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REGULAR ARTICLE

Nutrient uptake of catch crops under non-limiting growth conditions

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Abstract

Background: Catch crops enhance nutrient cycling of cropping systems. Considering possible limitations of catch crop studies in field and greenhouse experiments, a new approach was chosen to combine the advantages of both systems in quantifying the potential for nutrient retention by catch crops.

Aims: This study aimed at identifying N, P, and K uptake of different catch crop species grown in monoculture and as a mixture under non-limiting growth conditions in terms of water and nutrient availability.

Methods: Catch crops were cultivated under semi-controlled conditions in large containers (August to November 2020). Shoot N, P, and K uptake, leachate accumulation, and soil N_{min}, CAL-P, and CAL-K (0–30 cm) were quantified after harvest. After washing, root parameters were quantified with a root scanner.

Results: Nutrient uptake of N, P, and K was highest for phacelia. The mixture of seven different catch crops performed equally well. Nutrient uptake was closely related to root length and root surface area.

Conclusions: Under non-limiting growth conditions, phacelia has the highest potential to conserve N, P, and K for a succeeding crop; however, the low C : N ratio of the frost-sensitive crop could promote nutrient losses during winter. We conclude that growing a single catch crop can be as effective in reducing the nutrient leaching potential as cultivating a mixture of catch crops when nutrients and water are no growth-limiting factors.

KEYWORDS
nitrogen, nutrient use efficiency, phosphorus, potassium, root architecture

1 | INTRODUCTION

Well-known benefits of long-term use of catch crops are improvements of soil physical (Basche et al., 2016), chemical (Kwiatkowski et al., 2020) and biological properties (Basche et al., 2016; Wanic et al., 2019), protection from soil erosion and run-off (Derpsch et al., 1986), weed suppression (Brust et al., 2014), and increased nutrient use efficiency of the farming system (Dabney et al., 2001).

Several agronomic and climatic factors influence the suitability of different catch crops to reduce nutrient leaching and increase nutrient availability for a succeeding crop: precipitation and temperature (Liu et al., 2014; Thorup-Kristensen & Nielsen, 1998), soil type, soil nutrient content (Thorup-Kristensen & Nielsen, 1998), catch crop species (Eichler-Löbermann et al., 2008; Rinnofner et al., 2008), sowing date (Hashemi et al., 2013; Komainda et al., 2016), biomass production and nutrient uptake (Thorup-Kristensen, 1994), chemical composition of catch crop residues (Kaleeem Abbasi et al., 2015), rooting depth, and persistency of the catch crop (Thorup-Kristensen, 1994, 2001).

While many studies have focused on the effect of catch crops on N (Janušauskaitė et al., 2013; E. S. Jensen, 1992; McLenaghen et al., 1996;

Thorup-Kristensen, 1994) or P cycling (Eichler-Löbermann et al., 2008; Liu et al., 2015), studies that include data on the three nutrients N, P, and K—the main components of common agricultural fertilizers—are scarce (Möller et al., 2008; Wendling et al., 2016).

Catch crops differ in their ability to take up and conserve nutrients for a succeeding crop: N uptake by crucifers exceeds N uptake of monocots (e.g., ryegrass; Thorup-Kristensen, 1994, 2001). Rapid seedling emergence (Brust et al., 2014), vigorous growth, and deep rooting (Heuermann et al., 2019; Thorup-Kristensen, 2001) of the crucifers white mustard and oilseed radish have made them popular non-legume catch crop choices for N and K retention (Talgre et al., 2011). Nutrient losses by leaching are particularly relevant for coarse sandy soils, while lower porosity and processes such as ion sorption and reversible K fixation prevail on soils with high clay mineral contents (Askegaard et al., 2004; Gaines & Gaines, 1994); hence, nutrient leaching is reduced on those soils. Eichler-Löbermann et al. (2008) have investigated the effect of different catch crops on the bioavailability of P for a succeeding crop. They have shown that phacelia significantly increased P availability in comparison to a control. They also suggested that including P-mobilizing legumes could increase P and N availability for a succeeding crop at the same time (Eichler-Löbermann et al., 2008). One example of a P-mobilizing legume is white lupin, which forms root clusters for the secretion of root exudates to mobilize P (Kamh et al., 1999; Soltangheisi et al., 2018; Wasaki et al., 2005). Similarly, the Polygonaceae buckwheat is classified as an efficient crop under low-P conditions. It mobilizes Ca-bound P through acidification of the rhizosphere (Amann & Amberger, 1989; Teboh & Franzen, 2011; Zhu et al., 2002). Both white lupin and buckwheat have received much attention under P-deficient conditions. However, when the main aim of catch cropping is to reduce nutrient leaching, crops have to be able to extract easily leachable nutrient surpluses from the soil, which might otherwise be lost to aquatic ecosystems (Drinkwater & Snapp, 2007).

The nutrient acquisition is dependent on architectural root traits (P. J. White et al., 2013). For example, leaching losses of the highly mobile NO_3-N were most effectively reduced by catch crops with a deep-rooting system and high biomass production (Thorup-Kristensen, 2001; P. J. White et al., 2013). For example, Thorup-Kristensen (2001) found that high root frequency below the 50-cm soil layer strongly reduced NO_3-N content. Likewise, a deep-rooting system was proposed for effective K uptake, a nutrient that is mainly transported to the roots via diffusion, while the architectural root ideotype for P acquisition is characterized by high root length densities in the topsoil (P. J. White et al., 2013). In their investigation of 20 different catch crop species, Wendling et al. (2016) proposed the classification of different catch crop groups based on their relationship between nutrient uptake and leaf and root traits. Their findings support the root characteristics for high N, P, and K stated above. Therefore, differences in root architecture need to be considered in assessing the suitability of different catch crops to decrease nutrient leaching and enhance nutrient availability for a succeeding crop.

In the European Union, the cultivation of multi-species catch crop mixtures is being subsidized in the form of green direct payments for ecological focus areas (EC, 2017). Various studies suggest a positive relationship between species diversity and total biomass production (Finney et al., 2016; Rinnofner et al., 2008; Tilman et al., 2001). Therefore, catch crops mixtures could be more efficient in improving nutrient cycling efficiency than their single-species counterparts. The reasoning is that different species occupy complementary environmental niches (above and below ground), thereby enhancing the exploitation of all available resources (Hooper et al., 2005). However, the performance of species mixtures is highly dependent on nutrient availability, growth conditions, and species choice (root architecture, persistency, N_2-fixing ability, etc.; Baraibar et al., 2020). Different plant species interact on different levels. These interactions can be complementary, facilitative, or competitive. Complementary species do not influence each other as they occupy different ecological niches (Heuermann et al., 2019; Hooper et al., 2005). Thus, complementarity can lead to more efficient use of resources, compared to the cultivation of a single species. This has often been reported for mixtures of legumes and non-legume catch crops in terms of N use (e.g., Möller et al., 2008; Wendling et al., 2017). Facilitation describes the positive influence one crop has on another crop, for example, in terms of biomass production (Andersen et al., 2005; Wendling et al., 2017), competition for a limiting resource (water, nutrients, light, etc.) can have a negative influence on the overall performance of the catch crop mixture (Wendling et al., 2017).

Most studies with catch crops have been performed either in field experiments or under controlled greenhouse conditions. Aiming at combining the advantages of both systems, we conducted our experiment in large containers under semi-controlled conditions. The container technology has been well-established at Justus Liebig University with various crops and research objectives (Hohmann et al., 2016; Hütsch & Schubert, 2018; Keipp et al., 2020). In pot experiments, common factors that strongly affect plant growth are the limitation of soil volume for root proliferation due to small pot sizes (Greub & Roberts, 2020; Poorter et al., 2012), the lack of "neighbor effects" in experiments with one plant per pot (Hohmann et al., 2016), and the absence of natural variations of meteorological conditions and other abiotic factors. The 120-L containers used in this study provide an appropriate soil volume for root development, and crops can be sown at field densities (Hohmann et al., 2016). Moreover, soil properties in the containers are homogeneous, compared to field conditions (García-Palacios et al., 2012). In contrast to the aforementioned studies of catch crops in large containers that were performed in greenhouses, we decided to subject the catch crops to natural variations in meteorological conditions (radiation, temperature, humidity, wind, and precipitation) while closely monitoring water supply to the crops (hence the term "semi-controlled" conditions), as water is an important factor for seedling emergence and total biomass production (Dorsainvil et al., 2005). In doing so, we wanted to create controllable yet not artificial growth conditions to analyze maximum nutrient uptake (N, P, and K) of different catch crop species without limitations in terms of nutrient or water availability.

We hypothesized that catch crops differ in their efficiency to acquire and conserve N, P, and K for a succeeding crop and that these differences are due to (1) catch crop species: N and K accumulations are highest for crucifers, while P is most efficiently acquired by

TABLE 1 Overview of treatments, plant densities, and growth stage at final harvest [74 days after sowing (DAS)] of single-species treatments

Family	Species name	Common name	Cultivar	Plant density (plants m^{-2})	Growth stage at harvest
–	–	Bare fallow	–	–	–
Brassicaceae	*Sinapis alba* L.	White mustard	Gisilba	270	Fruit development
Brassicaceae	*Raphanus sativus* L. *var. oleiformis* Pers.	Oilseed radish	Bento	252	Vegetative
Fabaceae	*Lupinus albus* L.	White lupin	Feodora	70	Flowering
Boraginaceae	*Phacelia tanacetifolia* Benth.	Phacelia	Amerigo	525	Vegetative
Polygonaceae	*Fagopyrum esculentum* Moench	Buckwheat	Hajnalka	315	Fruit development
Poaceae	*Lolium perenne* L.	Ryegrass	Marava	1050	Vegetative
Asteraceae	*Helianthus annus* L.	Sunflower	SY Vivacio	12	Vegetative
		Mix (9% white mustard, 9% oilseed radish, 20% white lupin, 9% phacelia, 9% buckwheat, 9% ryegrass, 33% sunflower)			

phacelia, buckwheat, and white lupin; and (2) root architecture: N and K accumulations are highest for catch crops with deep-rooting systems, while P is most efficiently acquired by catch crops with high root length densities in the topsoil. We furthermore hypothesized that due to complementary and/or facilitative effects, a multi-species catch crop mixture outperforms its single-species counterparts in terms of nutrient uptake (N, P, and K) and root biomass.

