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Department of Soil and Environment

Potential uptake of phosphorus by catch crops in greenhouse conditions and release after freezing-thawing

Rafa Abdulhassan Khalaf

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Supervisor: Jian Liu, Department of Soil and Environment, SLU
Examiner: Barbro Ulén, Department of Soil and Environment, SLU

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Cover: Eight catch crops species (three replicates each) two days before the first harvest, 2011, photo by author

Abstract

Catch crops are an important component of cropping systems in Sweden and other Scandinavian countries, but may contribute to phosphorus (P) losses after freezing-thawing cycles (FTCs). Eight existing and new catch crop species in Swedish farming were grown in a greenhouse to study potential P uptake and P release from shoots, roots and whole plants after FTCs. The catch crop species were structurator (*Raphanus sativus* L. var. *longipinnatus*), white mustard (*Sinapis alba* L.), oilseed radish (*Raphanus sativus* var. *oleiferus*.), phacelia (*Phacelia tanacetifolia* L.), red clover (*Trifolium pratense* L.), chicory (*Cichorium intybus* L.), perennial ryegrass (*Lolium perenne* L.) and cocksfoot (*Dactylis glomerata* L).

The largest uptake of total P (TP) was found in phacelia and oilseed radish (~17 kg TP ha^{-1}), which also had the largest biomass (approx. 8 t DM ha^{-1}). Red clover had the smallest biomass (1.26 t DM ha^{-1}) and uptake of P (4.4 t TP ha^{-1}) and was excluded from the P release experiment due to its poor growth. Concentrations of TP ranged from 0.25 to 0.35% in shoots and 0.08 to 0.36% in roots. In general, concentrations increased with increasing root specific surface area or volume (except phacelia), but decreased with increasing ratio of root specific surface area to volume. Roots contributed 23-57% of the total biomass and 15-49% of the P content in the crops.

To examine P release, fresh shoot and root samples were exposed to different combinations of freezing thawing treatments (FTTs) and P was extracted with distilled water from these and from untreated controls. Shoot and root samples were dried and milled and total-P concentrations were determined.

Compared with the control, all freezing-thawing treatments caused significant release of P from both shoots and roots of every species, with the most P being released at the first extraction after freezing-thawing. The rate of P release then declined with extraction number and after four extractions it reached the pre-treatment level. In general, shoots of all species except grasses released more P than the roots, while grasses had similar release from both parts. The shoots of the here catch crops were affected most by continuous freezing thawing cycles (CFT-Cs) and discontinuous freezing thawing cycles (DFT-Cs) treatments and less by a single, long-lasting freezing and thawing (SFT-C), whereas roots were evenly affected by all FTTs.

Potential losses of P from the plant materials were consistent with the concentrations of P in the plants. On average for shoots and roots, structurator, white mustard and oilseed radish had the largest release of P among all species, mainly because of high release of P from the shoots, whereas chicory and phacelia had the lowest P release owing to low P release from the roots. The ranking of P amounts released calculated on an areal basis did not differ substantially from the ranking calculated on a concentration basis.

Chicory and phacelia were the best species in terms of P retention in this study. However, the results need to be validated in lysimeter or field studies under more realistic conditions.

Keywords: Catch crops, Freezing, Thawing, Phosphorus, Uptake, Release, Root morphology.

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List of abbreviations

Abbreviation	Description
CFT-Cs	Continuous freezing-thawing cycles
DFT-Cs	Discontinuous freezing-thawing cycles
DM	Dry matter
E	Extraction
FTC	Freezing thawing cycle
FTT	Freezing thawing treatment
SFT-C	One single, more long-lasting (4 days) freezing-thawing cycle
Tot-WEP	Total water extractable phosphorus
TP	Total phosphorus

1. Introduction

1.1 Phosphorus release from catch crops and other plants

Phosphorus (P) is of great importance in an environmental perspective and has been identified as the most limiting nutrient for phytoplankton growth in the majority of lakes (Schindler, 1977) and in marine environments such as the Baltic Sea (Boesch *et al*., 2005). Phosphorus transport from arable land is the main contributor to this enclosed brackish water body (HELCOM, 2007), with a typical load of 0.4 kg P ha^{-1} $year^{-1}$ from Sweden, 20-80% of which is in dissolved reactive form (Bergström *et al*., 2007). Besides soil erosion and use of P fertilizers, plants represent a potential source for P losses to water after drought or freezing-thawing, with the latter of high relevance under Nordic conditions (Uhlen, 1989; Børresen & Uhlen, 1991; White, 1973). Special consideration may be needed when introducing new plants that have not been cold-acclimated.

Phosphorus may be released from plants after the cells burst due to ice crystal formation and frost damage, which leads to declining water potential and withdrawal of water from adjacent cells (Jones, 1992). Cell damage or death due to freezing leads to the point of no return for recovery and can result in release of inter/intra-cellular P. Plant resistance to frost damage differs between species and different parts of the plant. In a study on two turfgrasses, perennial ryegrass (*Lolium perenne* L.) and supine bluegrass (*Poa supina* Schrad.), Stier *et al*. (2003) used an infrared video and observed that bluegrass was more sensitive to frost damage than perennial ryegrass. The most sensitive part of these plants to frost damage was the crown near the soil surface, which represented the joint between upper parts and roots. However, roots froze first, then crowns and lower shoots, and finally leave**.**

Catch crops are grown in the period between two main crops. They may be either under-sown with the previous main crop or sown after the main crop is harvested and before the succeeding crop is grown. They are also widely referred to as cover crops when they are grown to protect soil from erosion. Growing catch crops is an important mitigation option to reduce nitrogen (N) leaching after the main crop is harvested. The practice is widely used in the south of Sweden, as well as in the other Scandinavian countries (Aronsson, 2000; Ulén *et al*., 2007). The catch crop used should be able to establish quickly so that it can develop rapidly after the main crop is harvested, but should not compete with the main crop. With respect to P, the catch crop should have high abilities to store P, both in above-ground plant parts and in roots, and to resist freezing damage, which may cause P leaching. Therefore, it is very important to select appropriate catch crops without a high risk of P leaching.

Several studies have shown that water-extractable P (WEP) from plants (*e.g.* Bechmann *et al*., 2005) and soil (*e.g.* Vaz *et al*., 2006) increases with the number of FTCs. Since more frequent and greater fluctuations in temperature and more FTCs are predicted for Scandinavian countries with future climate change (Rummukainen *et al*., 2003), potential WEP should be carefully evaluated for the whole plant in connection with freezing-thawing.

The aim of this study was to investigate potential uptake of P by eight different catch crop species and release of P from their above-ground parts (referred to here as ‘shoots’) and roots after different FTTs. The following hypothesises were tested:

(1) Uptake of P differs with species and root characteristics such as specific root length; specific root surface area, thickness and general shape (*e.g.* tap roots compared with fibrous roots).

(2) Annual species release more P than perennial species.

(3) Shoots release more P than roots.

(4) Tap roots potentially release more P than fibrous roots following frost damage.

(5) The highest P release occurs after the first FTC in all catch crop species and parts.

(6) Repeated FT and extraction cycles can increase potential P release compared with a control treatment; and with other FTTs.

2. Materials and methods

2.1 Experimental catch crops

Eight new and existing catch crops used in Swedish agriculture were included in the study (Table 1). Many of the new catch crops share common characteristics, but leaf shape differs between species and roots vary in shape and potential penetration depth.

Table 1. *Catch crop life-form, description of leaf and root, potential rooting depth and potential resistance to frost, where # very good function; ## good performance; ### certain function; #### poor function (Aronsson et al., 2012)*

Catch crops	Life-form	Leaf	Root	Root depth (m)	Frost resistance
Structurator	Annual	Eleptic with more leaflets	Thick fleshy taproot with long, thin, hairy roots	2.2	#
White mustard	Annual	Eleptic with tendency for trifoliate leaflets in tip	Stout taproot	*	####
Oilseed radish	Annual	Eleptic leaflet	Fleshy taproot with more lateral branches	<2.2	###
Phacelia	Annual	Bipinnate and lobed	Dense fibrous	0.75	####
Red clover	Biennial	Orbicular	Deep taproots, branches, tubercle-rich	3	#
Chicory	Perennial	Oblanceolate	Long, stout taproots	*	#
Perennial ryegrass	Perennial	Aciculate	Tufted and fibrous	*	##
Cocksfoot	Perennial	Aciculate	Dense fibrous root mat	0.25	#

*Indicates missing data

Oilseed radish (*Raphanus sativus* var. *oleiferus*) is a winter or freeze-kill and fast-decompose catch crop. It is a type of mustard that is widely grown in Canada and North America as a catch crop and as forage for grazing. The plant was recently introduced as a subsidised catch crop in southern Sweden and is now intensively used in organic farming on clay soils in western Sweden (Källander, 2000). Oilseed radish shoots can reach 0.91 m height under good growing conditions. The root system is known to have a large P storage capacity and to be able to improve soil structure due to 'bio-tillage' during growth. The roots tend to have more lateral branches from the taproot system than structurator (*Raphanus sativus* var. *longipinnatus*). These branches improve the efficiency of uptake of N and other nutrients from the soil profile. Oilseed radish can suppress or delay emergence of weeds, improve the seedbed and increase soil organic matter content. However, since it is susceptible to clubroot disease caused by *Plasmodiophora brassicae* and to cabbage flies (*Delia radicum*), it should not be grown for two consecutive years (Weil & Williams, 2004; Weil & Kremen, 2007; Dean & Weil, 2009; Cavigelli *et al*., 1994).

