

Institute of Plant Nutrition
Research Centre for Biosystems, Land Use and Nutrition (iFZ)
Justus Liebig University Giessen
Prof. Dr. Sven Schubert

NUTRIENT CYCLING EFFICIENCY AND WATER REQUIREMENT OF VARIOUS CATCH CROPS UNDER VARYING CLIMATIC CONDITIONS

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Tabea Selzer

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Examination committee

Head of examination committee: Prof. Dr. Joachim Aurbacher

1st Examiner (supervisor): Prof. Dr. Sven Schubert

2nd Examiner (co-supervisor): Prof. Dr. Michael Frei

3rd Examiner: Prof. Dr. Andreas Gattinger

4th Examiner: Prof. Dr. Jan Siemens

Essentially, all life depends upon the soil [...].

There can be no life without soil and no soil without life.

- Dr. Charles E. Kellogg -

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Abbreviations

AMBAV	Agrometeorological model for the calculation of actual evaporation (<i>Agrarmeteorologisches Modell für die Berechnung der aktuellen Verdunstung</i>)
AMF	Arbuscular mycorrhizal fungi
ANOVA	Analysis of variance
BF	Bare fallow
BW	Buckwheat
CAL-K / CAL-P	Calcium-lactate extractable potassium / phosphorus
CAP	Common agriculture policy
CCC	Catch and cover crops
CDC	Climate data center
CO₂-e	CO ₂ -equivalent
DAS	Days after sowing
DW	Dry weight
DM	Dry matter
DWD	German meteorological service (<i>Deutscher Wetterdienst</i>)
DY	Dummy (non-transpiring plants)
E	Evaporation
EC	European Commission
EFA	Ecological focus areas
ET	Evapotranspiration
ET_m	Measured evapotranspiration
ET_{AMBAV}	Simulated evapotranspiration with the model AMBAV
EU	European Union
FDR	False discovery rate
FW	Fresh weight
GAEC	Good agricultural and environmental conditions
GDD	Growing degree days
GHG	Greenhouse gas
GW	Meteorological station 'Giessen-Wettenberg'

GUI	Graphical user interface
g_{st}	Stomatal conductance
h_{max}	Maximum crop height
I	Irrigation
KUE	Potassium use efficiency
LAI	Leaf area index
LAI_{max}	Maximum leaf area index
MAE	Mean absolute error
Mix	Mixture of seven different catch crops
N_{min}	Mineral nitrogen
NSE	Nash-Sutcliffe efficiency
NUE	Nutrient use efficiency / nitrogen use efficiency
OR	Oilseed radish
P	Precipitation
PAR	Plant available radiation
PH	Phacelia
PN	Experimental station of the Institute of Plant Nutrition
PUE	Phosphorus use efficiency
R^2	Coefficient of determination
$r_a / r_c / r_s / r_v$	Aerodynamic / canopy / soil / vegetation resistance
RG	Ryegrass
RLD	Root length density
RMSE	Root mean square error
RSA	Root surface area
SE	Standard error
SF	Sunflower
SOC	Soil organic carbon
SVAT	Soil-vegetation-atmosphere-transfer
SWC	Soil water content
T	Transpiration
VPD	Vapor pressure deficit

WG	Experimental station 'Weilburger Grenze'
WHC	Water-holding capacity
WL	White lupin
WM	White mustard
WUE	Water use efficiency
ZAMF	Agrometeorological Research Centre (<i>Zentrum für agrarmeteorologische Forschung</i>)

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Summary

Facing the combined challenges of climate change and consequences of high-input agricultural production, catch and cover crops (CCC) have gained importance for our agroecosystems. They can improve soil chemical, physical, and biological properties, they effectively suppress weeds, and increase the biodiversity and climate resilience of cropping systems. However, catch and cover cropping has its own challenges. For instance, ambiguous results were reported concerning the yield effect of CCC on a succeeding crop. The yield effect is dependent on both the nutrient and the water availability after catch crop cultivation. Therefore, (a) the nutrient cycling efficiency and (b) the water requirement of CCC were identified as two major challenges. The objective of this thesis was to quantify both processes. Specifically, (a) the maximum nutrient uptake under non-limiting growth conditions as an indicator for nutrient cycling efficiency was determined and (b) relevant water inputs (rainfall, irrigation, and occult precipitation) and water losses (transpiration, evaporation, and leaching) were quantified in container experiments. Seven different CCC were cultivated as pure stands and as a mixture in comparison to a bare fallow under semi-controlled conditions in 2020 and 2021. Furthermore, the model AMBAV by the German Meteorological Service was used to simulate evapotranspiration (ET) for three of the CCC. The simulated data were compared with measured data obtained in the container experiments.

(a) Nutrient cycling efficiency

Catch and cover crops with the highest biomass production (white mustard, oilseed radish, phacelia, and buckwheat) also had the highest N, P, and K uptake. Accordingly, CCC with lower biomass production (sunflower, ryegrass, and white lupin) had lower nutrient uptakes. Phacelia showed the highest potential for conservation of all three nutrients, although the low C : N ratio of the frost-sensitive catch crop could promote nutrient losses during winter. A clear differentiation of CCC ideotypes for N, P, and K uptake was not possible. However, a general relationship between nutrient uptake and increasing root surface area as well as root length density was established. In addition, it was shown that pure stands can be as efficient as a CCC mixture in terms of nutrient retention.

(b) Water requirement of catch and cover crops

Although favorable conditions occurred during both vegetation periods, no evidence of occult precipitation was found. In autumn, soil water was depleted by fast-growing CCC with high biomass production in comparison to a bare fallow. During winter, soil water was recharged in the treatments with frost-sensitive CCC due to the early preparation of a mulch layer in combination with favorable meteorological conditions, while in early spring rising temperatures increased transpiration losses of a winter-hardy cover crop, leading to a reduction of soil water.

Whether CCC deplete or conserve soil water is dependent on (a) climate, (b) soil type, and (c) management. From a water-budget viewpoint, the cultivation of CCC is neither economically nor agronomically feasible in (semi-)arid regions / in dry years. Effective management options for water conservation in regions where catch and cover cropping are feasible are (a) the early termination of CCC growth, (b) no tillage, and (c) the preparation of a mulch layer or (d) the cultivation of frost-sensitive CCC which form a natural mulch in winter. However, management practices which are beneficial from a water-budget viewpoint can have negative impacts on the nutrient cycling efficiency. Moreover, current legislation in Germany does not allow for early mechanical termination of CCC growth before 15 February. The necessity for water-smart agricultural production in times of a changing climate questions this regulation. A legislative framework which distinguishes between the aims of CCC cultivation in (semi-)arid regions / dry years and humid regions / wet years is proposed and challenges for such a framework are identified.

It was shown that simulations of ET with the model AMBAV severely underestimated measured ET. Further optimization of the model is needed for the reliable prediction of CCC water requirement. Temperature and humidity were identified as the most important meteorological parameters, and leaf area index as the most important crop-specific parameter for ET simulations with AMBAV. Small deviations of these parameters – which occur not only on a macro-climatic but also on a micro-climatic scale – had large effects on overall simulated water losses by ET. Thus, simulations should be made with site-specific data instead of default data. An optimized version of AMBAV which reliably predicts water fluxes of CCC could become an effective tool for farmers' water management decisions.

Zusammenfassung

Angesichts der kombinierten Herausforderungen des Klimawandels und der Folgen einer intensiven landwirtschaftlichen Produktion haben Zwischenfrüchte für unsere Agrarökosysteme an Bedeutung gewonnen. Sie können die chemischen, physikalischen und biologischen Eigenschaften des Bodens verbessern, haben eine Unkraut-unterdrückende Wirkung und erhöhen zudem die Biodiversität und Klima-Resilienz. Neben diesen Vorteilen birgt der Zwischenfruchtanbau einige Herausforderungen, die Landwirte davor abschrecken, Zwischenfrüchte anzubauen. So ist beispielsweise der Ertragseffekt von Zwischenfrüchten auf eine Folgefrucht bisher unklar. Der Ertragseffekt ist sowohl von der Nährstoff- als auch von der Wasserverfügbarkeit für die Folgefrucht abhängig. Daher wurden (a) die Effizienz von Nährstoffkreisläufen und (b) der Wasserbedarf als zwei Herausforderungen im Zwischenfruchtanbau identifiziert, die in dieser Arbeit quantifiziert werden sollten.

Insbesondere wurden (a) die maximale Nährstoffaufnahme unter nicht-limitierenden Wachstumsbedingungen als Indikator für die Effizienz der Nährstoffkreisläufe bestimmt und (b) relevante Wassereinträge (Regen, Bewässerung und Auskämmeffekt) und Wasserverluste (Transpiration, Verdunstung, und Sickerwasser) in Container-Versuchen mit sieben verschiedenen Zwischenfrüchten und einer Zwischenfruchtmischung im Vergleich zu einer Schwarzbrache quantifiziert. Des Weiteren wurde das Modell AMBAV des Deutschen Wetterdienstes verwendet, um die Evapotranspiration (ET) für drei dieser Zwischenfrüchte zu simulieren und die simulierten Daten anschließend mit den Messwerten aus den Container-Versuchen zu vergleichen.

(a) Effizienz von Nährstoffkreisläufen

Die Zwischenfrüchte mit der höchsten Biomasseproduktion (Weißer Senf, Ölrettich, Phacelia und Buchweizen) zeigten die höchste N-, P- und K-Aufnahme. Folglich zeigten Zwischenfrüchte mit geringerer Biomasseproduktion (Sonnenblume, Weidelgras und Weiße Lupine) eine geringere Aufnahme dieser Nährstoffe. Das höchste Potential der Nährstoffkonservierung der drei betrachteten Nährstoffe zeigte Phacelia. Dabei ist zu beachten, dass das niedrige C : N-Verhältnis dieser frostempfindlichen Zwischenfrucht Nährstoffverluste im Winter begünstigen könnte. Die Identifizierung eines Zwischenfrucht-Ideotypen für die N-, P- und K-Aufnahme war nicht möglich. Es wurde jedoch ein allgemeiner Zusammenhang zwischen Nährstoffaufnahme und großer Wurzeloberfläche sowie einer hohen Wurzellängendichte

festgestellt. Zudem konnte gezeigt werden, dass eine einzelne Zwischenfrucht in Bezug auf die Nährstoffretention genauso effizient sein kann wie eine Zwischenfruchtmischung.

(b) Wasserbedarf von Zwischenfrüchten

Obwohl in beiden Vegetationsperioden günstige Witterungsbedingungen auftraten, gab es keinen Wassereintrag durch Auskämmeffekt. Im Herbst wurde das Bodenwasser durch schnell wachsende Zwischenfrüchte mit hoher Biomasseproduktion im Vergleich zu einer Schwarzbrache erschöpft. Durch das frühe Anlegen einer Mulchschicht in den Varianten mit frostempfindlichen Zwischenfrüchten in Verbindung mit hohen Niederschlägen wurden die Bodenwasser-Speicher während des Winters aufgefüllt. Die winterharte Zwischenfrucht Weidelgras hingegen fing im Frühjahr bei steigenden Temperaturen wieder an, zu transpirieren. Dies führte zu einer Reduktion des Bodenwassergehalts im Vergleich zu einer Schwarzbrache.

Aus wasserhaushaltstechnischer Sicht ist der Anbau von Zwischenfrüchten in (semi-)ariden Regionen / in Trockenjahren weder wirtschaftlich noch agronomisch sinnvoll. Effektive Bewirtschaftungsmaßnahmen für die Konservierung von Wasser in Regionen, in denen Zwischenfruchtanbau sinnvoll ist, sind (a) eine frühe Terminierung des Zwischenfrucht-Wachstums, (b) keine Bodenbearbeitung und (c) das Anlegen einer Mulchschicht beziehungsweise (d) der Anbau von frostempfindlichen Zwischenfrüchten, die im Winter eine natürliche Mulchschicht bilden. Aus wasserhaushaltstechnischer Sicht vorteilhafte Bewirtschaftungsmaßnahmen können sich jedoch negativ auf die Effizienz der Nährstoffkreisläufe auswirken.

Darüber hinaus erlaubt die aktuelle Gesetzgebung in Deutschland keine mechanische Terminierung des Zwischenfrucht-Wachstums vor dem 15. Februar. Die Notwendigkeit einer landwirtschaftlichen Produktion, die in Zeiten des Klimawandels bewusst mit der Ressource Wasser umgeht, stellt diese gesetzliche Vorgabe in Frage. Eine Überarbeitung der Gesetzgebung, wird vorgeschlagen. Diese sollte darauf abzielen, Rahmenbedingungen zu schaffen, die klar zwischen den Zielen des Zwischenfruchtanbaus in (semi-)ariden Regionen / trockenen Jahren und feuchten Regionen / nassen Jahren differenziert. Eine solche Differenzierung ist erforderlich, jedoch mit einigen Herausforderungen verbunden, die in dieser Arbeit aufgezeigt werden.

In den Simulationen mit AMBAV konnte gezeigt werden, dass das Modell die gemessene Evapotranspiration sehr stark unterschätzt. Für eine zuverlässige Vorhersage des Wasserbedarfs von Zwischenfrüchten ist eine weitere Optimierung des Modells erforderlich. Das Modell reagierte besonders empfindlich auf Änderungen der meteorologischen Parameter Temperatur und relative Luftfeuchtigkeit sowie den pflanzenspezifischen Parameter Blattflächenindex. Kleine Abweichungen dieser Parameter – die nicht nur auf makroklimatischer, sondern auch auf mikroklimatischer Ebene auftreten können – hatten einen großen Einfluss auf die simulierten, kumulativen Wasserverluste. Daher sollten Simulationen mit standortspezifischen Daten anstelle von Standarddaten durchgeführt werden. Eine optimierte Version von AMBAV, die die Wasserflüsse von Zwischenfrüchten zuverlässig vorhersagen kann, könnte ein wirksames Instrument für Landwirte sein und sie in den Entscheidungsprozessen in Bezug auf die Nutzung der begrenzten Ressource Wasser unterstützen.

1 General introduction

1.1 Relevance of catch and cover cropping

Facing the consequences of resource and management-intensive agriculture in addition to a changing climate, we start to realize the need to protect the basis of life, the soil. The key to healthy and productive soils is the choice of suitable management options. One of these options, which is often mentioned in the context of sustainable, biodiverse, and climate resilient agriculture, is cover cropping. Cover crops – also known as catch crops – improve soil chemical, physical, and biological properties, they effectively suppress weeds, increase the biodiversity and climate resilience of cropping systems (Figure 1.1). While the term ‘catch crops’ is used for crops which are primarily grown to scavenge excess nutrients from the soil, ‘cover crops’ is a more general term which is mainly used in the context of erosion control in the time span between two cash crop cultivation periods when the soil would otherwise lie fallow (Klages et al., 2022). In this thesis, the term ‘catch and cover crops’ (CCC) will be used to include all agronomic utilization possibilities of these crops. Besides the reduction of nutrient leaching and erosion control, CCC provide various additional benefits to cropping systems.

1.1.1 Benefits of catch and cover cropping

1.1.1.1 Improvement of soil properties

Through the effective reduction of nutrient leaching (Askegaard and Eriksen, 2008; Herrera and Liedgens, 2009; McLenaghan et al., 1996; Thapa et al., 2018; Torstensson and Aronsson, 2000) and the enhancement of the nutrient cycling efficiency when residues are returned to the soil (Thorup-Kristensen, 1994; Vos and van der Putten, 2001), CCC can improve the chemical soil properties. Nitrate leaching can be reduced by 40-70% through CCC cultivation (Islam et al., 2021) (Figure 1.1). Improvements of nutrient cycling are not limited to the highly mobile NO_3^- -N, which catch crops effectively ‘catch’ and immobilize. It has been shown that CCC furthermore improve P and K cycling (Askegaard and Eriksen, 2008; Eichler-Löbermann et al., 2009). Moreover, CCC increase the soil organic carbon (SOC) content (Basche et al., 2016; Brust et al., 2014; Holmes et al., 2017; Kaye and Quemada, 2017) which in turn affects the biological and physical soil properties (Figure 1.1).

In a study by Basche et al. (2016), the long-term use of winter rye as a cover crop improved the water storage capacity in the topsoil and increased the soil water content (SWC) by 10-11% of field capacity. The authors propose that this could be the result of an overall improvement of physical soil properties which influence the infiltration of water. Furthermore, CCC have been shown to increase the percentage of water-stable aggregates by up to 17% (Villamil et al., 2006), reduce soil bulk density at the soil surface (Steele et al., 2012; Villamil et al., 2006), and increase hydraulic conductivity (Yu et al., 2016) (Figure 1.1). These changes of the physical soil properties are mainly due to (1) more residue biomass which serves as a carbon-input into the soil (Villamil et al., 2006) and (2) improved root penetration (Yu et al., 2016). Both processes can increase soil porosity, thereby contributing to the improvement of water infiltration (Bayhan, 2021) (Figure 1.1).

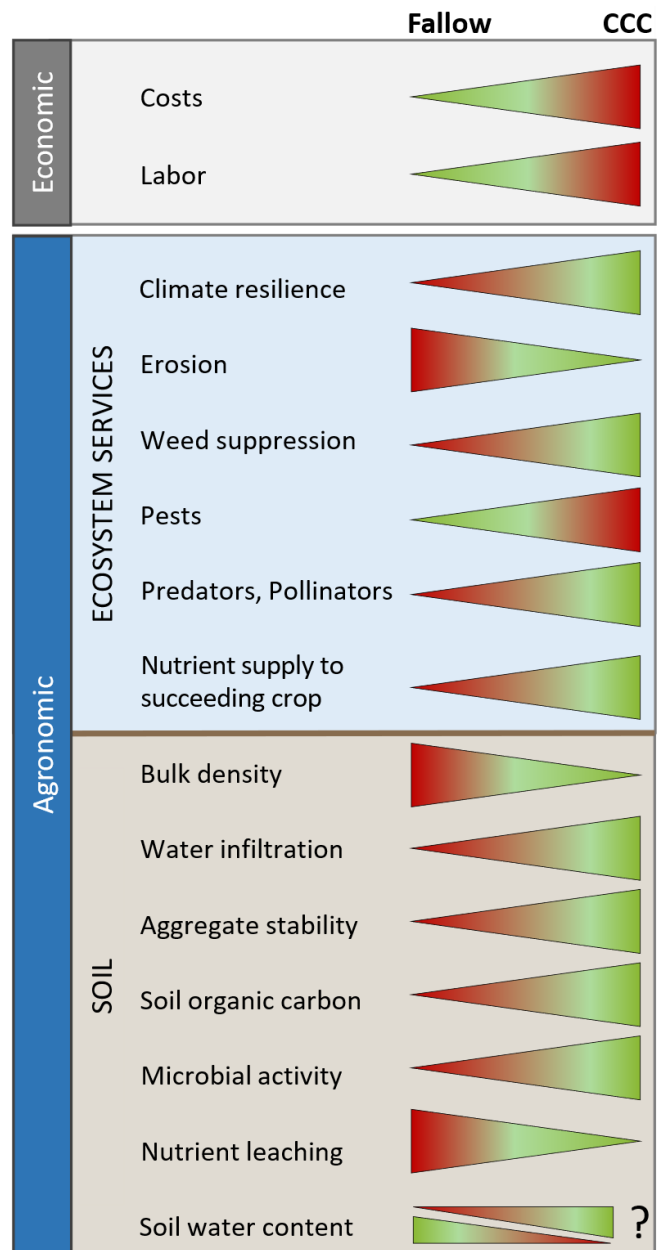


Figure 1.1 Benefits and disadvantages of catch and cover crops (CCC) in comparison to a bare fallow. Arrows indicate an increase (◀) or decrease (▶) of the economic or agronomic parameter. Red: Increase / decrease of the parameter is a disadvantage; green: Increase / decrease of the parameter is a benefit.

The chemical and physical changes of the soil furthermore impact the biological soil properties. The incorporation of CCC with a narrow C : N ratio (e.g., legumes) in the crop rotation stimulates microbial activity (Wanic et al., 2019) (Figure 1.1). Not only bacterial activity increases, but also fungal biomass and arbuscular mycorrhizal fungi (AMF) colonization are stimulated (Abdalla et al., 2019; Dabney et al., 2001; Schipanski et al., 2014). Higher microbial activity in turn leads to higher residue decomposition rates and the release of

nutrients which highlights the interconnectedness of the three categories of soil properties: Chemical, physical, and biological.

1.1.1.2 Weed control

Another benefit of catch and cover cropping is the suppression of weeds (Figure 1.1). The fast emergence and quick establishment of a closed soil cover in combination with the development of deep roots means that CCC can outcompete other crops in terms of light, water, and nutrient uptake (Brust et al., 2014). In addition to this competition for resources, CCC can restrict weed growth through the release of allelopathic compounds. Furthermore, germination of other plant seeds can be delayed when CCC cover the soil due to a reduction in soil temperature and light penetration (Brust et al., 2014; Mohler and Teasdale, 1993).

1.1.1.3 Biodiversity

In addition to the intended diversification of the crop rotation through the cultivation of CCC, this management practice has been shown to increase the biodiversity of flora and fauna by 21% on average (Beillouin et al., 2021). Various studies have shown the positive effect of CCC on fauna diversity: One advantage of catch and cover cropping related to biodiversity is their positive influence on predatory and pollinator insect abundance (Figure 1.1). Rivers et al. (2017) showed that carabid activity and carabid species richness increased through the cultivation of a mixture of hairy vetch and triticale. Species richness was not only influenced by the choice of CCC species but also by the termination date, with late termination of CCC favoring higher species richness than early termination (Rivers et al., 2017). Arthropod diversity in a pear orchard, measured by the Shannon-Wiener index, was significantly higher with CCC than without cover crops (De Pedro et al., 2020). In that environment, catch and cover crop cultivation was especially beneficial for several spider, beetle, and hymenoptera families (De Pedro et al., 2020). Furthermore, flowering summer CCC such as buckwheat and phacelia can increase the abundance of pollinators (Candelaria-Morales et al., 2022).

While AMF were already mentioned in the context of the stimulation of microbial activity through the cultivation of CCC (Chapter 1.1.1.1), Bowles et al. (2016) have shown in a meta-analysis that CCC also affect the diversity and abundance of AMF, both of which are highly dependent on CCC species and management practices. In general, legume and graminoid CCC improved the colonization of cash crops with arbuscular mycorrhizas (Bowles et al., 2016).

Although the positive impact of CCC on the biodiversity of beneficial insects and microorganisms are advantages of CCC cultivation (Figure 1.1), it should not be neglected that CCC can increase the abundance of pests at the same time (Smit et al., 2019) (Figure 1.1). It furthermore needs to be noted that while fauna biodiversity benefits from catch and cover cropping, the quick development of a closed soil cover can negatively affect above-ground flora biodiversity by suppressing the growth and development of non-target species, as mentioned previously (Chapter 1.1.1.2).

In addition to the overall positive impact of CCC on flora and fauna biodiversity (Beillouin et al., 2021), the cultivation of CCC mixtures, which include species with complementary traits, can also increase the 'functional trait diversity', that is they enhance multiple ecosystem functions at the same time (Blesh, 2018; Schipanski et al., 2014). This concept is also known as 'multifunctionality' (Byrnes et al., 2014). However, trade-offs among different ecosystem services may exist in CCC mixtures (Blesh, 2018; Finney and Kaye, 2017).

1.1.1.4 Climate resilience

One aspect of climate change is a shift in global rainfall patterns (Trenberth, 2011). As a consequence of increasingly intense precipitation events after long periods of drought, susceptibility of soils to water erosion increases (Li and Fang, 2016; Nearing et al., 2004). It was shown that cover crops can provide an effective protection from erosion (Figure 1.1). The erosion-reducing potential is dependent on above and below-ground plant characteristics. De Baets et al. (2011) have shown that root architecture of CCC determines the extent of protection from soil loss by concentrated flow erosion. Catch and cover crops with fine-branched roots had a higher erosion-reducing potential than those with tap roots (De Baets et al., 2011).

In relation to the mitigation of climate change, carbon sequestration has gained importance in recent years. Several studies have shown that catch and cover cropping is an effective management tool to store atmospheric carbon in the soil (*e.g.*, Blanco-Canqui et al., 2013; Chalise et al., 2019; Kaye and Quemada, 2017). Tribouillois et al. (2018) have proposed that the practice of incorporating CCC residues in the soil could potentially decrease greenhouse gas emissions by 315 kg CO₂-equivalent (CO₂-e) ha⁻¹ year⁻¹ in comparison to bare soil. Based on data by Poeplau and Don (2015), Kaye and Quemada (2017) even propose a mitigation rate of 1,170 kg CO₂-e ha⁻¹ year⁻¹ for both, legumes and non-legumes. The production of synthetic

fertilizers is a highly energy-intensive process which also contributes to agricultural greenhouse gas (GHG) emissions (Camargo et al., 2013; Kaye and Quemada, 2017). The enhancement of N cycling efficiency through CCC cultivation decreases the dependency on synthetic fertilizer application and provides another potentially effective means for climate change mitigation (Kaye and Quemada, 2017). Based on these results, CCC will play an important role for the reduction of GHG emissions from agriculture in the future, a fact which was also recognized by the European Union (EU) which seeks to promote catch and cover cropping as a climate change mitigation strategy (Smit et al., 2019) (Figure 1.1).

1.1.2 Adoption of catch and cover cropping

As a means to counteract the negative impact of agriculture on the environment and biodiversity, the European Union (EU) introduced 'Greening' measures in their Common Agriculture Policy (CAP) as a voluntary financial support option for farmers (Sarvia et al., 2022). In the new CAP (2023-2027), Greening will be compulsory in the member states (European Commission, 2022). Greening comprises the three agricultural practices (a) crop diversification, (b) maintenance of permanent meadows and pastures, and (c) Ecological Focus Areas (EFA). Management practices applicable for EFA are clearly defined by the European Commission (EC) and can only be applied to arable land (Sarvia et al., 2022). Each member state can choose from a common EU-list of approved EFA options where, depending on its importance for biodiversity, each option has its own weighting factor (European Commission, 2017).

On a European level, CCC are one of the most popular EFA options and only come second to nitrogen-fixing crops with 33% and 37% of declared EFA areas in 2015, respectively (European Commission, 2017). The highest adoption rates of CCC can be found in north-western Europe (European Commission, 2017), *e.g.*, 75% of all EFA were dedicated to catch and cover cropping in Germany in 2021 (corresponding to 44% after applying weighting factors) (BMEL, 2021) (Figure 1.2). This clearly illustrates the importance catch and cover cropping gained in recent years. Moreover, it shows the political motivation to increase the adoption of CCC cultivation even further.

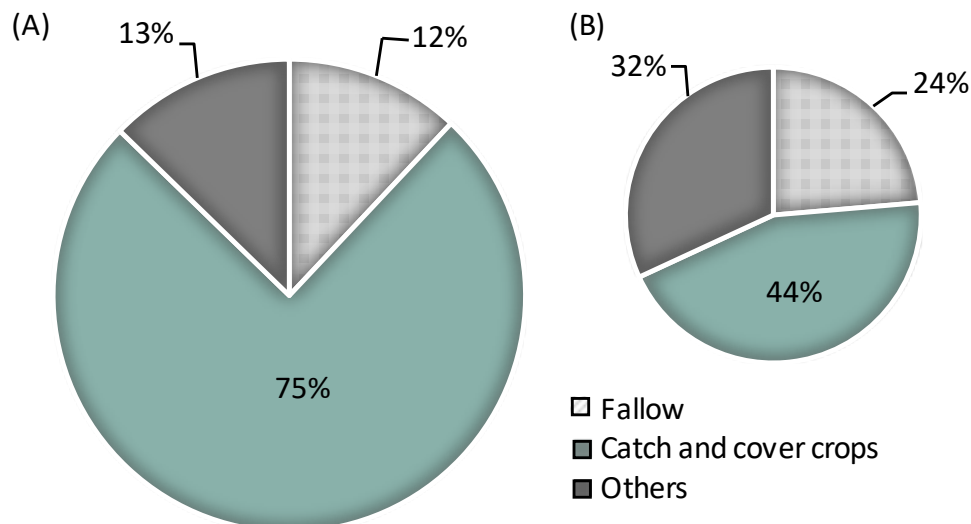


Figure 1.2 Proportion of Ecological Focus Areas (EFA) dedicated to catch and cover crops in comparison to fallow and other EFA in Germany in 2021 depicted as percentage of total EFA (A) without weighting factors and (B) after applying weighting factors. Based on data from BMEL (2021).