2 | MATERIALS AND METHODS

2.1 | Growth conditions and treatments

Catch crops were cultivated under semi-controlled growth conditions in 120-L containers (width × depth × height = 40 × 40 × 80 cm) at the experimental station of the Institute of Plant Nutrition in Giessen (50°35’53.30’’N, 8°40’1.56’’E) from August till November 2020. The container technology allowed to monitor and control important factors such as soil texture, soil nutrient content, and water supply (Hütsch & Schubert, 2018), while the plants were subjected to natural temperature, humidity, wind speed, and solar radiation. Water demand of the catch crops was monitored closely by weighing the containers twice a week. When natural precipitation did not suffice, the plants were irrigated manually to keep the soil at 50% water-holding capacity (WHC).

The containers were filled with 10-L glass gravel (Misapor, EN ISO 21898) as a drainage layer to prevent waterlogging during times of high precipitation. A valve was installed at the bottom of each container to allow the discharge and collection of leachate. A fibrous web of fleece (ACO Master Dränage, Trenn- und Filtervlies) separated the drainage layer from the soil. The containers were filled with 130 kg of a sandy loam subsoil (44.3% sand, 34.6% silt, 21.2% clay) equaling a depth of approximately 70 cm at a soil surface area of 0.16 m^2 (Supplementary Information 1). The low nutrient content of the soil (14.5 mg N_{min} kg^{-1}, 8.3 mg CAL-P kg^{-1}, 43.5 mg CAL-K kg^{-1}) allowed for a controlled supply of plant-available nutrients. The top 30 cm of soil were fertilized with a compound fertilizer (Nitrophoska spezial Blau-Dünger) and micronutrients. In total, all treatments received 300-kg N ha^{-1}, 131-kg P ha^{-1}, 353-kg K ha^{-1}, 30-kg Mg ha^{-1}, 168-kg S ha^{-1}, 20-kg Zn ha^{-1}, 10-kg Cu ha^{-1}, 5-kg Mn ha^{-1}, and 0.5-kg B ha^{-1}. Due to the comparably low natural pH of the soil (pH_{CaCl2} = 5.4), it was limed with 2.5-g $CaCO_3$ kg^{-1} prior to sowing to achieve a pH_{CaCl2} of 7.5.

A total of nine different treatments with seven replicates each was investigated (63 containers). The control treatment was a bare fallow. The eight catch crop treatments consisted of seven single-species treatments and one multi-species treatment. An overview of the treatments and plant densities is given in Table 1. One day prior to sowing, WHC of the soil was adjusted to 50%. On August 24, the catch crop seeds were evenly sown in four furrows per container in 1-cm depth at a row spacing of 8 cm. The seeds were covered with soil and evenly wetted with 1-L deionized water per container. Afterward, the containers were covered with a net to reduce evaporation until the first seedlings emerged 2 days after sowing (DAS) on August 26. Weeds were manually removed from the soil on a regular basis. Due to high pest pressure, the application of insecticides (Karate, Syngenta) was necessary twice during the vegetation period (17 and 71 DAS). Three of the seven replicates of each treatment were used to monitor biomass production throughout the vegetation period. Of those, plants of one container per treatment were harvested on September 16 (23 DAS), October 1 (38 DAS), and October 29 (66 DAS). Fresh weight was determined and the water supply to the catch crops was adjusted accordingly. Water supply by irrigation was recorded for every container individually. A completely randomized design was used, and the position of the 63 containers was changed twice a week.

2.2 | Monitoring of meteorological conditions

Temperature and humidity (DK 320 HumiLog Plus, Driesen+Kern GmbH), precipitation (rain gauge), and wind speed (Wind sensor WSW G0010, F&C GmbH) were monitored throughout the vegetation period. Temperature, humidity, and wind speed were recorded by data loggers. Precipitation in the rain gauge was quantified twice a week. Long-term average annual temperature and precipitation (1999–2019)

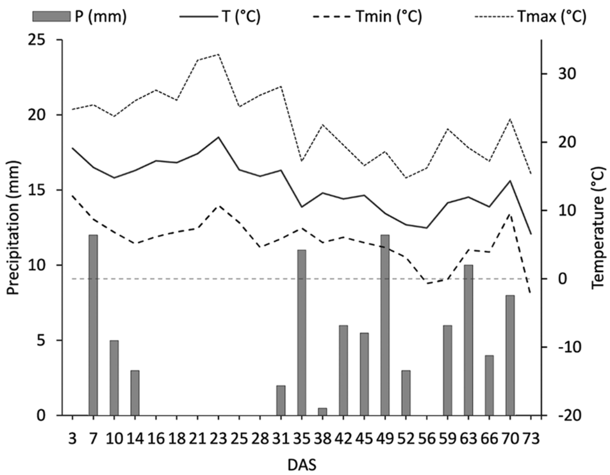

FIGURE 1 Measured precipitation (P) and average (T), minimum (T_{min}) and maximum (T_{max}) daily air temperature during the vegetation period. Harvest at 74 days after sowing (DAS)

in Giessen were 10.0°C and 619 mm (DWD, 2020). Climatic conditions during the vegetation period are depicted in Figure 1. Total precipitation during this period was 88 mm while the average daily temperature was 13.3°C. The maximum temperature of 33.4°C was reached at 22 DAS and the minimum temperature of –2.5°C at 73 DAS (Figure 1).

2.3 | Plant development and final harvest

2.3.1 | Shoot biomass

Following a frost event on November 5, from which the sunflower and buckwheat plants did not recover, the vegetation period was terminated on November 6 (74 DAS). Above-ground biomass was harvested, and fresh weight was determined. For the determination of shoot dry weight, the biomass was dried at 105°C.

2.3.2 | Root biomass

Using an auger (diameter 7.6 cm), a core soil sample was extracted from each container in successive 6-cm increments. The auger was positioned in the center of the container between catch crop rows. The individual samples were wrapped in plastic bags and stored at 5°C until the samples were soaked and roots were carefully separated from the soil and organic material in several sieving steps (max. diameter 1 mm) with cold water. Fresh weight was recorded before covering the roots with fixing solution [ethanol (70%) + acidic acid, 9:1] to prevent microbial decomposition. Root length and root surface area per sample were determined using the WinRhizo LA2400 Scanner (Regent Instruments Inc.). For the determination of root dry weight, the samples were dried at 80°C.

2.4 | Plant nutrient analyses

Total N concentration in 500 mg dried shoot material was determined using the Kjeldahl method (Keipp et al., 2020). NO_3-N reduction was achieved by incubating the samples with 10 mL salicylic-sulfuric acid (2.5 g salicylic acid dissolved in 100 mL concentrated (96%–98%) sulfuric acid) at room temperature for 15 min followed by another 15 min incubation of the samples with 1.5 g sodium thiosulphate. After the second incubation step, a Kjeldahl tab (Kjeltab AA009, K_2SO_4 + Se) and 10 mL concentrated sulfuric acid were added to achieve the conversion of the remaining N compounds to $(NH_4)_2SO_4$. Digestion was performed using the SpeedDigester K–436 (BÜCHI Laboratory Equipment). In the subsequent distillation (Destillation Unit B–324, BÜCHI Laboratory Equipment), NaOH solution was added to the samples that were boiled for another 10 min. Evaporating NH_3 was condensed in the cooling system and was collected in boric acid. Back-titration with hydrochloric acid was performed to determine the N concentration of the samples.

Phosphorus and K concentrations in the dried plant material were determined using photometry and atomic absorption spectroscopy, respectively. One gram of dried plant material was incinerated at 550°C for more than 12 h. After cooling, 2 mL deionized water and 2.5 mL 5 M HNO_3 were added to the ash. The mixture was boiled and filtered (MN 640, diameter 125 mm). The filtrate was collected in 50 mL flasks. Deionized water was used to fill the flasks to the mark. Ten milliliters of the filtrate were mixed with 3.5 mL deionized water, 0.5 mL 5 M HNO_3 and 6 mL vanadate solution (5 M HNO_3, ammonia-solution (50 g L^{-1}), ammonia-vanadate solution (2.5 g L^{-1} in 0.1 M HNO_3; 1:1:1)] for photometric P determination at 450 nm (Genesys™ 10S UV/Vis, Thermo Scientific Inc.). The K concentration in the filtrate was determined using atomic absorption spectrometry (SpectrAA 220 FS, Varian Inc.). The shoot C:N ratio was determined in dried, ball-milled plant material with an elemental analyzer (Unicube, Elementar Analysesysteme GmbH). Nutrient use efficiency (NUE) was defined as the ratio of shoot dry matter to fertilizer application:

$$NUE_i = \frac{DW_{cc}}{F_i}, \quad (1)$$

with NUE_i = nutrient use efficiency of nutrient i in g g^{-1}, DW_{cc} = shoot dry weight of the catch crop in g m^{-2}, and F_i = fertilizer application of nutrient i in g m^{-2} (Dobermann, 2005).

2.5 | Soil nutrient analyses

Soil samples (0–30 cm) were taken on November 11 (80 DAS). The soil was dried at 40°C and sieved to diameter ≤ 2 mm. Mineral nitrogen (N_{min} = NH_4-N + NO_3-N) concentration was measured after extraction with 0.01 M $CaCl_2$ (Houba et al., 1986). Of that solution, 100 mL were added to 10 g soil. The mixture was mixed for 90 min on an overhead shaker and filtered through MN 615 one-fourth ash-free filter paper (Macherey-Nagel GmbH & Co. KG). NH_4-N and NO_3-N concentrations in the filtrate were determined using an auto-analyzer (AA3, Bran+Luebbe GmbH).

Available P was determined with the CAL method. Activated charcoal and 100 mL of a CAL solution (calcium lactate + calcium acetate + acetic acid, pH = 4.1) were added to 5 g soil (diameter ≤ 2 mm) in 250 mL plastic bottles and mixed for 2 h on a horizontal shaker (Edmund Bühler GmbH). The mixture was filtered (MN 619 G ¼, Macherey-Nagel GmbH & Co. KG) and collected in 100 mL plastic bottles. A 12.5 mL filtrate was mixed with a 0.5 mL concentration of HNO_3 and 2.5 mL vanadate solution. After 30 min, P concentration in the filtrate was determined photometrically at 406 nm (Genesys 10S UV/Vis, Thermo Scientific Inc.). Potassium concentration in the filtrate was determined using atomic absorption spectrometry (SpectrAA 220 FS, Varian Inc.).