Structurator (*Raphanus sativus* L. var. *longipinnatus*) is a variety of oilseed radish that shares many characteristics with common oilseed radish, but has some morphological differences. The root of this variety has an even stronger ability to penetrate down into the soil than the root of common oilseed radish. The lower taproot can penetrate to ~1.8 m and the fleshy part can be on average 0.4 m long, with an average protrusion length of 0.1 m. It can be planted after harvest of the main crop to capture N in the autumn. The plant can tolerate temperatures down to -3 ºC and can survive for several nights before it dies and decomposes to leave a thin tissue of residue after the winter (Weil & Williams, 2004; Weil & Kremen, 2007; Dean & Weil, 2009).

White mustard (*Sinapis alba* L.) is an annual plant that can reach 1 m height. The crop is used for forage or for extracting food oil from the seeds. The root system consists of a small, stout taproot and a large quantity of fibrous roots with a large root mass (root mat) confined to the topsoil (Economic Plants and their Diseases, Pests and Weeds, 2003-2009).

Phacelia (*Phacelia tanacetifolia* L.) is an annual herbaceous plant, originally from the USA and Mexico. The crop can adapt to a wide range of climate and soil types. When winter-killed at approx. -8 ºC, the plant material decomposes rapidly.

Phacelia is used intensively in Europe as a catch crop and bee forage plant and is reported to have a high nutrient scavenging ability (Leslie, 2003). The plant has a fibrous root that can reach 0.75 m depth, which branches at a high rate at 0.15 m depth. There are no pathogens associated with phacelia roots (Wyland *et al*., 1996). Phacelia is one of the catch crops used in biodynamic farming (Diver, 1999).

Red clover (*Trifolium pratense* L.) is a biennial (two-year) legume, widely used as a forage crop. Red clover shoots can reach ~0.4 m height. The longest observed depth of roots is ~1.2 m in the first growing season and ~3 m for mature plants in rich moist and silt loam soil. Lateral branches can extend out to around 0.02 m in deeper parts before turning downwards without branching (Weaver, 1926). The root system is rich in tubercles to deep within the soil (Weaver, 1926). Tubercles are small rounded nodules occupied by the soil bacteria *Rhizobium,* which are essential for atmospheric N fixation in the roots of legumes (Lindemann & Glover, 2003). Due to its ability to fix N in the roots, red clover is very important in maintaining soil productivity throughout the crop rotation.

Chicory (*Cichorium intybus* L.) is a member of the sunflower family, Asteraceae (Compositae), and the aerial parts of the crop can be consumed fresh or cooked, while the roots have medical benefits to humans and can be roasted and used as a coffee supplement or coffee substitute (Innocenti *et al*., 2005). Chicory can resist drought relatively well, and can stand for 5-7 years depending on grazing management practices (Hall & Jung, 2008). Chicory shoots can reach 0.3-1.2 m, with grooved, stiffly erect stems (Clapham *et al*., 1981). Its leaves are overall spatulate or oblanceolate, rounded or broadest towards the tip and tapering towards the base and can reach 20 cm long and 5 cm wide. The perennial chicory root system has a long, stout taproot that has the ability to break up the subsoil (Rumball, 1986).

Perennial ryegrass (*Lolium perenne* L.) is currently the most widely used catch crop for N scavenging in Sweden. Ryegrass is a perennial grass that can bear heavy grazing and treading. Roots are mostly clumps of shallow fibrous form (English Ryegrass Grasses, 2013). In pasture around Canterbury, New Zealand, where the climate is similar to that in Northern Europe, the crop produces 4 t DM ha^{-1} in the fifth year (Morris, 2011).

Cocksfoot (*Dactylis glomerata* L), also called orchard grass, is a perennial pasture crop used as hay grass. It can grow to 1 m high. Cocksfoot has been established in Canada and Scandinavia to improve its winter hardness and tolerance to drought. Since the crop does not produce any harmful alkaloids, it has no impaired animal grazing (Mills, 2007). Potential yield of cocksfoot shoots in Canterbury, NZ, ranges from 7.5 to 28.6 t DM ha^{-1} y^{-1} from 10 years old under limited and unlimited pasture conditions, respectively (Mills, 2007). The root system consists of dense fibrous roots that form a mat in the first 0.25 m of the soil profile (Weaver, 1926; Ridley & Simpson, 1994).

The eight catch crops described above were cultivated on pure sand (90% of particles 0.25-1 mm) produced by Sibelco Nordic on 16 February 2011. The mineral composition of the sand was mainly SiO_2 (> 99%).

Each catch crop was cultivated in a plastic box (36 cm x 26 cm x 22 cm), with three replicates. These 24 growing boxes were randomly distributed on a bench in the greenhouse. Before sowing the seeds, a volume of 16.8 L dry sand was added to fill each plastic box to a depth of 18 cm, after which the soil was saturated with 6 L tap water. The sowing rate was 48 seeds per box, corresponding to 8 kg ha^{-1} for grasses and 20 kg ha^{-1} for the other species, which are common seed rates for catch crops in Sweden. After sowing, another 1.5 cm of dry soil was added to cover the seeds. Finally, the soil surface was covered with plastic to prevent high evaporation until the seeds had germinated.

In the greenhouse, light was provided by 10 white halogen bulbs (400 W, Manufacturer) that turned on and off automatically, giving approximately 15 hours of illumination and 9 hours of darkness. Temperature, recorded every hour, fluctuated between day and night, especially when the lights were off and the temperature outside the greenhouse was very low. The temperature was regulated to +15 ºC in the first five days after seeding to provide good germination conditions and avoid unnecessarily high evaporation rates. Average temperature during the next five weeks was increased to an average of approximately +21 ^{o}C in order to accelerate the growth rate, and then at 40 days after sowing the temperature was lowered to approximately +10 ^{o}C. The catch crops were irrigated with tap water when needed during the whole growing period. A total of 100 kg N ha^{-1} and 20 kg P ha^{-1} and additional necessary elements were applied during the growing period, one-third while saturating the soil with water before sowing and the remaining two-thirds when the catch crops started to show signs of nutrient deficiency after one month of growth.

2.1.1 Growth in the last weeks and harvest

Catch crop species were harvested at different times (Table 2), which were determined by the work load and their rate of maturation, *i.e*. early maturing species were harvested first. White mustard and structurator were harvested first when they started flowering, 34 days after sowing. Phacelia and oilseed radish were harvested 47 days after sowing, and red clover and chicory 54 days after sowing. The latest harvested catch crops were perennial ryegrass and cocksfoot, 62 days after sowing.

Table 2. *Catch crop species, date of harvest, mean air temperature for the week before harvest, number (No.) of days of growth, total number of plants and average height of the three replicates at harvest*

Catch crops	Harvest	Temperature, ^{o}C	No. days	No. of plants	Height, cm
Structurator	22/3/2011	21	34	95	28
White mustard	22/3/2011	21	34	133	40
Oilssed radish	4/4/2011	13	47	128	30
Phacelia	4/4/2011	13	47	107	50
Red clover	11/4/2011	9	54	72	18
Chicory	11/4/2011	9	54	113	30
Perennial ryegrass	19/4/2011	10	62	122	35
Cocksfoot	19/4/2011	10	62	111	35

Harvesting was done by cutting off the shoots with a pair of scissors from the root crown, and the shoots and roots were separately collected. The number of shoots per plant and shoot height were recorded. Roots were collected in a 2-mm sieve by slowly and carefully washing away adhering sand with tap water while minimising damage to the roots. The collected roots were air-dried for 2 hours at room temperature (20±2 ºC) on paper tissues, which were changed when it was wet. The shoots and air-dried roots were weighed to determine fresh weight and then the replicates were pooled before sampling for further analysis and experiments.

2.1.2 Root scanning

To determine root morphological characteristics, a 100-170 g subsample of fresh roots from each of the catch crops was scanned with an Epson perfection 4990 PHOTO scanner at the Department of Crop Production Ecology, SLU. Before scanning, the roots were separated and fitted into a transparent box filled with distilled water. The scanner produced a raster image format, *i.e*. an array of square pixels dots per inch (dpi), in resolution 4800 * 9600 dpi. Professional Win RHIZO (Pro V. 2007a) software was used to analyse the scanned images and to determine root morphological parameters such as root specific (length, surface area, volume, surface area to volume and average diameter).

2.2 Phosphorus release experiment

2.2.1 Sampling and extraction under initial conditions

To examine P release under various freezing-thawing treatments (see detailed description in the section below), 2 g fresh shoot or root samples (3 replicates per treatment) were extracted with distilled water and WEP was analysed. The shoot samples were taken from the youngest growing part and the root samples were taken to include a complete root, *i.e.* the main root with as many branches as possible. Red clover, which had low biomass production, was excluded from the study on P release.

To obtain the initial concentration of WEP, the first extraction (E0) took place on all samples directly after sampling. A pre-test with seven extractions after treatments on structurator and white mustard showed that P release after four extractions (excluding E0) became consistently small. Therefore, four extractions (excluding E0) were made on all other species. Extraction was made by adding 100 mL distilled water to a plastic bottle filled with 2 g plant sample and end-to-end shaking at a rate of 16 rpm for 1 hour at room temperature (20±2 °C). After the initial extraction, the plant samples were kept intact inside the plastic bottles during the subsequent FT treatments. Water samples were filtered through a 100-cm filtering area on 00H filter paper at 40 mL min^{-1}. The filtrate was stored in glass bottles at +1 ºC before further analysis of total P (TP) and dissolved reactive P (DRP), which took place within 3 days.