1.2 Challenges of catch and cover cropping

Even though catch and cover cropping is widely promoted and has been shown to provide various benefits to agroecosystems, the cultivation of an additional crop during otherwise fallow periods faces challenges (Figure 1.1).

Roesch-McNally et al. (2018) have conducted focus-group discussions with farmers in Iowa, USA, to identify barriers to the adoption of catch and cover cropping. Field-level barriers for the farmers were the additional labor required for planting and terminating the CCC, the timing of catch and cover crop cultivation in a corn/soybean-dominated cropping system, and the lack of ‘facilitating infrastructure’ for CCC (Roesch-McNally et al., 2018). Other agronomical issues with CCC are (a) the risk of increasing pest populations, (b) CCC turning into weeds in a succeeding cash crop cultivation period, and (c) soil water depletion (Smit et al., 2019). While pest populations might increase through catch and cover crop cultivation, predators of those pests also benefit from CCC (Figure 1.1). Although flowering CCC can indeed increase the number of weed seeds, the predominant effect of a quickly developing CCC with high LAI is that of weed suppression, as mentioned earlier. Thus, agronomical issues (a) and (b) can be overcome by smart CCC management. However, the effect of CCC on soil water is still subject to discussion (Figure 1.1). While the long-term effects of catch and cover cropping improve the water-related physical properties of the soil (Chapter 1.1.1), CCC use significant amounts of water which, in the context of global warming, could potentially lead to an

increased drought stress for a succeeding cash crop not only in arid but also in humid regions of the world (Islam et al., 2021; Unger and Vigil, 1998).

Moreover, costs (direct and opportunity costs) associated with catch and cover cropping were identified as another important barrier to adoption (Figure 1.1), especially as the yield effect of CCC on a succeeding crop is perceived as uncertain by some farmers (Roesch-McNally et al., 2018). Whether CCC are effective not only in the reduction of nutrient losses but also in the provision of nutrients to a succeeding crop is highly dependent on species selection which, in combination with catch crop management and growth conditions, determines maximum nutrient uptake.

The present study focuses on two of those challenges concerning catch and cover crop cultivation: (1) Maximum nutrient uptake by CCC for effective nutrient cycling efficiency and (2) the water requirement of CCC.

1.2.1 Challenge 1: Nutrient cycling efficiency

It was established above that CCC can provide many different ecosystem services to a cropping system. However, the main reason for the cultivation of CCC still is the improvement of the nutrient cycling efficiency through two processes: (1) The reduction of nutrient losses and (2) increasing the nutrient availability for a succeeding crop. These two processes are each linked to a challenge: (1) The maximization of the nutrient uptake through the choice of suitable catch crop species and (2) the synchronization of nutrient mineralization from catch crop residues and the nutrient uptake by the succeeding cash crop. Here, the focus lies on the challenge of maximizing the nutrient uptake.

In addition to agronomic characteristics and the suitability of a particular catch crop for the inclusion in an existing crop rotation, the maximum nutrient retention capacity of a catch or cover crop species is an important factor for farmers to choose a particular species over another. A catch crop's maximum nutrient retention capacity can only be determined under non-limiting growth conditions. Therefore, experiments for the determination of maximum nutrient uptake of various CCC were performed in 120 L containers under semi-controlled conditions where neither water nor nutrient availability were growth-constraining factors (Selzer and Schubert, 2021).

Nutrient acquisition of crops is species-dependent. Specifically, it depends on how well a crop is adapted to the particular growth conditions, on quick emergence (Brust et al., 2014), how

fast the crop can produce a significant amount of above and below-ground biomass (Heuermann et al., 2019; Thorup-Kristensen, 2001), and on architectural root traits (White et al., 2013).

In the past, a myriad of studies has been conducted on the ability of various catch crops to reduce NO_3^- -N leaching and on improvements of the N cycling efficiency (e.g., Herrera et al., 2010; Jensen, 1992; Justes et al., 1999; Kuo et al., 2001; McLenaghan et al., 1996; Thapa et al., 2018; Thorup-Kristensen, 1994). The possibility of using CCC to increase P cycling of cropping systems has gained some attention in more recent years (e.g., Eichler-Löbermann et al., 2008; Liu et al., 2015). However, studies which do not focus on just one nutrient but include several important macronutrients are scarce.

Cruciferous CCC have a higher N-scavenging ability than monocots (Thorup-Kristensen, 2001, 1994). Common characteristics of those crucifers are the quick development of root and shoot biomass (Thorup-Kristensen, 2001). Especially *Sinapis alba* and *Raphanus sativus* are popular CCC species for the reduction of NO_3^- -N losses. Characteristics for K retention are similar to those of N scavenging (Figure 1.3): Talgre et al. (2011) found that K uptake by white mustard and fodder radish was up to 82 kg ha^{-1} . Species choice for maximum P uptake, however, differs from that for maximum N and K cycling efficiency (Figure 1.3). Catch and cover crop species which were proposed as being P-efficient include *Phacelia tanacetifolia* (Eichler-Löbermann et al., 2008), *Lupinus albus* (Soltangheisi et al., 2018), and *Fagopyrum esculentum* (Teboh and Franzen, 2011).

Architectural root traits which are important for nutrient acquisition differ depending on the nutrient in question. The ideotype for an effective N and K uptake has a deep root system (White et al., 2013) (Figure 1.3). In temperate latitudes, N in soils occurs predominantly in form of the highly mobile nitrate (NO_3^-). It has been shown that *Sinapis alba*,

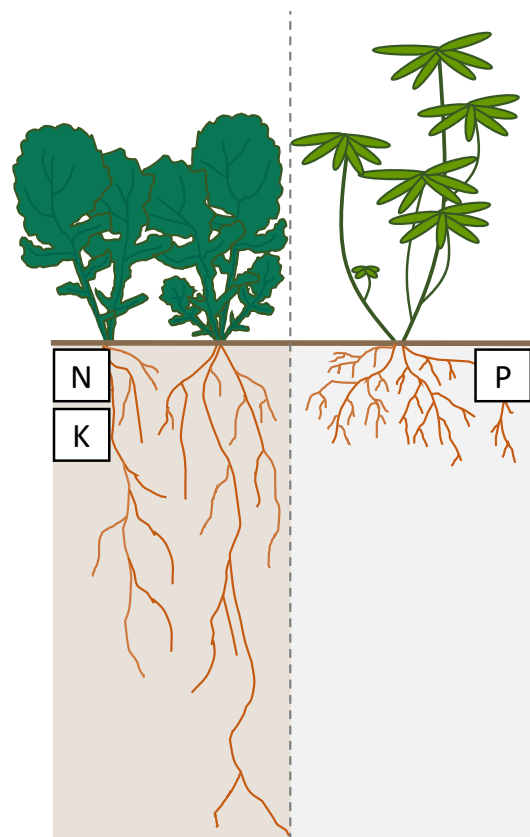


Figure 1.3 Proposed catch crop ideotypes for maximum N, K, and P uptake (1st hypothesis). Catch crop species displayed are examples of those ideotypes. Left side: Oilseed radish (*Raphanus sativus* L. var. *oleiformis* Pers.); right side: White lupin (*Lupinus albus* L.)

Phacelia tanacetifolia, and *Avena strigosa* were able to deplete the NO_3^- -N pool at 20-30 and at 50-60 cm soil depths while the shallow rooting *Trifolium alexandrinum* had little effect on N_{min} in comparison to a fallow control (Heuermann et al., 2019). Furthermore, Thorup-Kristensen (2001) has established that NO_3^- -N leaching is strongly reduced by catch crops with a high root frequency in soil layers deeper than 50 cm. Potassium differs in its soil dynamic from N in the way that it is not highly mobile but rather sorptively bound to clay minerals. Nevertheless, due to the necessity of transport of K to the roots via diffusion (Lynch, 2007), making the proximity of the roots to the K source the limiting factor for K acquisition, effective K uptake is also achieved by a dense and deep root system (White et al., 2013). In contrast, the root ideotype for P uptake is a shallow root system with high root length densities in the upper 30 cm (Liu, 2021; Lynch and Brown, 2001; White et al., 2013) (Figure 1.3). Again, this ideotype is determined by soil dynamics of the nutrient. Phosphorus availability is generally higher in the topsoil than in deeper soil layers, giving plants with a high topsoil foraging ability, *i.e.*, plants with a high root length density (RLD) and root surface area (RSA) in that layer, an advantage in P acquisition (Lynch and Brown, 2001). However, the architectural root traits for effective N, P, and K uptake displayed in Figure 1.3 are generally based on results under experimental conditions where the plants were deprived of the respective nutrient. Catch crops which are grown to reduce nutrient leaching, however, do not face nutrient scarcity but rather an excess of nutrients.

One objective of this study was to test whether the CCC ideotypes proposed in Figure 1.3 also apply to non-limiting growth conditions in terms of water and nutrient availability. Thus, it was hypothesized that:

- 1 Catch crops differ in their efficiency to acquire and conserve N, P, and K for a succeeding crop. These differences are due to (1) catch crop species: N and K accumulation are highest for crucifers, while P is most efficiently acquired by phacelia, buckwheat, and white lupin, and (2) root architecture: N and K accumulation 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 (Figure 1.3). This hypothesis was tested in Article 1 (Chapter 2.1; Selzer and Schubert, 2021).

The stringent rules by the European Commission (EC) mandate that the recipients of EFA subsidies need to cultivate a mixture of at least two different CCC species (Sarvia et al., 2022). Interactions between different species in a mixture can be complementary, facilitative, or competitive (Figure 1.4). While complementarity (*i.e.*, the species occupy different ecological niches) and facilitation (*i.e.*, one plant species has a positive impact on the development of another plant species (Andersen et al., 2005)) can lead to higher resource use efficiency (Heuermann et al., 2019; Hooper et al., 2005), inter-specific competition has a negative impact on overall CCC performance (Wendling et al., 2017). Catch and cover crop mixtures are often designed to include a diversity of species

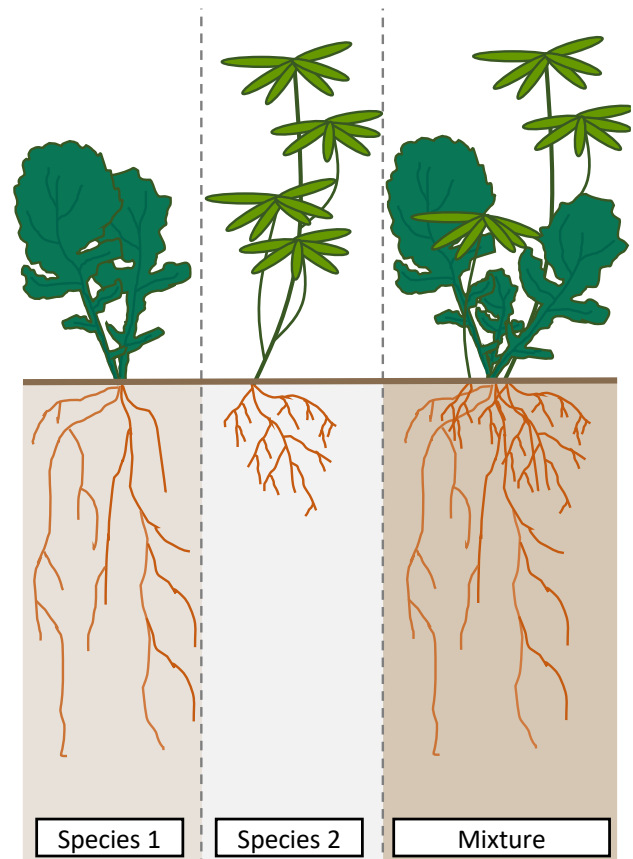


Figure 1.4 Illustration of complementary, facilitative, and competitive interactions of species in a mixture (right side) compared to their single species counterparts (left side) (2nd hypothesis).

which are complementary in their growth requirements. For example, it is very common to maximize N cycling efficiency by making use of the complementary N acquisition strategies of legumes and non-legume CCC (Möller et al., 2008; Wendling et al., 2017). Species diversity can furthermore increase total biomass production (Finney et al., 2016; Rinnofner et al., 2008; Tilman et al., 2001). Since biomass production is closely related to nutrient uptake, it was hypothesized that:

- 2 Due to complementary and/or facilitative effects a multi-species catch and cover crop mixture outperforms its single-species counterparts in terms of nutrient uptake (N, P, and K) and root biomass (Figure 1.4). This hypothesis was tested in Article 1 (Chapter 2.1; Selzer and Schubert, 2021).

1.2.2 Challenge 2: Water requirement of catch and cover crops

1.2.2.1 Water dynamics of catch and cover crops

The occurrence of droughts not only in arid regions but also in temperate zones is predicted to increase as a consequence of anthropogenic climate change (IPCC, 2022). This has direct consequences for cropping systems where the scarcity of the growth-limiting factor water can have detrimental effects on the yield of cash crops (Leng, 2021; Prodhon et al., 2022; Senapati et al., 2021). Hence, the current level of agricultural productivity can only be maintained if water is conserved. Farmers are concerned that the cultivation of an additional crop might deplete SWC and lead to an increased drought stress for a succeeding crop (McGuire et al., 1998).

As indicated in Figure 1.1, ambiguous results exist about the influence of CCC on soil water. The main water fluxes to be considered are water inputs in form of precipitation and water losses in form of transpiration and evaporation. While CCC increase transpiration losses, evaporation can be effectively reduced by winter-killed CCC or through the mechanical or chemical termination of CCC crop growth (Bodner et al., 2011; Campiglia et al., 2011; Gentsch et al., 2022; Meyer et al., 2019; Pedrosa De Azevedo et al., 1999; Qi et al., 2011; Unger and Vigil, 1998). The ambiguity found in the literature as to whether these processes lead to a net water loss or a net water benefit for the agroecosystem is a result of differences in climatic conditions, the duration of catch and cover crop cultivation, management, and species selection. In addition to the aforementioned relevant water fluxes, the process of occult precipitation could be a relevant water input in temperate climates where CCC are mainly cultivated during a period with relatively high atmospheric humidity and low temperatures (PIK, 2020) (Figure 1.5). The process of occult

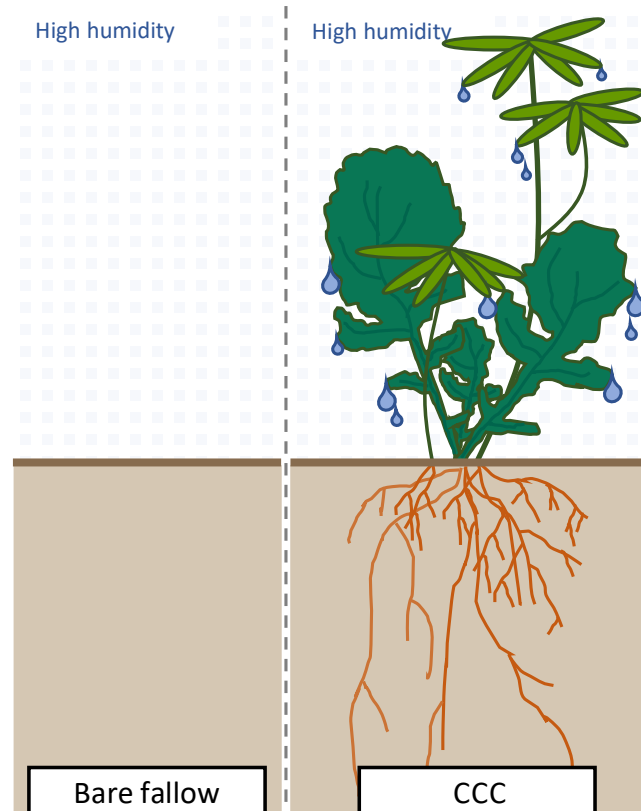


Figure 1.5 Illustration of expected water input through occult precipitation for a catch and cover crop mixture (CCC; right side) in comparison to a bare fallow (left side) (3rd hypothesis).

precipitation has been described for almost all biomes (Matos et al., 2022). In high-humidity locations such as rainforests, occult precipitation can make up 5-20% of total precipitation (Remmert, 2013). An additional water input could counteract transpiration losses and increase SWC during the CCC cultivation period. It was therefore hypothesized that:

- 3 Under middle European climatic conditions, catch and cover crops increase the water input from the atmosphere into the soil through occult precipitation in comparison to a bare fallow control (Figure 1.5).
- 4 The effect is more pronounced for non-transpiring (artificial) plants than for transpiring catch and cover crops. Both hypotheses were tested in Article 2 (Chapter 3.1; Selzer and Schubert, accepted).

Smart management of CCC can improve water conservation and minimize the potential water deficit for a succeeding crop. The aim is to reduce water losses through transpiration (T) and evaporation (E). Choosing frost-sensitive instead of winter-hardy CCC can be an effective tool for soil water recharge during winter (Gentsch et al., 2022). The winter-killed CCC serve as a mulch layer. This has two effects: (1) Winter-killed or terminated CCC do not transpire and (2) the mulch layer reduces evaporation losses (Figure 1.6). The cultivation of a winter-hardy CCC, however, may even increase water losses through transpiration in early spring when growth conditions are favorable (Qi et al., 2011). It was therefore hypothesized that:

- 5 Soil moisture can be recharged during winter when frost-sensitive catch and cover crops are mulched after the first frost event, while a winter-hardy catch or cover crop depletes soil water in early spring (Figure 1.6). This hypothesis was tested in Article 2 (Chapter 3.1; Selzer and Schubert, accepted).

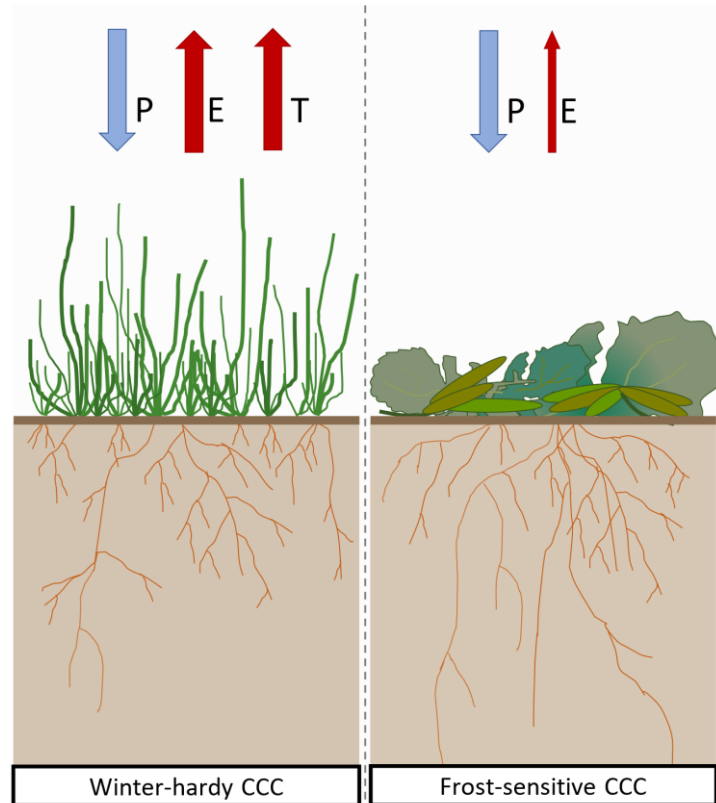


Figure 1.6 Illustration of different water fluxes in spring after the cultivation of winter-hardy (left side) or frost-sensitive (right side) catch and cover crops (CCC). Water input (blue arrow): P = precipitation; Water loss (red arrows): E = evaporation, T = transpiration (5th hypothesis).

1.2.2.2 Prediction of water requirement

As mentioned previously, the fear of creating a water deficit for a succeeding crop discourages farmers from the adoption of catch and cover cropping (Chapter 1.2.2.1). From a water-budget viewpoint, deciding whether CCC cultivation is a feasible option necessitates not only deeper knowledge about general estimates of the maximum water uptake by those crops but rather a site-specific prediction of ET losses which consider meteorological, crop, and soil specific data. One option for farmers is the installation of a complex network of soil moisture probes, temperature, and humidity sensors as used in smart irrigation management systems. A simpler way of deriving the relevant data are computer models which simulate the development of ET based on site-specific input data including meteorological (*e.g.*, humidity, temperature), crop (*e.g.*, LAI, height, developmental stage), and soil (*e.g.*, soil type, bulk density) specific data. Based on the results of these computer models, farmers can make well-founded management decisions.

In Germany, the Agrometeorological Research Centre (ZAMF) of the German Meteorological Service (DWD) uses the model AMBAV (agrometeorological model for the prediction of actual evaporation; German: *'Agrarmeteorologisches Modell zur Berechnung der aktuellen*

Verdunstung') to simulate ET for several crops, including the catch and cover crops mustard, oilseed radish, and phacelia. Based on the simulations, the DWD instructs farmers on their (irrigation) management (Löpmeier, 1983). Since farmers rely on the accuracy of these predictions, it was hypothesized that:

- 6 There are no significant differences between measured evapotranspiration (ET_m) determined in a container experiment and simulated evapotranspiration (ET_{AMBAV}) using AMBAV. This hypothesis was tested in Article 3 (Chapter 3.2; Selzer and Schubert, submitted).

Evapotranspiration losses are dependent on several different meteorological, crop, and soil-specific parameters. The higher the water availability, the higher the measured water losses (own data). Crop-specific factors influence ET as well: LAI not only influences transpiration losses (a high LAI favors high transpiration) but also evaporation (a high LAI restricts soil evaporation). Plant height, another parameter considered by AMBAV, influences ET losses more indirectly. It determines the stratification of the plant which, in combination with LAI, influences soil evaporation (Allen et al., 1998). Accordingly, it was hypothesized that:

- 7 ET_{AMBAV} is most sensitive to variations of (a) the meteorological parameter water supply (precipitation and irrigation) and (b) the crop-specific parameter leaf area index. This hypothesis was tested in Article 3 (Chapter 3.1; Selzer and Schubert, submitted).

2 Nutrient cycling efficiency

2.1 Article 1: Nutrient uptake of catch crops under non-limiting growth conditions^{1, 2}

Selzer, T.^a and Schubert, S.^a

^a Institute of Plant Nutrition, Research Centre for Biosystems, Land Use and Nutrition (iFZ), Justus Liebig University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany

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² Supplementary Material for this chapter can be found in Appendix A.



REGULAR ARTICLE

Nutrient uptake of catch crops under non-limiting growth conditions

Tabea Selzer | Sven Schubert

Institute of Plant Nutrition, Research Centre for Biosystems, Land Use and Nutrition (IFZ), Justus Liebig University, Giessen, Germany

Correspondence

Tabea Selzer, Institute of Plant Nutrition, Research Centre for Biosystems, Land Use and Nutrition (IFZ), Justus Liebig University, Heinrich-Buff-Ring 26–32, 35392 Giessen, Germany.
Email: tabea.selzer@ernaehrung.uni-giessen.de

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; Rinnoferner 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 (Kaleem 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; McLenaghan et al., 1996;

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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 $\text{NO}_3\text{-N}$ 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 $\text{NO}_3\text{-N}$ 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 crop 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	<i>Snapis alba</i> L.	White mustard	Gisilba	270	Fruit development
Brassicaceae	<i>Raphanus sativus</i> L. var. <i>oleiformis</i> Pers.	Oilseed radish	Bento	252	Vegetative
Fabaceae	<i>Lupinus albus</i> L.	White lupin	Feodora	70	Flowering
Boraginaceae	<i>Phacelia tanacetifolia</i> Benth.	Phacelia	Amerigo	525	Vegetative
Polygonaceae	<i>Fagopyrum esculentum</i> Moench	Buckwheat	Hajnalka	315	Fruit development
Poaceae	<i>Lolium perenne</i> L.	Ryegrass	Marava	1050	Vegetative
Asteraceae	<i>Helianthus annuus</i> 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 Drainage, 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 m² (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 CaCO₃ 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)

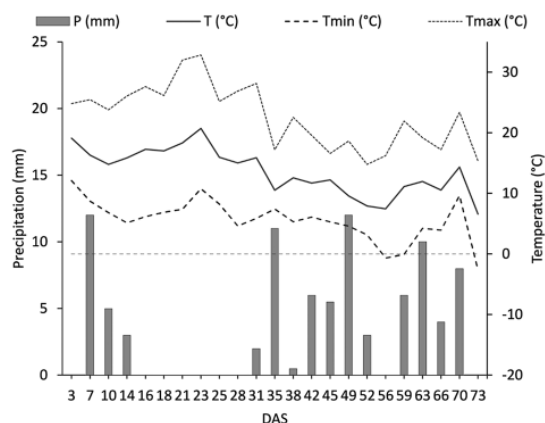


FIGURE 1 Measured precipitation (P) and average (T), minimum (T_{\min}) and maximum (T_{\max}) daily air temperature during the vegetation period. Harvest at 74 days after sowing (DAS)

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%) + acetic 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). $\text{NO}_3\text{-N}$ 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, $\text{K}_2\text{SO}_4 + \text{Se}$) and 10 mL concentrated sulfuric acid were added to achieve the conversion of the remaining N compounds to $(\text{NH}_4)_2\text{SO}_4$. Digestion was performed using the SpeedDigester K-436 (BÜCHI Laboratory Equipment). In the subsequent distillation (Distillation 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 (Ucube, Elementar Analysensysteme GmbH). Nutrient use efficiency (NUE) was defined as the ratio of shoot dry matter to fertilizer application:

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

with NUE_i = nutrient use efficiency of nutrient i in g g^{-1} , DW_{oc} = 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 ($N_{\min} = \text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) 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). $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$

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 \leq 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 $\frac{1}{4}$, 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 HNO₃ and 2.5 mL vanadate solution. After 30 min, P concentration in the filtrate was determined photometrically at 406 nm (Genesys 10SUV/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 $\frac{1}{4}$ Macherey-Nagel GmbH & Co. KG) before measuring N as the sum of NH₄-N and NO₃-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 = $\frac{T_{\max} - T_{\min}}{2} - T_{\text{base}}$, with $T_{\text{base}} = 5^\circ\text{C}$ (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 $> 1 \text{ kg DW m}^{-2}$, 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 $> 50 \text{ cm}$ 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 $< 5 \text{ km m}^{-2}$ 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 $< 7 \text{ g N}^{-1}$; 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).

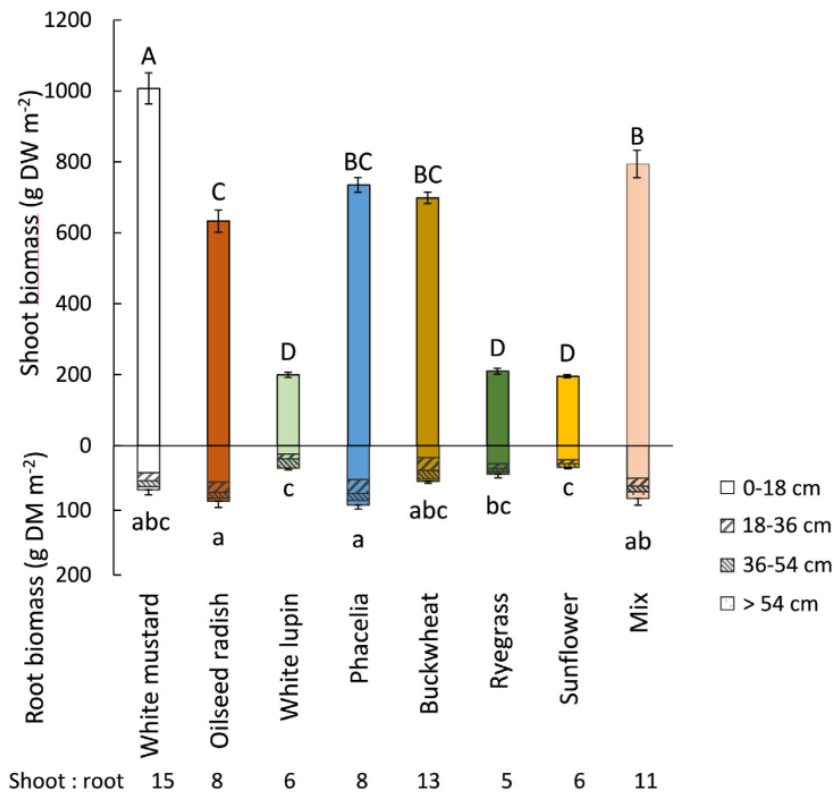


FIGURE 2 Shoot and root dry weights of various catch crops in four successive soil depths (0–18 cm, 18–36 cm, 36–54 cm, and > 54 cm) and shoot:root ratio of the catch crops at final harvest (74 DAS). Soil volume per $m^2 = 0.71 m^3$. One-way analysis of variance (ANOVA) and comparison of means adjusted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

relation 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).