2.6 | Leachate collection and analysis

The containers were regularly checked for leachate accumulation in the drainage layer. The leachate was quantified gravimetrically and volumetrically. An aliquot of approximately 50 mL was filtered (MN 615 ¼ Macherey-Nagel GmbH & Co. KG) before measuring N as the sum of NH_4-N and NO_3-N concentrations using an auto-analyzer (AA3, Bran+Luebbe GmbH). Phosphorus concentration in the samples was determined photometrically at 882 nm (Genesys™ 10S UV/Vis, Thermo Scientific Inc.) with the molybdenum blue method described by Murphy and Riley (1962), and K concentration was determined by atomic absorption spectrometry (SpectrAA 220 FS, Varian Inc.).

2.7 | Statistical analysis

Statistical analysis was performed with RStudio (R version 3.5.1) and Microsoft Office Excel (2016). Parameters were compared with a one-way analysis of variance (ANOVA) and a post hoc false discovery rate (FDR) test at a significance level of $p < 0.05$. For heteroscedastic data, a White-adjusted ANOVA was performed according to H. White (1980) and Long and Ervin (2000) followed by a post hoc FDR-test. Root biomass and root length densities were calculated under the assumption that the core samples were representative of root distribution in the whole container.

3 | RESULTS

3.1 | Growth conditions

The growth period was characterized by a total of 666°C growing degree days [GDD = $\frac{T_{max} - T_{min}}{2} - T_{base}$, with T_{base} = 5°C (DWD, 2020)]. In the single-crop treatments, white mustard and buckwheat started flowering at GDD = 409°C (31 DAS), while white lupin needed 657°C until flowering (69 DAS).

3.2 | Shoot and root biomass

With > 1 kg DW m^{-2}, white mustard produced the highest shoot biomass during the vegetation period (Figure 2). White lupin, ryegrass, and sunflower had a significantly lower shoot and root biomass than white mustard, phacelia, and oilseed radish at harvest. All catch crops developed roots to a depth of > 50 cm and—with the exception of white lupin—the largest proportion of roots was found in the first 18 cm. The majority of roots (40%) of white lupin was found in the soil layers 36–54 cm and 0–18 cm (36%; Figure 2). Shoot:root ratios ranged between 5 (ryegrass) and 15 (white mustard).

Significant differences among the various catch crops were not only evident for the shoot and root biomass but also for root length at different soil depths. Together with sunflower and ryegrass, buckwheat and white lupin had lower root length densities in the 0–18 cm layer than oilseed radish, phacelia, and the mix treatment. However, roots of buckwheat and white lupin were more evenly distributed over the different soil layers in terms of biomass and root length (Figures 2 and 3), while root length densities of oilseed, phacelia, and mix radish declined steeply from > 16 to < 5 km m^{-2} from the 0–18 cm-layer to the 18–36 cm-layer.

3.3 | Catch crop nutrient concentration, nutrient uptake, and nutrient use efficiency

3.3.1 | Nitrogen

Phacelia was the single catch crop with the highest N uptake, equivalent to 74% of fertilizer N, however, the NUE of phacelia was lower than that of white mustard (Table 2) due to lower biomass production (Figure 2). Although shoot N concentration in the catch crop mixture was lower than that of phacelia, the treatments did not differ in total N uptake. Ryegrass was the catch crop with the highest shoot N concentration (Table 2). Due to its relatively low above-ground biomass (Figure 2), however, total N uptake by ryegrass was lower than that of phacelia, white mustard, oilseed radish, buckwheat, and the mix. White lupin showed the lowest N uptake equivalent to only 18% of total fertilizer N and consequently resulting in a leaching potential of 24.6-g N m^{-2}. It is not surprising, therefore, that NUE of white lupin, ryegrass, and sunflower indicated the least efficient use of fertilizer N for biomass production [NUE < 7 g DW (g N)$^{-1}$; Table 2].

3.3.2 | Phosphorus

With 4.4 and 4.1 mg P (g DW)$^{-1}$, respectively, phacelia and oilseed radish had higher shoot P concentrations than all other catch crops with the exception of ryegrass (Table 2). Similar to N uptake, P uptake by phacelia was higher than that of all other single catch crops. Only the mix treatment showed an equally high P uptake (Table 2). Since fertilization rate did not differ between the treatments, catch crops with the highest shoot biomass (Figure 2) had the highest PUE (Table 2).

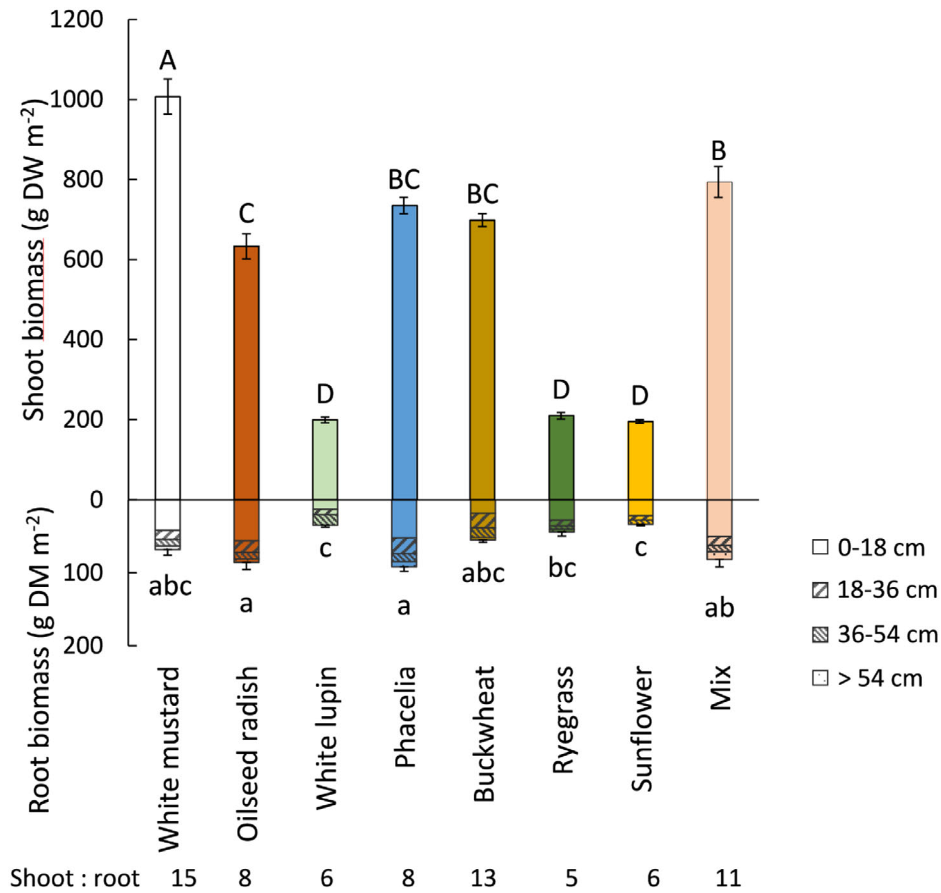

FIGURE 2 Shoot and root dry weights of various catch crops in four successive soil depths (0–18 cm, 18–36 cm, 36–54 cm, and > 54 cm) and shoot:root ratio of the catch crops at final harvest (74 DAS). Soil volume per $m^2 = 0.71\ m^3$. One-way analysis of variance (ANOVA) and comparison of means adjusted according to FDR. Letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$) ± SE

3.3.3 | Potassium

Phacelia and sunflower had significantly higher shoot K concentrations than the other catch crops (Table 2). As previously seen for N and P, KUE was highest for high-yielding catch crops (Table 2). With 26.54 and 31.42-g K m^{-2}, K uptake by white mustard and oilseed radish amounted to 75% and 89% of applied fertilizer K, respectively. However, as a consequence of high shoot K concentrations in combination with high shoot biomass (Figure 2), K uptake by phacelia was significantly higher than in all other treatments. In fact, K uptake by phacelia (42.23-g K m^{-2}) exceeded applied fertilizer K (35.30-g K m^{-2}) by 20%. Although biomass production of white mustard was significantly higher than for the other catch crops (Figure 2), K uptake was lower than that of phacelia and oilseed radish due to lower shoot K concentrations (Table 2).

3.3.4 | Nutrient uptake and root parameters

Nutrient uptake of all seven catch crops and the mixture was closely related to root length and root surface area ($p < 0.001$). The higher the root length, the more the nutrients were stored in the shoot. This correlation was highest for K ($R^2 \geq 0.95$) and lowest for P ($R^2 \leq 0.80$) for both root parameters (Figure 4).

3.3.5 | C:N ratio

With C:N ratios ≥ 22, white mustard and buckwheat, crops that had already reached a generative growth stage at the time of harvest (Table 1), had the highest C:N ratios. Catch crops that were still in a vegetative growth stage (Table 1) showed significantly lower C:N ratios (Figure 4). Ryegrass and sunflower had the lowest C:N ratios (≤ 10; Figure 5), while white lupin and the mix showed medium C:N ratios of approximately 15.

3.4 | Soil nutrient concentrations (0–30 cm)

Figure 6 depicts N, P, and K concentrations in the upper 30 cm of soil after harvest, compared to initial soil nutrient content and soil nutrient content after fertilization. In all treatments, mineral N concentration (N_{min}) was significantly lower after harvest than before sowing and ranged between 2.2 (phacelia) and 6.3 mg N (kg soil)$^{-1}$ (ryegrass).