2.2.2 Freezing-thawing treatments and extraction sequences

The shoots and roots of the catch crops were treated in four different ways (Table 3), following Bechmann *et al*. (2005) in a similar study.

The treatments were as follows (Table 3)

- Control, no freezing: Four extractions (excluding E0) each after samples were kept without freezing at +4 °C for 20 hours.
- DFT-Cs (discontinuous freezing-thawing cycles): Four extractions (excluding E0) each after one FTC, *i.e*. frozen at -18 °C for 10 hours and thawed at +18±2 °C for 10 hours.
- CFT-Cs (continuous freezing-thawing cycles): Four extractions (excluding E0) with a 6-hour interval between two consecutive extractions, when the samples were kept at +4 °C after completing four continuous FTCs consisting of freezing at -18 °C for 10 hours and thawing at +18±2 °C for 10 hours.
- SFT-C (one single, more long-lasting freezing and thawing cycle): Four extractions (excluding E0) after completing the long-lasting freezing (4 days) and thawing (10 hours), with a 6-hour interval between two consecutive extractions, when the samples were kept at +4 °C.

Table 3. *Treatment names and experimental procedures for the shoots and roots of the eight catch crops studied. DFT-Cs = discontinuous freezing-thawing cycles, CFT-Cs = continuous freezing-thawing cycles, SFT-C, one single and more long-lasting (4 days) freezing-thawing cycle, N = no freezing, E = extraction, F = freezing, T = thawing*

Treatments	Procedures
Control	E-N-N-E-N-N-E-N-N-E-N-N-E
DFT-Cs	E-F-T-E- F-T-E- F-T-E- F-T-E
CFT-Cs	E-F-T- F-T- F-T- F-T-E-E-E-E
SFT-C	E-F-F-F-F-F-F-F-F-T-E-E-E-E

2.3 Chemical analysis

A sample of 20-50 g shoots and roots of each catch crop (3 replicates) was dried at +40 ºC, weighed to determine dry matter content and milled for TP analysis. The TP analysis was carried out by the Plant Nutrition Laboratory at the Department of Soil and Environment, SLU. To analyse TP concentration, ~1.5 g DM plant samples were added to a 50-mL Kjeltec tube and digested with 10 mL concentrated nitric acid (HNO_3). Samples were left overnight to break down organic matter and then boiled with stepwise increasing temperature, for one hour at 60 ºC, one hour at 100 ºC and four hours at 125 ºC. After two hours at 125 ºC, an additional 5 mL of concentrated nitric acid were added. The samples were diluted to 50 mL with distilled water after cooling, and P was determined by inductively coupled plasma (ICP).

Concentrations of DRP and TP in water extracts were determined respectively before and after the water samples were oxidised, in a spectrophotometer at a wavelength of 904 nm according to Murphy & Riley (1962). Oxidation of the water samples were performed according to European Standard EN 1189.

2.4 Statistical analysis

A large quantity of data was obtained in this study, including 1032 measurements of DRP and TP concentrations in water samples, 48 measurements of TP in plant samples and 237 measurements of root morphological characteristics on the scanned images. All data are presented on a dry matter basis unless otherwise stated.

The SAS software (Version 9.2) was used for statistical analysis (Littell *et al.*, 2006). The General Linear Model (GLM) was used for analysis of differences in plant biomass and plant P concentrations between the catch crops and for regressions of root morphology parameters with plant P content. Differences in P release from the catch crops were analysed with a Mixed Model for repeated measurements, where the “repeated” statement was used to realise the repeated extractions on the same sample. The complete model including all the factors (species, crop part, treatment, extraction time) and their interactions was used and WEP concentrations at E0 were included in the model as baseline values. A significance level of α=0.05 was used throughout this study unless otherwise stated.

3. Results

3.1 Harvested biomass and uptake of P

Germination rate and growth were good for almost all the experimental catch crops. The biomass and concentrations of P in the shoots and roots and total biomass and uptake of P in the whole plant are shown in Table 4. Oilseed radish and phacelia each produced more than 5 t ha^{-1} of biomass in shoots, which was substantially more than the other species, while chicory, structurator and white mustard produced around 3 t ha^{-1}, and the two grasses, perennial ryegrass and cocksfoot, produced approximately 2 tons ha^{-1}. For unknown reasons, red clover had a small shoot biomass (0.87 t ha^{-1}), which was significantly lower than for any of the other species. Concentrations of P in the shoots ranged from 0.21% in perennial ryegrass to 0.35% in red clover. The ranking of P concentration in the shoots was: red clover = structurator = white mustard > oilseed radish = phacelia = chicory = cocksfoot = perennial ryegrass. No clear pattern was found between shoot P concentrations and crop species.

Table 4. *Biomass (Biom) and concentration of total phosphorus (TP) in the shoots and roots of the catch crops, and total biomass and uptake of TP by the whole plant determined at harvest. Different letters indicate significant differences in each column (α=0.05, n=3)*

	Shoots		Roots		Whole plant	
Catch crops	Biom (t ha^{-1})	TP (%)	Biom (t ha^{-1})	TP (%)	Biom (t ha^{-1})	TP uptake (kg ha^{-1})
Structurator	3.4 C	0.35 C	1.1 B	0.22 B	4.5 B	14.1 CD
White mustard	3.0 C	0.32 BC	0.9 B	0.18 AB	3.9 B	11.4 C
Oilseed radish	5.3 D	0.27 B	2.5 D	0.13 AB	7.8 C	17.5 E
Phacelia	5.3 D	0.26 AB	3.1 E	0.09 A	8.4 C	16.4 DE
Red clover	0.9 A	0.35 C	0.4 A	0.36 C	1.3 A	4.4 A
Chicory	3.6 C	0.24 AB	4.8 F	0.08 A	8.4 C	12.4 C
Perennial ryegrass	1.9 B	0.21 A	2.3 CD	0.17 AB	4.2 B	7.8 B
Cocksfoot	1.8 B	0.22 AB	1.9 C	0.13 AB	3.7 B	6.3 AB

In general, biomass production was lower for roots than shoots within species with the exception of chicory, perennial ryegrass and cocksfoot (Table 4). Chicory produced 4.78 t DM ha^{-1} roots, which was higher than that of the chicory shoots (3.59 t DM ha^{-1}) and was the highest among all the roots. It was followed by phacelia roots (3.10 t ha^{-1}). Phosphorus concentrations in the roots were lower than in the shoots. The lowest P concentration was in phacelia and chicory among all the species. The ranking of P concentration in the roots was: red clover > structurator = white mustard = perennial ryegrass = oilseed radish = cocksfoot > phacelia = chicory. Red clover had the largest specific root length (85.1 m g^{-1}), specific root surface area (10.7 dm^2 g^{-1}), and specific root volume 10.9 cm^3 g^{-1} among all the species (Table 5).

Concentration of TP in the roots increased significantly with increasing root specific surface area except phacelia (Figure 1).

Table 5. *Specific root length, specific root surface area, specific root volume and ratio of specific surface area (sa) to specific volume (vol) (sa/vol)*

Catch crops	Specific length ($m\ g^{-1}$)	Specific surface ($dm^2\ g^{-1}$)	Specific volume ($cm^3\ g^{-1}$)	sa/vol (cm^{-1})
Structurator	58	7.2	7.1	101
White mustard	34.6	4.5	4.83	94
Oilseed radish	25.1	3.2	3.23	98
Phacelia	48.5	5.9	5.78	102
Red clover	85.1	10.7	10.9	99
Chicory	20.7	2.4	2.25	107
Perennial ryegrass	52.4	5.5	4.55	120
Cocksfoot	62.2	5.3	3.64	146

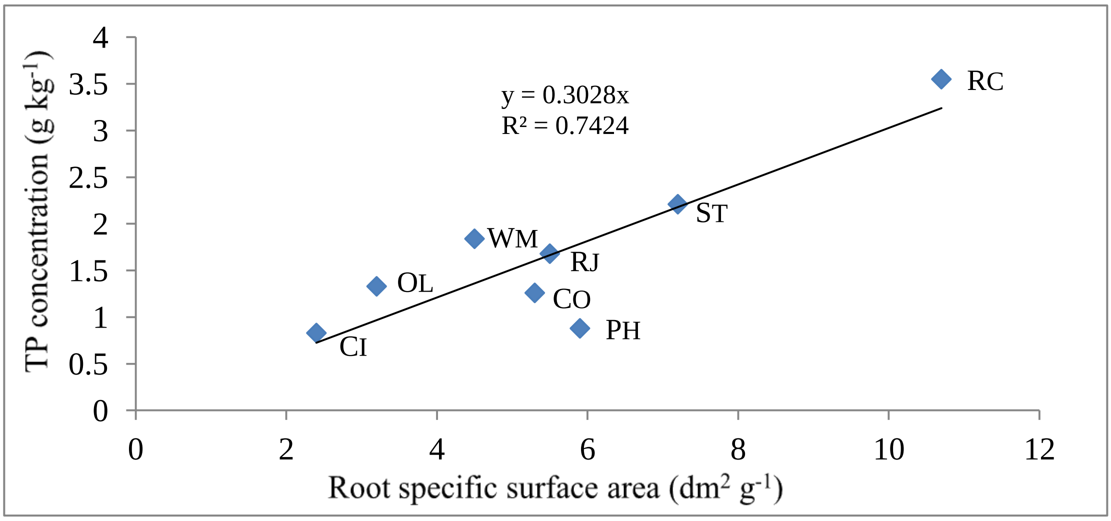

Figure 1. Correlation between concentrations of TP in the roots and root specific surface area for 8 tested catch crops. Abbreviates for the catch crops names, (ST = Structurator, WM = White mustard, PH = Phacelia, OL = Oilseed radish, RC = Red clover, CI = Chicory, RJ = Perennial ryegrass, CO = Cocksfoot).