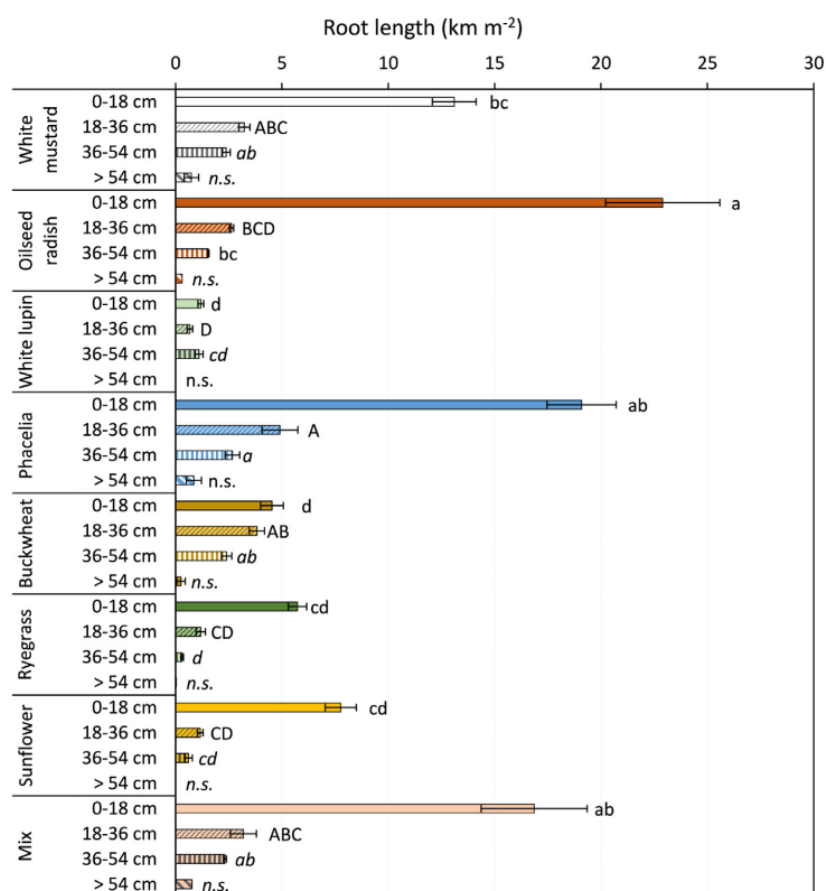


FIGURE 3 Root lengths of various catch crops in four successive soil depths (0–18 cm, 18–36 cm, 36–54 cm, and > 54 cm) at final harvest (74 DAS). One-way ANOVA and comparison of means adjusted according to FDR. Lowercase letters, uppercase letters, and letters in italics indicate significant differences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

Treatment	N			P			K		
	Concentration mg N (g DW)^{-1}	Uptake g N m^{-2}	NUE g DW (g N)^{-1}	Concentration mg P (g DW)^{-1}	Uptake g P m^{-2}	PUE g DW (g P)^{-1}	Concentration mg K (g DW)^{-1}	Uptake g K m^{-2}	KUE 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

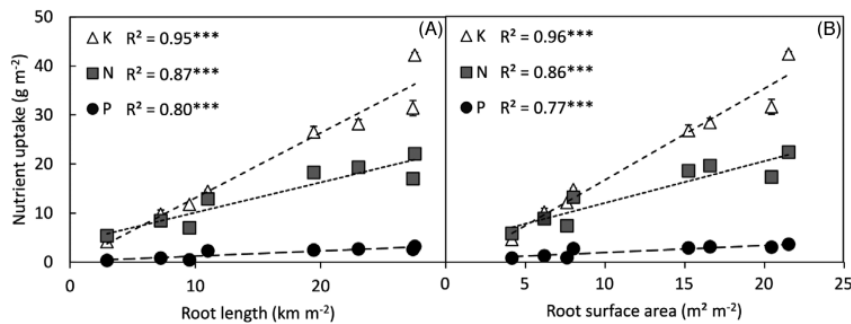


FIGURE 4 Catch crop N, P, and K uptake in relation to (A) root length and (B) root surface area at final harvest (74 DAS). Linear regression analysis ($p < 0.05$). Mean values ($n = 4$) \pm SE. Coefficients of determination (R^2) are given for each nutrient (***) = $p < 0.001$)

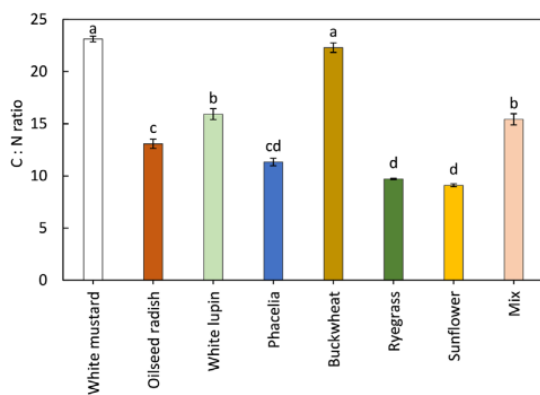


FIGURE 5 C:N ratios of various catch crops at final harvest (74 DAS). One-way ANOVA and comparison of means adjusted according to FDR. Letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$ with the exception of phacelia and sunflower where $n = 3$) \pm SE

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).

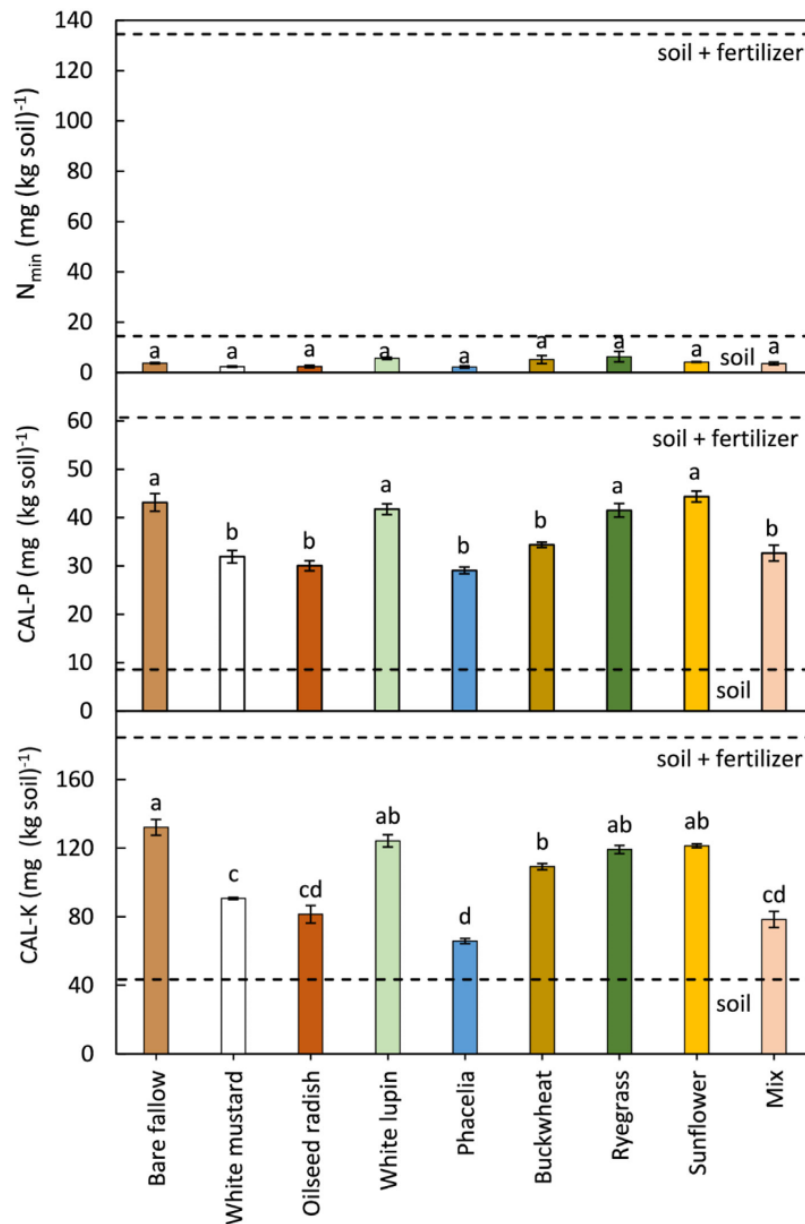


FIGURE 6 Soil mineral nitrogen concentration (N_{\min}), CAL-extractable P concentration (CAL-P), and CAL-extractable K concentration (CAL-K) in the topsoil (0–30 cm) after final harvest (74 DAS) of various catch crops in comparison to a bare fallow control treatment. One-way ANOVA and comparison of means adjusted according to FDR. Different letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$) \pm 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 $\geq 50\%$ 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 mineralogy, 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 shrinkage 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 leaf 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 N₂ fixation. However, symbiotic N₂ 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 N₂ 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) NO₃-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 Ca²⁺ 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 (Aman & 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 $< 6.5 \text{ mg N (kg soil)}^{-1}$, equivalent to less than half of the initial N_{\min} before fertilization [$14.5 \text{ mg N (kg soil)}^{-1}$; 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 ($> 30 \text{ cm}$) 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 $\text{NO}_3\text{-N}$ 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 $\text{NO}_3\text{-N}$ uptake by catch crops in combination with high $\text{NO}_3\text{-N}$ 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 $\text{NO}_3\text{-N}$ 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 comparatively 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 $\text{NO}_3\text{-N}$ 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 N₂. 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 NO₃⁻ 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 eco-

logical 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.

ORCID

Tabea Selzer <https://orcid.org/0000-0002-2507-6568>

Sven Schubert <https://orcid.org/0000-0003-2069-3994>

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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3 Water requirement of catch and cover crops

3.1 Article 2: Water dynamics of cover crops: No evidence for relevant water input through occult precipitation^{3,4}

Selzer, T.^a and Schubert, S.^a

^a Institute of Plant Nutrition, Research Centre for Biosystems, Land Use and Nutrition (iFZ), Justus Liebig University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany

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⁴ Supplementary Material for this chapter can be found in Appendix B.

Abstract

Rising temperatures and a disruption of rainfall patterns due to climate change make water a limiting growth factor even in regions of temperate climates. Thus, producing ‘more crop per drop’ is of utmost importance. While cover crops provide many benefits to cropping systems, their influence on soil water is discussed controversially. While an increase in transpiration can lead to soil water depletion, the reduction of evaporation in combination with possible additional water inputs could provide a water benefit for a succeeding crop. Occult precipitation could be such an additional water input. The objective of this study was to quantify whether cover crops provide a net water benefit over a bare fallow due to the occurrence of occult precipitation.

In a 2-year experiment seven different cover crops were cultivated in pure stands and as a mixture under semi-controlled conditions in a container experiment. Water fluxes and meteorological conditions were closely monitored. Although favourable conditions occurred during both vegetation periods, we found no evidence of occult precipitation. In autumn, soil water was depleted by fast-growing cover crops. In winter, soil water was recharged due to the early preparation of a mulch layer combined with high winter precipitation while in early spring rising temperatures increased transpiration losses of a winter-hardy cover crop, leading to a reduction of soil water.

For middle European conditions, this shows that (1) living cover crops do not provide any water benefits and that (2) soil water recharge in winter is highly dependent on meteorological conditions and cover crop management. From a water budget viewpoint, negative effects on a succeeding cash crop can only be prevented if cover crops are terminated early enough for replenishment of soil water.

1 Introduction

Catch crops – also known as cover crops – are primarily grown to prevent nutrient leaching during times of high precipitation (Thorup-Kristensen and Nielsen, 1998; Kaye and Quemada, 2017). By incorporating the plant into the soil as green manure the nutrients are returned to the soil and can be used by a succeeding crop (Dinesh et al., 2001; Langelier et al., 2021; Torstensson and Aronsson, 2000). Further benefits of cover crops are improvements in

biological, chemical, and physical soil properties (Blanco-Canqui and Ruis, 2020; Dabney et al., 2001; Delgado, 1998; Haruna and Nkongolo, 2015).

Since agriculture is highly dependent on favourable growth conditions, the effects of climate change on temperature as well as on global and regional rainfall patterns affect agricultural productivity. Although different meteorological simulations predict that average annual precipitation will remain constant in the future, dry periods without rainfall are projected to become longer while the intensity of precipitation events is likely to increase (IPCC, 2022; Trenberth, 2011).

Especially the overlap of critical, water-dependent growth stages of grain crops with periods of low precipitation and high temperatures is a major concern for farmers on a global scale (Mase et al., 2017; Woods et al., 2017; Zingrebe et al., 2017). Considering these developments, water – which has already been a growth-limiting factor in the past – is predicted to become even more so in the future (Trnka et al., 2011). Thus, notwithstanding the benefits of cover crops on different soil properties and nutrient cycling efficiency of cropping systems (Selzer and Schubert, 2021), farmers are concerned that the vigorous growth of cover crops will lead to the depletion of soil water, thereby increasing drought stress for the main crop (Basche et al., 2016; McGuire et al., 1998). Nielsen et al. (2016) have reported a grain yield reduction of 3-40% in the Great Plains after cover crop cultivation due to lower water availability than after a fallow.

The main water fluxes in cropping systems include water losses due to (1) transpiration, (2) evaporation, and (3) leaching and water gains in the form of (1) precipitation, (2) irrigation and (3) occult precipitation (Datta et al., 2021; Matos et al., 2022).

Most of the studies with cover crops have focused on water losses caused by evaporation and transpiration. While cover crops increase transpiration losses, they can reduce evaporation in comparison to fallow soil when used as a mulch layer (Bodner et al., 2011; Campiglia et al., 2011; Meyer et al., 2019; Pedrosa De Azevedo et al., 1999; Qi et al., 2011; Unger and Vigil, 1998). The studies show contradictory results as to whether the reduction of evaporation outweighs the increased transpiration losses depending on the duration of the vegetation period, cover crop species (winter-hardy vs. frost-sensitive) and meteorological growth conditions.

In this study, next to exploring evaporation and transpiration losses of various cover crops, we explored possible additional water gains by quantifying relevant water fluxes in a semi-controlled environment. It has been shown that when atmospheric humidity is high, the condensation and coalescence of water droplets on plant surfaces can cause stemflow generation independent of precipitation. This process of ‘fog combing’ or ‘occult precipitation’, that is precipitation which is not detected by standard rain gauges (Holwerda et al., 2010), has been described for different locations around the world. In rainforests, it can amount to up to 5%-20% of gross precipitation (Remmert, 2013). In Californian redwood forests, occult precipitation accounted for 34% of the total annual water input in comparison to 17% when trees were absent (Dawson, 1998). Plants in semi-arid regions and deserts are specialized in using fog combing to meet their water demand in a highly strenuous environment (Ebner et al., 2011). The magnitude of these fluxes, independent of geographic location, is determined by (1) meteorological conditions such as humidity, precipitation, atmospheric temperature, and wind speed (Van Stan et al., 2014) and (2) crop-specific parameters. The latter include plant height and architecture, leaf morphology (*i.e.* diameter and length-to-width ratio), leaf area index (LAI), leaf surface roughness, and the chemical composition of the leaf surface (Ebner et al., 2011; Holloway, 1970; Mali et al., 2020).

While changes of soil physical properties through cover cropping have been studied extensively to explain changes in soil water dynamics (*i.e.*, Irmak et al. 2011; Steele et al., 2012; Blanco-Canqui and Ruis, 2020), the possibility that cover crops could positively affect water inputs through occult precipitation has not been considered yet.

The typical growing season for cover crops in middle Europe starts at the end of August and lasts until the cultivation of a main crop in the following year. This period, especially the months in late autumn and winter, is characterized by relatively high atmospheric humidity and low temperatures (PIK, 2020), providing optimum meteorological conditions for the occurrence of occult precipitation (Zimmermann and Zimmermann, 2002).

We hypothesized that under middle European climatic conditions cover crops increase the water input from the atmosphere into the soil through occult precipitation in comparison to a bare fallow control. We furthermore hypothesized that the effect would be more pronounced for non-transpiring (artificial) plants than for transpiring cover crops.

It has been shown previously that the management of cover crops, especially the timing of cover crop termination, plays an important role in soil moisture dynamics (Alonso-Ayuso et al., 2014, 2018). Mulching of cover crops is an effective tool to increase soil moisture through the reduction of evaporation and the termination of transpiration (Chalise et al., 2019; Ji and Unger, 2001). At the same time, winter-hardy cover crops may increase water losses in spring when radiation intensity and temperature increase, thereby promoting transpiration (Qi et al., 2011). This can cause soil water depletion and hamper the development of a succeeding crop. We hypothesized that soil moisture can be recharged during winter when frost-sensitive cover crops are mulched after the first frost event while a winter-hardy cover crop depletes soil water in early spring.

2 Materials and Methods

2.1 Container experiments

Cover crops were cultivated at the experimental station of the Institute of Plant Nutrition in Giessen (50°35'53.30"N, 8°40'1.56"E) in 2020 and 2021. The crops were grown in large containers (width × depth × height = 40 cm × 40 cm × 80 cm) which allowed for semi-controlled growth conditions (Selzer and Schubert, 2021). While subjected to natural variations of meteorological conditions, soil moisture was kept at a given water-holding capacity (WHC) of 50% in 2020 and 45% in 2021 through irrigation and nutrients were supplied in a mineral form to create non-limiting growth conditions. This ensured the production of maximum cover crop biomass, creating optimum conditions for maximum water inputs through occult precipitation.

Each container was filled with 130 kg limed ($2.5 \text{ g CaCO}_3 \text{ kg}^{-1}$), homogenized, air-dried soil (Table 1) in four consecutive layers as described by Hütsch and Schubert (2018). Fertilizer application followed Selzer and Schubert (2021) in both years: The top 40 kg of soil (equating approximately 0-30 cm) were fertilized with 40 g compound fertilizer (Nitrophoska spezial Blau-Dünger) and micronutrients.

Table 1 Comparison of container experiments in 2020 and 2021 with respect to cultivation practices, irrigation, soil properties, length and meteorological conditions during vegetation periods.

	2020	2021
Cultivation		
Sowing	24 August	25 August
Intermediate harvest 1	16 September	17 September
Intermediate harvest 2	1 October	5 October
Intermediate harvest 3	29 October	27 October
Preparation of mulch layer	-	27 October
Final harvest	6 November	29 March 2022
Soil properties		
Sand (%)	44.3%	52.9%
Silt (%)	34.6%	28.2%
Clay (%)	21.2%	19.9%
pH _{CaCl2}	5.4	5.6
pH _{CaCl2} (limed)	7.5	7.4
Vegetation period (d)		
Precipitation (mm)	88	35
T _{mean} (°C)	13.3	13.1
GDD ^a (°C)	666	586
Irrigation	50% WHC	45% WHC

$$^a \text{GDD (growing degree days)} = \frac{T_{\max} - T_{\min}}{2} - T_{\text{base}}, \text{ with } T_{\text{base}} = 5^\circ\text{C (DWD, 2020)}$$

Abbreviation: WHC = water-holding capacity

An overview of the 10 different treatments ($n = 7$) and cover crop plant densities is given in Table 2. Sowing densities were 20% higher than the aspired plant densities. One week after germination plant density in the containers was adjusted to the values shown in Table 2. Plant densities of sunflower and the mixture were adjusted in 2021. The plant density of sunflower was increased to 80 plants m^{-2} (Wendling et al., 2016) and the proportions of the individual cover crops in the mixture were adjusted to 14.3% of their respective plant densities in monoculture (Table 2). Two control treatments were included in the study, (1) a bare fallow and (2) a ‘dummy’ with non-transpiring, artificial plants (Figure S1). The height and leaf area index (LAI) of these artificial plants was adjusted according to the overall average height and LAI of the cover crops on a weekly basis.

Table 2 *Treatments and plant densities.*

Treatment	Plant density (plants m ⁻²)
Bare fallow	-
Dummy	93
<i>Sinapis alba</i> L. cv. Gisilba	270
<i>Raphanus sativus</i> L. var. oleiformis Pers. cv. Bento	252
<i>Lupinus albus</i> L. cv. Feodora	70
<i>Phacelia tanacetifolia</i> Benth. cv. Amerigo	525
<i>Fagopyrum esculentum</i> Moench cv. Hainalka	315
<i>Lolium perenne</i> L. cv. Marava	1050
<i>Helianthus annuus</i> L. cv. SY Vivacio	12 (80)
Mix	9% (14%) white mustard – 16 (39) 9% (14%) oilseed radish – 15 (36) 20% (14%) white lupin – 14 (10) 9% (14%) phacelia – 32 (75) 9% (14%) buckwheat – 19 (45) 9% (14%) ryegrass – 63 (150) 33% (14%) sunflower – 4 (11)

Note: Mix: plant densities of the individual species are given as the percentage of their respective plant density in pure stands and as number of plants per square meter. Changes for the cultivation period 2021 in comparison to 2020 are given in parentheses.

2.1.1 Meteorological conditions

Sensors were installed in radiation shields 161 cm above the ground (75 cm above soil surface in the containers) and connected to data loggers (DK 320 HumiLog Plus, Driesen+Kern GmbH) which recorded temperature and relative humidity in 1 min intervals. Wind speed was measured using a cup anemometer (WSW G0010, F&C GmbH) linked to a data logger (DK312 MultiLog, Driesen+Kern GmbH) at a height of 350 cm above ground (270 cm above the soil surface in containers).

The main water fluxes in the container experiment are depicted in Figure 1. The main water input consists of precipitation in the form of rainfall. In 2020, precipitation was quantified with a rain gauge which was checked twice a week. Rain gauge data were compared to hourly precipitation recorded with a tipping bucket at the nearby experimental station 'Weilburger Grenze' (50°36'6.12''N, 8°39'12.96''E). Since data from the rain gauge were comparable to those of the rain gauge, the hourly precipitation recordings from Weilburger Grenze were used in this study. Missing data were supplemented with data from the weather station in Giessen-Wettenberg (50°37'5.04''N, 8°39'38.04''E) of the German meteorological service (DWD). In October 2021, maximum wind speed data were neither recorded at Weilburger

Grenze nor in Giessen-Wettenberg. Consequently, data for this parameter are missing from the results.

The temperature sum was calculated as growing degree days (GDD) based on Equation 1.

$$GDD = \frac{T_{max} - T_{min}}{2} - T_{base} \quad (1)$$

With T_{max} = daily maximum temperature in °C, T_{min} = daily minimum temperature in °C, and T_{base} = base temperature in °C which was set at 5°C (DWD, 2020).

2.1.2 Biomass production

Plant height and LAI (ACCUPAR LP-80 PAR/LAI Ceptometer, METER Group) were determined weekly throughout the vegetation period as the mean of four and three measurements per container, respectively. The length of the LAI sensor exceeded the width of the containers. Therefore, measured values were multiplied with a factor of 2.14 which was determined calibration measurements ($n = 10$ for seven different lengths).

Three intermediate harvests were performed to assess above-ground biomass production (Table 1). On those dates, one container of each cover crop treatment was harvested by cutting the plants 1 cm above the ground. Fresh weight was determined gravimetrically.

In 2020, the vegetation period was terminated following the first frost event 74 days after sowing (DAS) from which sunflower and buckwheat plants did not recover (Selzer and Schubert, 2021). Cover crop fresh and dry weights (drying at 105°C) were determined gravimetrically. In 2021, after the first frost event 63 DAS, shoot fresh weight was determined gravimetrically before the biomass of frost-sensitive cover crops was cut into 3-5 cm pieces and placed back on top of the soil as a mulch layer. The fresh weight to dry weight ratio of the third intermediate harvest, which took place on the same day as the preparation of the mulch layer (Table 1), was used to determine biomass dry weight after the first frost (Equation 2).

$$DW = FW \cdot \frac{DW_{IH3}}{FW_{IH3}} \quad (2)$$

with DW = dry weight in kg m⁻², FW = fresh weight in kg m⁻², DW_{IH3} = dry weight at third intermediate harvest in kg m⁻², FW_{IH3} = fresh weight at third intermediate harvest in kg m⁻².

The winter-hardy cover crop ryegrass was not mulched. Therefore, fresh weight of ryegrass was only determined for one container which was harvested for the third intermediate

harvest. The experiment was terminated at 216 DAS on 29 March 2022 (Table 1). On that date, the fresh weight of ryegrass and the cover crop residues was determined.

2.1.3 Plant water dynamics

Two of the water losses by plants depicted in Figure 1 consist of evaporation (E) and transpiration (T). Evapotranspiration (ET) is defined as the sum of E and T. ET was calculated for each container using Equation 3 under the assumption that 1 L H₂O = 1 kg:

$$ET_{ij} = (C_i - L_{hi} + P_{ij} + I_{ij} - FW_{CCj} - C_j) \cdot 6.25 \quad (3)$$

With ET_{ij} = evapotranspiration between time i and time j in L m⁻², C_i = weight of container at time i in kg, L_{hi} = leachate accumulation between time h and time i , P = precipitation between time i and time j in L container⁻¹, I = irrigation between time i and time j in L container⁻¹, FW_{CC} = cover crop shoot fresh weight in kg container⁻¹, and C_j = weight of container at time j in kg. The operational procedure made it necessary to determine the weight of the containers (C_i) before releasing the leachate from the drainage layer. Therefore, leachate accumulation until time point i (L_{hi}) was quantified and subtracted from C_i to determine the actual weight of the containers without leachate. Since the containers had a surface area of 0.16 m² the results were multiplied with the factor 6.25 to get ET losses in L m⁻². FW_{CC} was obtained from the different intermediate harvests.

Relevant water gains by plants, that is the occurrence of occult precipitation (Figure 1), was defined as periods with water inputs which could neither be explained by precipitation nor irrigation, that is $ET_{ij} > 0$.

Water use efficiency (WUE) is defined as the ratio of biomass accumulation to total water input to the system (Sinclair et al., 1984) (Equation 4).

$$WUE = \frac{DW}{(I + P)} \quad (4)$$

with WUE = water use efficiency in kg L⁻¹, DW = shoot dry weight in kg m⁻², I = irrigation in L m⁻², and P = precipitation in L m⁻².

2.1.4 Soil water dynamics

Water gains

Water inputs by precipitation were recorded with a tipping bucket. Water inputs by irrigation (Figure 1) were recorded for each container. Cover crops were irrigated with deionized water twice a week to keep soil moisture at 50% WHC in 2020. Since we suspected luxury water consumption in that year, we decided to reduce soil moisture to 45% WHC in 2021.

Water losses

The drainage layer at the bottom of the containers (Selzer and Schubert, 2021) allowed for the quantification and collection of leachate (Figure 1) throughout the vegetation period. The accumulated leachate was discharged through a valve and quantified gravimetrically after precipitation events on a weekly basis.

Water-holding capacity (WHC)

The soil water-holding capacity (WHC) of each container was calculated using Equation 5.

$$WHC_i = \frac{C_i - C_e - G - S - FW_{CCi}}{WC_{100\%}} \quad (5)$$

WHC_i = water-holding capacity at the time i in %, C_i = weight of container at the time i in kg, C_e = weight of the empty container in kg, G = weight of gravel in drainage layer in kg, S = weight of dry soil in kg, FW_{CC} = cover crop shoot fresh weight in kg container⁻¹, and $WC_{100\%}$ = water content of soil at 100% WHC in kg.