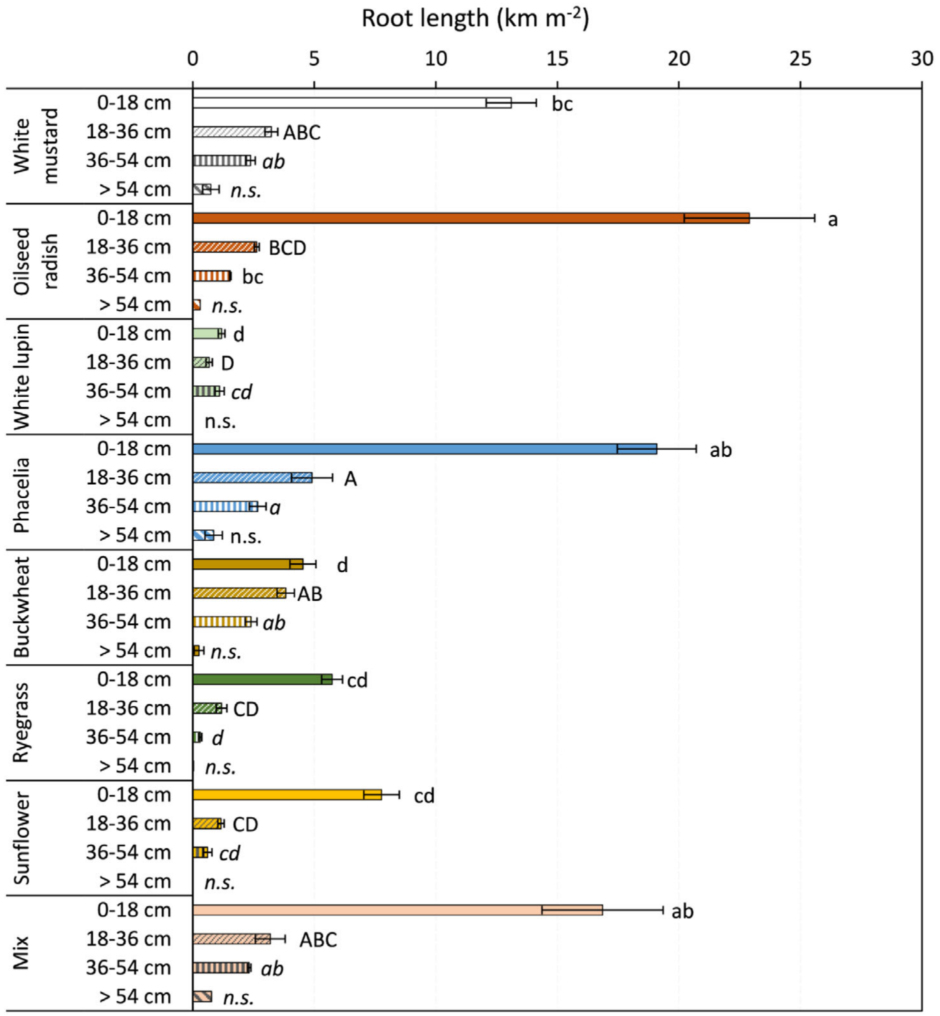

FIGURE 3 Root lengths of various catch crops in four successive soil depths (0–18 cm, 18–36 cm, 36–54 cm, and > 54 cm) at final harvest (74 DAS). One-way ANOVA and comparison of means adjusted according to FDR. Lowercase letters, uppercase letters, and letters in italics indicate significant differences ($p < 0.05$) in the layers 0–18 cm, 18–36 cm, and 36–54 cm, respectively; *n.s.* = not significant. Mean values ($n = 4$) ± SE

TABLE 2 Shoot nutrient concentration, nutrient uptake, and nutrient use efficiency of various catch crops. N concentration, N uptake, N use efficiency (NUE), P concentration, P uptake, P use efficiency (PUE), K concentration, K uptake, and K use efficiency (KUE) at final harvest (74 DAS). One-way analysis of variance and comparison of means adjusted according to FDR. Different superscript letters within a column indicate significant differences ($p < 0.05$). Mean values ($n = 4$) ± SE

	N			P			K		
	Concentration	Uptake	NUE	Concentration	Uptake	PUE	Concentration	Uptake	KUE
Treatment	mg N (g DW)$^{-1}$	g N m^{-2}	g DW (g N)$^{-1}$	mg P (g DW)$^{-1}$	g P m^{-2}	g DW (g P)$^{-1}$	mg K (g DW)$^{-1}$	g K m^{-2}	g DW (g K)$^{-1}$
White mustard	18.17 ± 0.40^{e}	18.28 ± 0.81^{b}	33.58 ± 1.46^{a}	2.44 ± 0.08^{d}	2.45 ± 0.10^{b}	76.90 ± 3.35^{a}	26.37 ± 0.54^{d}	26.54 ± 1.15^{c}	28.56 ± 1.24^{a}
Oilseed radish	26.92 ± 0.78^{cd}	17.00 ± 0.72^{b}	21.11 ± 1.05^{c}	4.10± 0.05^{ab}	2.60 ± 0.16^{b}	48.33 ± 2.41^{c}	49.64 ± 0.31^{b}	31.42 ± 1.55^{b}	17.95 ± 0.89^{c}
White lupin	27.12 ± 0.88^{cd}	5.40 ± 0.24^{e}	6.64 ± 0.23^{d}	1.83 ± 0.06^{e}	0.37 ± 0.02^{c}	15.20 ± 0.53^{d}	20.83 ± 0.50^{d}	4.15 ± 0.19^{f}	5.65 ± 0.20^{d}
Phacelia	30.13 ± 0.60^{c}	22.11 ± 0.30^{a}	24.50 ± 0.68^{bc}	4.36 ± 0.05^{a}	3.21 ± 0.10^{a}	56.11 ± 1.57^{bc}	57.56 ± 1.04^{a}	42.23 ± 0.52^{a}	20.84 ± 0.58^{bc}
Buckwheat	18.42 ± 0.18^{e}	12.88 ± 0.42^{c}	23.29 ± 0.54^{bc}	3.31 ± 0.16^{c}	2.32 ± 0.15^{b}	53.33 ± 1.24^{bc}	20.69 ± 0.35^{d}	14.44 ± 0.30^{d}	19.80 ± 0.46^{bc}
Ryegrass	40.41 ± 0.39^{a}	8.47 ± 0.29^{d}	6.99 ± 0.27^{d}	3.91 ± 0.04^{b}	0.82 ± 0.03^{c}	16.02 ± 0.63^{d}	46.36 ± 2.56^{b}	9.80 ± 0.84^{e}	5.95 ± 0.23^{d}
Sunflower	35.97 ± 0.50^{b}	7.01 ± 0.05^{de}	6.51 ± 0.14^{d}	2.34 ± 0.04^{d}	0.46 ± 0.00^{c}	14.90 ± 0.33^{d}	60.26 ± 0.94^{a}	11.75 ± 0.12^{de}	5.53 ± 0.12^{d}
Mix	24.47 ± 0.76^{d}	19.36 ± 0.72^{ab}	26.47 ± 1.29^{b}	3.40 ± 0.09^{c}	2.69 ± 0.12^{ab}	60.61 ± 2.95^{b}	35.78 ± 1.74^{c}	28.20 ± 0.89^{bc}	22.51 ± 1.10^{b}

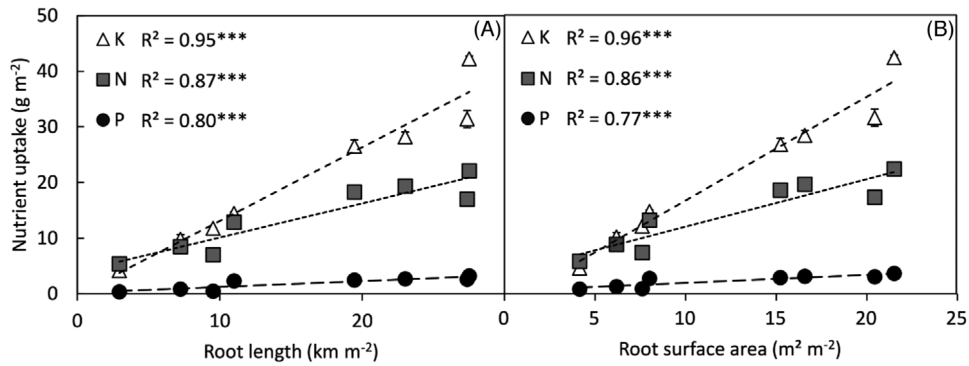

FIGURE 4 Catch crop N, P, and K uptake in relation to (A) root length and (B) root surface area at final harvest (74 DAS). Linear regression analysis ($p < 0.05$). Mean values ($n = 4$) ± SE. Coefficients of determination (R^2) are given for each nutrient (*** = $p < 0.001$)

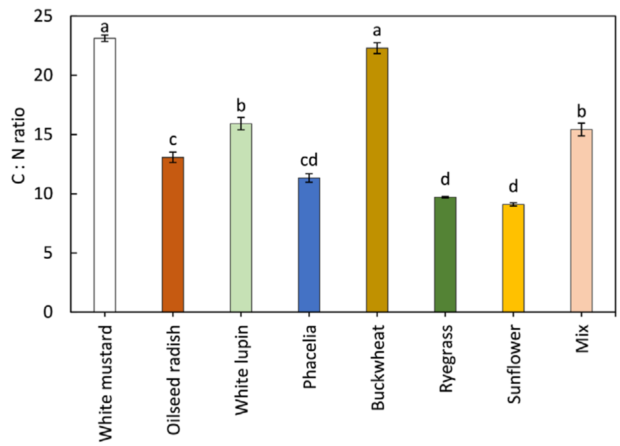

FIGURE 5 C:N ratios of various catch crops at final harvest (74 DAS). One-way ANOVA and comparison of means adjusted according to FDR. Letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$ with the exception of phacelia and sunflower where $n = 3$) ± SE

Residual N_{min} was lower than the initial, unfertilized N_{min} of the soil in all treatments. Although catch crops showed differences in N uptake and N concentration (Table 2), this did not result in significant differences in the N_{min} concentration among the different treatments. While the reduction of N_{min} in the catch crop treatments can mostly be attributed to catch crop N uptake (Table 2), the low N_{min} concentrations in the bare fallow treatment (Figure 6) must have been a result of translocation of N to deeper soil layers. White mustard, oilseed radish, phacelia, buckwheat, and mix were most efficient in depleting the upper 30 cm of the soil of P and K. Soil P and K concentrations after cultivation of white lupin, ryegrass, and sunflower did not differ from the bare fallow control treatment.