Taking the whole plant into account, the species with fleshy or dense fibrous roots took up around 11-18 kg P ha^{-1}, while the plants with fine fibrous roots took up less (perennial ryegrass ~8 kg ha^{-1}, cocksfoot ~6 kg ha^{-1} and red clover <5 kg ha^{-1}).

Oilseed radish and phacelia took up most P, mainly in their shoots, during 47 days of growth (Figure 2).

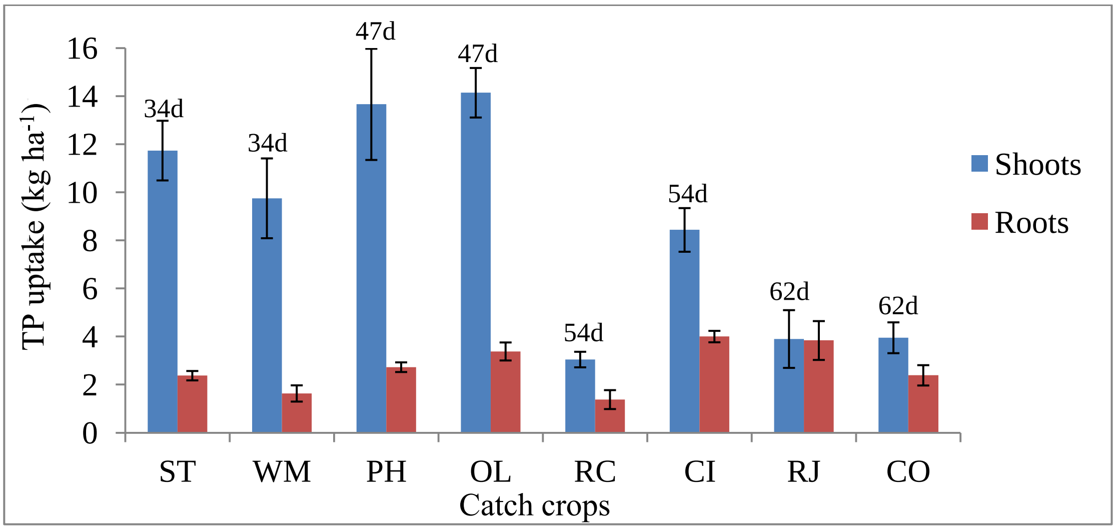

Figure 2. Mean total P uptake in the shoots and roots of the eight catch crops. Abbreviates for the catch crops names, (ST = Structurator, WM = White mustard, PH = Phacelia, OL = Oilseed radish, RC = Red clover, CI = Chicory, RJ = Perennial ryegrass, CO = Cocksfoot, d = days). The small bars represent standard deviations (n=3).

3.2 Phosphorus release from catch crops in water extract

Statistical results based on WEP concentrations (g P kg^{-1} DM) for individual catch crops and parts of plants at each extraction, with interactions, are shown in Tables 6-8. Overall, release of P from the catch crops was significantly affected by crop species ($p<0.0001$), crop part, *i.e.* shoot or root ($p<0.0001$), freezing treatment ($p<0.0001$), and extraction event ($p<0.0001$). The interactions between these factors were also found to be highly significant, *e.g.* crop species x crop part, crop species x treatment, *etc*. ($p<0.0001$).

3.2.1 Phosphorus release from shoots

Overall, catch crop shoots were highly affected by FTTs compared with the control. Susceptibility to P release in respect to treatments was ranked as CFT-Cs = DFT-Cs > SFT-C > Control (Table 6). FTCs also caused much higher P release from the shoots than at the initial extraction (E0, 0.02 g P kg^{-1}) and, for the FTTs, the highest release of P was at E1 (0.92 g P kg^{-1}), *i.e.* after the first FTC (Table 7). Tot-WEP significantly declined after E1 until E4 (0.17 g P kg^{-1}). Release of P from shoots of strucutrator, white mustard and oilseed radish was much higher than that from the other species, giving the ranking stracturator > white mustard > oilseed radish > chicory = perennial ryegrass = phacelia = cocksfoot (Table 8).

Table 6. *WEP (g P kg^{-1} DM) as a mean of five extractions (including E0) for shoots, roots and the whole plant (mean) of all species under different treatments. Different letters indicate statistically significant differences within rows, (see Table 3 for treatments abbreviation)*

	Treatments			
Plant parts	Control	DFT-Cs	CFT-Cs	SFT-C
Shoot	0.01 a	0.51 c	0.52 c	0.41 b
Roots	0.04 a	0.26 b	0.25 b	0.28 b
Mean	0.02 a	0.39 c	0.39 c	0.34 b

Table 7. *WEP (g P kg^{-1} DM) as a mean of four treatments for shoots, roots and the whole plant (mean) of all species at various extractions. Different letters indicate statistically significant differences within rows*

	Extractions				
Plant parts	E0	E1	E2	E3	E4
Shoots	0.02 a	0.92 e	0.42 d	0.28 c	0.17 b
Roots	0.06 b	0.73 d	0.14 c	0.07 b	0.03 a
Mean	0.04 a	0.82 e	0.28 d	0.17 c	0.10 b

Table 8. *WEP (g P kg^{-1} DM) as a mean of all treatments and extractions (including E0) for shoots and roots of different species. Different small letters indicate statistically significant differences within rows, capital letters significant differences within columns*

	Catch crops						
Plant parts	Structurator	White mustard	Oilseed radish	Phacelia	Chicory	Perennial ryegrass	Cocksfoot
Shoots	0.83 d B	0.57 c B	0.29 b B	0.21 a B	0.23 a B	0.21 a A	0.21 a A
Roots	0.38 d A	0.32 c A	0.21 b A	0.09 a A	0.09 a A	0.17 b A	0.18 b A

Table 9. *WEP (g P kg^{-1} DM) as a mean of five extractions (including E0) for shoots and roots of different species under various treatments. Different small letters indicate statistically significant differences within rows, capital letters significant differences within columns, (see Table 3 for treatments abbreviation)*

Plant parts	Treatments	Catch crops: Structurator	White mustard	Oilseed radish	Phacelia	Chicory	Perennial ryegrass	Cocksfoot
Shoots	Control	0.02 a A	0.03 a A	0.002 a A	0.01 a A	0.00 a A	0.01 a A	0.004 a A
	DFT-Cs	1.30 e E	0.72 d C	0.38 c C	0.29 ab C	0.35 bc D	0.27 ab CD	0.23 a B
	CFT-Cs	1.10 d D	0.82 c C	0.49 b D	0.30 a C	0.29 a CD	0.31 a D	0.33 a C
	SFT-C	0.89 c C	0.72 b C	0.28 a B	0.23 a C	0.26 a C	0.23 a BC	0.27 a BC
Roots	Control	0.05 ab A	0.10 b A	0.01 a A	0.01 a A	0.002 a A	0.04 ab A	0.04 ab A
	DFT-Cs	0.52 d B	0.37 c B	0.25 b B	0.11 a B	0.12 a B	0.23 b BC	0.25 b BC
	CFT-Cs	0.48 e B	0.38 d B	0.30 c B	0.11 a B	0.10 a B	0.19 b B	0.19 b B
	SFT-C	0.48 c B	0.43 c B	0.28 b B	0.14 a B	0.14 a B	0.24 b BCD	0.21 ab B

Table 9 shows mean P release from each catch crop and treatment. Chicory, perennial ryegrass, cocksfoot and phacelia had lower P release from shoots than structurator, white mustard and oilseed radish in the CFT-Cs and DFT-Cs treatments. For instance, in the CFT-Cs treatment, cumulative release of all extractions was 1.50 g P kg^{-1} DM from phacelia and 1.45 g P kg^{-1} DM from chicory, which was much lower than that from structurator that had the highest release (5.50 g P kg^{-1} DM), and also lower than that from white mustard (4.10 g P kg^{-1}DM) and oilseed radish (2.45 g P kg^{-1}DM). SFT-C resulted in the same trend of P release as CFT-Cs except that oilseed radish was statistically equal to chicory, perennial ryegrass, cocksfoot and phacelia instead of being higher. Among the FTTs, DFT-Cs had the largest impact on structurator and chicory and the least impact on cocksfoot. CFT-Cs impacted most on structurator, oilseed radish, perennial ryegrass and chicory. White mustard and phacelia were equally affected by FTCs. Statistically similar, low P release was observed among the catch crops in the control treatment.

Figure 3 shows the dynamics of TP release from the shoots of the catch crops at the different extraction times. For the control treatment, the highest tot-WEP concentration was at the initial extraction (E0), although there were no significant differences between any of the tot-WEP concentrations (Figure 3A). For the FTTs, the highest P concentrations were observed at E1 (Figure 3B, C, D) and the concentrations decreased thereafter with extraction number. In general, the magnitude of WEP was lower for SFT-C than for the other FTTs.