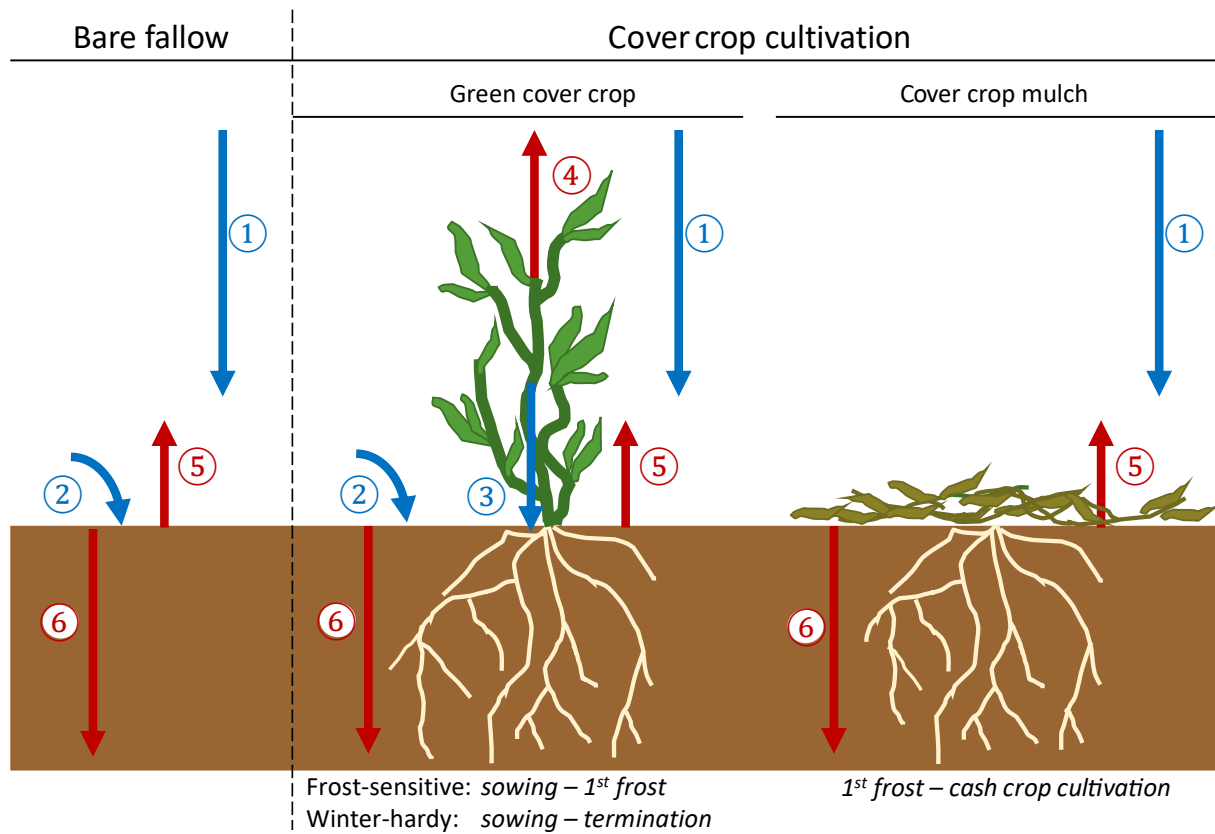


Figure 1 Water fluxes in the cover crop experiment. Water gains (blue): 1 = precipitation, 2 = irrigation, 3 = occult precipitation. Water losses (red): 4 = transpiration, 5 = evaporation, 6 = leaching.

2.2 Climate chamber experiments

2.2.1 Experiment 1

A climate chamber experiment was carried out to identify under which climatic conditions occult precipitation occurs. The same plastic leaves that were used in the container experiments for the 'dummy' treatment were used to simulate a non-transpiring crop. Mitscherlich pots (\varnothing 30 cm) were filled with quartz sand. The plastic leaves were attached to 50 cm long stalks at a 45° angle and positioned in the quartz sand. The total height of the stalks and leaves was 73 cm and the LAI equaled 1.6 (uncorrected average LAI over all cover crop treatments in 2020). A ventilator (KE-60, 160 W, Kesser) was positioned 100 cm in front of the pot to regulate wind speed. Humidity in the climate chamber was set to 95% while a combination of various temperatures (5, 10, 15, and 20°C) and wind speeds (0.6 and 1.4 m s⁻¹) was tested in separate runs. The pots were weighed 0, 2, 4, 6, and 8 h after the start of each run to quantify occult precipitation. Each combination of meteorological conditions was repeated three times.

2.2.2 Experiment 2

The same setup, wind speeds (0.6 and 1.4 m s⁻¹), and relative humidity (95%) as in Experiment 1 were used for Experiment 2. However, the temperature was not held constant over the weighing period. Creating more realistic conditions for fog formation, we simulated a temperature drop from 20 to 5°C while the other influencing factors were kept constant. The pots were weighed 0, 10, 20, 30, 60, and 120 min after the start of the temperature drop to quantify occult precipitation.

2.3 Statistical analysis

Biomass and water fluxes of the different treatments were compared with a one-way analysis of variance (ANOVA) followed by a post-hoc FDR-test for each year. A White-adjusted ANOVA according to White (1980) and Long and Ervin (2000) was used for heteroscedastic data. A Grubb test was performed to identify outliers. This was relevant for WHC and leachate accumulation of white mustard on February 22, February 25, and March 1, 2022. For these dates, only three of the four replicates were included in the results shown below. Where applicable, results from the two consecutive years were compared using a two-sided Student's t-test. Although the experimental setup was the same in both years, differences in water supply, the duration of the vegetation period, and meteorological differences need to be considered when interpreting the results. The significance levels of all tests were chosen at $p < 0.05$. All tests were performed with RStudio (R version 4.1.0). The figures depict the means \pm standard error (SE) which was calculated using Microsoft Office Excel (2019).

3 Results

3.1 Meteorological conditions

In 2020 the average temperature during the 74-day vegetation period was 13.3°C with a maximum of 33.4°C 22 DAS and a minimum of -2.5°C (73 DAS) (Figure 2 a). The average temperature during the vegetation period in 2021 was 13.1°C with a maximum of 30.4°C (12 DAS) and a minimum of -2.0°C (61 DAS) (Figure 2 d). At the time of the first frost event, after which cover crops were either harvested (2020) or mulched (2021), a temperature sum of 666 and 586 growing degree days (GDD) was reached in 2020 and 2021, respectively.

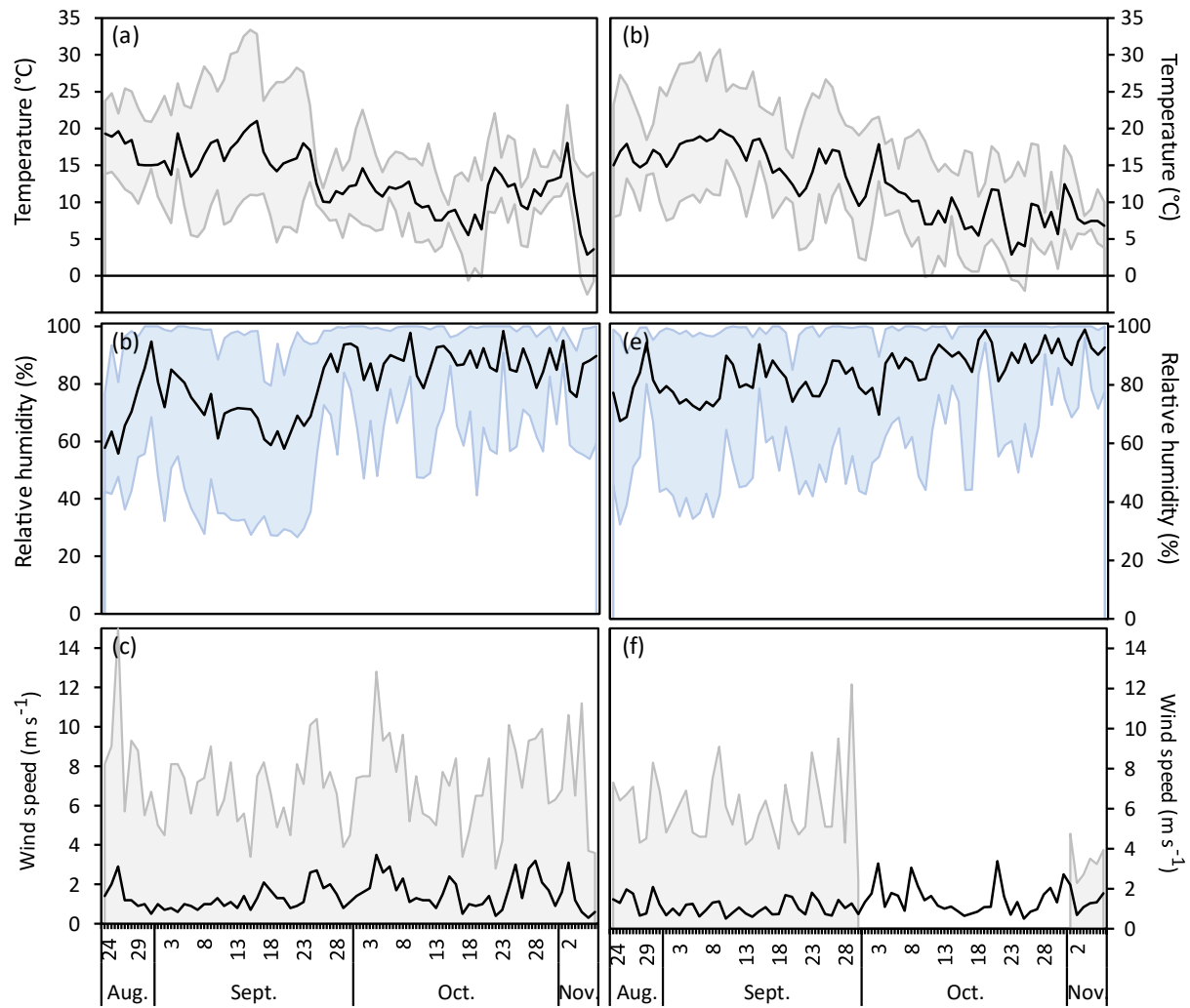


Figure 2 Meteorological conditions during the cover crop vegetation periods in 2020 (a-c and 2021 (d-f). Depicted are (1) mean daily temperature (a + d, black solid line) and range between maximum and minimum daily temperature (grey area), (2) mean relative humidity (b + e, black solid line) and range between maximum and minimum daily humidity (grey area), and (3) mean daily wind speed (c + f, black solid line) and range between maximum and minimum daily wind speed (grey area).

Mean humidity during the first 35 days was < 80% in 2020 (Figure 2 b). Except for September, relative humidity was comparable in 2020 and 2021. Due to the absence of rain between 4 September and 22 September 2020, relative humidity was comparably low. From 28 September (35 DAS) onwards, mean relative humidity exceeded 80% and reached maximum values of 100% every day until harvest (74 DAS). In 2021, the mean humidity in September was higher than in 2020 (Figure 2 b, e) due to more precipitation events. Wind speed reached maximum values of 4 m s⁻¹ on several occasions while the overall mean wind speed was 1.4 m s⁻¹ in 2020 and 1.3 in 2021 (Figure 2 c, f).

3.2 Biomass production

White mustard was the cover crop with the highest shoot biomass in both years with ≥ 1 kg DW m^{-2} (Figure 3). Oilseed radish, phacelia, buckwheat, and the mix of different cover crops also showed a quick development, good soil cover (Table S1), and high biomass production (Figure 3). Adjusting the plant density of sunflower in 2021 led to a significant increase in shoot dry weight in comparison to 2020, while white lupin and phacelia produced $> 20\%$ less biomass in 2021 than in 2020 (Figure 3) due to differences in water supply, temperature sum, and length of the vegetation period.

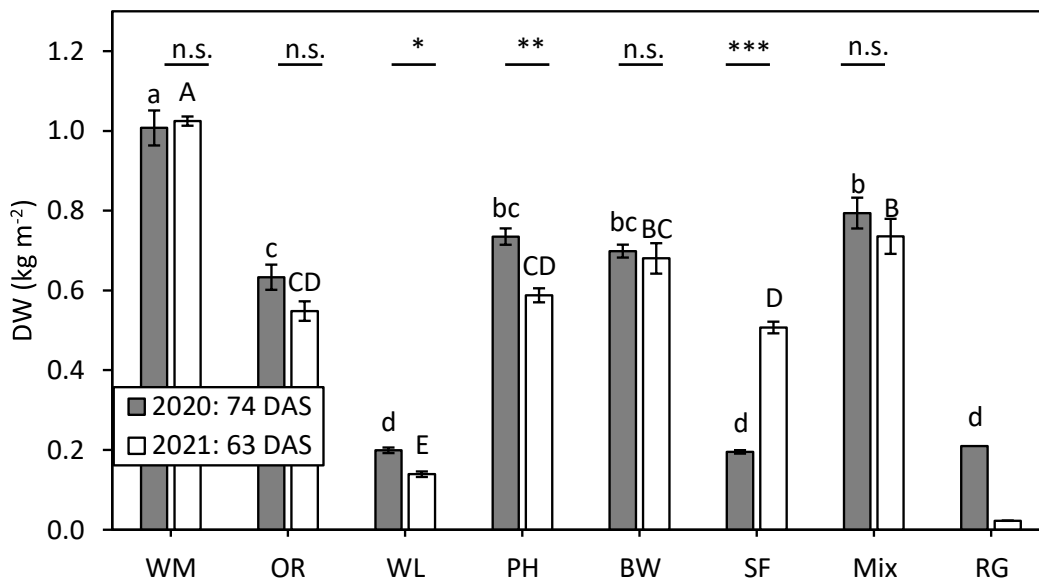


Figure 3 Shoot dry weight (DW) of various cover crops at the time of the first frost event 74 and 63 days after sowing (DAS) in 2020 and 2021, respectively (BW, buckwheat; OR, oilseed radish; PH, phacelia; RG, ryegrass; SF, sunflower; WL, white lupin; WM, white mustard). One-way ANOVA and comparison of means adjusted according to FDR. Different letters indicate significant differences ($p < .05$), whereas small and capital letters indicate differences between cover crop species in 2020 and 2021, respectively. DW of the individual cover crops between the two consecutive years was compared using a two-sided Student's *t*-test (n.s. = not significant; * $p < .05$; ** $p < .01$; *** $p < .001$). Mean values ($n = 4$, 2021: $n_{RG} = 1$) \pm SE.

3.3 Plant water dynamics

3.3.1 Water gains

Figure 4 and 5 depict plant water dynamics in the form of water inputs (irrigation and precipitation) and water losses (ET) for 2020 and 2021, respectively. Total precipitation during the vegetation period amounted to 88 mm in 2020 (Figure 4) and 35 mm in 2021 (Figure 5). Precipitation events were higher and more frequent in 2020 than in 2021. However, during the main growth period of cover crops in September 2020 (8-37 DAS), no precipitation occurred over a 20-day period (Figure 4). Accordingly, irrigation with up to 96 mm (white

mustard) was necessary to keep soil moisture at 50% WHC (Figure 4). In both years, total precipitation in September was far below the long-term (1991-2020) average of 50 mm in Giessen (calculated based on data from the DWD) with 16 and 12 mm in 2020 and 2021, respectively. Precipitation in October 2020 (38-68 DAS) was within the range of the long-term average of 50 mm. However, October 2021 (37-67 DAS) was unusually dry with 68% less rainfall than in an average year.

The amount of irrigation in each treatment reflects the water losses through plant water use (transpiration), evaporation, and leaching. Irrigation was applied to keep soil moisture at 50% and 45% WHC in 2020 and 2021, respectively. Accordingly, more irrigation water was needed in 2020 than in 2021, with the exception of sunflowers which had a higher irrigation requirement in 2021 due to the adjusted plant density (Table 2). Irrigation necessity was directly linked to biomass production. White mustard, the cover crop with the highest biomass in 2020 (Figure 3) was also among the cover crops with the highest total irrigation necessity (184 mm, Figure 4). For phacelia, water supply by irrigation (176 mm, Figure 4) was similarly high in 2020 although biomass production was significantly lower than for white mustard (Figure 3). Cover crops with low biomass production (white lupin, ryegrass, and sunflower) needed significantly less irrigation water (Figure 4). For example, total irrigation necessity of ryegrass was 80% lower than that of white mustard in 2020 (Figure 4). Similarly, differences in total irrigation were reflective of differences in biomass production in 2021 (Figures 3 and 5). For most of the vegetation period, the bare fallow and dummy did not require any irrigation to keep soil moisture at 50% and 45% WHC in 2020 and 2021, respectively (Figures 4 and 5).

The occurrence of occult precipitation was defined as periods in which $ET > 0$. This condition was neither met in 2020 (Figure 4) nor during the vegetation period 2021 (Figure 5) in any of the treatments. No water inputs via occult precipitation were quantifiable.

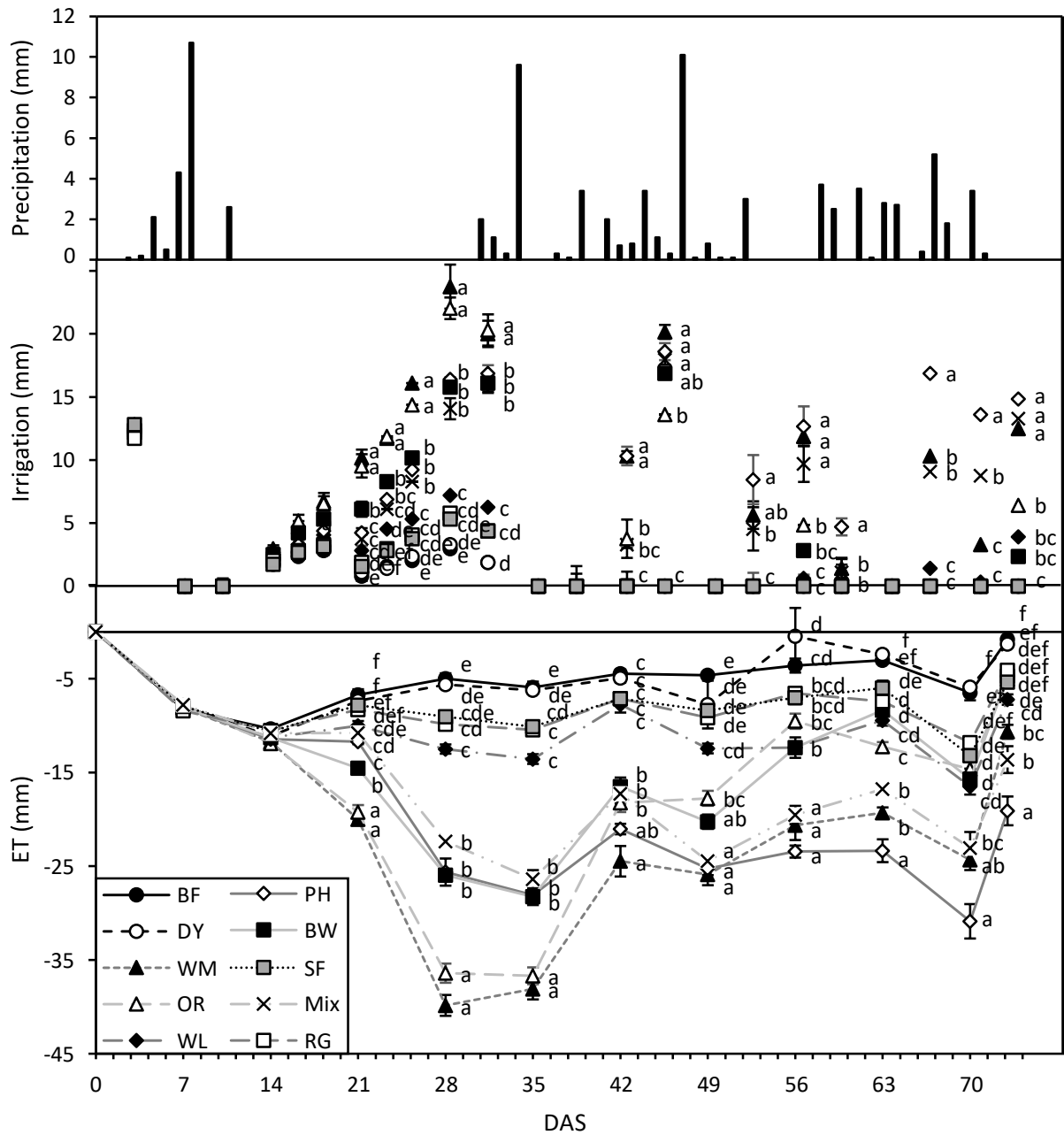


Figure 4 Water gains (precipitation and irrigation) and weekly water losses (ET) in 2020 until 74 days after sowing (DAS) (BF, bare fallow; BW, buckwheat; DY, dummy; OR, oilseed radish; PH, phacelia; RG, ryegrass; SF, sunflower; WL, white lupin; WM, white mustard). One-way ANOVA and comparison of means adjusted according to FDR. Different superscript letters indicate significant differences ($p < .05$) between treatments for that date. Mean values ($n = 4$) \pm SE.

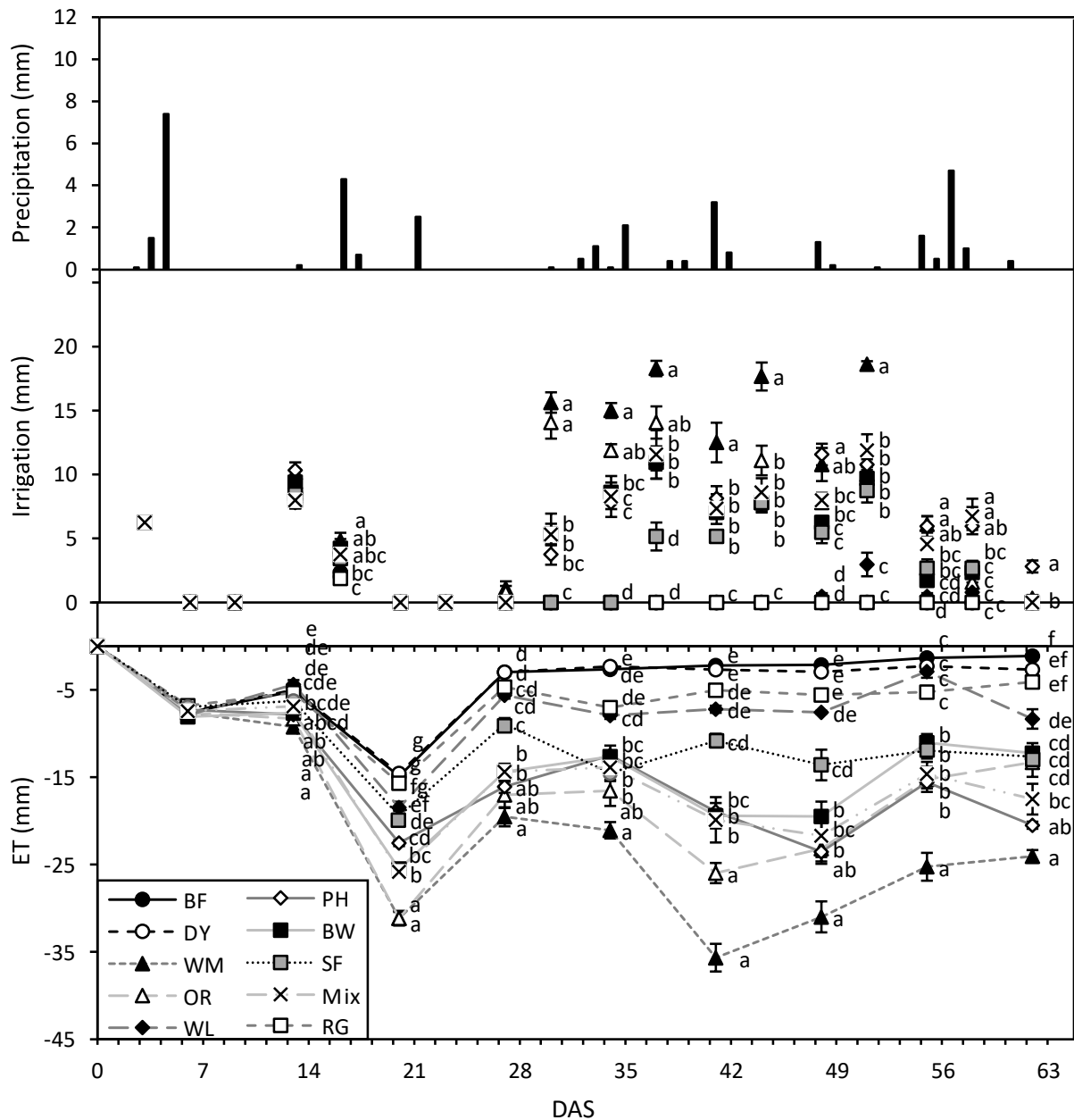


Figure 5 Water gains (precipitation and irrigation) and water losses (ET) in 2021 until 63 days after sowing (DAS) (BF, bare fallow; BW, buckwheat; DY, dummy; OR, oilseed radish; PH, phacelia; RG, ryegrass; SF, sunflower; WL, white lupin; WM, white mustard). One-way ANOVA and comparison of means adjusted according to FDR. Different superscript letters indicate significant differences ($p < .05$) between treatments for that date. Mean values ($n = 4$) \pm SE.

3.3.2 Water losses

The crops with the highest biomass production, namely white mustard, oilseed radish, phacelia, and the mixture of seven cover crops showed the highest ET losses in both years (Figures 4 and 5). The highest water losses by buckwheat and white mustard coincided with the beginning of flowering (both 31 DAS) in 2020 (Figure 4) while in 2021 white mustard lost most of its water after flowering began.

Although artificial plants provided a shading effect, there were no significant differences in the irrigation necessity or evaporative water losses between the two control treatments bare fallow and dummy (Figures 4 and 5). Total ET was significantly lower in those treatments compared to the cover crop treatments in both years (Figure 6).

Total ET was representative of differences in shoot biomass production (Figures 3 and 6). With > 256 mm white mustard and phacelia showed significantly higher ET than the other single and mixed cover crop treatments in 2020 (Figure 6). ET losses by cover crops were lowest for ryegrass and sunflower in that year (Figure 6), which were also among the cover crops with the lowest biomass production (Figure 3). Similar results were found in 2021. However, due to different meteorological conditions, management, and a shorter growth period before the first frost event, cumulative ET in 2021 was on average 36% lower than in 2020. This difference was statistically significant for all cover crops with the exception of sunflowers (Figure 6). This can be attributed to the adjusted plant density of sunflower in 2021 compared to 2020 (Table 2).