3.5 | Nutrient leaching

As a consequence of low precipitation and moderate irrigation during the vegetation period, leachate accumulation only occurred in three out of 63 containers. Leachate volume was 405 ± 328 (phacelia) and 320 (buckwheat) mL container^{-1} with N concentrations of 1.44 ± 0.39 and 1.54 mg N L^{-1} and K concentrations of 2.03 ± 0.73 and 1.77 mg K L^{-1}, respectively. P concentrations in the samples were below the detection limit.

4 | DISCUSSION

4.1 | Methodology

Reasons for choosing a study design with container technology rather than conducting a field experiment were stated above. Here, we want to illustrate a few of the limitations of this specific design that need to be kept in mind for the interpretation of the results: The experiment was conducted under very controlled conditions with optimum soil moisture and high nutrient availability. The containers were filled with a disturbed subsoil. Consequently, microbial activity and organic matter content can be expected to be lower than in a natural, undisturbed soil profile (e.g., Federle et al., 1986; Fierer et al., 2003; Liebmann et al., 2020). Microorganisms are vital for the decomposition and mineralization of organic matter and are essential for nutrient cycling. Since nutrients were already provided in a plant-available, mineral form, the role of microbial activity for catch crop growth can be neglected in this study, which justifies the use of subsoil for our purposes. However, when looking at organic matter decomposition, nutrient supply to a succeeding crop, and improvement of soil physical and chemical properties, the importance of soil microorganisms should not be neglected (Hallama et al., 2019).

Hohmann et al. (2016) have shown a good correlation between stress response of oilseed rape grown in containers and under field conditions at different locations. Due to the drainage layer at the bottom of the containers, the maximum possible rooting depth was reduced to approximately 65 cm, which is only a fraction of the 2.4-m rooting depth reported for oilseed radish by Kristensen and Thorup-Kristensen (2004). However, significant differences in root characteristics were still evident in the present study (Figures 2 and 3), and the soil volume was sufficient to prevent typical “pot effects” (Hohmann et al., 2016).

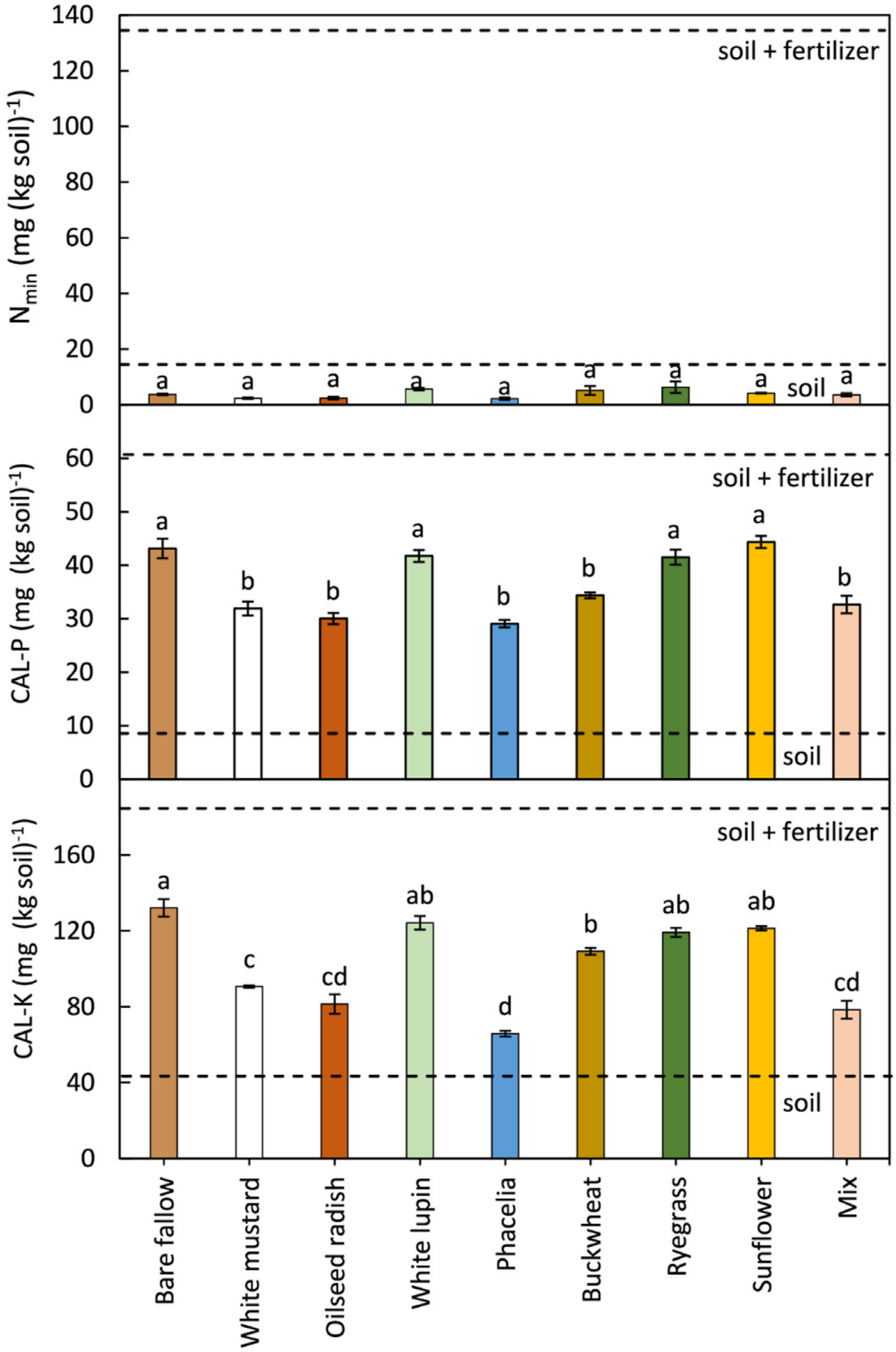

FIGURE 6 Soil mineral nitrogen concentration (N_{min}), CAL-extractable P concentration (CAL-P), and CAL-extractable K concentration (CAL-K) in the topsoil (0–30 cm) after final harvest (74 DAS) of various catch crops in comparison to a bare fallow control treatment. One-way ANOVA and comparison of means adjusted according to FDR. Different letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$) ± SE. Dashed lines *soil* and *soil+fertilizer* indicate initial nutrient content and nutrient content after mineral fertilization, respectively

When interpreting the soil nutrient balances (Figure 6), it should be considered that several factors in the study design might have contributed to nutrient translocation from the topsoil to deeper soil layers: First, irrigation was provided twice a week to keep soil moisture at ≥ 50% WHC, thereby supporting nutrient mobility (Mengel & von Braunschweig, 1972; Sato & Morgan, 2012). Moreover, soil moisture is important for cation exchange processes (Brown, 1953), which, depending on clay minerology, could have reduced CAL-extractable K concentrations in the topsoil due to K fixation (Askegaard et al., 2004). Second, the soil in this study was a relatively sandy subsoil with low organic matter content. N, P, and K movement in the soil are strongly affected by soil texture, organic matter, and sorption/desorption properties of the soil with leaching generally being favored by a coarse texture, low organic matter content, and low sorption capacity (Andersson et al., 2013; Askegaard et al., 2004; Gaines & Gaines 1994). Third, nutrient translocation is favored by preferential flow (Alfaro et al., 2004; Djodjic et al., 2004; Sinaj et al., 2002). Although soil heterogeneity was reduced in the container experiment in comparison to field conditions and soil was kept moist by regular irrigation, the formation of shrinking cracks between the container and the soil was unavoidable. These cracks could have provided a preferential flow way for water and nutrients, which could also explain why leachate accumulation was evident in three out of 63 containers even though, taking into account, water supply by irrigation and precipitation soil moisture never exceeded 70% WHC in any of the treatments (data not shown). Soil penetration by taproots could furthermore have supported nutrient translocation via preferential flow in some of the catch crop treatments (Mitchell et al., 1995).

4.2 | Performance of individual catch crops

This study has shown that catch crops differ in their efficiency to acquire N, P, and K. Nutrient acquisition was described in terms of total shoot nutrient uptake. Root nutrient contents were neglected since root biomass accounted for only approximately one-tenth of shoot biomass (Figure 2).

4.2.1 | Nutrient uptake

Catch crop species

Important traits for nutrient scavenging catch crops are rapid emergence, high biomass production, and quick establishment of a deep rooting system (Brust et al., 2014; Herrera et al., 2010; Holmes et al., 2017; Thorup-Kristensen, 2001). The same characteristics were suggested for high K uptake. All these traits apply to the crucifers white mustard and oilseed radish, which were included in this study. Although both crucifers were the first to emerge and produce a closed soil cover (Supplementary Informations 2 and 3), total N, P, and K uptake of white mustard and oilseed radish was significantly lower than that of phacelia (Table 2). In fact, K uptake by phacelia even exceeded fertilizer K application by 20%, which highlights the efficacy of the crop to acquire and store K under the given growth conditions and could be relevant for the effective prevention of K leaching on sandy soils with high fertilization rates (Askegaard et al., 2004; Munson & Nelson, 1963), which are common in intensive vegetable production. Moreover, the high nutrient uptake suggests a high nutrient supply to a succeeding crop if phacelia is incorporated into the soil.

Differences in shoot nutrient uptake between the two crucifers and phacelia were due to lower shoot nutrient concentration (white mustard) and differences in growth stages (white mustard and oilseed radish). While phacelia was in a vegetative state at harvest, white mustard was in the stage of fruit development (Table 1), and both, white mustard and oilseed radish, started to become senescent 56 DAS. Leaf senescence is defined as the controlled, age-dependent deterioration of leaves (Lim et al., 2007), which is influenced by various environmental conditions. Leaf senescence of oilseed radish coincided with biotic stress by a severe aphid infestation as well as abiotic stress following a decline in temperature (Figure 1). As senescence serves the remobilization of nutrients (Lim et al., 2007), shoot N, P, and K concentrations of white mustard and oilseed radish are likely to have decreased in comparison to phacelia, which showed no signs of leave senescence at the end of the cultivation period. We thus conclude that not only catch crop species but also the developmental stage of the catch crops plays an important role in total N, P, and K uptake and prevention of nutrient leaching.