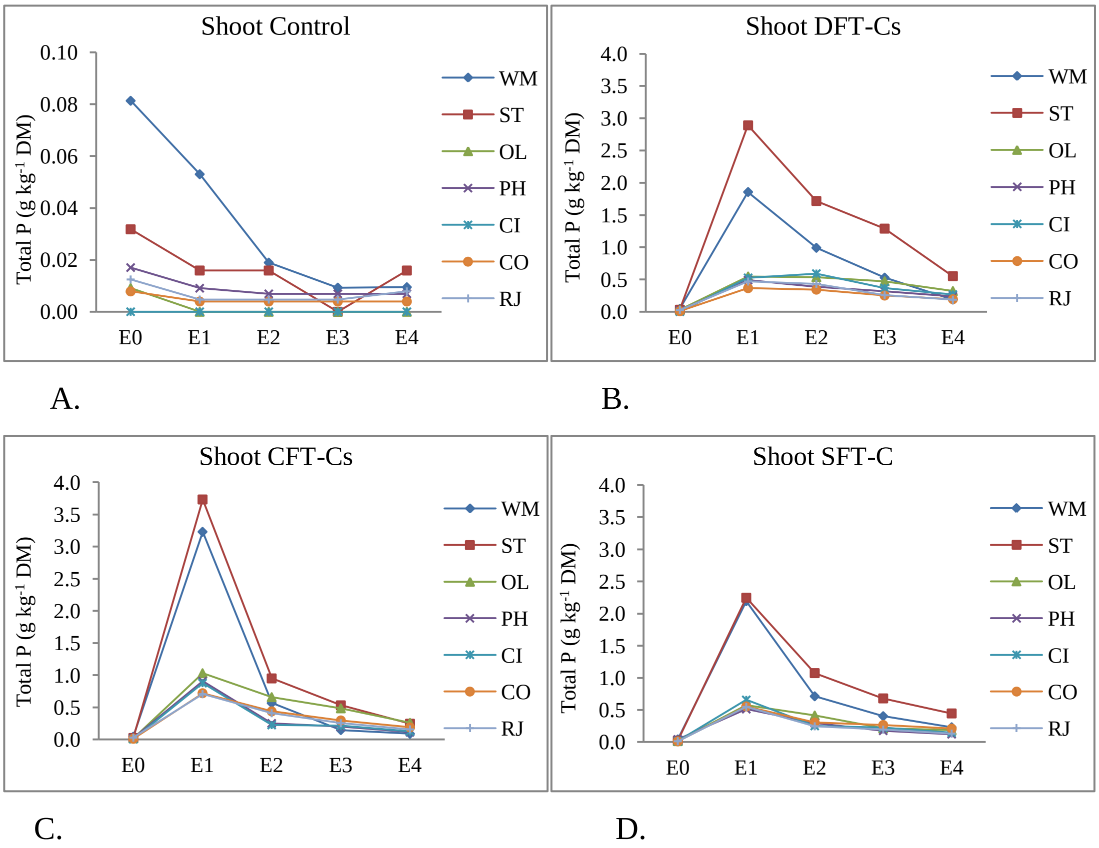

Figure 3. WEP release (g P kg^{-1} DM) from shoots of seven catch crops in five consecutive extractions (E0-E4) under four different treatments. Abbreviates for the catch crops names, (ST = Structurator, WM = White mustard, PH = Phacelia, OL = Oilseed radish, RC = Red clover, CI = Chicory, RJ = Perennial ryegrass, CO = Cocksfoot). Note different scale on y-axis for control.

3.2.2 Phosphorus release from the roots

Overall, roots had lower P losses than shoots for all catch crops, treatments and extractions tested. On average, roots released 0.21 g P kg^{-1} DM at each extraction, which was 40% lower than for shoots (0.36 g P kg^{-1} DM). Specifically, the roots of most catch crops tested had lower P release than the shoots, except for those with fibrous roots, which had similar release rates to their shoots (Table 8). Despite this similarity in terms of shoots, roots of structurator, white mustard and oilseed radish had the highest release of P among all species, whilst phacelia and chicory had the lowest. Ranking of species in releasing P from the roots based on all treatments was: structurator > white mustard > oilseed radish = cocksfoot = Perennial ryegrass > phacelia = chicory (Table 8).

Roots were equally affected by FTTs and the least effect on all catch crops was in the control treatment. Ranking of tot-WEP release from roots due to treatments was: SFT-C = CFT-Cs = DFT-Cs > Control (Table 6). In contrast to shoots, catch crop roots varied in P losses in the control treatment (Table 9), where white mustard had the highest release and chicory, phacelia and oilseed radish had the lowest. The dynamics of root P release with extraction time differed in shoots, *i.e.* E1>E2>E3=E0>E4 (Table 7).

For any species, root P release in the control was significantly lower than that in FTTs, while a similar pattern was found for shoots (Table 9). In contrast to shoots, different FTTs caused almost the same P release from the roots of each species. The same trend was found in structurator, white mustard, oilseed radish, phacelia and chicory: DEF-C = CFT-C = SFT-C > control; whereas the trend was slightly different in perennial ryegrass (SFT-C ≥ DEF-C ≥ CFT-C > control) and cocksfoot (DEF-C ≥ CFT-C = SFT-C > control).

Figure 4 shows the dynamics of TP release from the roots of the catch crops with extraction time. A similar P release trend as in the shoots was observed among FTTs. For the FTCs on every species, the highest release was at E1 and the release at other extractions was rather low. The highest release of P in the control was at E0 and WEP concentration declined with further extractions. The highest P release at a single extraction was observed in structurator under DFT-Cs, followed by white mustard.

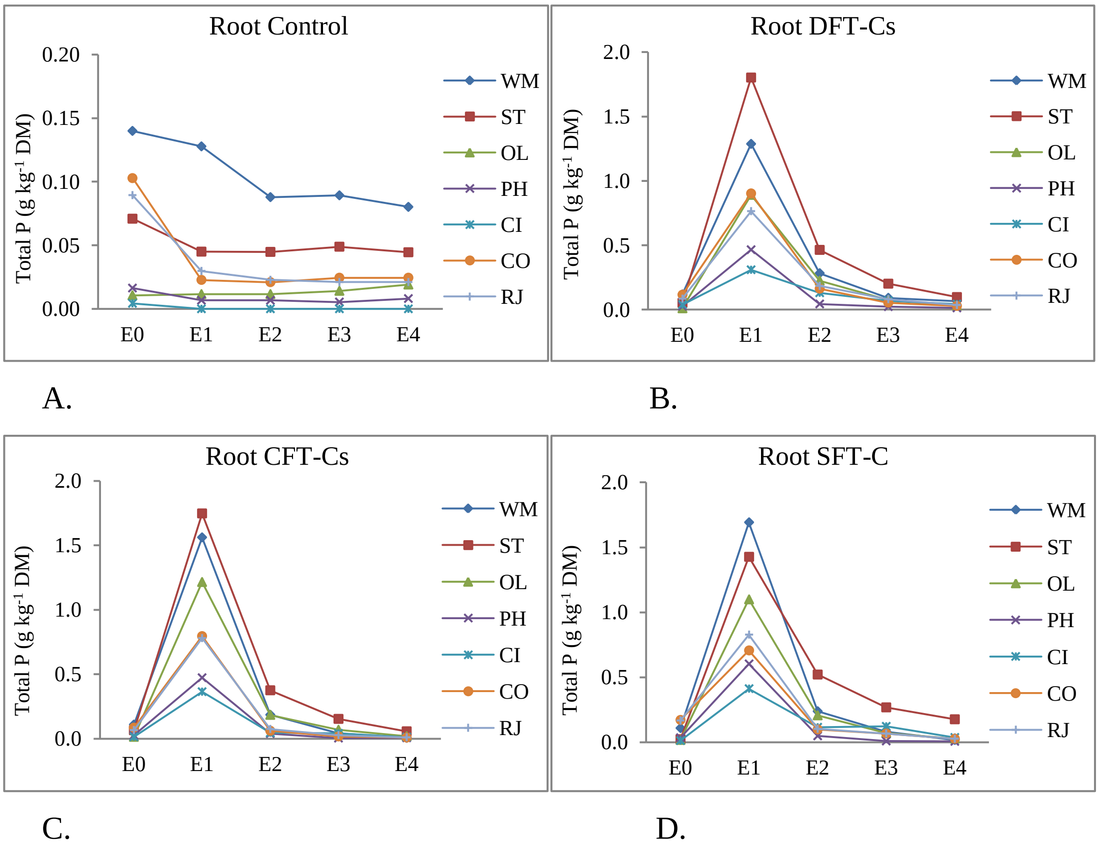

Figure 4. WEP release (g P kg^{-1} DM) from roots of seven catch crops in five consecutive extractions (E0-E4) under four different treatments. Abbreviates for the catch crops names, (ST = Structurator, WM = White mustard, PH = Phacelia, OL = Oilseed radish, RC = Red clover, CI = Chicory, RJ = Perennial ryegrass, CO = Cocksfoot). Note different scale on y-axis for control.

3.2.3 Phosphorus release from the whole plant

The general trend of WEP differing with species with consideration of all treatments (Table 10) was ranked as structurator > white mustard > oilseed radish > perennial ryegrass = cocksfoot > chicory = phacelia. Table 10 also shows the mean WEP at one extraction from each species in different treatments. Overall, WEP in respect to treatments was ranked as DFT-Cs = CFT-Cs > SFT-C > Control (Table 6). This indicated that the seven catch crops tested on the whole were more susceptible to DFT-Cs and CFT-Cs than SFT-C, whereas the control treatment had the lowest loss of P for any species. The highest impact of DFT-Cs on P release was observed in white mustard, followed by structurator and oilseed radish, while the impact was lower in phacelia, chicory, cocksfoot and perennial ryegrass. CFT-Cs had the greatest impact on structurator and least on chicory and phacelia. SFT-C had a similar impact to CFT-Cs. In the control, white mustard and structurator released more P (0.07 and

0.03 g P kg^{-1} DM, respectively) than the other species, *e.g*. oilseed radish (0.01 g P kg^{-1} DM) and chicory (0.00 g P kg^{-1} DM).