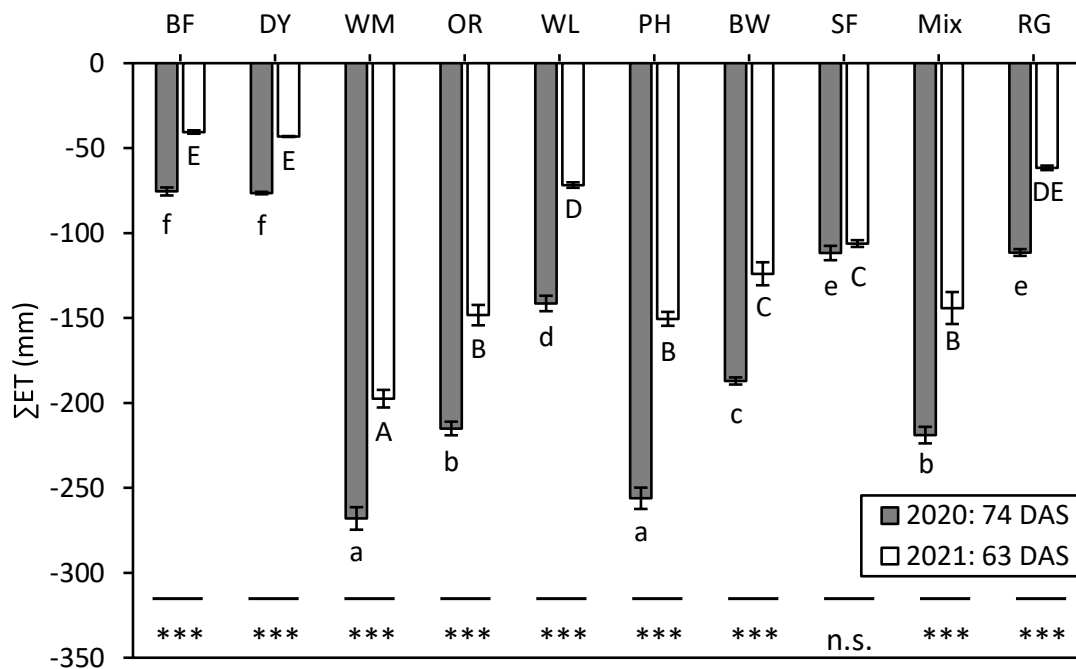


Figure 6 Cumulative evapotranspiration (ET) during the vegetation period of various cover (BW, buckwheat; OR, oilseed radish; PH, phacelia; RG, ryegrass; SF, sunflower; WL, white lupin; WM, white mustard) in 2020 and 2021 compared to two control treatments (BF, bare fallow; DY, dummy). One-way ANOVA and comparison of means adjusted according to FDR. Different letters indicate significant differences ($p < .05$) where small and capital letters indicate differences between cover crop species in 2020 and 2021, respectively. ET of the individual cover crops between the two consecutive years was compared using a two-sided Student's *t*-test (n.s. = not significant; * $p < .05$; ** $p < .01$; *** $p < .001$). Mean values ($n = 4$) \pm SE.

Water losses in the form of leaching did not occur in the 63-day vegetation period in 2021 and leachate accumulation was only evident in three out of 40 containers in 2020 which could be explained by the preferential flow of irrigation water along the rim of the containers.

Water use efficiency (WUE) was defined as the ratio of shoot biomass production to total available water (Equation 4). Of the single-species treatments, white mustard and buckwheat showed the highest WUE followed by oilseed radish and phacelia in both years. WUEs of white lupin, ryegrass and sunflower, the cover crops with the lowest shoot biomass in 2020 (Figure 3), were $< 1.5 \text{ g DW L}^{-1}$ in that year (Figure 7). The mix of various cover crops used the available water equally well as the most efficient single cover crops in both years. With an average increase of 55%, the WUE of frost-sensitive cover crops in 2021 was significantly higher than in 2020. The increased WUE was due to reduced water inputs while biomass production only declined marginally for some of the crops (Figure 3). The adjustment of plant densities for sunflowers increased WUE by 249% in 2021. With 5.4 g DW L^{-1} it had one of the highest WUEs and did not differ from white mustard, buckwheat or the mixture in that year (Figure 7).

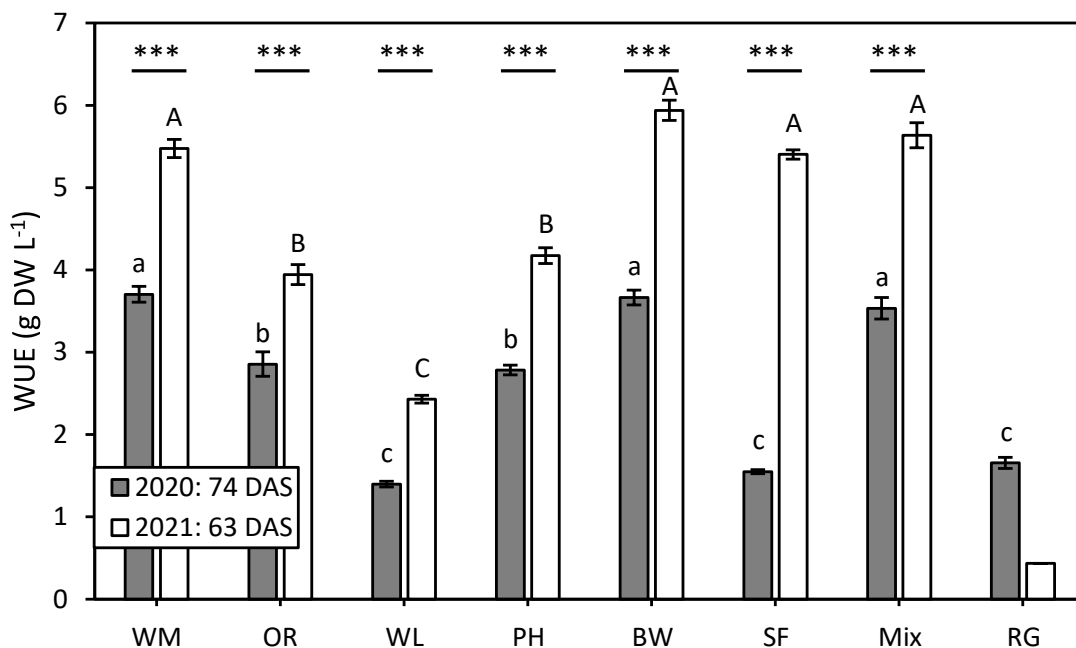


Figure 7 Water use efficiency (WUE) of various cover crops at the time of the first frost event 74 and 63 days after sowing (DAS) in 2020 and 2021, respectively (BW, buckwheat; OR, oilseed radish; PH, phacelia; RG, ryegrass; SF, sunflower; WL, white lupin; WM, white mustard). One-way ANOVA and comparison of means adjusted according to FDR. Different letters indicate significant differences ($p < .05$) where small and capital letters indicate differences between cover crop species in 2020 and 2021, respectively. WUE of the individual cover crops between the two consecutive years was compared using a two-sided Student's *t*-test (*n.s.* = not significant; * $p < .05$; ** $p < .01$; *** $p < .001$). Mean values ($n = 4$, 2021: $n_{RG} = 1$) \pm SE.

3.4 Soil water dynamics

The water gains and losses shown above directly influenced soil water dynamics. Although the soil was kept moist throughout the vegetation period, WHC differed significantly between treatments at the time of the first frost event. With > 73% and > 58% WHC in 2020 and 2021, respectively, soil moisture in the two control treatments bare fallow and dummy was significantly higher than in the cover crop treatments (Table 3).

Table 3 Soil water-holding capacity (WHC) at the first frost event in 2020 (74 DAS) and 2021 (63 DAS) and at the termination of the experiment (216 DAS).

	WHC (%)		
	2020	2021	
	First frost	First frost	Termination
Control			
BF	73.4 ± 0.5 ^a	60.0 ± 0.4 ^a	91.3 ± 1.5 ^a
DY	73.8 ± 0.3 ^a	58.4 ± 0.2 ^a	92.3 ± 1.4 ^a
Frost-sensitive			
WM	42.7 ± 0.4 ^d	39.4 ± 0.4 ^{ef}	87.0 ± 1.1 ^a
OR	47.1 ± 0.8 ^c	43.3 ± 1.2 ^{bcd}	86.8 ± 1.4 ^a
WL	47.6 ± 0.6 ^c	44.8 ± 0.7 ^{bc}	92.4 ± 1.9 ^a
PH	41.4 ± 0.3 ^d	36.6 ± 0.4 ^f	85.6 ± 1.4 ^a
BW	48.8 ± 0.1 ^c	46.0 ± 0.4 ^b	88.1 ± 1.6 ^a
SF	56.8 ± 1.8 ^b	41.2 ± 0.6 ^{cde}	84.0 ± 1.7 ^a
Mix	42.6 ± 0.3 ^d	40.6 ± 0.7 ^{de}	89.1 ± 1.9 ^a
Winter-hardy			
RG	57.8 ± 0.7 ^b	46.8 ± 0.8 ^b	68.2 ± 1.5 ^b

Abbreviations: BF, bare fallow; BW, buckwheat; DY, dummy; OR, oilseed radish; PH, phacelia; RG, ryegrass; SF, sunflower; WL, white lupin; WM, white mustard

Note: One-way ANOVA and comparison of means adjusted according to FDR. Different superscript letters in a column indicate significant differences ($p < .05$). Mean values ($n = 4$) ± SE.

This difference in soil moisture between the different treatments at the end of the vegetation period 2021 on October 27 (first frost) was no longer evident at the termination of the experiment in March 2022 (Table 3). Soil moisture increased after the preparation of the mulch layer in the treatments with frost-sensitive cover crops. During winter, soil moisture was restored to levels comparable to the control treatments. Soil moisture even exceeded 100% WHC on several occasions leading to leaching (Figure 8). For the winter-hardy cover crop ryegrass, soil moisture also increased. However, since ryegrass was not mulched, soil water recharge was slower than in the other treatments leading to significantly lower leaching. In early spring, when temperatures rose to 23.5°C (28 March, 215 DAS), WHC in the ryegrass

treatment declined sharply from 90.4% on March 18 (205 DAS) to 68.2% on March 29 (216 DAS) (Figure 8) resulting in significantly lower soil moisture than in the other treatments (Table 3).

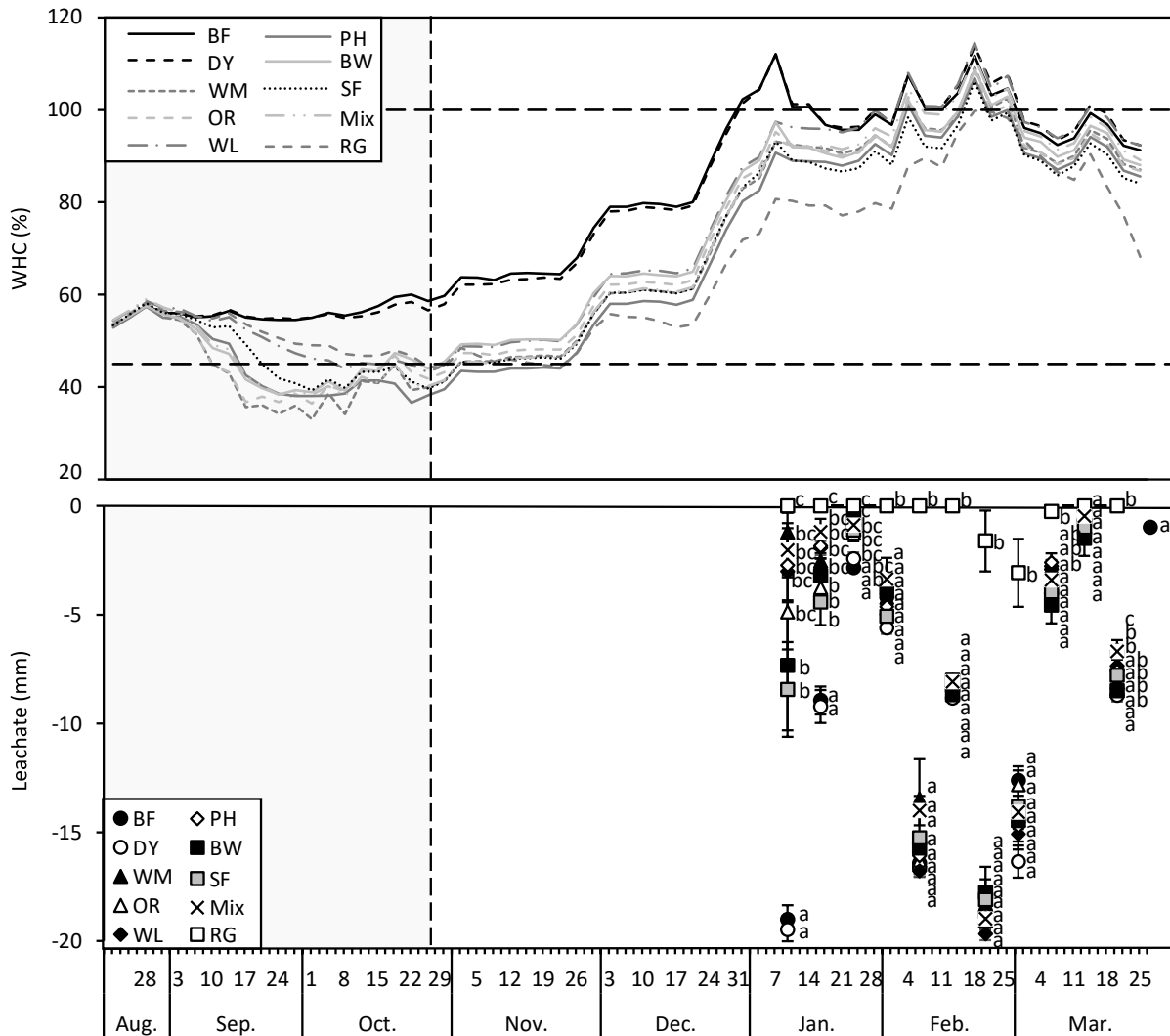


Figure 8 Time course of soil water-holding capacity (WHC) and leachate accumulation in the cover crop experiment in 2021. Preparation of mulch layer (dashed line) after first frost event 63 days after sowing (October 27) in frost-sensitive cover crop treatments (BW, buckwheat; OR, oilseed radish; PH, phacelia; RG, ryegrass; SF, sunflower; WL, white lupin; WM, white mustard) with exception of the winter-hardy cover crop ryegrass (RG) in comparison to the control treatments bare fallow (BF) and a dummy (DY) with non-transpiring plants. One-way ANOVA and comparison of means adjusted according to FDR. WHC: mean values ($n = 4$). Leachate: different letters indicate significant differences ($p < .05$) between treatments for that date. Mean values ($n = 4$) \pm SE.

4 Discussion

4.1 Methodology

4.1.1 Determination of water fluxes

Calculating ET based on measurements which were performed twice a week can only give rather rough estimates of the various water fluxes shown in Figure 1. It is possible therefore, that minor events of occult precipitation of a few millilitres per container might have been overlooked by this approach. However, since we were only interested in quantifying those water inputs with a quantifiable and relevant contribution to the cover crops' and the succeeding crops' water supply, the approach is justified. The results clearly illustrate that more precise measurements would not have changed the overall conclusion that occult precipitation did not have a relevant influence on the water balance of the cover crops.

Soil water storage is determined by the complex interplay of soil physical and chemical properties (Basche et al., 2016). While the focus of our experiments was on the effect of cover crops on water fluxes during two individual growth seasons it has been shown previously that cover crops can have long-term effects on soil physical, biological, and chemical properties which in turn enhance soil water storage capacity (McDaniel et al., 2014; Poepflau and Don, 2015) by increasing soil porosity (Villamil et al., 2006), reducing soil bulk density (Steele et al., 2012), increasing soil hydraulic conductivity (Klik et al., 1998), and promoting aggregate stability (Sainju et al., 2003; Villamil et al., 2006). These processes can improve water infiltration leading to an increasingly fast soil water recharge (Mubvumba et al., 2021) while the formation of crusts as a consequence of heavy rainfall restricts infiltration in bare soil (Hardie and Almajmaie, 2019). These long-term effects should not be neglected when considering the overall effects of cover cropping on soil water dynamics.

4.1.2 Water supply

Since ET was positively correlated with water supply in all treatments in 2020, when soil moisture was kept at 50% WHC, we suspected that the high cumulative ET of up to 268 mm by white mustard (Figure 6) was caused by luxury water consumption. Figures 6 and 7 support the assumption of luxury water consumption. Although biomass production of white mustard did not differ between 2020 and 2021 (Figure 3), the cumulative ET of white mustard was 26%

lower when soil moisture was kept at 45% compared to 50% WHC (Figure 6). In addition, the reduction of water availability led to a significant increase of WUE (Figure 7).

In both years, keeping the soil moist is likely to have increased cumulative ET losses compared to field conditions without irrigation. Thus, the ET of cover crops grown in the field is likely to be lower than the values shown in Figure 6. In this study, keeping the soil moist was justified by the attempt to create conditions for maximum water inputs through occult precipitation.

4.2 Can we save water with cover crops?

Relevant amounts of occult precipitation, that is water inputs which could neither be explained by rainfall nor irrigation ($ET > 0$) (Holwerda et al., 2010), did not occur in the container experiment although preferential meteorological conditions for occult precipitation occurred on several occasions during both vegetation periods (Figure 2). Instead, substantial water losses in the form of ET were evident (Figure 6) especially for cover crops with high biomass production and LAI (Figure 3, Table S1). Hence, the hypothesis that the occurrence of occult precipitation in cover crop treatments provides a water benefit in comparison to a bare fallow has to be rejected. At no point during the two vegetation periods were we able to quantify relevant water inputs through occult precipitation. This finding is supported by other studies which found that cover crops deplete soil water due to increased transpiration losses (McGuire et al., 1998; Mubvumba et al., 2021; Nielsen et al., 2015). Contradicting results have been presented in other studies which have found either an increase or no difference between the water content after cover crop cultivation and a bare fallow control (Alonso-Ayuso et al., 2014; Basche et al., 2016; Mubvumba et al., 2021; Rinnofner et al., 2008). However, in most of these studies cover crop growth was terminated and the water content increased only after this termination (Alonso-Ayuso et al., 2014; Basche et al., 2016; Gentsch et al., 2022; Mubvumba et al., 2021). This clearly shows that increases in soil water cannot be attributed to an additional water input (occult precipitation) but to a reduction of water losses (transpiration and evaporation).

The aim of including a second control treatment, namely a dummy with non-transpiring plants, was to determine the net water input through occult precipitation without transpiration losses. It was hypothesized that net water inputs would be higher in the dummy treatment than in the cover crop treatments. Although ET losses from the dummy were

significantly lower than those of the cover crops, they did not differ from the bare fallow at any time during the vegetation periods (Figures 4 and 5) leading to the rejection of the second hypothesis. The results were supported by the climate chamber experiments in which the dummy did not harness any significant amounts of atmospheric moisture (Figure S2).

4.3 Can we afford cover crops in times of increasing water scarcity?

Based on the results in Figure 8 and Table 3, we can accept the third hypothesis that soil moisture is recharged during the winter if cover crops are mulched while the winter-hardy cover crop ryegrass depletes soil water in spring due to an increase in transpiration. This may suggest that water is not a problem in cover crop cultivation when only frost-sensitive cover crops are grown. However, soil water recharge is not only dependent on the type of cover crop used but also depends on meteorological conditions and the management of the cover crops.

4.3.1 Meteorological conditions

Sharma and Irmak (2019) pointed out that the net effect of cover cropping on soil water dynamics is highly dependent on timing and amount of precipitation. In 2021, the soil moisture of the bare fallow and dummy was higher than that of the cover crop treatments until the middle of January (Figure 8). Only due to exceptionally high rainfall in February with 72 mm compared to a long-term (1991-2020) average of 38 mm (calculated based on data from the DWD) soil water was restored and even exceeded 100% WHC. In areas with limited precipitation cover crop cultivation can deplete soil water which adversely affects the yield of a succeeding crop (Islam et al., 2021). For semi-arid regions it was shown that the soil water content in spring was 25%-35% lower under a green manure cover crop in comparison to a bare fallow resulting in a reduced yield of the subsequent wheat crop (Unger and Vigil, 1998). With increasingly irregular precipitation patterns (Trenberth, 2011) there is no guarantee that winter precipitation will restore soil water storage after cover crop cultivation not only in arid but also in (sub-)humid regions.

4.3.2 Cover crop management

Alonso-Ayuso et al. (2018) have shown that the termination date is a meaningful tool for the regulation of water losses. In their study, a late termination (mid-April) of cover crops led to

soil water depletion which increased pre-emptive competition with a succeeding crop. This was in agreement with results from this study where the winter-hardy cover crop reduced the soil water content in early spring (Figure 8). Similar results were found by Unger and Vigil (1998) who have shown that due to lower water availability the yield of a succeeding grain crop decreased if cover crops were allowed to reach maturity in comparison to a cover crop which was desiccated. It is shown in this study that early termination of cover crop growth allows soil water to recharge during winter under favourable weather conditions (Figure 8). However, early termination can have negative effects on other ecosystem services provided by cover crops: Leachate volume was significantly higher in the mulched cover crop treatments in comparison to the winter-hardy ryegrass (Figure 8).

Not only the time of termination but also the management of cover crop residues directly affects soil water dynamics. One management option which was tested in this study is mulching. At termination, the soil water content in the mulched treatments was significantly higher than in the treatment with winter-hardy ryegrass. However, it did not differ from the water content in the bare fallow treatment (Table 3). Even though a mulch layer effectively increases soil water content due to the termination of transpiration losses and the significant reduction of evaporation in comparison to a bare fallow (Chalise et al., 2019), soil moisture in the cover crop treatments declined equally fast as in the bare fallow treatment in this study (Figure 8).

Possible reasons for this reduction of soil moisture in the mulched treatments are threefold: Firstly, decomposition processes during winter reduced cover crop biomass to $\leq 10\%$ of its original fresh weight (Figure S3). Tolk et al. (1998) have shown that next to the evaporative demand of the atmosphere, the thickness of the residue determines the rate of evaporation. While the mulch effectively covered the soil in November 2021, it hardly provided a closed cover in February and March 2022 (Figure S4) when temperatures rose and evaporative water losses started to increase again. The decomposition rate is determined by (1) microbial activity which depends on temperature and soil pH, (2) the chemical composition of the organic matter, and (3) water availability. Coppens et al. (2007) have shown that moisture limitation is even more important than N limitation for mulch decomposition. In this study, neither N availability nor soil moisture were limiting factors. The C:N ratio of the cover crops was ≤ 23 in 2020 (Selzer and Schubert, 2021) and after the preparation of the mulch layer soil moisture increased steadily in all treatments (Figure 8), providing good conditions for mineralization.

The rapid decomposition of cover crop residues was also evident in a semi-arid environment where it reduced the positive effect of cover crops on soil physical properties (Blanco-Canqui et al., 2013) which are closely related to soil water dynamics.

Secondly, returning residue to the soil as a mulch has been shown to increase soil water retention in the upper 5 cm of soil due to an increased soil organic carbon content and a reduction of soil bulk density (Chalise et al., 2019). This improved water retention in the topsoil might have contributed to higher evaporation losses at the soil surface in comparison to the bare fallow treatment which has a lower water retention at the soil surface.

Thirdly, the darker colour of the mulch in comparison to the bare soil surface could have increased the absorption of solar radiation (Masse and Cary, 1978) thereby promoting faster heating of the upper few centimetres of the soil, leading to higher water losses due to evaporation.

Thus, from a water budget viewpoint, cover cropping can only be afforded if cover crop growth is terminated early enough to minimize water losses through transpiration while simultaneously maximizing the other benefits cover crops provide to a cropping system. However, cover crop management is not the only determining factor. Water scarcity is already one of the main reasons for farmers to decide against the adaptation of cover crops in some regions in Germany (personal communication). Consequently, even with good management practices in place, cover crops can only be afforded in regions where winter precipitation is sufficient for soil water recharge after the depletion of soil water by cover crops in autumn.

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3.2 Article 3: Cover crop water consumption: Analyzing performance of the agrometeorological model for the calculation of actual evapotranspiration (AMBAV) in a container experiment ^{5,6}

Selzer, T.^a and Schubert, S.^a

^a Institute of Plant Nutrition, Research Centre for Biosystems, Land Use and Nutrition (iFZ), Justus Liebig University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany

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⁶ Supplementary Material for this chapter can be found in Appendix C.

Abstract

Due to anthropogenic climate change, cover crop water consumption in winter could potentially increase drought stress for a succeeding crop. Simulation of cover crop evapotranspiration (ET) losses could be a tool for farmers to make smart management decisions. In Germany, the model AMBAV is used by the German Meteorological Service (DWD) to advise farmers in irrigation management. We compared measured ET of phacelia (*Phacelia tanacetifolia*), oilseed radish (*Raphanus sativus* var. *oleiformis*), and white mustard (*Sinapis alba*) cultivated in a container experiment with simulated data and conducted a sensitivity analysis to identify the meteorological and crop-specific parameters which had the strongest effect on simulated ET. In general, measured ET exceeded simulated ET. Different statistical criteria showed that AMBAV performed best for simulation of evaporation from a bare soil surface. Model performance was also strongly influenced by the irrigation regime in the container experiment. However, the sensitivity analysis showed that changes of irrigation hardly had an influence on simulated ET. We recommend optimization of the model for irrigated agriculture. Furthermore, we identified temperature and humidity as the most important meteorological and leaf area index as the most important crop-specific parameter for ET simulations with AMBAV. Since farmers' management decisions depend on the accuracy of ET simulations, they should be aware that even small regional deviations of meteorological conditions and soil cover can significantly affect model predictions.

1 Introduction

Anthropogenic climate change has increased the occurrence of weather extremes such as drought or heavy precipitation events on a global scale. In central Europe and the Mediterranean, an increase of agricultural and ecological drought has been observed since the 1950s (IPCC, 2021). Evapotranspiration (ET) losses – the sum of evaporation (E) and crop transpiration (T) – are projected to increase with rising temperatures due to an increasing atmospheric water demand. This increase in ET will potentially lead to a decrease in soil moisture (Arias et al., 2021). In consequence, the growth-limiting factor water could become even more scarce during the vegetation period of grain and other cash crops. Zhu et al. (2021) found that between 1980 and 2018, water limitation accounted for 32% of all wheat yield

decreases. In their study, high ET corresponded to high yield shock probability across various regions in Europe (Zhu et al., 2021).

The increasingly common practice of cover cropping – the cultivation of crops in otherwise fallow periods to reduce nutrient losses – might intensify the drought stress for a succeeding cash crop as cover crops consume up to 270 mm water during their vegetation period (Selzer and Schubert, accepted). This is a major concern for farmers who have to choose between the benefits of cover cropping and cash crop yields (Mase et al., 2017; Woods et al., 2017; Zinngrebe et al., 2017). As a decision-making tool, farmers oftentimes rely on computer models to predict the evapotranspirative water demand of different cash and cover crops in relation to the changing climatic conditions since the direct measurement of actual ET in the field is highly complex. Many of the models used today are based on the Penman-Monteith equation (Monteith, 1965; Penman, 1948). They include meteorological data as well as crop and soil-specific characteristics and are regularly validated in field experiments. On the basis of model simulations, farmers can be supported in different decision-making processes: Which cash and cover crops are most suitable for cultivation under the given climatic conditions? Does the water supply support these crops? Is additional irrigation necessary? Do the benefits of cover cropping outweigh the additional water losses linked to their growth?

One of those models is AMBAV (Agrarmeteorologisches Modell zur Berechnung der aktuellen Verdunstung). It is a SVAT (soil-vegetation-atmosphere-transfer) model developed by the German Meteorological Service (DWD). The model was updated and adapted several times since its first introduction in 1983 (Löpmeier, 1983) to precisely calculate historic ET and predict ET under various climate scenarios (Braden, 2013). While the focus of these calculations lay on cash crops in the past, the DWD incorporated three of the most important cover crops in Germany – white mustard, oilseed radish, and phacelia – through parametrization in lysimeter experiments in recent years. Based on ET simulations with AMBAV, the DWD advises farmers and uses the model for irrigation necessity prognoses (Friesland and Löpmeier, 2007). Model evaluations have shown that ET simulations with AMBAV show ‘reasonably good accordance’ with measured ET of different cash crops under varying climatic and environmental conditions (Friesland and Löpmeier, 2007). However, except for two validation trials (Helle, 2021; Kollhorst, 2019), model performance of AMBAV for cover crops has not yet been investigated intensively.

Cover crop trials are performed under varying conditions ranging from field experiments to container, minirhizotron, and pot experiments. The controllability of water inputs increases with decreasing scale while the value for farmers increases with increasing scale. Selzer and Schubert (2021) have shown that the container technology established in the Institute of Plant Nutrition of the Justus Liebig University in Giessen can be used to investigate the nutrient use efficiency of various cover crops. The container technology provides a sufficient soil volume for natural root development, crops can be sown at field densities, and the containers can be subjected to natural meteorological conditions while closely monitoring water fluxes such as ET (Hohmann et al., 2016; Hütsch and Schubert, 2021; Selzer and Schubert, 2021). However, since cover crop parametrization for AMBAV took place in lysimeters in field experiments of limited regional variation, it has not been investigated yet whether the simulation of water fluxes with AMBAV can be applied to different cover crops grown under various climatic and soil conditions.