Including legumes in a cropping rotation can be beneficial in many ways, especially in terms of N_2 fixation. However, symbiotic N_2 fixation is limited in the presence of inorganic nitrogen (Evans et al., 1987). It is not surprising, therefore, that roots of white lupin were not nodulated, that is, no biological N_2 fixation occurred, and N demand of white lupin was solely met by inorganic fertilizer N. Additionally, above- and below-ground biomass production of white lupin was lower than that of the non-legume catch crops (Figure 1). This poor performance led to potential N losses of 82% of applied fertilizer N. This is in line with studies that found that leguminous catch crops do not always reduce (Tosti et al., 2014) or even increase (Campiglia et al., 2011; Kuo et al., 2001) NO_3-N leaching losses, compared to a control. Poor performance of white lupin on the previously limed soil in the present study could be explained in terms of high pH_{CaCl2} (7.5) and high Ca^{2+} concentrations, which have been shown to adversely affect shoot and root development of the crop (Kerley & Huyghe, 2002; Tang et al., 1992). Accordingly, the effective P acquisition strategy of white lupin (Kamh et al., 1999; Soltangheisi et al., 2018; Wasaki et al., 2005) did not provide a benefit over the other catch crops in terms of PUE or total P uptake, while the PUE of buckwheat, another "P-efficient" crop (Amann & Amberger, 1989; Teboh & Franzen, 2011; Zhu et al., 2002), which showed rapid development and high biomass production, did not differ from that of phacelia.

These results indicate that biomass accumulation is one of the driving factors for nutrient acquisition under non-limiting nutrient conditions. We can distinguish between two groups: (1) phacelia, white mustard, oilseed radish, and buckwheat forming a group of catch crops with high biomass production and high N, P, and K accumulation and (2) sunflower, ryegrass, and white lupin a group of catch crops with low biomass production and low N, P, and K accumulation. The study by Wendling et al. (2016) supports the finding that differences in nutrient uptake are mainly driven by differences in shoot biomass.

Root architecture

Although rooting depth did not differ between the crops grown in containers (Supplementary Information 4) we showed that nutrient uptake is determined by different root parameters such as root surface area and root length. The positive relationship and the high coefficients of determination between N, P, and K uptake and these parameters (Figure 4) underline the importance of root development for nutrient acquisition (Lynch, 2007; Wendling et al., 2016). Similar to shoot biomass, crops with high root biomass and root length densities in the topsoil accumulated more N, P, and K than those with lower root biomass and root length densities. However, a distinct classification of architectural root traits of individual catch crops in relation to nutrient acquisition is not possible since rooting depth was limited to a maximum of 70 cm in this study, which is deeper than in other studies (Wendling et al., 2016) but does not allow undisturbed root development since several of the catch crops selected for this study have been shown to develop roots far below 70-cm soil depth (Kristensen & Thorup-Kristensen, 2004; Thorup-Kristensen, 2001).

4.2.2 | Soil nutrient concentrations and nutrient translocation

Nutrient concentrations in the fertilized soil layer (0–30 cm) were significantly lower after the harvest of the catch crops than before. In fact, N_{min} plummeted to values < 6.5 mg N (kg soil)$^{-1}$, equivalent to less than half of the initial N_{min} before fertilization [14.5 mg N (kg soil)$^{-1}$; Figure 6]. Significant differences in soil P and K contents responded to differences in P and K uptake of the catch crops. However, in spite of differences in catch crop N, uptake residual N_{min} content (0–30 cm) did not differ between the treatments. In general, N, P, and K uptake by the catch crops reduces potential nutrient losses in comparison to a bare fallow control. However, the gap between soil nutrient content before and after cultivation of catch crops (Figure 6) cannot be explained solely by catch crop nutrient uptake.

The lack of data on nutrient concentrations in deeper soil levels (> 30 cm) and the lack of leachate accumulation in most of the treatments due to low precipitation during the cultivation period make it difficult to retrace the exact movement of the nutrients. However, by looking at soil nutrient concentrations in the bare fallow control, we can assume with great certainty that such a movement or translocation of nutrients took place: N, P, and K concentrations (0–30 cm) in this treatment declined significantly during the vegetation period.

Other studies have shown that N_{min} was significantly reduced through catch crop cultivation in comparison to a bare fallow control (Janušauskaitė et al., 2013; Thorup-Kristensen, 1994). The fact that N_{min} of the bare fallow did not differ from N_{min} in the catch crop treatments in the present study can only be explained by one of two processes: either catch crop N uptake did not result in a significant reduction in N_{min} in the topsoil or N uptake by catch crops was significant; however, all residual NO_3-N that was not taken up by crops was translocated to deeper soil layers in both the catch crop and the control treatments so that no difference in N_{min} (0–30 cm) was detectable. Considering results in Table 2 and the arguments given above that support the assumption that nutrient translocation took place not only in the bare fallow but also in the catch crop treatments, the latter explanation seems more plausible. Similarly, in a field study by Hashemi et al. (2013), initially high soil N levels decreased between September and December to approximately zero down to 60-cm soil depth with and without catch crops. The authors explained this by high NO_3-N uptake by catch crops in combination with high NO_3-N leaching losses in the control (Hashemi et al., 2013). This underlines that although P and K losses can be significant for an agroecosystem (Andersson et al., 2013; Askegaard et al., 2004), quantitatively speaking, it is mainly the highly mobile NO_3-N that is lost for a succeeding crop if soil N contents exceed maximum N uptake by catch crops. This study has shown that N uptake of a high-yielding catch crop such as phacelia can take up 74% of applied fertilizer N, while the N leaching potential can remain as high as 82% of applied fertilizer N after the cultivation of a low-yielding catch crop with low shoot N concentration such as white lupin.

4.2.3 | Nutrient availability for a succeeding crop

The availability of nutrients stored in catch crop biomass to a succeeding crop is determined by (1) the decomposition rate, (2) nutrient losses during winter, (3) synchronization of catch crop nutrient release and nutrient uptake by the succeeding crop, and (4) soil cultivation practices. While the latter ones were not part of this particular study, we analyzed shoot C:N ratios as an indicator for the decomposition rate of organic substances (H. L. Jensen, 1929; Quemada & Cabrera, 1995). The C:N ratio was shown to be one of the best predictors for the net N mineralization of catch crops (Quemada & Cabrera, 1995; Thomsen et al., 2016). While C:N ratios below 25 provide favorable conditions for decomposition, microbial immobilization of N can occur at C:N ratios above 25 (Justes et al., 2009). All catch crop C:N ratios in this study were below 25 (Figure 5), indicating a medium to good nutrient availability for decomposition. Although decomposition is necessary to provide nutrients to the succeeding crop, frost-sensitive catch crops with low C:N ratio have been shown to increase nutrient leaching during winter (Liu et al., 2015). For P, leaching is facilitated by freezing-thawing cycles and high precipitation (Liu et al., 2014, 2015), common climatic conditions in Northern Europe. Thus, although nutrient uptake by phacelia was effective in reducing soil N, P, and K concentrations, its comparingly low C:N ratio (Figure 5) and its sensitivity to frost (Liu et al., 2014) could promote quick microbial decomposition and facilitate high nutrient losses in winter. For example, Hashemi et al. (2013) showed that NO_3-N stored in the above-ground biomass of oat decreased by 47% between December and spring of the following year. Similar results were reported by Thorup-Kristensen (1994) who showed for different non-persistent catch crops that after decomposition, between 50% and 80% of previously stored N were lost during winter, resulting in higher N leaching losses in comparison to persistent catch crops (Böldt et al., 2021; Gollner et al., 2020). These losses can significantly reduce nutrient availability to a succeeding crop. Consequently, the results presented above have to be viewed with great caution as the catch crops were harvested immediately after the first frost to prevent nutrient losses caused by decomposition.

4.3 | Performance of a catch crop mixture

The catch crop mixture had comparably high shoot and root biomass (Figure 2) and showed high N, P, and K uptake (Table 2). However, it did not outperform the best-performing single-species treatment.

Although the design of this study does not allow a clear distinction between the three inter-species interactions (complementarity, facilitation, and competition) these results indicate that a high diversity catch crop mixture does not necessarily provide benefits in the form of higher nutrient use efficiencies or nutrient uptake under non-limiting growth conditions. We, therefore, conclude that any facilitative effects that might have occurred between some of the catch crops in the seven-species mixture were (1) either not quantifiable with the parameters we analyzed or (2) they were superimposed by simultaneous antagonistic effects.

Since N was not a growth-limiting factor in this study, the benefits of complementary N use by legumes and non-legumes (Möller et al., 2008; Wendling et al., 2017) are unlikely to have had a positive impact on the performance of the mixture. In fact, as mentioned earlier, roots of white lupin were not nodulated and therefore not able to fix atmospheric N_2. However, the absence of complementary N acquisition in the mixture does not necessarily mean that N availability did not affect species interactions. Various studies have shown that N fertilization influences the competitiveness of catch crop species grown in mixtures (Andersen et al., 2005; Wendling et al., 2017), similar to the effect of N on weed competitiveness (Blackshaw & Brandt, 2008). The irrigation practice of keeping soil moisture at 50% WHC might have supported NO_3^- translocation to deeper soil layers, thereby providing a competitive advantage to the two crucifers white mustard and oilseed radish over the other species in the mixture due to rapid seedling emergence and root establishment. According to Wendling et al. (2017), high N availability favors the competitiveness of mustard in mixtures. This is also reflected in the high NUE of white mustard grown in monoculture in this study and the fact that white mustard was the most dominant species in the mix treatment (Supplementary Information 5).

Nevertheless, results on mixture performance provided here have to be regarded with caution as we only considered one specific mixture with a specific number and composition of species and specific sowing densities, under very specific growth conditions (water and nutrient availability). It has been shown that already a small variation of one of these parameters can affect overall mixture performance (Baraibar et al., 2020; Connolly et al., 1990). Additionally, reasons for and benefits provided by the cultivation of catch crop mixtures cover a very broad spectrum (Blesh, 2018; Chapagain et al., 2020; Couëdel et al., 2018; Finney et al., 2016) while we only focused on biomass production and nutrient uptake.