General WEP release from all seven catch crops tested under all treatments at different extractions differed, but followed a similar pattern. The mean P release with respect to extractions followed the order: E1>E2>E3>E4>E0 (Table 7). All FTTs showed a similar trend of P release, with P concentrations increasing from E0 to reach a peak at E1 (*i.e.* after the first FTC) and then declining gradually to level out at values close to those at E0 (Figure 3B-D, Figure 4B-4D). The highest single P release from the whole plant was from structurator (5.48 g P kg^{-1} DM) and white mustard (4.79 g P kg^{-1} DM) at the first extraction under CFT-Cs. Peak P release from the other species was highest in oilseed radish (2.25 g P kg^{-1} DM) under CFT-C and lowest in chicory (0.84 g P kg^{-1} DM) under DFT-C. The highest magnitude of P release from the whole crop at E1 was observed in CFT-C.

Table 10. *WEP (g P kg^{-1} DM) as a mean of five extractions (including E0) for whole plants of different species under various treatments. Different small letters indicate statistically significant differences within rows, capital letters significant differences within columns, (see Table 3 for treatments abbreviation)*

	Catch crops						
Treatments	Structurator	White mustard	Oilseed radish	Phacelia	Chicory	Perennial ryegrass	Cocksfoot
Control	0.03 b A	0.07 b A	0.01 a A	0.01 a A	0.00 a A	0.02 a A	0.02 a A
DFT-Cs	0.91 d D	0.55 c B	0.31 b B	0.20 a B	0.23 a B	0.25 a B	0.24 a B
CFT-Cs	0.79 f C	0.60 e B	0.40 d C	0.20 ab B	0.19 a B	0.25 bc B	0.26 c B
SFT-Cs	0.69 e B	0.57 d B	0.28 c B	0.19 a B	0.20 ab B	0.23 abc B	0.24 bc B
Mean	0.61 e	0.45 d	0.25 c	0.15 a	0.16 a	0.19 b	0.19 b

3.2.4 Phosphorus release (area-based)

Cumulative P release after five extractions (including E0) was calculated on an areal basis, by multiplying WEP with biomass, as shown in kg P ha^{-1} in Table 11. There was no appreciable difference between the amounts of P lost from roots or shoots in the control. For most catch crops, shoots had the highest P release under FTTs, particularly DFT-Cs and CFT-Cs. Under FTTs, structurator, white mustard and oilseed radish shoots released more P than other species, *e.g.* structurator released approximately 10 times more P than cocksfoot in the DFT-Cs treatment.

The percentage of DRP in total WEP ranged between 36 and 100% and differed between treatments and catch crops. In general, P release and the majority of DRP-% were lower in roots than in shoots after FTTs. In the shoots, the proportion of DRP in total P released was relatively more for structurator, white mustard and oilseed radish than for the other species, with cocksfoot and perennial ryegrass releasing little. Proportion of DRP in roots showed no appreciable differences among most of catch crops and FTTs.

Table 11. *Release of tot-WEP after five extractions (including E0) from different parts of each catch crop in different treatments, area-based calculations (kg P ha^{-1}) and percentage of DRP in total WEP in brackets, (see Table 3 for treatments abbreviation)*

	Shoots				Roots			
Crops	Control	DFT-Cs	CFT-Cs	SFT-C	Control	DFT-Cs	CFT-Cs	SFT-C
ST	0.3 (36)	21.1 (66)	18.6 (94)	15.2 (99)	0.3 (65)	2.8 (79)	2.6 (88)	2.6 (96)
WM	0.5 (73)	10.9 (87)	12.3 (100)	10.8 (96)	0.5 (89)	1.7 (85)	1.7 (77)	1.9 (88)
OL	0.05 (60)	10 (93)	12.9 (95)	7.4 (95)	0.2 (51)	3.1 (88)	3.8 (93)	3.6 (92)
PH	0.3 (86)	7.7 (93)	7.87 (95)	6 (93)	0.1 (74)	1.8 (76)	1.7 (85)	2.2 (85)
CI	0.00 (0)	6.3 (91)	5.20 (89)	4.7 (93)	0.02 (100)	2.8 (64)	2.3 (77)	3.3 (80)
RJ	0.06 (53)	2.6 (80)	2.94 (75)	2.1 (78)	0.4 (74)	2.6 (80)	2.2 (69)	2.7 (74)
CO	0.04 (44)	2.1 (87)	2.9 (82)	2.4 (89)	0.4 (86)	2.4 (77)	1.8 (69)	2 (68)

Abbreviates for the catch crops names, (ST = Structurator, WM = White mustard, PH = Phacelia, OL = Oilseed radish, RC = Red clover, CI = Chicory, RJ = Perennial ryegrass, CO = Cocksfoot).

4. Discussion

4.1 Experimental conditions

The use of pure sand soil in the greenhouse growing experiment was to allow uniform and fast distribution of nutrients throughout the growing medium and facilitate root collection after harvest. This allowed most of the catch crop roots to be collected, with large amounts of root hairs retained within the collected roots. Fertilisation at a rate of 20 kg P ha^{-1} was presumably sufficient for the needs of the catch crops, since it is slightly higher than the amount of P removed annually by grain crops in Sweden. The nutrients were added in two steps to avoid potentially high concentrations of nutrients at the start, which might have inhibited or reduced the potential germination of seeds. It also reduced potential nutrient losses with excess irrigation water due to high hydraulic conductivity and low affinity of P with the coarse sand soil particles. The concentration of P applied was 116 mmol m^{-3} in the first step and 232 mmol m^{-3} in the second. These P concentrations fall within the range for suitable root growth and development (between 7-500 mmol P m^{-3}) according to studies on *Arabidopsis thaliana* (Bates & Lynch, 2000, 2006).

Catch crops, including phacelia, white mustard, oilseed radish, oilseed rape (*Brassica napus* L.) and Italian ryegrass (*Lolium multiflorum* L.), need at least a 50-day growing period with 9 ºC daily effective temperature for good biomass production (Talgre *et al*., 2011). Since the present experiment was started in February, with unfavourable low natural illumination and temperature, supplementary light and warming were used in the greenhouse to accelerate plant growth and maturation (Boivin *et al*., 1987; McCall, 1992, 1996). Plant emergence was recorded every second day after sowing and it was found that the trend of flowering, maturation and harvest of the catch crops, especially for the first four species listed in Table 2, followed the emergence rate. Thus there may be a relationship between catch crop maturity and emergence, with structurator and white mustard emerging first, followed by oilseed radish and phacelia. The last catch crops to emerge were perennial ryegrass and cocksfoot. The interval between emergences of each catch crop was ~48 h. By start of harvest, red clover had the lowest emergence rate (50%) and white mustard had the highest (90%). For other crops the rate ranged between 66% for structurator and 89% for oilseed radish.

It was assumed that plant injuries at cutting would not cause large amounts of P to be released, as Timmons & Holt (1970) measured plant exudates from cut ends and their contribution to early leaching losses of P and found no differences when sample cut ends were submerged in leaching water. This indicated that the majority of the measured P release was from plant material rather than cut injuries.

4.2 Biomass and P uptake

The eight catch crops were harvested at different times according to their growth and development stage; white mustard, structurator, oilseed radish and phacelia at start of flowering, and red clover, chicory, perennial ryegrass and cocksfoot before flowering. This probably resulted in uncertainties when comparing the biomass and P uptake between species at different harvest times. However, harvesting according to development was consistent with crop life cycle, *i.e*. perennial species after annual species, and seems to be rational when relating the results to field conditions. For instance, Talgre *et al*. (2011) demonstrated that white mustard started flowering earlier than other species when it was grown in an environment with long periods of sunlight and high air temperature. Leslie (2003) reported that phacelia started flowering 6-8 weeks after sowing, which was similar to the maturation period in the present study.

Biomass production differed with species. Phacelia, chicory and oilseed radish had the largest total biomass. Higher biomass was observed in shoots than in roots for most species, with the exception of chicory, perennial ryegrass and cocksfoot. The biomass production in the present study differed from that reported in other studies, probably due to different growing conditions and periods. For instance, the biomass of oilseed radish, phacelia and chicory was almost two-fold higher than that reported by Riddle (2011). Oilseed radish biomass was also two-fold higher than that found by Talgre *et al*. (2011). However, oilseed total biomass was around 20% lower than that reported by Cavigelli *et al*. (1994). As regards P uptake in the whole plant, oilseed radish and phacelia ranked top of the catch crops tested, followed by structurator, chicory and white mustard. Oilseed radish and phacelia showed no significant difference in P concentrations in whole plant or plant parts or in total biomass and TP uptake. In another greenhouse experiment, Riddle (2011) reported much higher TP uptake at a P fertilizer application rate that was relatively low (14.3 kg P ha^{-1}) compared with that in the present experiment (20 kg ha^{-1}).