The objective of this study was to investigate whether AMBAV is suitable to accurately simulate cover crop water losses in the form of ET. Simulated ET (ET_{AMBAV}) was compared to measured ET (ET_m) from a cover crop experiment conducted under semi-controlled conditions in container technology in 2020 and 2021 (Selzer and Schubert, accepted). We hypothesized that there were no significant differences between ET_m and ET_{AMBAV} .

Simulations are always dependent on the accuracy of data input. If used for irrigation scheduling, ET_{AMBAV} estimates should be reliable. It has been shown, however, that seemingly small errors of ET estimates can amount to substantial amounts of water (Allen et al., 2011b). Moreover, Kroes et al. (2006) have highlighted that AMBAV is strongly influenced not only by meteorological input data but also by crop and soil characteristics. For simulation purposes, the DWD often uses generalized default data since crop specific measurements of leaf area index (LAI) or crop height rarely exist for individual farms. Our aim was to identify the parameters with the highest impact on ET_{AMBAV} . Since variations in water supply (precipitation and irrigation) were responsible for up to 65% of cover crop ET_m in the container experiment in 2020 (own data), we hypothesized that ET_{AMBAV} is most sensitive to this meteorological parameter. A high LAI is positively correlated with high transpiration losses and negatively correlated with soil evaporation (Allen et al., 1998). Therefore, we hypothesized that ET_{AMBAV} is more sensitive to changes in the crop specific parameter LAI than to changes in crop height.

2 Material and Methods

2.1 Cover crop cultivation

Cover crops were cultivated in container technology under semi-controlled conditions at the experimental station of the Institute of Plant Nutrition (PN), Justus Liebig University from August 24 till November 6 2020 (50.5981°N, 8.6671°E). The three cover crops relevant for this study are white mustard (*Sinapis alba* L. cv. Gisilba), oilseed radish (*Raphanus sativus* L. var. *oleiformis* Pers. cv. Bento), and phacelia (*Phacelia tanacetifolia* Benth. cv. Amerigo) sown at plant densities of 270, 252, and 525 plants m⁻², respectively. Prior to sowing, soil moisture was adjusted to 50% of its maximum water-holding capacity (WHC). A detailed description of cultivation and nutrient supply to the cover crops can be derived from Selzer and Schubert (2021). Soil characteristics are shown in Table 1. A bare fallow was included as a control treatment to monitor evaporation from a bare soil surface. Each treatment had seven replicates, three of which were used for intermediate harvests (2020: 23, 38, and 66 days after sowing (DAS); 2021: 23, 41, and 63 DAS) to monitor biomass production for precise ET measurements. The four remaining replicates were harvested after the first frost event 74 and 63 DAS in 2020 and 2021, respectively.

Table 1 Soil characteristics for cover crop cultivation in 2020 and 2021.

	2020	2021
Sand (%)	44.3	52.9
Silt (%)	34.6	28.2
Clay (%)	21.2	18.9
Organic matter (%)	≤ 2	≤ 2
pH _{CaCl2}	7.5	7.4
N _{min} (mg kg ⁻¹)	14.5	2.1
CAL-P (mg kg ⁻¹)	8.3	10.3
CAL-K (mg kg ⁻¹)	43.5	66.5

2.1.1 Crop development

During the vegetation period, the phenological growth stages of the three cover crops were closely monitored. Plant height and leaf area index (ACCUPAR LP-80 PAR/LAI Ceptometer, METER Group, USA) were measured weekly. Since the length of the LAI sensor exceeded the width of the containers, LAI had to be corrected with the transformation factor 2.14 (Selzer and Schubert, accepted).

At final harvest, shoot fresh and dry (105°C) weights were determined for each container (0.16 m²). Results were extrapolated to 1 m². In 2020, maximum rooting depth was determined by placing an auger (∅ 7.6 cm) between the rows of cover crops to sample core soils in 6 cm-increments. The depth of the last soil sample that included roots was recorded as the maximum rooting depth. Maximum rooting depth was not measured separately in 2021, since roots of all three cover crops equaled depth of the container in 2020.

2.1.2 Meteorological conditions

Meteorological conditions were monitored throughout the vegetation period. Wind speed was measured using the WSW G0010 wind sensor (F&C GmbH, Germany) in 2.67 m height in combination with a data logger (DK312 MultiLog rugged Plus, Driesen+Kern GmbH, Germany) at 60 s intervals. The same frequency was used to record temperature and relative humidity (DK320 HumiLog Plus, Driesen+Kern GmbH, Germany). Hourly rainfall data were derived from a tipping bucket at the nearby experimental station 'Weilburger Grenze' (WG) (50.6017°N, 8.6536°E). Data on relative short wave and long wave radiation as well as sunshine duration were provided by the meteorological station 'Giessen-Wettenberg' (GW) (50.6°N, 8.65°E) run by the DWD.

In 2020, with a total of 88 mm, precipitation during the 74-day cultivation period was lower than during the same period in the previous ten years in Giessen (2010-2019: 114 ± 12 mm) (Figure 1a). With 13.3°C the average temperature was close to the mean for this period between 2010 and 2019 (12.3 ± 0.3°C). In 2021, precipitation in the 63-day cultivation period only amounted to 35 mm and the average temperature was similar to 2020 (13.1°C) (Figure 1b).

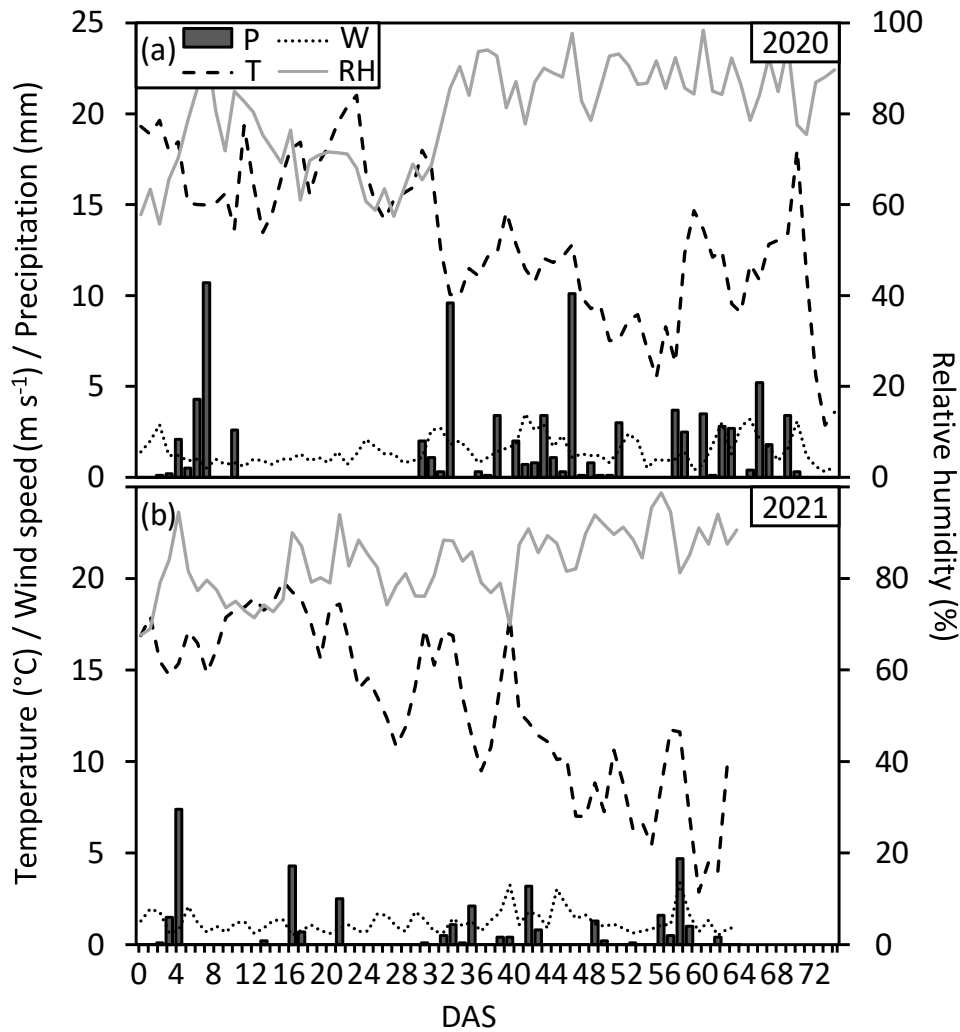


Figure 1 Meteorological conditions during the vegetation periods (a) 2020 (until 74 DAS) and (b) 2021 (until 63 DAS). P = daily precipitation sum, T = daily mean temperature, W = daily mean wind speed, RH = daily mean relative humidity.

2.1.3 Measured evapotranspiration (ET_m)

Measured evapotranspiration (ET_m) of cover crops in the container experiment was quantified gravimetrically by weighing the containers twice a week as described by Selzer and Schubert (2021). A drainage layer at the bottom of each container allowed for the collection and quantification of leachate. ET_m was determined using Equation 1 (Selzer and Schubert, accepted).

$$ET_{m(ij)} = (C_i - L_{hi} + P_{ij} + I_{ij} - FW_{CC} - C_j) \cdot 6.25 \quad (1)$$

with $ET_{m(ij)}$ = measured evapotranspiration between time i and time j in $L\ m^{-2}$, C_i = weight of container at time i in kg, L_{hi} = leachate accumulation between time h and time i , P = precipitation between time i and time j in $L\ container^{-1}$, I = irrigation between time i and time j in $L\ container^{-1}$, FW_{CC} = cover crop shoot fresh weight in kg, C_j = weight of container at time j

in kg, and 6.25 = conversion factor from an individual container (surface area = 0.16 m²) to 1 m².

2.2 Simulated evapotranspiration (ET_{AMBAV})

2.2.1 Data requirement for AMBAV

Evapotranspiration for the vegetation period was simulated using the graphical user interface AMBAV Global GUI (V0.9509). Data requirements and data availability for simulation of potential evapotranspiration with AMBAV can be derived from Table 2. The required measurement frequency for meteorological data is 1 h⁻¹. Due to technical difficulties with the above-mentioned wind sensor, wind speed data from WG were used for the simulations (measuring height = 10 m).

In 2020, maximum leaf area index (LAI_{max}) 4.33, 5.79, and 5.7 m² m⁻² for white mustard, oilseed radish, and phacelia, respectively. Maximum crop height (h_{max}) in that year was 1.24, 0.69, and 0.64 m for white mustard, oilseed radish, and phacelia, respectively. With LAI_{max} of 3.81, 5.56, and 4.71 m² m⁻² and h_{max} of 1.23, 0.45, and 0.52 m white mustard, oilseed radish and phacelia were a bit shorter and had slightly lower LAI_{max} in 2021 than in 2020. Since root depth was only measured after the termination of the growth period, data for the parameter 'days until maximum root depth reached' were not available (Table 2). The default value in AMBAV assumes maximum rooting depth to be reached at crop maturity (DWD, 2021). For 2021, maximum root depth was not measured separately since roots reached the bottom of the containers in all treatments in 2020. Therefore, maximum root depth was set at 0.7 m which is equivalent to the soil depth in the containers.

Irrigation was simulated using the 'drip irrigation' option in AMBAV which is defined as the addition of water 'which only wets the soil' (DWD, 2021). Time of irrigation was set to 8:00-9:00 am which resembles the timespan of irrigation in the experiment.

Table 2 AMBAV input data (DWD, 2020)(DWD, 2020). Availability of data is indicated: “x” = data available; “-” = data not available. Location of meteorological data measuring point indicated in brackets: PN = Plant Nutrition (50.5981°N, 8.6671°E), WG = Weilburger Grenze (50.6017°N, 8.6536°E), GW = Giessen-Wettenberg (50.6°N, 8.65°E).

METEOROLOGICAL DATA		Availability of data
Air temperature 2 m above ground surface (°C)		x (PN)
Precipitation 2 m above ground surface (mm)		x (WG)
Relative humidity 2 m above ground surface (%)		x (PN)
Wind speed in 10 m measuring height (m s ⁻¹)		x (WG)
Downward short-wave radiation (W m ⁻²)		x (GW)
Downward long-wave radiation (W m ⁻²)		x (GW)
CROP-SPECIFIC DATA		
Shoot	Maximum LAI [†] (m ² m ⁻²)	x
	Maximum crop height (m)	x
Roots	Maximum root depth (m)	x
	Root expansion shape factor	x
	Days until maximum root depth was reached	-
Phenology	Crop-specific growth stages	x
Daily irrigation (L m ⁻²)		x
SOIL DATA		
Clay (%)		x
Silt (%)		x
Bulk density (g cm ⁻³)		x
Water potential at wilting point (m ³ m ⁻³)		x

[†] LAI = leaf area index

2.2.2 Comparison of measured and simulated ET

The performance of simulated evapotranspiration (ET_{AMBAV}) in comparison to the measured data was evaluated using the statistical criteria (a) coefficient of determination (R², Equation 2), (b) Nash-Sutcliffe efficiency (NSE, Equation 3), (c) root mean square error (RMSE, Equation 4), and (d) mean absolute error (MAE, Equation 5).

$$R^2 = \left[\frac{\sum_{t=1}^T (ET_m^t - \overline{ET}_m) (ET_{AMBAV}^t - \overline{ET}_{AMBAV})}{\sqrt{\sum_{t=1}^T (ET_m^t - \overline{ET}_m)^2} \sqrt{\sum_{t=1}^T (ET_{AMBAV}^t - \overline{ET}_{AMBAV})^2}} \right]^2 \quad (2)$$

$$NSE = 1 - \frac{\sum_{t=1}^T (ET_m^t - ET_{AMBAV}^t)^2}{\sum_{t=1}^T (ET_m^t - \overline{ET}_m)^2} \quad (3)$$

$$RMSE = \sqrt{\frac{\sum_{t=1}^T (ET_{AMBAV}^t - ET_m^t)^2}{N}} \quad (4)$$

$$MAE = N^{-1} \sum_{t=1}^N |ET_m^t - ET_{AMBAV}^t| \quad (5)$$

With ET_m = measured evapotranspiration at time t in mm, \overline{ET}_m = average measured evapotranspiration in mm, ET_{AMBAV} = simulated evapotranspiration at time t in mm, \overline{ET}_{AMBAV} = average simulated evapotranspiration in mm, t = timesteps between ET measurements, and N = number of observations.

The coefficient of determination (R^2 , $0 \leq R^2 \leq 1$) shows which proportion of ET_m can be described by ET_{AMBAV} . NSE was described by Nash and Sutcliffe (1970) and is also known as the coefficient of efficiency. Values can range from $-\infty < NSE \leq 1$ and is an indicator of how well a model can predict peaks. Negative values of NSE indicate that \overline{ET}_m is a better predictor than the model (Legates and McCabe, 1999). Since both R^2 and NSE are dimensionless and sensitive to outliers, calculations of RMSE and MAE were included which estimate the difference of the simulated and the measured values in their respective units. RMSE ($0 \leq RMSE < \infty$) and MAE ($0 \leq MAE < \infty$) differ in how they weigh errors: Errors with larger absolute values are given more weight than errors with small absolute values by RMSE while the MAE does not make that distinction. All errors are treated as equal by MAE (Chai and Draxler, 2014).

2.2.3 Sensitivity analysis

Sensitivity analysis of AMBAV was performed similar to Bormann et al. (2007) by calculating relative changes of simulated evapotranspiration (ET_{AMBAV}) where one meteorological parameter was changed in the range of $i = -50\%$ to $i = +50\%$ of its original value ($ET_{AMBAV,0 \pm i}$) in 10% increments relative to simulated evapotranspiration using the original, hourly measured meteorological data from 2020 and 2021, respectively. The analysis was performed for the parameters (1) temperature (max. = 40°C (Helle, 2021)), (2) wind speed, (3)

precipitation, (4) irrigation, and (5) relative humidity (min. = 20%, max. = 100%). The same analysis was performed for the crop-specific parameters maximum leaf area index and maximum crop height.

2.3 Statistical analysis

Simulated and measured ET were compared using a Student's t-test for each measuring date. Irrigation was compared with a one-way ANOVA followed by a post-hoc FDR-test. Heteroscedastic data was compared using the White-adjusted one-way ANOVA and which was also followed by a post-hoc FDR-test. All statistical analyses were performed in RStudio (R version 4.1.0). The significance level for the tests was chosen at $p < 0.05$. Mean values ($n = 4$) and the standard error (SE) were calculated with Microsoft Office Excel (2019). In the context of this study, ET is defined as a water loss and therefore depicted with negative values.

3 Results

3.1 Comparison of measured and simulated ET

3.1.1 Vegetation period 2020

In general, simulated evapotranspiration losses ($ET_{AMB\Delta V}$) were lower than measured evapotranspiration losses (ET_m) in 2020. From 16 DAS onwards, this difference was significant for phacelia and white mustard (Figure 2). Differences between $ET_{AMB\Delta V}$ and ET_m were especially pronounced between 21 and 38 DAS for the three cover crop treatments (Figure 2 b-d) and from 59 DAS onwards for white mustard and phacelia (Figure 2 b, d). While the period from 21-38 DAS was characterized by low precipitation ($\Sigma P = 2$ mm), high temperatures, relatively high maximum wind speeds, and low relative humidity (Figure 1a) which led to the high measured ET losses in all treatments, the period from 59 DAS onwards was characterized by a mixture of low ($T_{min} = -2.6^\circ\text{C}$, 73 DAS) and high ($T_{max} = 23.2^\circ\text{C}$, 70 DAS) temperatures, high wind speeds, and high relative humidity (Figure 1b).

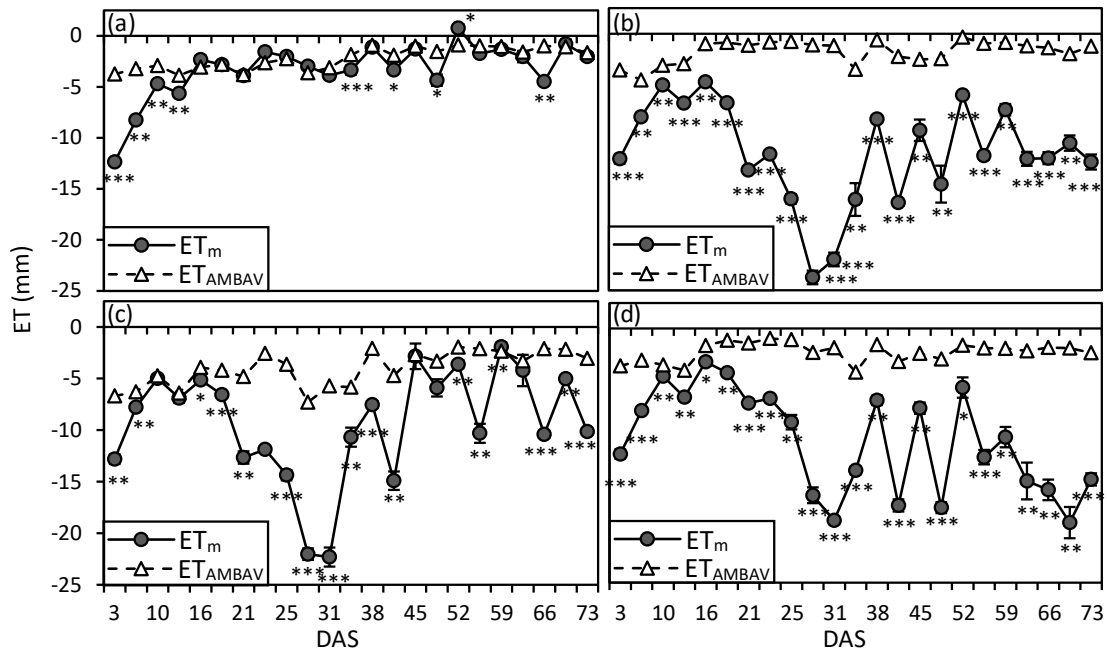


Figure 2 Comparison of simulated (ET_{AMBAV} , Δ) and measured (ET_m , \bullet) evapotranspiration of (a) a bare fallow, (b) white mustard, (c) oilseed radish, and (d) phacelia throughout the vegetation period from August 24, 2020 until harvest at 74 DAS. Comparison of ET_m and ET_{AMBAV} with a two-sided Student's *t*-test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Mean values ($n = 4$) \pm SE.

Since water supply was adjusted according to the water demand of the cover crops, high ET_m coincided with high water supply in the form of irrigation (Figure 3). ET_{AMBAV} most accurately resembled ET_m of all treatments in times of low ET_m (Figure 2) and consequently low to none irrigation necessity (Figure 3).

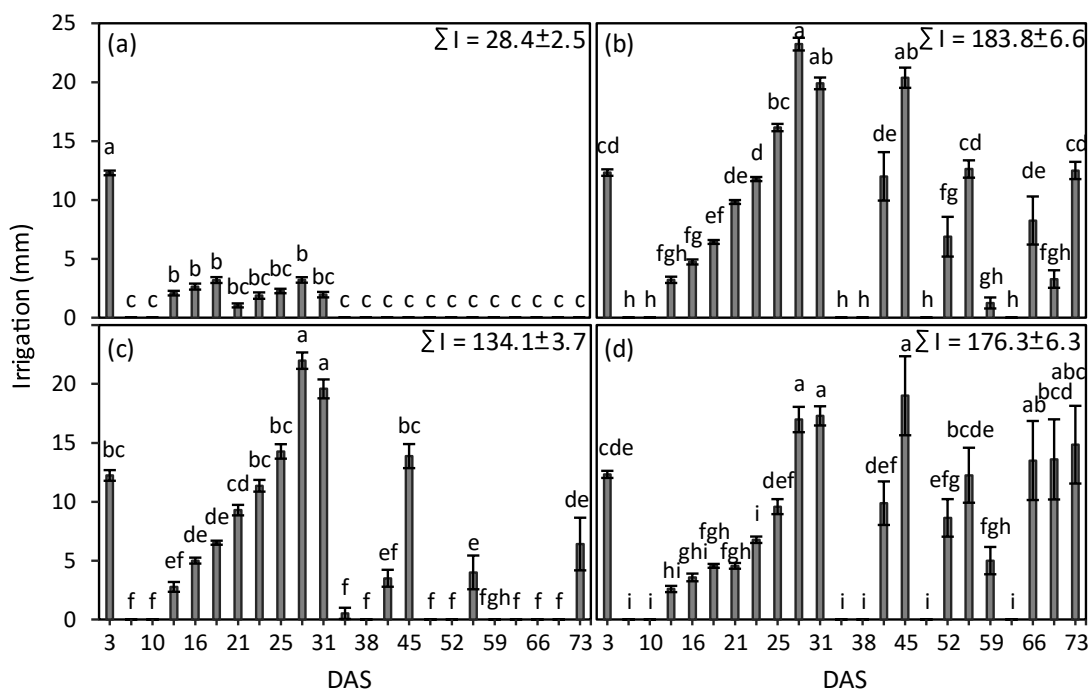


Figure 3 Irrigation to (a) a bare fallow, (b) white mustard, (c) oilseed radish, and (d) phacelia during the vegetation period 2020 until harvest at 74 DAS. One-way ANOVA and comparison of means adjusted according to FDR for irrigation. Different letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$) \pm SE.

In 2020, AMBAV performed best in the simulation of evaporation from a bare soil surface as indicated in Figure 2 a and in Table 3. Total ET_{AMBAV} was only 25 mm lower than ET_m while ET_m and ET_{AMBAV} in the cover crop treatments differed by 123 (oilseed radish) to 228 mm (white mustard). Out of the three cover crops, model performance of AMBAV was poorest for white mustard and phacelia, indicated by low R^2 and NSE, high RMSE and MAE, and a high discrepancy between $\sum ET_m$ and $\sum ET_{AMBAV}$ (white mustard: 228; phacelia: 202.3 mm) (Table 3). The model performed better for oilseed radish (higher NSE, lower RMSE and MAE, and less discrepancy was observed between $\sum ET_m$ and $\sum ET_{AMBAV}$). The bare fallow was the only treatment with $RMSE < MAE$. Based on the statistical criteria in Table 3, performance of AMBAV in 2020 followed the order: Bare fallow > oilseed radish > phacelia > white mustard.

Table 3 Comparison of simulated (ET_{AMBAV}) and measured (ET_m) evapotranspiration of three cover crops and a bare fallow on the basis of different statistical criteria. $\sum ET$ = cumulative evapotranspiration, R^2 = coefficient of determination, NSE = Nash-Sutcliffe efficiency, RMSE = root mean square error, MAE = mean absolute error.

	Bare fallow	White mustard	Oilseed radish	Phacelia
2020				
$\sum ET_m$ (mm)	-75.5	-268.0	-215.0	-256.1
$\sum ET_{AMBAV}$ (mm)	-50.5	-40.0	-92.0	-53.8
R^2	0.39	0.00	0.28	0.04
NSE	0.2	-4.2	-0.8	-3.1
RMSE (mm)	1.3	11.0	6.5	9.8
MAE (mm)	1.5	9.9	5.4	8.8
2021				
$\sum ET_m$ (mm)	-40.5	-197.5	-148.3	-150.5
$\sum ET_{AMBAV}$ (mm)	-36.5	-32.7	-82.3	-45.3
R^2	0.59	0.11	0.44	0.02
NSE	0.6	-3.3	-0.4	-3.9
RMSE (mm)	0.7	10.6	4.8	6.4
MAE (mm)	1.2	9.2	4.4	6.0

3.1.2 Vegetation period 2021

Water supply to the cover crops was reduced to keep soil moisture at 45% of its water-holding capacity in 2021. Consequently, total ET in 2021 was lower than in 2020. Furthermore, the reduction of soil moisture improved the performance of AMBAV in comparison to the previous vegetation period. ET_{AMBAV} of the bare fallow showed a close resemblance of ET_m (Figure 4 a). Overall, discrepancies between ET_{AMBAV} and ET_m of the cover crops were not as severe as in 2020. Similar to 2020, discrepancies became more pronounced 20-23 DAS (Figure 4 b-d). The maximum difference between ET_{AMBAV} and ET_m amounted to 18.8, 10.6, and 9.3 mm for white mustard, phacelia, and oilseed radish 34 DAS, respectively.

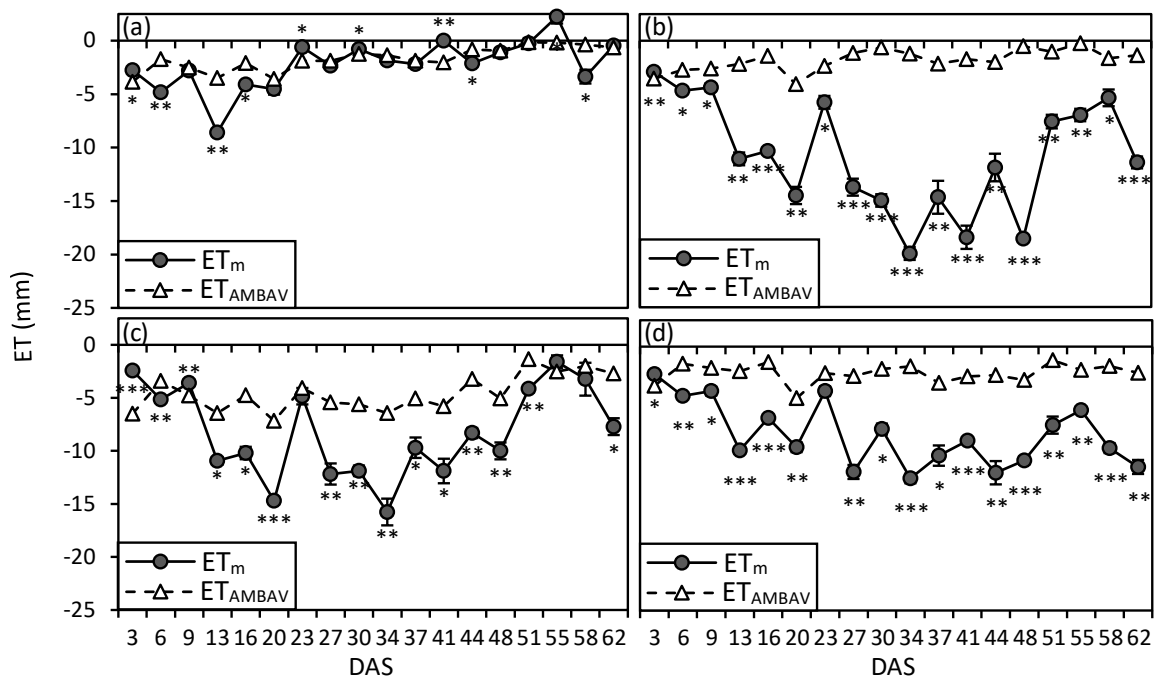


Figure 4 Comparison of simulated (ET_{AMBAV} , Δ) and measured (ET_m , \bullet) of (a) a bare fallow, (b) white mustard, (c) oilseed radish, and (d) phacelia throughout the vegetation period from August 25, 2021 until harvest at 63 DAS. Comparison of ET_m and ET_{AMBAV} with a two-sided Student's *t*-test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Mean values ($n = 4$) \pm SE.