5 | CONCLUSION

The new approach to study catch crop nutrient retention under semi-controlled conditions was suitable to identify differences in root characteristics and nutrient uptake. Under non-limiting growth conditions—in terms of water and nutrient supply—*Phacelia tanacetifolia* had the highest N, P, and K uptake out of the seven single catch crops in this study. Phacelia was also characterized by a narrow C:N ratio, an indicator for good nutrient availability for a succeeding crop. However, the occurrence of nutrient losses between the first frost event and the cultivation of a succeeding main crop has to be considered when choosing a frost-sensitive winter catch crop. The catch crop mixture tested in this study, consisting of catch crops that occupy various ecological niches, did not outperform the best-performing single-species treatment. High N availability increased the dominance of competitive species (quick development and nutrient accumulation) in the mixture while potential benefits of the legume *Lupinus alba* were diminished. Thus, when nutrient and water availability are not limited, cultivation of a single catch crop could be as (or even more) effective in reducing nutrient losses as a diverse catch crop mixture. However, the cultivation of a mixture of species might provide additional ecosystem services to a cropping system, which were not analyzed in this study.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Alfaro, M. A., Jarvis, S. C., & Gregory, P. J. (2004). Factors affecting potassium leaching in different soils. *Soil Use and Management*, *20*(2), 182–189.

Amann, C., & Amberger, A. (1989). Phosphorus efficiency of buckwheat (*Fagopyrum esculentum*). *Zeitschrift für Pflanzenernährung und Bodenkunde*, *152*(2), 181–189.

Andersen, M. K., Hauggaard-Nielsen, H., Ambus, P., & Jensen, E. S. (2005). Biomass production, symbiotic nitrogen fixation and inorganic N use in dual and tri-component annual intercrops. *Plant and Soil*, *266*(1), 273–287.

Andersson, H., Bergström, L., Djodjic, F., Ulén, B., & Kirchmann, H. (2013). Topsoil and subsoil properties influence phosphorus leaching from four agricultural soils. *Journal of Environmental Quality*, *42*(2), 455–463.

Askegaard, M., Eriksen, J., Johnston, A. E. (2004). Sustainable management of potassium. In P. Schijønning, S. Elmholdt, & B. T. Christensen (Eds.), *Managing soil quality: challenges in modern agriculture* (pp. 85–102). CAB International.

Baraibar, B., Murrell, E. G., Bradley, B. A., Barbercheck, M. E., Mortensen, D. A., Kaye, J. P., & White, C. M. (2020). Cover crop mixture expression is influenced by nitrogen availability and growing degree days. *PLoS ONE*, *15*(7), e0235868. https://doi.org/10.1371/journal.pone.0235868

Basche, A. D., Archontoulis, S. V., Kaspar, T. C., Jaynes, D. B., Parkin, T. B., & Miguez, F. E. (2016). Simulating long-term impacts of cover crops and climate change on crop production and environmental outcomes in the Midwestern United States. *Agriculture, Ecosystems & Environment*, *218*, 95–106.

Blackshaw, R. E., & Brandt, R. N. (2008). Nitrogen fertilizer rate effects on weed competitiveness is species dependent. *Weed Science*, *56*(5), 743–747.

Blesh, J. (2018). Functional traits in cover crop mixtures: Biological nitrogen fixation and multifunctionality. *Journal of Applied Ecology*, *55*(1), 38–48.

Böldt, M., Taube, F., Vogeler, I., Reinsch, T., Kluß, C., & Loges, R. (2021). Evaluating different catch crop strategies for closing the nitrogen cycle in cropping systems—field experiments and modelling. *Sustainability*, *13*(1), 394. https://doi.org/10.3390/su13010394

Brown, D. A. (1953). Cation exchange in soils through the moisture range, saturation to the wilting percentage. *Soil Science Society of America Journal*, *17*(2), 92–96.

Brust, J., Claupein, W., & Gerhards, R. (2014). Growth and weed suppression ability of common and new cover crops in Germany. *Crop Protection*, *63*, 1–8.

Campiglia, E., Mancinelli, R., Radicetti, E., & Marinari, S. (2011). Legume cover crops and mulches: effects on nitrate leaching and nitrogen input in a pepper crop (*Capsicum annuum* L.). *Nutrient Cycling in Agroecosystems*, *89*(3), 399–412.

Chapagain, T., Lee, E. A., & Raizada, M. N. (2020). The potential of multi-species mixtures to diversify cover crop benefits. *Sustainability*, *12*(5), 2058. https://doi.org/10.3390/su12052058

Connolly, J., Wayne, P., & Murray, R. (1990). Time course of plant-plant interactions in experimental mixtures of annuals: density, frequency, and nutrient effects. *Oecologia*, *82*(4), 513–526.

Couëdel, A., Alletto, L., & Justes, É. (2018). Crucifer-legume cover crop mixtures provide effective sulphate catch crop and sulphur green manure services. *Plant and Soil*, *426*(1), 61–76.

Dabney, S. M., Delgado, J. A., & Reeves, D. W. (2001). Using winter cover crops to improve soil and water quality. *Communications in Soil Science and Plant Analysis*, *32*(7–8), 1221–1250.

Derpsch, R., Sidiras, N., & Roth, C. H. (1986). Results of studies made from 1977 to 1984 to control erosion by cover crops and no-tillage techniques in Paraná, Brazil. *Soil and Tillage Research*, *8*, 253–263.

Djodjic, F., Börling, K., & Bergström, L. (2004). Phosphorus leaching in relation to soil type and soil phosphorus content. *Journal of Environmental Quality*, *33*(2), 678–684.

Dobermann, A. R. (2005). Nitrogen use efficiency-state of the art. *Agronomy–Faculty Publications*, 316.

Dorsainvil, F., Dürr, C., Justes, E., & Carrera, A. (2005). Characterisation and modelling of white mustard (*Sinapis alba* L.) emergence under several sowing conditions. *European Journal of Agronomy*, *23*(2), 146–158.

Drinkwater, L. E., & Snapp, S. (2007). Nutrients in agroecosystems: rethinking the management paradigm. *Advances in Agronomy*, *92*, 163–186.

DWD (2020). *Deutscher Wetterdienst—Wetter Und Klima*. *Bundesministerium für Verkehr und Digitale Infrastruktur*. http://dwd.de.

EC (2017). Report from the commission to the European Parliament and the council on the implementation of the ecological focus area obligation under the green direct payment scheme. European Commission.

Eichler-Löbermann, B., Köhne, S., Kowalski, B., & Schnug, E. (2008). Effect of catch cropping on phosphorus bioavailability in comparison to organic and inorganic fertilization. *Journal of Plant Nutrition*, *31*(4), 659–676.

Evans, J., O'Connor, G. E., Turner, G. L., & Bergersen, F. J. (1987). Influence of mineral nitrogen on nitrogen fixation by lupin (*Lupinus angustifolius*) as assessed by ^{15}N isotope dilution methods. *Field Crops Research*, *17*(2), 109–120.

Federle, T. W., Dobbins, D. C., Thornton-Manning, J. R., & Jones, D. D. (1986). Microbial biomass, activity, and community structure in subsurface soils. *Groundwater*, *24*(3), 365–374.

Fierer, N., Schimel, J. P., & Holden, P. A. (2003). Variations in microbial community composition through two soil depth profiles. *Soil Biology and Biochemistry*, *35*(1), 167–176.

Finney, D. M., White, C. M., & Kaye, J. P. (2016). Biomass production and carbon/nitrogen ratio influence ecosystem services from cover crop mixtures. *Agronomy Journal*, *108*(1), 39–52.

Gaines, T. P., & Gaines, S. T. (1994). Soil texture effect on nitrate leaching in soil percolates. *Communications in Soil Science and Plant Analysis*, *25*(13–14), 2561–2570.

García-Palacios, P., Maestre, F. T., Bardgett, R. D., & De Kroon, H. (2012). Plant responses to soil heterogeneity and global environmental change. *Journal of Ecology*, *100*(6), 1303–1314.

Gollner, G., Fohrafellner, J., & Friedel, J. K. (2020). Winter-hardy vs. freeze-killed cover crop mixtures before maize in an organic farming system with reduced soil cultivation. *Organic Agriculture*, *10*(1), 5–11.

Greub, K. L., & Roberts, T. L. (2020). ^{15}N fertilizer recovery and partitioning by cover crops under greenhouse conditions. *Agronomy Journal*, *112*(6), 5300–5311.

Hallama, M., Pekrun, C., Lambers, H., & Kandeler, E. (2019). Hidden miners—the roles of cover crops and soil microorganisms in phosphorus cycling through agroecosystems. *Plant and Soil*, *434*(1), 7–45.

Hashemi, M., Farsad, A., Sadeghpour, A., Weis, S. A., & Herbert, S. J. (2013). Cover-crop seeding-date influence on fall nitrogen recovery. *Journal of Plant Nutrition and Soil Science*, *176*(1), 69–75.

Herrera, J. M., Feil, B., Stamp, P., & Liedgens, M. (2010). Root growth and nitrate-nitrogen leaching of catch crops following spring wheat. *Journal of Environmental Quality*, *39*(3), 845–854.

Heuermann, D., Gentsch, N., Boy, J., Schweneker, D., Feuerstein, U., Groß, J., Bauer, B., Guggenberger, G., von Wirén, N. (2019). Interspecific competition among catch crops modifies vertical root biomass distribution and nitrate scavenging in soils. *Scientific Reports*, *9*(1), 1–11.

Hohmann, M., Stahl, A., Rudloff, J., Wittkop, B., & Snowdon, R. J. (2016). Not a load of rubbish: simulated field trials in large-scale containers. *Plant, Cell and Environment 39*(9), 2064–2073.

Holmes, A. A., Thompson, A. A., & Wortman, S. E. (2017). Species-specific contributions to productivity and weed suppression in cover crop mixtures. *Agronomy Journal*, *109*(6), 2808–2819.

Hooper, D. U., Chapin Iii, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Set, H., Symstad, A. J., Vandermeer, J., Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, *75*(1), 3–35.

Houba, V. J. G., Novozamsky, I., Huybregts, A. W. M., & Van der Lee, J. J. (1986). Comparison of soil extractions by 0.01 M $CaCl_2$, by EUF and by some conventional extraction procedures. *Plant and Soil*, *96*(3), 433–437.

Hütsch, B. W., & Schubert, S. (2018). Maize harvest index and water use efficiency can be improved by inhibition of gibberellin biosynthesis. *Journal of Agronomy and Crop Science*, *204*(2), 209–218.