Structurator had slightly larger shoot and root biomass and P concentrations than white mustard, though the difference was not significant. The shoot and root biomass of structurator was in the low part of the biomass range reported by Lawley *et al*. (2011), although those authors stressed that the biomass greatly depended on the length of the growing period and field management. Despite the shoot biomass of white mustard being lower than that reported by Gondek (2005) and higher than reported by Talgre *et al.* (2011), the concentration of P in the shoots were almost the same as in those two studies. The root biomass of white mustard was higher than that reported by both Gondek (2005) and Talgre *et al*. (2011), but the concentration of P in the roots was lower. For the whole plant, total biomass and P uptake in white mustard were slightly higher than reported by Talgre *et al*. (2011) and lower than reported by Gondek (2005). While white mustard had low root biomass, even lower than the two grasses, the high shoot biomass and P concentrations in the shoots made it the species with the third highest uptake of P in terms of kg ha^{-1}.

Oilseed radish grew fast and both the shoot and root biomasses were twice that recorded by Talgre *et al*. (2011), but lower than that observed in by Cavigelli *et al*. (1994). The P concentration in oilseed radish shoots (0.27%) was higher than the 0.13-0.23% reported by others (Cavigelli *et al*., 1994; Talgre *et al*., 2011; Riddle, 2011), whereas the P concentration in the roots (0.13%) was lower than the 0.19-0.39% reported by Talgre *et al*. (2011) and Riddle (2011). Even though the concentration of P in the roots of oilseed radish was similar to that in white mustard, cocksfoot and phacelia, its roots had higher total P than the latter three, due to high root biomass.

The shoot and root biomass of phacelia were unexpectedly high compared with values reported by Jackson *et al*. (1993) and Talgre *et al*. (2001), 3- to 4-fold higher for shoots and 6- to 7-fold higher for roots. The low biomass production in previous studies might have been due to the fact that field conditions were not optimal for phacelia growth, *i.e*. cold and drought during the growing period, and to lower seed rate than in the present study. Furthermore, the root branches of phacelia are fragile and easily broken, which makes them difficult to collect intact. This is likely to lead to underestimation of root biomass in field studies on fine-textured soils. The concentration of P in the shoots of phacelia was similar to that reported by Talgre *et al*. (2011), but the root P concentration was only 20% of the latter. However, large biomass made phacelia rank top in terms of uptake of P in kg ha^{-1}. Phacelia is considered to be a good catch crop due to its good root mass production during a relatively short time and significant contribution to increased P uptake.

Red clover had rather high P concentration but very small biomass in both shoots and roots compared with the other species, which gave it the smallest uptake of P among all species. The reason for the low biomass of red clover is not clear, but Hart *et al*. (1981) found that the relationship between red clover yield and P supply was not linear. This might indicate that the low biomass of red clover in the present study was limited by factors other than P. Germination rate of red clover was low compared with that of the other species, perhaps because the temperature in the greenhouse was too high and inhibited germination (Hill & Luck 1991).

Chicory had similar shoot biomass to that reported by Hall & Jung (2008) for the first year as a forage crop, after which biomass may increase two-fold for the next two to three years under grazing conditions (Li & Kemp, 2005). Chicory had the largest root biomass among all the species in the present study, even larger than the shoot biomass. The concentration of P in the shoots was similar to that reported by Riddle (2011), but the P concentration in the roots was much lower. Along with phacelia, chicory had the lowest P concentration in the roots. The concentration of P in the shoots of chicory was higher than in grass shoots, supporting findings by Li & Kemp (2008). The significantly higher root biomass in chicory resulted in high total biomass and total P uptake in chicory whole plants, despite the low P concentration. Total P uptake in chicory was statistically similar to that in white mustard and structurator.

Perennial ryegrass and cocksfoot had similar biomass and concentration of P in shoots and roots and in whole plant. The whole plant biomass of the two grasses was statistically similar to that of structurator and white mustard. The whole plant P uptake in the two grasses was the lowest of almost all species studied except red clover. The root biomass of cocksfoot was substantially lower than that observed by Davis (1995). Mills (2007) demonstrated that cocksfoot biomass production can be up to 20 t DM ha^{-1} under favourable environmental conditions. The concentrations of P in the roots and shoots of both perennial ryegrass and cocksfoot were higher than those reported by Riddle (2011) and Davis (1995). Uptake of P in the perennial ryegrass whole plant was almost double that found by Riddle (2011) and almost four-fold higher than that reported by Talgre *et al.* (2011). Davis (1995) found almost double the total biomass and TP uptake in cocksfoot grown with abundant soil P than was found in the present study.

There was a relatively good linear correlation between total biomass and total P uptake (R^2>0.5), where P uptake increased with increasing biomass. However, P concentration also had a considerable impact on the final amount of P uptake. For instance, structurator total biomass was half that in chicory, but TP uptake in the two species was statistically similar.

Lynch (1995) reported that increasing the ratio of root specific surface area (sa) to volume (vol) increased nutrient uptake. In contrast, the present study showed that P concentrations of all catch crop roots increased with decreasing sa/vol; *e.g.* cocksfoot had the highest sa/vol ratio of all the species tested, which indicates that it should have had the highest P concentration, but in fact did not. The present study also found a poor correlation between sa/vol and total P uptake (R^2<-0.25) (Table 5). However, there was a significant correlation between surface area or volume and root P content (R^2>0.74) (Figure 1). Red clover had the longest roots and the highest surface area and volume, which may explain why it had the highest root P concentration. Chicory had the smallest root specific surface area or volume and thus the lowest P content. In addition, most fleshy roots had relatively high P content. The concentration of P was little in phacelia root though the latest had similar root specific surface area or volume to those in structurator and white mustard and about two times more compared to chicory and oilseed radish roots (Table 5).

4.3 Phosphorus release

It was very difficult to find literature that was comparable with the present study in terms of including so many species and examining the effects of FTTs on both shoots and roots. Therefore, the results were mainly compared within the study and to a certain extent with the very few similar existing studies on P release. This is why much of the discussion below concerning specific extractions and interactions with treatments lack a respective reference.

4.3.1 Overall pattern

The concentrations of total WEP (tot-WEP) significantly increased after freezing-thawing compared with the control (no freezing) for all catch crops (red clover was excluded from this part of the study) and for both shoots and roots. This was consistent with findings by Bechmann *et al.* (2005) of significantly elevated concentrations of dissolved P in water extracts from annual ryegrass biomass due to repeated freezing-thawing. Freezing can damage plant cells and potentially cause release of dissolved P. Reid & Palazzo (1990) concluded that freezing damage to plant cells can be the result of two main effects: rupture of cell membranes and walls, and ion imbalance as freezing removes water from the plant solution.

For a particular treatment, the increase in concentration of tot-WEP after freezing-thawing differed with species and extraction time. In general, concentrations of tot-WEP peaked after the first FTC and then declined significantly after the second FTC for both crop parts (Table 7). A similar trend of the first FTC causing most of the P release has been found for shoots of bluegrass (Timmons & Holt, 1970) and annual ryegrass (Bechmann *et al*., 2005). However, the pattern of P release from the shoots and roots differed in a few ways in the present study. Firstly, the shoots had larger P release than roots under different treatments and extractions, with the exception of the two grasses, for which tot-WEP in shoots and roots was similar. The differences in tot-WEP between grasses and non-grasses were probably due to differences in genotype, although the specific reason is unknown. Secondly, roots responded similarly to the different freezing-thawing treatments, whereas shoots responded differently. Moreover, the concentrations of tot-WEP released from the shoots after the fourth FTC were still higher than the initial tot-WEP concentrations, which may indicate possible future release of P if freezing-thawing and extraction continue, though the magnitude of further tot-WEP is not likely to exceed E4 under FT treatments. In contrast, the tot-WEP from the roots after the fourth FTC was lower than the initial tot-WEP, which indicated that all potential P release after freezing-thawing had been extracted. This may also indicate that the roots were more susceptible to FTCs than the shoots.

Another general trend was that structurator, white mustard and oilseed radish had higher tot-WEP than the other species. This is probably due to higher concentrations of P in these than in the other species, probably as a result of their genotype. It may also to some extent be the effect of temperature differences at different harvest times. As our first harvest was done under the high growing temperature inside the greenhouse, this may have increased the effect of further freezing-thawing treatments on P release compared with other species that were harvested at a lower temperature. Bechmann *et al*. (2005) reported that abrupt changes in temperature from +10 to -18 ºC may increase the effect of freezing-thawing, while Teutonico *et al*. (1993) found that acclimation increased freezing tolerance of *Brassica napus* and *Brassica rapa* and decreased ion leakage from these two species. However, a significant difference in tot-WEP was also found between the two species harvested at the same time, *i.e*. structurator and white mustard, and oilseed radish and phacelia, which may indicate that temperature at harvest was not the main cause of tot-WEP differences between species.

4.3.2 Interaction between treatments, catch crop parts and extraction

Type of FTTs, species and extractions interacted and resulted in different trends of TP release. Most crop shoots were more highly affected by DFT-Cs and CFT-Cs than SFT-C, with structurator, oilseed radish and chicory being most affected by DFT-Cs. On the other hand, almost all crop roots were evenly affected by all FTTs except perennial ryegrass, which was more affected by SFT-C and DFT-Cs, and cocksfoot, which was more affected by DFT-Cs. Even though most of the species were less affected by SFT-C for both parts, the shoots of structurator and white mustard had almost 4-fold and 3-fold larger release of P, respectively, under SFT-C than the other species. The roots of these two crops under SFT-C released almost twice as much P as the other species in the same treatment. The shoots of phacelia, chicory, perennial ryegrass and cocksfoot were least affected by all FTTs among other crops, with phacelia and chicory roots being least affected.