With 35.2 mm total precipitation during the vegetation period was 60% less in 2021 than in 2020 (Figure 1). However, the amount of irrigation water needed was < 80% of irrigation in 2020 (Figure 3, Figure 5) due to the reduction of soil moisture.

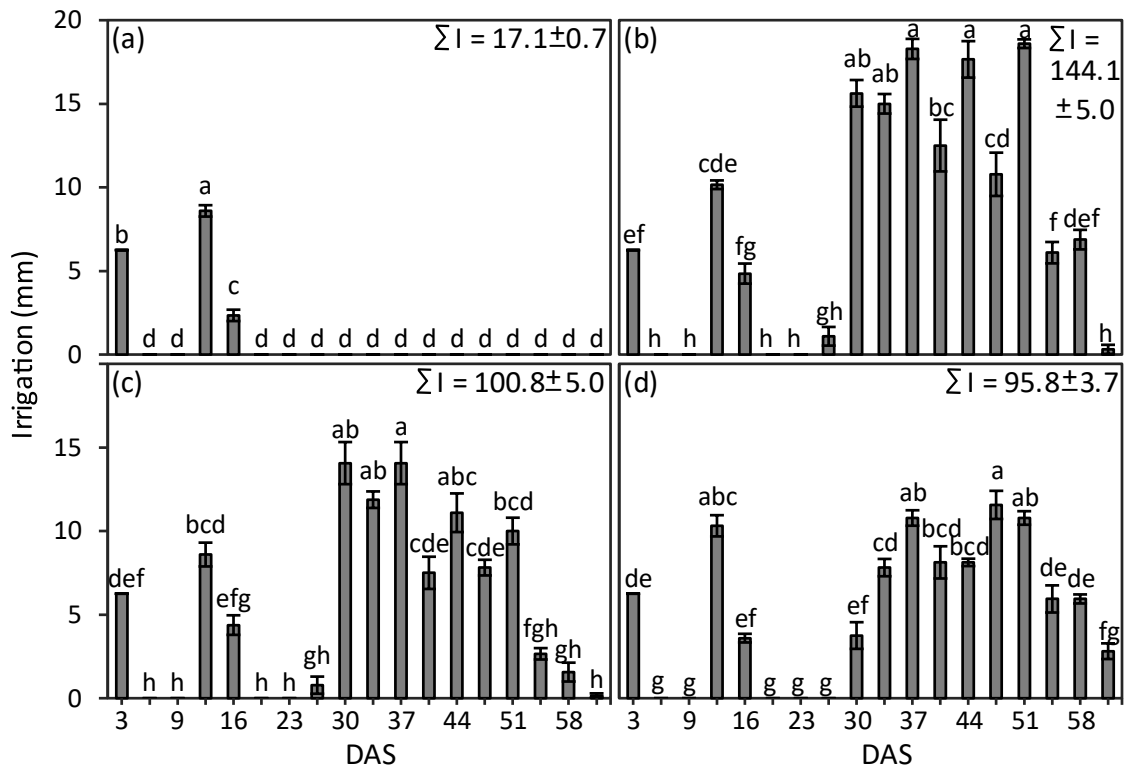


Figure 5 Irrigation to (a) a bare fallow, (b) white mustard, (c) oilseed radish, and (d) phacelia during the vegetation period 2021 until harvest at 63 DAS. One-way ANOVA and comparison of means adjusted according to FDR for irrigation. Different letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$) \pm SE.

The better performance of AMBAV with data from 2021 was also reflected in the statistical indicators which describe model performance (Table 3). With a difference of just 4 mm, model performance for the bare fallow was very good. This impression was confirmed by the high R^2 , high NSE, and low RMSE and MAE (Table 3). For the cover crop treatments, performance of AMBAV was best for oilseed radish ($R^2 = 0.44$). For white mustard, AMBAV model performance was better in 2021 than in 2020. The most pronounced improvement was the 11% increase of R^2 which was coupled with slight improvements of the other statistical criteria (Table 3). There was also a slight improvement in the accuracy for phacelia: In 2020, $\sum ET_{AMBAV}$ was 79% lower than $\sum ET_m$. In 2021, $\sum ET_{AMBAV}$ was 70% of $\sum ET_m$. The errors decreased from RMSE = 9.8 and MAE = 8.8 in 2020 to RMSE = 6.4 and MAE = 6.0 in 2021. However, R^2 and NSE for phacelia decreased, which indicates that almost no variability of ET_m was detected by ET_{AMBAV} and it failed to precisely predict peaks of ET_m .

Based on RMSE and MAE, performance of AMBAV in 2021 followed the same order as in 2020. However, based on R^2 and NSE, performance of AMBAV in 2021 followed the order: Bare fallow > oilseed radish > white mustard > phacelia.

3.2 Sensitivity analysis

The sensitivity analysis (Figure 6) showed for all treatments that changes in temperature and relative humidity had the greatest influence on $\sum ET_{AMB\Delta V}$. For the meteorological data from 2020 (Figure 1 a), a 50% reduction of mean daily temperature led to an increase of $\sum ET_{AMB\Delta V}$ by 61% and 27% for phacelia and oilseed radish, respectively, while $\sum ET_{AMB\Delta V}$ of white mustard was unaffected by a temperature decrease and simulated evaporation of the bare fallow even decreased by 13% (Figure 6 a). With increasing temperature $\sum ET_{AMB\Delta V}$ decreased in all treatments by up to 52% (oilseed radish) (Figure 6 a). Similar results were found for the vegetation period 2021 for oilseed radish (Figure 6 b). However, $\sum ET_{AMB\Delta V}$ of phacelia was less sensitive to changes in temperature in 2021 compared to 2020.

The influence of relative humidity on $\sum ET_{AMB\Delta V}$ was even more pronounced than that of changes in temperature (Figure 6 c, d). In 2020, a change of relative humidity by -50% and +50% resulted in a change of $\sum ET_{AMB\Delta V}$ by +76% (oilseed radish) to +119% (bare fallow) and -44% (oilseed radish) to -68% (bare fallow), respectively (Figure 6 c). The analysis for the vegetation period 2021 supported this highly sensitive reaction of $\sum ET_{AMB\Delta V}$ to changes in relative humidity (Figure 6 d).

The model was less sensitive to changes in wind speed (Figure 6 e, f) and precipitation (Figure 6 g, h), although a close correlation between water supply and ET_m was shown (Figure 2, 3). Due to higher total water availability in 2020, when soil moisture was kept at 50% WHC, increasing precipitation resulted in a < 5% increase of $\sum ET_{AMB\Delta V}$ (Figure 6 g). In comparison, changes in precipitation had a more pronounced effect on $\sum ET_{AMB\Delta V}$ in 2021 when soil moisture and total precipitation were lower (Figure 6 h). The effect of decreasing precipitation was most significant for white mustard in that year while $\sum ET_{AMB\Delta V}$ of oilseed radish was hardly affected by these changes at all.

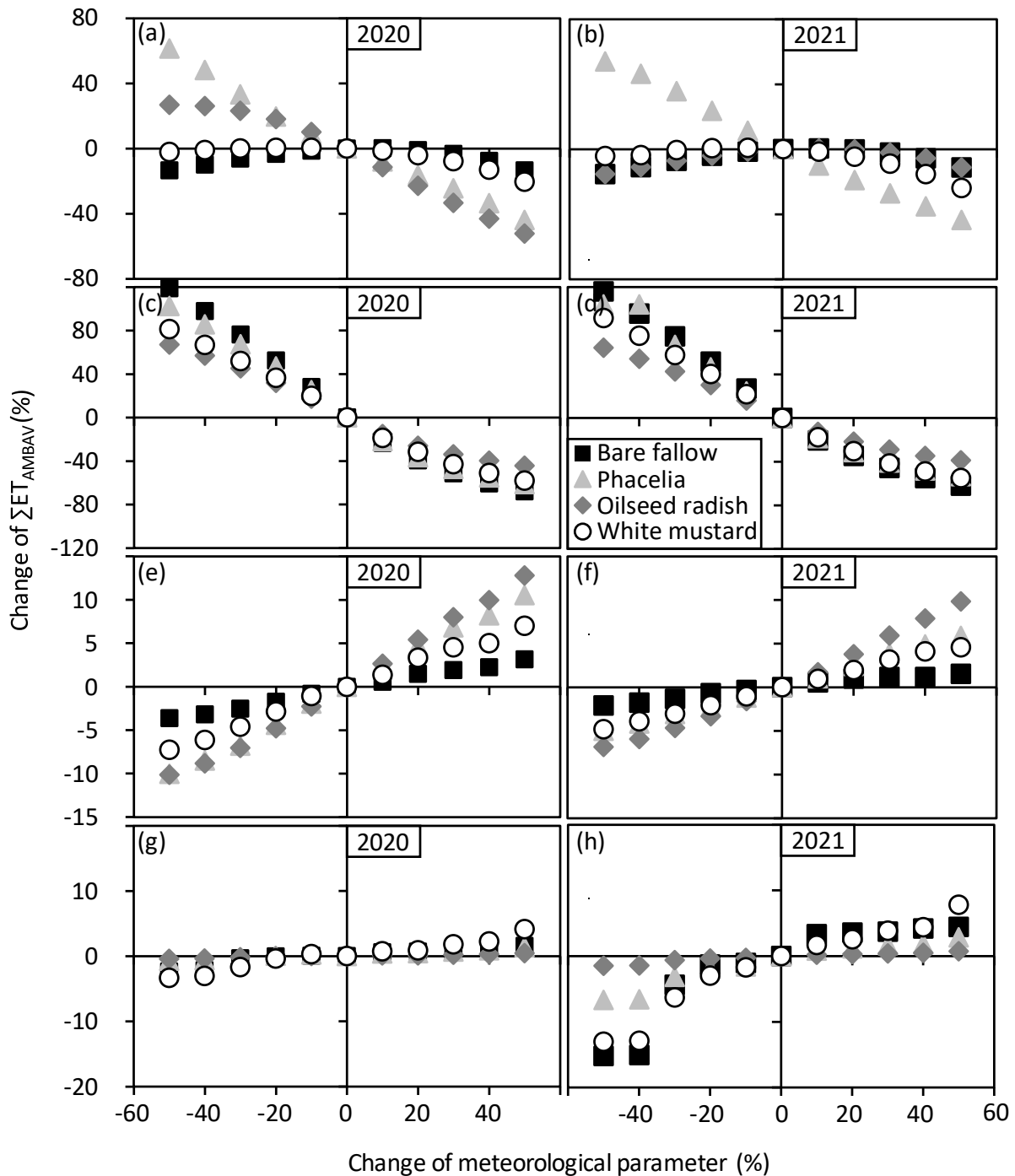


Figure 6 Sensitivity analysis for AMBAV simulation of cumulative evapotranspiration (ΣET_{AMBAV}) based on meteorological data (Figure 5) at the experimental station of the Institute of Plant Nutrition in Giessen ($50^{\circ}35'53.30''N$, $8^{\circ}40'1.56''E$) for the vegetation periods 2020 and 2021. Influence of percentage change ($\pm 50\%$) of measured temperature (a, b), wind speed (c, d), relative humidity (e, f), and precipitation (g, h) on ΣET_{AMBAV} of a bare fallow (■), phacelia (▲), oilseed radish (◆), and white mustard (○).

Out of all the parameters tested, the model was least sensitive for changes in irrigation: An increase in irrigation of up to 50% only resulted in a $< 1\%$ increase of ΣET_{AMBAV} in both years (Figure 7).

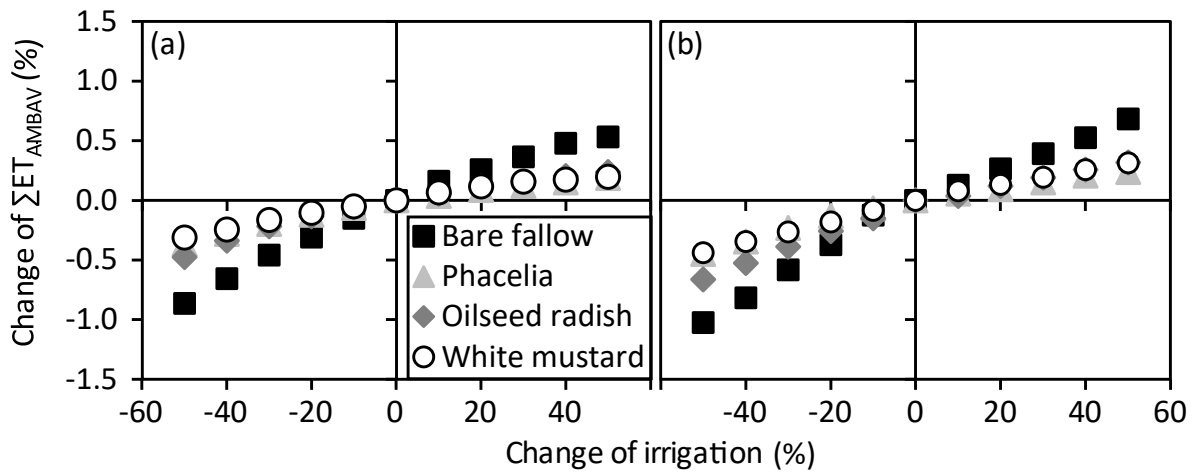


Figure 7 Sensitivity analysis for AMBAV simulation of cumulative evapotranspiration (ΣET_{AMBAV}) based on irrigation during the vegetation periods 2020 and 2021. Influence of $\pm 50\%$ change of irrigation (min. = 0 mm) of a bare fallow (■), phacelia (▲), oilseed radish (◆), and white mustard (○) on ΣET_{AMBAV} of the same treatments in (a) 2020 and (b) 2021.

Out of the two plant-specific parameters tested in this study, changes of maximum leaf area index (LAI_{max}) had the highest influence on ΣET_{AMBAV} for phacelia and oilseed radish while ΣET_{AMBAV} response of white mustard was somewhat inconsistent to changes of LAI_{max} (Figure 8). ΣET_{AMBAV} of oilseed radish decreased by 12% with a 50% reduction of LAI_{max} and increased by 2% with a 50% increase in LAI in 2020 (Figure 8 a). ΣET_{AMBAV} of phacelia responded similarly to changes of LAI_{max} in 2020 (Figure 8 a) while the changes were less pronounced in 2021 (Figure 8 c). Changes of maximum plant height (h_{max}) resulted in changes of $\Sigma ET_{AMBAV} < \pm 5\%$ for all three crops in 2020 (Figure 8 b) and 2021 (Figure 8 d). Consistent with results for changes of LAI_{max} , ΣET_{AMBAV} of oilseed radish and phacelia was more sensitive to changes of h_{max} than ΣET_{AMBAV} of white mustard.

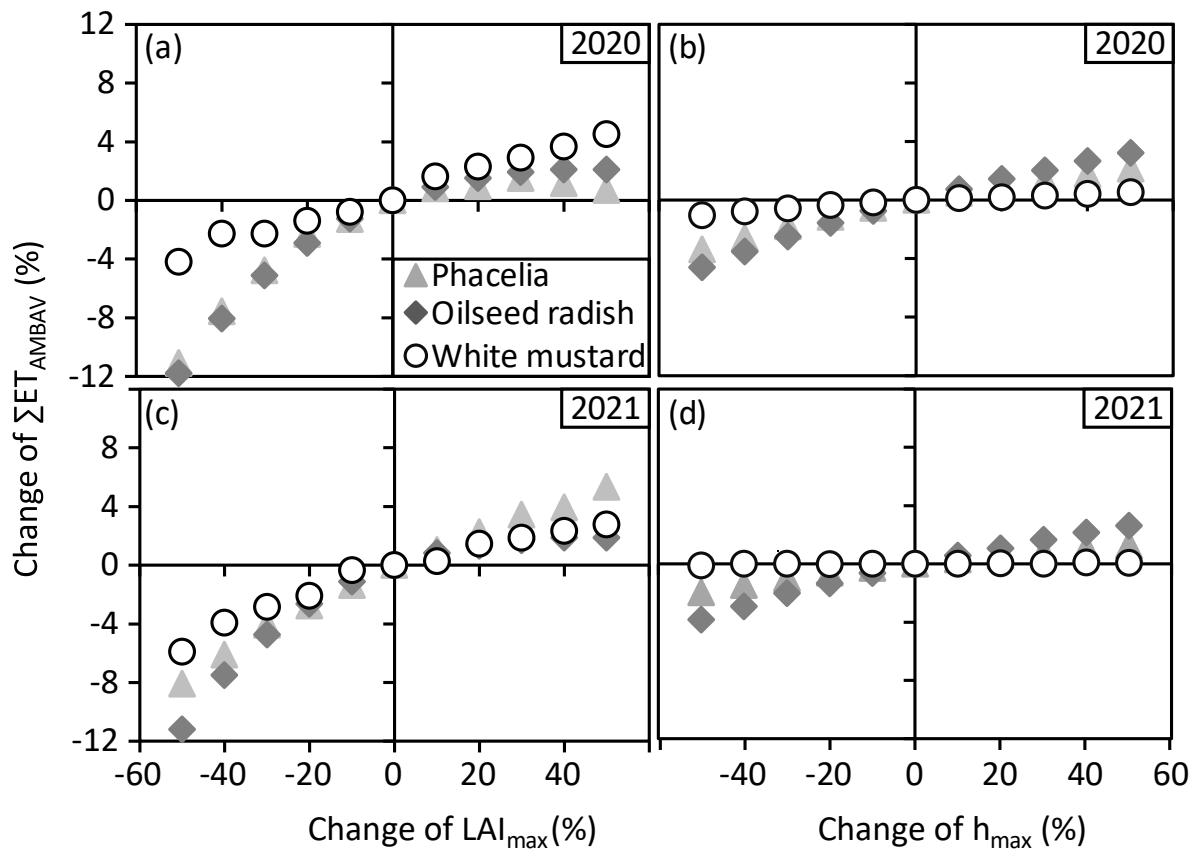


Figure 8 Sensitivity analysis for AMBAV simulation of cumulative evapotranspiration (ΣET_{AMBAV}) based on plant-specific parameters from the vegetation periods 2020 and 2021. Change of ΣET_{AMBAV} in response to $\pm 50\%$ change of maximum leaf area index (LAI_{max}) (a, c) and maximum crop height (h_{max}) (b, d) of phacelia (\blacktriangle), oilseed radish (\blacklozenge), and white mustard (\circ).

4 Discussion

4.1 Methodology as main source for discrepancies between ET_m and ET_{AMBAV} ?

The results presented above clearly show that ET_m exceeded ET_{AMBAV} for all three cover crops (Figure 2, 4), indicating that AMBAV is not suitable to simulate ET of cover crops grown in container technology. The magnitude of the discrepancy is surprisingly high considering that the model was parametrized especially for these crops. Hence, we must assume that the discrepancy is likely to be a result of differences between the experimental setup of the container trial and the field lysimeter experiment which the DWD used for the parametrization of AMBAV. We chose to conduct our experiments in containers instead of a field trial to avoid typical problems associated with other forms of ET measurements, *e.g.*, spatial and vertical variability of soil properties, unquantifiable deep percolation losses, and other factors affecting the accuracy of ET measurements which are explained extensively by Allen et al. (2011a).

Here, we want to illustrate a few of the methodological differences that are likely to have impacted ET_m and ET_{AMBAV} :

(1) The cover crops were manually irrigated with a watering can twice a week to keep soil moisture at 50% WHC in 2020 and 45% WHC in 2021. The option 'irrigation' in AMBAV only provides the choice between 'drip' or 'sprinkler' irrigation. By choosing 'drip' irrigation the model calculated ET_{AMBAV} under the assumption that the irrigation water was supplied evenly over the specified time range and not instantaneous, as was the case in the container experiment. Thus, the actual water content of the topsoil might have differed from the simulated water content. This would also explain why, with the exception of phacelia, model performance was generally better in 2021 (Table 3) when the amount of irrigation was reduced to keep soil moisture at 45% WHC.

(2) The model simulates soil water content (SWC) at a given soil bulk density and soil type (Table 1) and uses these data to calculate ET. However, the confinement of the soil in the containers might have inhibited the natural flow of water in the soil leading to a higher SWC than under field conditions, where water can 'escape' not only vertically but also horizontally. In the container experiment, high SWC in the topsoil could have resulted in increased ET_m while the model calculated ET_{AMBAV} for field conditions.

(3) The containers were set up closely together to minimize wind exposure. However, since containers were moved regularly and the bare fallow containers were mixed with the containers for cover crop cultivation, a closed soil cover with minimum wind exposure similar to field conditions could not be achieved. It is likely that wind had a stronger influence on ET_m in the container experiment than shown in Figure 6 e, f for ET_{AMBAV} . The influence of wind on ET is more pronounced under dry air conditions than under humid conditions (Allen et al., 1998) which relates well to the high ET_m losses during the first 38 DAS in 2020 (Figure 3) when humidity was low and temperature was relatively high, as well as to lower ET_m losses from 52 DAS onwards when humidity was higher (Figure 1).

(4) Another aspect that needs to be considered are differences in soil temperature. Daily soil temperature fluctuations are more pronounced when using the container technology than under field conditions (Figure S1). Deviating from field conditions, the soil in the containers is subjected to the atmospheric temperature and solar radiation. In the field, the surrounding soil acts as a buffer which regulates soil temperature. Since this buffer is missing in container

experiments, the soil is heating and cooling more quickly than under field conditions. In addition, the dark green color of the containers can cause an increased absorption of solar radiation thereby increasing the already existing temperature differences. Soil temperature is an important factor for evaporation. Quick heating of the soil promotes soil evaporation (Allen et al., 1998) and could have contributed to higher ET_m losses that were not recognized by the model.

For the identification of how significant the methodological error was, the best-performing treatment needs to be considered. Based on the statistical criteria, AMBAV performed best in the simulation of evaporation from a bare soil surface (Table 3) which means that only a discrepancy of 25 mm and 4.0 mm can be explained by the above-mentioned methodological differences (1) to (4) in 2020 and 2021, respectively (Table 3). The vast majority of the error, however, was caused by crop-specific parameters which determine transpiration losses. These parameters (LAI, height, rooting depth) were closely monitored.

The experimental setup only allowed a maximum rooting depth of approximately 70 cm. This does not represent all field conditions where oilseed radish has been shown to reach rooting depths of > 2 m (Thorup-Kristensen, 2006). However, the sensitivity analysis showed that changes of rooting depth did not have a significant influence on ET_{AMBAV} (max. $\pm 0.01\%$ change of ET_{AMBAV} with $\pm 50\%$ change of rooting depth) which indicates that rooting depth is negligible for ET simulations with AMBAV (data not shown).

Since LAI is the main variable in computer models for the calculation of photosynthetic activity and ET (Weiss et al., 2004), we might assume that LAI measurements in this study conducted with the ACCUPAR LP-80 PAR/LAI Ceptometer, henceforth abbreviated 'LP 80', were not accurate enough for the model. Adeboye et al. (2019) have shown that LAI measurements with the LP 80 overestimate LAI in the initial growth phase of soybeans and once LAI reaches $\geq 1.11 \text{ m}^2 \text{ m}^{-2}$, the ceptometer underestimates LAI. Although a very good correlation ($R^2 \geq 0.85$) was found between LAI measured with the LP 80 and measurements with the central leaflet width method, the underestimation in the mid-season amounted to a difference of up to approximately $2 \text{ m}^2 \text{ m}^{-2}$ (Adeboye et al., 2019). Additionally, Pokovai and Fodor (2019) have shown that the accuracy of LAI measurements with LP 80 is highly sensitive to light conditions. They conclude that inadequate light conditions of plant-available radiation ($PAR < 1700 \mu\text{mol m}^{-2} \text{ s}^{-1}$, which are common during the winter cover crop growing season in Germany, lead to an underestimation of LAI. Especially towards the end of the vegetation period of the

container experiment PAR even fell below $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the measurements which were taken at the same time of day on a weekly basis. It is likely therefore, that LAI_{max} , which was used for calculation of ET_{AMBAV} , was underestimated and caused $\text{ET}_{\text{AMBAV}} < \text{ET}_m$ in this study. Correction of LAI measurements on overshadowed days should be considered in future experiments.

4.2 Arguments against methodology as sole reason for discrepancies between ET_m and ET_{AMBAV}

Although significant differences between the container technology and field experiments are apparent, based on the results presented above we cannot assume that these were the sole reasons for the strong discrepancies between ET_m and ET_{AMBAV} . The following arguments suggest that the model itself needs further optimization for a reliable application for ET simulation of cover crops:

(1) It seems that the water input through irrigation is not recognized by the model. Although significant amounts of water were added to the soil in times of high evaporative and transpirative water losses, ET_{AMBAV} did not peak after this additional water input. Changes in the amount of irrigation rarely had an effect on ET_{AMBAV} (Figure 7). This unsensitivity cannot be a simple result of differences in soil moisture after irrigation between field conditions and the container technology, as suggested above. According to the technical documentation of the model, total precipitation (P_t) is defined as the sum of natural rainfall (P) and irrigation (I) (DWD, 2021), suggesting that both parameters should have the same weight for calculation of ET_{AMBAV} . However, the sensitivity analysis showed that the model was less sensitive to changes of irrigation (Figure 7) than to changes of precipitation (Figure 6 g, h). This assumption is supported by the close relationship between ΔET ($\Delta\text{ET} = \sum\text{ET}_m - \sum\text{ET}_{\text{AMBAV}}$) and $\sum I$ (Figure S2). The higher sensitivity of ET_{AMBAV} to natural rainfall can be partly explained by the fact that while irrigation water was applied directly to the soil, natural rainfall can be intercepted by leaves, thus increasing direct evaporation of water from the leaf surface resulting in higher $\sum\text{ET}_{\text{AMBAV}}$. If this were to be the main reason for the differences in sensitivity, we would expect the crop with the highest soil coverage (LAI_{max}), *i.e.*, the highest rain storage capacity (S_{max}), to have the highest $\sum\text{ET}_{\text{AMBAV}}$ under high-precipitation conditions. According to Figure 6 g, h this was clearly not the case. In fact, oilseed radish had the highest LAI_{max} in both years but was

least sensitive to changes in precipitation. This is likely due to the restriction of soil evaporation under a closed biomass cover (Allen et al., 1998). Furthermore, it must be noted that (1) evaporation of intercepted water can only occur after leaves are wetted by natural rainfall and that (2) the transpiration rate from wet leaves is lower than that of dry leaves (Klaassen et al., 1998). Consequently, the effects of higher evaporation and lower transpiration after natural rainfall may override each other. We therefore come to the conclusion that in times of high irrigation, the model is not able to reliably predict ET.