Janušauskaitė, D., Arlauskienė, A., & Maikštėnienė, S. (2013). Soil mineral nitrogen and microbial parameters as influenced by catch crops and straw management. *Zemdirbyste-Agriculture*, *100*(1), 9–18.

Jensen, E. S. (1992). The release and fate of nitrogen from catch-crop materials decomposing under field conditions. *Journal of Soil Science*, *43*(2), 335–345.

Jensen, H. L. (1929). On the influence of the carbon: nitrogen ratios of organic material on the mineralisation of nitrogen. *The Journal of Agricultural Science*, *19*(1), 71–82.

Justes, E., Mary, B., & Nicolardot, B. (2009). Quantifying and modelling C and N mineralization kinetics of catch crop residues in soil: parameterization of the residue decomposition module of STICS model for mature and non mature residues. *Plant and Soil*, *325*(1), 171–185.

Kaleeem Abbasi, M., Mahmood Tahir, M., Sabir, N., & Khurshid, M. (2015). Impact of the addition of different plant residues on nitrogen mineralization–immobilization turnover and carbon content of a soil incubated under laboratory conditions. *Solid Earth*, *6*(1), 197–205.

Kamh, M., Horst, W. J., Amer, F., Mostafa, H., & Maier, P. (1999). Mobilization of soil and fertilizer phosphate by cover crops. *Plant and Soil*, *211*(1), 19–27.

Keipp, K., Hütsch, B. W., Ehlers, K., & Schubert, S. (2020). Drought stress in sunflower causes inhibition of seed filling due to reduced cell-extension growth. *Journal of Agronomy and Crop Science*, *206*(5), 517–528.

Kerley, S. J., & Huyghe, C. (2002). Stress-induced changes in the root architecture of white lupin (*Lupinus albus*) in response to pH, bicarbonate, and calcium in liquid culture. *Annals of Applied Biology*, *141*(2), 171–181.

Komainda, M., Taube, F., Kluß, C., & Herrmann, A. (2016). Above-and below-ground nitrogen uptake of winter catch crops sown after silage maize as affected by sowing date. *European Journal of Agronomy*, *79*, 31–42.

Kristensen, H. L., & Thorup-Kristensen, K. (2004). Root growth and nitrate uptake of three different catch crops in deep soil layers. *Soil Science Society of America Journal*, *68*, 529–537.

Kuo, S., Huang, B., & Bembenek, R. (2001). Effect of winter cover crops on soil nitrogen availability, corn yield, and nitrate leaching. *The Scientific World Journal*, *1*, 22–29.

Kwiatkowski, C. A., Harasim, E., & Staniak, M. (2020). Effect of catch crops and tillage systems on some chemical properties of loess soil in a short-term monoculture of spring wheat. *Journal of Elementology*, *25*(1), 35–43.

Liebmann, P., Wordell-Dietrich, P., Kalbitz, K., Mikutta, R., Kalks, F., Don, A., Woche, S. K., Dsilva, L. R., Guggenberger, G. (2020). Relevance of aboveground litter for soil organic matter formation—a soil profile perspective. *Biogeosciences*, *17*(12), 3099–3113.

Lim, P. O., Kim, H. J., & Gil Nam, H. (2007). Leaf senescence. *Annual Reviews of Plant Biology*, *58*, 115–136.

Liu, J., Bergkvist, G., & Ulén, B. (2015). Biomass production and phosphorus retention by catch crops on clayey soils in southern and central Sweden. *Field Crops Research*, *171*, 130–137.

Liu, J., Ulén, B., Bergkvist, G., & Aronsson, H. (2014). Freezing–thawing effects on phosphorus leaching from catch crops. *Nutrient Cycling in Agroecosystems*, *99*(1), 17–30.

Long, J. S., & Ervin, L. H. (2000). Using heteroscedasticity consistent standard errors in the linear regression model. *The American Statistician*, *54*(3), 217–224.

Lynch, J. P. (2007). Roots of the second green revolution. *Australian Journal of Botany*, *55*(5), 493–512.

McLenaghen, R. D., Cameron, K. C., Lampkin, N. H., Daly, M. L., & Deo, B. (1996). Nitrate leaching from ploughed pasture and the effectiveness of winter catch crops in reducing leaching losses. *New Zealand Journal of Agricultural Research*, *39*(3), 413–420.

Mengel, K., & Von Braunschweig, L. C. (1972). The effect of soil moisture upon the availability of potassium and its influence on the growth of young maize plants (*Zea Mays* L.). *Soil Science*, *114*(2), 142–148.

Mitchell, A. R., Ellsworth, T. R., & Meek, B. D. (1995). Effect of root systems on preferential flow in swelling soil. *Communications in Soil Science and Plant Analysis*, *26*(15–16), 2655–2666.

Möller, K., Stinner, W., & Leithold, G. (2008). Growth, composition, biological N_2 fixation and nutrient uptake of a leguminous cover crop mixture and the effect of their removal on field nitrogen balances and nitrate leaching risk. *Nutrient Cycling in Agroecosystems*, *82*(3), 233–249.

Munson, R. D., & Nelson, W. L. (1963). Movement of applied potassium in soils. *Journal of Agricultural and Food Chemistry*, *11*(3), 193–201.

Murphy, J., & Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, *27*, 31–36.

Poorter, H., Bühler, J., van Dusschoten, D., Climent, J., & Postma, J. A. (2012). Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Functional Plant Biology*, *39*(11), 839–850.

Quemada, M., & Cabrera, M. L. (1995). Carbon and nitrogen mineralized from leaves and stems of four cover crops. *Soil Science Society of America Journal*, *59*(2), 471–477.

Rinnofner, T., Friedel, J. K., De Kruijff, R., Pietsch, G., & Freyer, B. (2008). Effect of catch crops on N dynamics and following crops in organic farming. *Agronomy for Sustainable Development*, *28*(4), 551–558.

Sato, S., Morgan, K. T. (2012) Nutrient mobility and availability with selected irrigation and drainage systems for vegetable crops on sandy soils, in M. H. Soriano (Ed.), *Soil health and land use management* (pp. 89–110). InteсhOpen.

Sinaj, S., Stamm, C., Toor, G. S., Condron, L. M., Hendry, T., Di, H. J., Cameron, K. C., Frossard, E. (2002). Phosphorus exchangeability and leaching losses from two grassland soils. *Journal of Environmental Quality*, *31*(1), 319–330.

Soltangheisi, A., Rodrigues, M., Coelho, M. J. A., Gasperini, A. M., Sartor, L. R., & Pavinato, P. S. (2018). Changes in soil phosphorus lability promoted by phosphate sources and cover crops. *Soil and Tillage Research*, *179*, 20–28.

Talgre, L., Lauringson, E., Makke, A., & Lauk, R. (2011). Biomass production and nutrient binding of catch crops. *Zemdirbyste-Agriculture*, *98*(3), 251–258.

Tang, C., Longnecker, N. E., Thomson, C. J., Greenway, H., & Robson, A. D. (1992). Lupin (*Lupinus angustifolius* L.) and pea (*Pisum sativum* L.) roots differ in their sensitivity to pH above 6.0. *Journal of Plant Physiology*, *140*(6), 715–719.

Teboh, J. M., & Franzen, D. W. (2011). Buckwheat (*Fagopyrum esculentum* Moench) potential to contribute solubilized soil phosphorus to subsequent crops. *Communications in Soil Science and Plant Analysis*, *42*(13), 1544–1550.

Thomsen, I. K., Elsgaard, L., Olesen, J. E., & Christensen, B. T. (2016). Nitrogen release from differently aged *Raphanus sativus* L. nitrate catch crops during mineralization at autumn temperatures. *Soil Use and Management*, *32*(2), 183–191.

Thorup-Kristensen, K. (1994). The effect of nitrogen catch crop species on the nitrogen nutrition of succeeding crops. *Fertilizer Research*, *37*(3), 227–234.

Thorup-Kristensen, K. (2001). Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? *Plant and Soil*, *230*(2), 185–195.

Thorup-Kristensen, K., & Nielsen, N. E. (1998). Modelling and measuring the effect of nitrogen catch crops on the nitrogen supply for succeeding crops. *Plant and Soil*, *203*(1), 79–89.

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, *294*(5543), 843–845.

Tosti, G., Benincasa, P., Farneselli, M., Tei, F., & Guiducci, M. (2014). Barley–hairy vetch mixture as cover crop for green manuring and the mitigation of N leaching risk. *European Journal of Agronomy*, *54*, 34–39.

Wanic, M., Zuk-Golaszewska, K., & Orzech, K. (2019). Catch crops and the soil environment–a review of the literature. *Journal of Elementology*, *24*(1), 31–45.

Wasaki, J., Rothe, A., Kania, A., Neumann, G., Römheld, V., Shinano, T., Osaki, M., Kandeler, E. (2005). Root exudation, phosphorus acquisition, and microbial diversity in the rhizosphere of white lupine as affected by phosphorus supply and atmospheric carbon dioxide concentration. *Journal of Environmental Quality*, *34*(6), 2157–2166.

Wendling, M., Büchi, L., Amossé, C., Jeangros, B., Walter, A., & Charles, R. (2017). Specific interactions leading to transgressive overyielding in cover crop mixtures. *Agriculture, Ecosystems & Environment*, *241*, 88–99.

Wendling, M., Büchi, L., Amossé, C., Sinaj, S., Walter, A., & Charles, R. (2016). Influence of root and leaf traits on the uptake of nutrients in cover crops. *Plant and Soil*, *409*(1), 419–434.

White, H. (1980). A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. *Econometrica*, *48*, 817–838.

White, P. J., George, T. S., Dupuy, L. X., Karley, A. J., Valentine, T. A., Wiesel, L., & Wishart, J. (2013). Root traits for infertile soils. *Frontiers in Plant Science*, *4*, 193. https://doi.org/10.3389/fpls.2013.00193

Zhu, Y. G., He, Y. Q., Smith, S. E., & Smith, F. A. (2002). Buckwheat (*Fagopyrum esculentum* Moench) has high capacity to take up phosphorus (P) from a calcium (Ca)-bound source. *Plant and Soil*, *239*(1), 1–8.

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