For most species, the first FTC had the highest effect and thus caused the largest TP release compared with further FTCs or the initial extraction. However, chicory shoot had 12% higher tot-WEP release at E2 than at E1. Shoots of the two grasses were much less resistant to P release due to DFT-Cs at E2 than at E3 and E4, with a P release at E2 that was only 7% lower than the peak release (at E1), whereas that at E3 and E4 was 45% and 60% lower, respectively, than at E1. A similar trend was found in chicory, phacelia and oilseed radish shoots. On the other hand, P release from oilseed radish shoots had extremely small differences between E1, E2 and E3. In contrast, for structurator and white mustard the difference in TP release was lower in over 40% at E2 and 80% at E4 than E1.

WEP decreased with increasing number of extractions in the control treatment. It should be noted that chicory shoot had no detected tot-WEP in any extraction and oilseed radish shoot and chicory root had TP detected only at the initial extraction. Therefore, tot-WEP release from oilseed radish increased with extraction numbers instead of decreasing (Figure 3A, Figure 4A). Nevertheless, both shoots and roots of all catch crops at any extraction released significantly less tot-WEP under the control than in the FT treatments.

The catch crops had different extents of increase in WEP after FTCs compared with WEP in the control. For the shoots, on average, FT resulted in an increased release of P that was 22-fold higher for white mustard, 29-fold higher for phacelia, 39-fold higher for perennial ryegrass, 68-fold higher for structurator, and 209-fold higher for oilseed radish. Chicory shoots had no detected TP release in the control and therefore it was difficult to compare the FT values. Elsewhere, Bechmann *et al.* (2005) found that freezing and thawing increased WEP from annual ryegrass by over 40-fold compared with the control without freezing. Timmons & Holt (1970) found for common meadowgrass (*Poa pratensis* L.) that air-drying or freezing increased WEP release from the shoots by over 11-fold and that further oven drying released almost twice as much P as under FTTs. Roots had a noticeably lower difference in tot-WEP release than the respective crop shoots. Compared with the control, FTTs significantly increased release of P from roots, by 4-fold for white mustard, 10-fold for structurator, 21-fold for oilseed radish, 6-fold for the two grasses, 14-fold for phacelia, and 140-fold for chicory. The high increase of P release from chicory caused by FTTs was due to a very low release from the control treatment. Release of P from the whole plant did not differ substantially with treatments compared with the trend of P release from individual parts. As previously discussed, the control had very low release of P compared with the FTTs. The trend for the whole plant was similar, *i.e.* FTTs gave a large elevation in P release compared with the control. The current study also showed that tot-WEP release for the whole plant was lowest from phacelia and chicory despite the fact that these two crops had appreciable P uptake which was larger than for the grasses and white mustard.

4.3.3 Release per unit area calculations

In terms of P release per unit area, white mustard shoots released large amounts of cumulative tot-WEP, of which 73% was DRP, in the control treatment. This was almost double the tot-WEP and DRP fraction from the shoots of the next closest crop, structurator, followed by oilseed radish and the two grasses. Unexpectedly, phacelia shoots in the control released almost as much P as structurator due to high biomass in the former. Moreover, the DRP proportion in tot-WEP from phacelia was twice as large as that from structurator. Chicory shoot had no recorded tot-WEP loss. Surprisingly, the loss of P from the roots of the catch crops was similar, if not higher, than that from the shoots under the control treatment.

The FTTs caused much higher P release per unit area than the control. For instance, chicory roots had the lowest tot-WEP loss among all the species in the control treatment and despite the fact that DRP was 100% of WEP; chicory lost only 0.02 kg P ha^{-1}. In contrast, the average DRP loss was 1.8 kg P ha^{-1} under DFT-Cs and CFT-Cs. As another example, the P loss under FTTs was 21-fold larger than under the control for structurator shoot and 44-fold larger for perennial ryegrass. However, perennial ryegrass had roughly 2.5-3 kg P ha^{-1} loss, with 75-80% in DRP, under FTTs, which represented almost 25% of the losses from white mustard and roughly 50% of the losses from chicory under the same treatments. This indicated that the amount of P lost due to FTTs may not be described well when compared with the control. Hence, using the ratio of loss due to FTTs and that in the control may not reflect the real effect of FTC on P release.

One notable fact is that most shoot DRP was higher under DFT-Cs and CFT-Cs, with an almost similar trend for tot-WEP loss. For instance, DRP in tot-WEP from oilseed radish was 12.3 kg P ha^{-1} and 9.3 kg P ha^{-1} under CFT-Cs and DFT-Cs, which were higher than under SFT-C.

As DRP is the most reactive form of P affecting water quality (Duan *et al*., 2011), low DRP loss from catch crops is desirable. With respect to DRP loss, shoots of structurator had the largest loss of P among all the species, especially under CFT-Cs, followed by white mustard and oilseed radish. Chicory and phacelia had around half the DRP losses of structurator. The two grasses had the lowest DRP loads from shoots.

Compared with P release in mg kg^{-1} DM, release per unit area, where biomass was included in the calculations, considerably changed the ranking of species. For instance, root of white mustard was even not within the top catch crops as tot-WEP loaders under FTTs. This is one good example of the complexity of evaluating catch crops in terms of nutrient losses.

4.4 Phosphorus retention in catch crops in laboratory experiment

Efficiency of P retention in catch crops was estimated as a percentage of P content at the end of the experiment. The control treatment had the highest retention of P and the best crop, which retained almost 100% of P in both parts, was chicory, followed by oilseed radish, which retained slightly less than 100% of P in the shoots, and phacelia, with retention of 95% of P in the roots. Cocksfoot also retained almost 100% of P in the shoots, but only 84% P remained in the roots. This was similar in perennial ryegrass and structurator, while white mustard roots had the least retention of P (72%).

Freezing-thawing treatments caused completely different P retention patterns. White mustard and structurator lost all plant P and thus had no retention of P after freezing-thawing. The lost P was even more in some of the parameters than total plant P before freezing, *e.g.* in the DFT-Cs, perhaps because of the small amount of plant material used. Bechmann *et al.* (2005) also found that WEP exceeded TP after eight FTCs on annual ryegrass shoots.

Shoots of oilseed radish, which had the largest uptake of P, had almost 50% P retention under SFT-C. The corresponding rate of retention under CFT-Cs and DFT-Cs was only 8% and 29% of TP uptake, respectively. Phacelia shoots had the best retention of P under FTTs among all the species, around 42% of TP uptake under DFT-Cs and CFT-Cs and 56% under SFT-C. Chicory, perennial ryegrass and cocksfoot shoots also had relatively good retention of P, 43-48% of TP uptake.

The roots of all crops tested behaved similarly to the shoots. For instance, structurator and white mustard roots had no retention of P after freezing-thawing in one or more FTTs. In addition, oilseed radish roots had no retention of P in CFT-Cs and SFT-C and only 8% of P retention in DFT-Cs. In contrast, chicory and perennial ryegrass retained slightly more than 42% of P under CFT-Cs, 31% under DFT-Cs, and 16-29% under SFT-C. Phacelia retained around 35% of TP under CFT-Cs and DFT-Cs and 21% under SFT-C.

These results are consistent with the previous statement that SFT-C had the least effect on catch crop shoots among the FTTs. Hence the catch crops studied had higher P retention in the shoots under SFT-C than in other FTTs; SFT-C had the largest effect on the roots and thus resulted in lower P retention in the roots than the other FTTs (Table 11). Which FT treatment is most likely with future climate change?

5. Summary and Conclusions

Uptake and release of P differed with species. With the exception of phacelia, the annual species (radish crops and white mustard) had higher uptake and release of P after freezing-thawing than the perennial species. Phacelia and chicory had moderate uptake but lower release for individual plant parts and the whole plant, and thus seem to be promising catch crops for P. In addition, the shoots of all catch crops tested except the two grasses had higher P uptake and release than the roots. The grasses had equal P release between shoots and roots, though P uptake was not equal.

Freezing-thawing significantly increased release of P from all species and plant parts. The highest P release occurred after the first cycle of freezing-thawing and extraction. Release of P at further extractions significantly declined, but still contributed to cumulative release of P. Finally, after four extractions release of P reached lower than the pre-treatment level at roots. However, in the control treatment the first extraction caused the highest release of P, except for oilseed radish root.

Root characteristics played an important role in uptake and release of P, which increased with increasing values of root parameters, *e.g.* root specific surface area. The only exception was phacelia roots, which had similar characteristics to structurator and white mustard roots, but one of the lowest TP concentrations after chicory. In addition, after freezing-thawing fibrous roots released lower amounts of P than most taproots and fleshy roots which might be due to the fact that fibrous roots had lower P uptake than fleshy or taproots.

Overall, phacelia and chicory roots proved susceptible to SFT-C and released higher amounts of P than after other FTTs. Hence, P retention was very low for these crops compared with in the DFT-Cs and CFT-Cs. Moreover, DRP in tot-WEP was higher under CFT-Cs and SFT-C than for other treatments. The control (no freezing) gave considerably lower P release than other treatments. The percentage of DRP was also low in the control, perhaps because plant cell damage was low compared with after freezing thawing, especially for structurator, perennial ryegrass and cocksfoot shoots and structurator and oilseed roots.

This study provides a good insight into the behaviour of common catch crops as regards P uptake and release after freezing-thawing. This can help improve the efficiency of these crops in reducing P leaching to groundwater and surface waters. The Nordic countries have recently introduced white mustard and oilseed radish as N catch crops and provide subsidies for these crops, but according to the present study there may be adverse effects from their use due to their high potential loss of P. However, it should be noted that evaluation of catch crops is complicated and that greenhouse studies under controlled conditions should be complemented with lysimeter or field studies to obtain a more complete picture.

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