(2) Simulated evaporation from a bare soil surface hardly differed from $ET_{AMB\text{AV}}$ of the three cover crops during both vegetation periods (Figure 4, 6), indicating that the model underestimates transpiration losses. For instance, bare soil evaporation was higher than $ET_{AMB\text{AV}}$ of white mustard and phacelia several times in 2020 and 2021 although these crops had already produced a significant amount of biomass and soil coverage (Figure S3). Factors which are included in the calculation of transpiration losses in AMBAV are the aerodynamic resistance (r_a) and the canopy resistance (r_c). While r_a affects the water-vapor transfer between the crop and the atmosphere that surrounds the crop, r_c is a term that describes the water transfer within the crop as well as the water transfer within the soil. Therefore, calculation of r_c requires knowledge of vegetation resistance (r_v) and soil resistance (r_s) (DWD, 2021). Vegetation resistance (r_v) depends on leaf stomatal resistance which is highly influenced by meteorological conditions such as light intensity, humidity, and vapor pressure deficit (VPD) (Damour et al., 2010). However, AMBAV uses 'fixed daytime and nighttime leaf stomatal resistances' for white mustard and phacelia (DWD, 2021). Thus, crop-specific variations of r_s during the course of the day cannot be reflected by $ET_{AMB\text{AV}}$ and might explain the under-estimation of transpiration losses which resulted in poor model performance for these crops (Table 3). For oilseed radish, which had an overall better model performance (Table 3), a parametrization was already prepared for AMBAV (DWD, 2021) following the Jarvis model (Jarvis, 1976). Parametrization of phacelia and white mustard for AMBAV could improve estimation of transpiration and thereby improve the accuracy of the simulation output. Helle (2021) has performed measurements of stomatal conductance on all three cover crops for implementation in AMBAV. It will have to be tested whether this leads to an improvement in model performance once the adjusted model is available.

(3) The driving force for ET is solar radiation which not only provides the energy for water vaporization but also heats the atmosphere, thereby increasing air temperature and VPD

(Allen et al., 1998). VPD is furthermore influenced by humidity: The higher the relative humidity, the lower the evapotranspirative demand of the atmosphere (Allen et al., 1998). Thus, high ET losses generally occur on clear (high radiation), warm (high temperature), and dry (low humidity) days. It is peculiar, therefore, that the sensitivity analysis showed a general decrease of $ET_{AMB\Delta V}$ with increasing temperature for phacelia (2020) and oilseed radish (2020, 2021) (Figure 6 a, b). Considering the quick development of the cover crops (Figure S3), we can assume that ET was governed by transpiration during most of the vegetation period. As mentioned above, transpiration is determined by a combination of meteorological conditions and crop-specific factors such as stomatal conductance. Based on the multiplicative relationship between different environmental drivers which affect stomatal conductance (g_{st}) proposed by Jarvis (1976), AMBAV calculates g_{st} as follows (Equation 6):

$$g_{st} = g_{st,max} \prod_{i=1}^n F_{v,i} \quad (6)$$

With $g_{st,max}$ = crop-specific maximum leaf stomatal conductance in $m s^{-1}$, n = number of drivers considered for the calculation of g_{st} , and $F_{v,i} = F_v(VPD) \cdot F_v(T_a) \cdot F_v(S\downarrow) \cdot F_v(\theta)$ with VPD = vapor pressure deficit in kPa, T_a = air temperature in $^{\circ}C$, $S\downarrow$ = shortwave radiation in $W m^{-2}$, and θ = volumetric soil water content in $m^3 m^{-3}$. It is widely accepted that in addition to these drivers, stomatal conductance is affected by ambient CO_2 concentration (Jarvis, 1976; Kirschbaum and McMillan, 2018). For simplification of the modeling process and due to the short-term nature of crop cultivation, atmospheric CO_2 concentrations are considered to be constant at 400 ppm in the simulation. Equations for the calculation of the single drivers can be derived from DWD (2021). The dependence of g_{st} on temperature is given by $F_v(T_a)$ which is defined as (Equation 7):

$$F_v(T_a) = \left[\frac{(T_a - T_{min})(T_{max} - T_a)}{(T_{opt} - T_{min})(T_{max} - T_{opt})} \right]^c \quad (0 \leq F_v(T_a) \leq 1) \quad (7)$$

With T_{min} = crop-specific minimum temperature in $^{\circ}C$ ($T_{min} = 0^{\circ}C$ (Helle, 2021)), T_{max} = crop-specific maximum temperature in $^{\circ}C$ ($T_{max} = 40^{\circ}C$ (Helle, 2021)), T_{opt} = crop-specific constant, and $c = (T_{max} - T_{opt}) / (T_{opt} - T_{min})$ (DWD, 2021). T_{opt} values for the three cover crops proposed by Helle (2021) are 15, 24, and $16^{\circ}C$ for white mustard, oilseed radish, and phacelia, respectively. Thus, we would expect maximum stomatal conductance ($F_v(T_a) = 1$) and maximum transpiration to be reached at these temperatures if all other drivers are neglected. Due to the comparatively high T_{opt} of oilseed radish, we would also expect this cover crop to have higher transpiration losses when temperature increases than white mustard and

phacelia which have approximately the same T_{opt} . Calculating the temperature dependent term $F_v(T_a)$ for the meteorological data on which we based our sensitivity analysis confirms these assumptions (Figure S4 a, b). However, this increase in stomatal conductance with increasing temperature is not reflected in Figure 6 a, b, eliminating this explanation.

Another possible explanation for decreasing ΣET with increasing temperature is stomatal closure to prevent water losses at high atmospheric temperatures (Damour et al., 2010). When ambient air temperature significantly surpasses T_{opt} , stomata close, *i.e.*, $F_v(T_a) \approx 0$. Consequently, g_{st} decreases to values close to zero. We tested this by calculating $F_v(T_a)$ for each measuring point. The number of values where $F_v(T_a) < 0.1$ (near stomatal closure) was higher for white mustard and phacelia than for oilseed radish in both years (Figure S4 c, d) so that stomatal closure at high / low temperatures cannot explain the unexpected relationship between changes in temperature and ΣET for oilseed radish.

The sensitivity analysis shown in Figure 6 was performed several times with the same results and the technical documentation for AMBAV does not provide a satisfying explanation as to why a temperature increase might cause a decline of ET_{AMBAV} apart from the two possibilities discussed above. Further insight into the programming script behind the calculations would be necessary to identify the cause for this finding.

4.3 Sensitive parameters for simulation of ET_{AMBAV}

The sensitivity analysis showed that, differently than hypothesized, ET_{AMBAV} is most sensitive to changes in temperature and humidity and not to changes in water supply (Figure 6). Changes in irrigation and precipitation did not affect ET_{AMBAV} although we found a highly significant relationship between water supply and ET_m ($p < 0.001$). As previously discussed, this could be due to methodological differences and internal model configurations.

As for the crop-specific parameters, the sensitivity analysis confirmed our hypothesis that ET_{AMBAV} is most sensitive to changes in LAI_{max} . The general increase of ET_{AMBAV} with increasing LAI_{max} for all three cover crops (Figure 8) clearly shows that the increased water loss through transpiration outweighs the reduction of evaporation losses with increasingly closed soil cover (Allen et al., 1998). Due to the comparably high sensitivity to this parameter, the analysis furthermore shows that when using AMBAV for irrigation scheduling or other applications, using the default LAI_{max} provided by model can result in a severe under- or overestimation of

actual ET. This is in agreement with Kroes et al. (2006) who recommend farmers to provide their own crop and soil-specific data to reduce the uncertainty of the model. Since manual measurements are time-consuming, digital imaging could be a solution for farmers. Different web-based and mobile applications have been developed in recent years to estimate soil cover based on digital images taken approximately 1 m above the ground (Riegler-Nurscher et al., 2018) or – depending on field size – on drone or satellite imaging (Kavoosi et al., 2020). These applications allow for a precise pixel-wise classification to distinguish between soil, stones, living and dead plant material (Riegler-Nurscher et al., 2018). The suitability of this soil cover data for estimation of LAI_{max} and its use for simulation of ET_{AMBAV} should be investigated further to provide farmers with an appropriate method to quickly determine LAI non-destructively for precise ET prognoses.

In the same way as LAI, using meteorological data (temperature and humidity) from a nearby meteorological station cannot guarantee reliable simulation of cover crop ET since regional deviations of relative humidity and temperature have been shown to have a significant influence on ET_{AMBAV} (Figure 6). It is not realistic, however, that farmers monitor meteorological conditions for each of their fields to obtain more reliable ET prognoses.

5 Conclusions

The study has shown that measured evapotranspiration (ET_m) losses in a container experiment with three different cover crops were underestimated by the simulation with AMBAV. Sensitivity analysis showed that ET_{AMBAV} is most sensitive to changes in temperature, humidity, and LAI_{max} while changes in wind speed, water supply, and crop height only had minor effects on ET_{AMBAV} . Poor performance of AMBAV in the given study is partly due to the experimental setup which strongly differed from the conditions under which the initial parametrization of the cover crops for AMBAV took place. In addition, the model parametrization for the cover crops needs further optimization through validation trials. Furthermore, we found that simulations of ET_{AMBAV} are highly dependent on the accuracy of the input data. Using the default data of the model can lead to a severe deviation of ET_{AMBAV} from actual ET which farmers should bear in mind when using simulated data for irrigation scheduling or other applications.

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4 General discussion

Catch and cover cropping is an increasingly popular addition to an existing crop rotation that can be beneficial for the agroecosystem in many aspects. However, several agronomic and economic challenges for the adoption of CCC have been identified (Figure 1.1). The agronomic issues include the risk of increasing pest populations (Smit et al., 2019), CCC turning into weeds in a succeeding cash crop cultivation period (Smit et al., 2019), uncertainty about the yield effects of CCC on succeeding crops (Roesch-McNally et al., 2018) which is directly linked to nutrient cycling, and soil water depletion (Islam et al., 2021; Smit et al., 2019). Economic issues are higher labor requirements as well as increased indirect and direct costs (Roesch-McNally et al., 2018). While all of these challenges are relevant and important, this thesis focused on two of those challenges, namely (1) maximizing the nutrient cycling efficiency and (2) determining the water requirement of catch and cover crops. In this chapter, the importance of the results presented in this thesis for the future of CCC cultivation in Germany will be discussed.

4.1 Challenge 1: Nutrient cycling efficiency

4.1.1 Maximization of N, P, and K uptake is directly linked to biomass production and root parameters

Maximum nutrient uptake was used as a simple predictor for the potential of increasing overall nutrient cycling efficiency (Selzer and Schubert, 2021). For non-limiting growth conditions, it has been shown that biomass production was the driving factor for nutrient uptake. Hence, the CCC species with the highest biomass production (white mustard, oilseed radish, phacelia, and buckwheat) also had the highest N, P, and K uptake, while nutrient uptake by CCC with lower biomass production (sunflower, ryegrass, and white lupin) was low. Under the given conditions, no clear differentiation of CCC ideotypes for N, P, and K uptake was possible. Therefore, the first hypothesis that N and K uptake is highest for crucifers with deep roots, and P uptake is highest by catch crops with high root length densities in the topsoil, was rejected. Nevertheless, a general increase of nutrient uptake with increasing root surface area (RSA) and root length density (RLD) was established (Selzer and Schubert, 2021).

However, if the aim of catch cropping is to maximize nutrient cycling efficiency, not only total N, P, and K uptake are of interest but also their availability to a succeeding crop. Both, nutrient and water dynamics are highly dependent on climatic conditions, species choice, and CCC

management (Selzer and Schubert, accepted). While early termination and the preparation of a mulch layer might be good choices for the reduction of the water deficit (Gentsch et al., 2022; Selzer and Schubert, accepted), nutrient losses were shown to increase when CCC were terminated early or killed by frost due to the onset of decomposition processes (Böldt et al., 2021; Gentsch et al., 2022; Thorup-Kristensen, 1994). The earlier the termination, the lower the C : N ratio of the plant material and the higher the leaching losses (Böldt et al., 2021; Gollner et al., 2020; Odhiambo and Bomke, 2007). Thus, phacelia – which showed the highest N, P, and K uptake of the pure stands – and other frost-sensitive CCC might turn from a sink to a source for nutrient losses during winter (Figure 4.1). Gollner et al. (2020) showed that N_{\min} values after cultivation of a frost-sensitive CCC were almost twice as high as N_{\min} after winter-hardy catch crops. This is in agreement with results by Thorup-Kristensen (1994) who reported a 50-80% loss of N that was previously taken up by frost-sensitive catch crops. These nutrient losses in combination with high humidity and rainfall events can result in nutrient leaching. This was also observed by Liu et al. (2015, 2014) who found increased P leaching

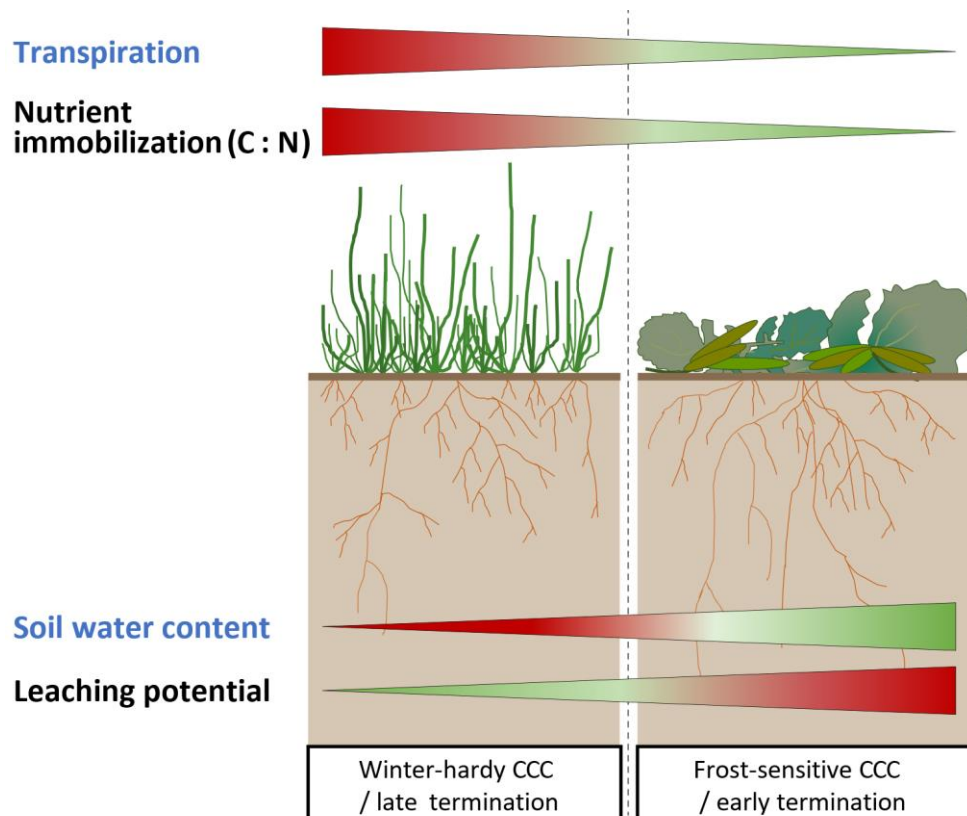


Figure 4.1 Influence (increase = ◀, decrease = ▶) of winter-hardy (left side) and frost-sensitive (right side) catch and cover crop (CCC) cultivation on different nutrient and water-related parameters at the end of the cultivation period. Red: Increase / decrease of the parameter is negative for the nutrient (black letters) or water (blue letters) dynamics of the agroecosystem; green: Increase / decrease of the parameter is positive for the nutrient (black letters) or water (blue letters) dynamics of the agroecosystem.

losses from frost-sensitive CCC after freezing-thawing cycles. On the other hand, the increasingly high C : N ratio of CCC which are terminated late in the season can lead to an immobilization and reduce the nutrient availability to a succeeding crop (Odhiambo and Bomke, 2007) (Figure 4.1). For the assessment of maximum nutrient cycling efficiency, it is therefore recommended to analyze nutrient dynamics from sowing of the CCC until cultivation of the cash crop under non-limiting growth conditions.

4.1.2 Pure stands can be as effective as mixtures in reducing the nutrient leaching potential

It has been shown that under non-limiting growth conditions, CCC pure stands can be as effective in reducing the nutrient leaching potential and thereby maximizing the nutrient cycling efficiency as a mixture of seven catch crops (Selzer and Schubert, 2021). Thus, the second hypothesis that due to complementary and/or facilitative effects a multi-species CCC mixture outperforms its single-species counterparts in terms of nutrient uptake (N, P, and K) and root biomass is rejected (Selzer and Schubert, 2021). This result is likely due to the fact that biomass production was the most important parameter for total nutrient uptake when nutrients are provided in excess. The complementarity of different species in terms of nutrient acquisition strategies can, however, be beneficial under conditions deviating from those in our experiment. For example, other studies have shown that mixtures of CCC which occupy different ecological niches complement each other and outperform their single CCC counterparts (Heuermann et al., 2019; Wendling et al., 2017).

4.1.3 Implications for the legislative framework in Germany

If the primary goal of catch cropping is to reduce nutrient leaching, it has been shown that growing a CCC mixture does not lead to a higher nutrient uptake compared to the cultivation of a fast-growing single CCC species under non-limiting growth conditions (Selzer and Schubert, 2021). Thus, in regions with high residual soil nutrient concentrations a single catch crop can be as effective in reducing the nutrient leaching potential as a mixture of various catch crop species. However, it is mandatory for farmers in Germany to grow mixtures of at least two species for the declaration as EFAs (Sarvia et al., 2022). The proportion of one species in the mixture is not allowed to exceed 60% (LLH, 2020). The requirement of cultivating mixtures instead of pure stands in Germany was derived from the European Greening regulations which state that EFAs were introduced “*in particular, [...] to safeguard and improve biodiversity on farms*” (European Commission, 2017) and to adapt “*agricultural practices*

beneficial for the climate and the environment” (European Parliament; Council of the European Union, 2013).

The legislative framework for the implementation of the Greening measures in the individual member states is an important factor in determining the effectiveness of CCC to increase the nutrient cycling efficiency. According to Klages et al. (2022) the frame conditions in Germany were a key cause for the lack of a reduction of water pollution through catch cropping in the federal state of Lower Saxony. This state is known for its intensive animal production which resulted in high groundwater NO_3^- -N levels (Eysholdt et al., 2022). Since 2015, catch and cover crops make up > 86% of all declared EFAs in Lower Saxony. Nevertheless, groundwater NO_3^- -concentrations stagnated in the same time span. Klages et al. (2022) suspect that the high CCC adoption rates in Lower Saxony cannot solely be explained by the farmers’ willingness to reduce NO_3^- -N levels, but that they are linked to the fact that during the 2015-2022 CAP period no restriction on fertilizer use for CCC cultivation existed from the European Commission. Therefore, farmers only needed to adhere to the German Fertilization Ordinance which allowed them to apply considerable amounts of manure in autumn (Klages et al., 2022). The authors suggest that improvements of the legislative framework are necessary to increase the effectiveness of CCC in reducing groundwater pollution and improving the nutrient cycling efficiency. They propose the compulsory cultivation of winter CCC in combination with stricter rules on fertilization allowance (no fertilization), mixture composition (no legumes), and cultivation period (times of high leaching risk) to be effective frame conditions (Klages et al., 2022). Especially in areas with high residual nutrient levels, as is the case in many parts of Lower Saxony, the results presented above can be a first indicator as to which CCC might be suitable choices for achieving this goal, keeping in mind the influence of different management options on nutrient availability to a succeeding crop (Figure 4.1).

While the proposed changes to the legislative framework might be beneficial for the enhancement of the nutrient cycling efficiency in specific regions (high precipitation, high nutrient inputs), other measures might be necessary in (a) other regions or (b) when the ecosystem services of catch crops are outweighed by their disservices (see below). Frame conditions for CCC cultivation which are suitable to reduce NO_3^- -N leaching in Lower Saxony might not be effective for water and nutrient conservation on sandy soils in Brandenburg or erosion control in hilly regions in Bavaria. The national and federal legislative frameworks

should reflect these soil-related, geographic, and climatic differences. This will be discussed in more detail in Chapter 4.2.1.3 with a focus on water-smart CCC cultivation.

4.2 Challenge 2: Water requirement of catch and cover crops

4.2.1 Water dynamics of catch and cover crops

4.2.1.1 Water depletion: No relevant occult precipitation but high ET losses

It was shown that CCC use significant amounts of water and that any form of water input through occult precipitation was by far not sufficient to counteract ET water losses (Selzer and Schubert, accepted). The process of occult precipitation is determined by meteorological conditions and crop-specific parameters (Holloway, 1970; Mali et al., 2020; Van Stan et al., 2014). As for the meteorological conditions, mean relative humidity exceeded 80% and reached a maximum value of 100% almost daily starting from the beginning of October in both vegetation periods (Selzer and Schubert, accepted) so that availability of moisture was not a limiting factor. Among the crop-specific parameters which determine occult precipitation are plant height, leaf morphology and roughness, and LAI (Ebner et al., 2011; Holloway, 1970; Mali et al., 2020). Plants can exhibit different direct and indirect strategies to make use of atmospheric water and the nutrients dissolved in that water. The direct interception and absorption by plant organs from the atmosphere belongs to the former category while an indirect strategy is the redistribution of the intercepted atmospheric water to the soil via (a) dewfall and adsorption, (b) throughfall, or (c) hydraulic redistribution (Matos et al., 2022). The direct strategy of water absorption by the plant is highly unlikely for CCC as the water gradient between plant and atmosphere generally favors water losses through transpiration (Matos et al., 2022), as seen in the experiments described above (Selzer and Schubert, accepted). As for the indirect strategies, although they might occur under the meteorological conditions common for winter CCC cultivation in Europe, an ecological relevance of dew and throughfall can only be expected under arid conditions when soil moisture is already limiting and the survival of the plant is dependent on every additional source of water it can find (Matos et al., 2022). Under the given conditions, soil moisture was kept at 50 and 45% WHC in 2020 and 2021, respectively, to avoid drought stress and allow the production of significant amounts of biomass (Selzer and Schubert, accepted). Thus, any additional water inputs which might have occurred via occult precipitation were not relevant for the CCC themselves as they had access to water via their root system.

Possible reasons why occult precipitation was not quantifiable under the experimental conditions described above are: (a) The intercepted water directly evaporated from the leaf surface and did not reach the soil, (b) the intercepted water reached the soil via dew or throughfall and was directly taken up by the plant so that by the subtraction of plant fresh weight for the calculation of ET it was falsely assumed that no occult precipitation occurred, or (c) the amount of occult precipitation was below the detection limit of or experimental setup.

However, the question of interest was not whether occult precipitation occurs but whether it is a relevant water input which reduces the water deficit and drought stress risk for a succeeding crop. Based on the results shown above it can clearly be stated that even though the amount of occult precipitation was not quantifiable, the CCC did not provide a water benefit for a succeeding crop but rather depleted soil water in autumn in comparison to a bare fallow. This was supported by the results from the climate chamber experiments where a non-transpiring 'dummy' plant was subjected to a variation of meteorological conditions (humidity, wind speed, and temperature) and where, over an eight-hour period no water input was found (Selzer and Schubert, accepted). Thus, the third hypothesis which stated that under middle European climatic conditions CCC increase the water input from the atmosphere into the soil through occult precipitation in comparison to a bare fallow control has to be rejected (Selzer and Schubert, accepted).

4.2.1.2 Water conservation: Influencing factors

Although soil water depletion was clearly evident in autumn, SWC did not differ between the bare fallow and the mulched, frost-sensitive CCC treatments in spring (Selzer and Schubert, accepted) (Figure 4.1). Thus, if winter precipitation is sufficient and with water-smart management it is possible to achieve water conservation in addition to the many other benefits CCC provide to agroecosystems. Whether CCC deplete or conserve water is dependent on several factors which include (a) soil type (higher water losses on sandy soil), (b) climate, and (c) management. The latter includes choices about (I) the date of termination, (II) catch or cover crop species, (III) tillage, and (IV) residue management (Figure 4.2).

Soil moisture at the end of March did not differ between early terminated, mulched, frost-sensitive CCC and a bare fallow (Selzer and Schubert, accepted) which shows that a combination of these management tools can help to conserve water. Hence, the fifth

hypothesis that soil moisture can be recharged during winter when frost-sensitive CCC are mulched after the first frost event while winter-hardy CCC deplete soil water in early spring can be accepted (Selzer and Schubert, accepted). These results are in agreement with those by Gentsch et al. (2022) who pointed out that CCC can be useful “*tools for soil water management*”.

MANAGEMENT	SWC	
I. Termination	Late	Early
II. Catch or cover crop choice	Winter-hardy	Frost-sensitive
III. Tillage	Plowing	No tillage
IV. Residue management	Removal	Mulching

Figure 4.2 Management strategies for water conservation in catch and cover crop cultivation. SWC = soil water content.

4.2.1.3 Feasibility of catch and cover crop cultivation dependent on climatic conditions

However, water-smart management alone is not enough to counteract the severe soil water deficit which results from vigorous CCC growth in autumn. In addition, the climatic conditions determine whether the soil water deficit can be recharged during winter (Selzer and Schubert, accepted). While management can play an important role for water conservation, it is clear that any crop needs water for its growth – CCC are no exception. Hence, water losses in autumn cannot be eliminated. Based on these findings the question arises under which climatic conditions the cultivation of CCC is agronomically and economically feasible.

Arid regions / dry years

The cultivation of CCC can only be afforded in regions where winter precipitation is sufficient to counterbalance autumn water losses. Thus, catch and cover cropping in (semi-)arid regions / in dry years is often not a feasible option (Abdalla et al., 2019), as it has been shown that soil water depletion by CCC strongly exceeds evaporation losses from a bare soil surface under these conditions (Nielsen et al., 2015; Unger and Vigil, 1998). From an agronomic viewpoint, the first problem in (semi-)arid regions / in dry years is CCC seed germination. After the cultivation of a main crop in an increasingly warmer climate with more frequent extreme drought events, *e.g.*, in Central Europe (Samaniego et al., 2018), water availability is a limiting factor for seed germination and the subsequent establishment of a closed soil cover. In Germany, farmers in regions with increasingly high soil water deficits, *e.g.*, in the federal states

Brandenburg, Saxony-Anhalt or Saxony (UFZ, 2022), quit catch and cover cropping in recent years as they were afraid to deplete soil water even further through this management practice (personal communication). Assuring seed germination in these regions would necessitate irrigation of the CCC during the first few weeks of cultivation. However, this is not an economically feasible option since CCC – in contrast to cash crops – generally do not provide a marketable product which generates a monetary revenue for farmers (with the exception of CCC which can be used as animal fodder). Except for the Greening subsidies (CAP 2015-2022), there are no immediate monetary benefits provided by CCC which could counterbalance the economic costs linked to irrigation. Of course, long-term catch and cover cropping can provide ecosystem services to a cropping system (Figure 1.1). However, (a) these services currently do not have a monetary value and (b) especially in (semi-)arid regions / dry years there is a trade-off between ecosystem services and disservices provided by CCC that needs to be taken into account (Alonso-Ayuso et al., 2014; Garba et al., 2022).

A second agronomic consideration for (semi-)arid regions is that – in contrast to humid regions – the main reason for catch and cover crop cultivation, *i.e.*, the prevention of nutrient losses through leaching, is not a relevant problem (Garba et al., 2022). Thus, the cultivation of an additional crop is not necessary for the reduction of leaching losses and consequently the agronomic and economic benefits linked to an enhanced nutrient cycling efficiency are lower. Thirdly, potential improvements of soil properties which are linked to an increased field capacity (*e.g.*, higher soil organic carbon content, increased aggregate stability, and the reduction of runoff) have been shown to be short-lived in a semi-arid climate and are lost quickly after termination of CCC cultivation due to rapid decomposition (Blanco-Canqui et al., 2013).

From an economic perspective, CCC cultivation is only feasible for farmers if it does not result in a yield reduction of a succeeding cash crop. Garba et al. (2022) proposed a break-even point of approximately 700 mm annual precipitation: In their meta-analysis they showed that precipitation < 693 mm a⁻¹ severely decreases cash crop yield after CCC cultivation, while annual precipitation > 693 mm in combination with CCC cultivation had a neutral or positive effect (Garba et al., 2022). However, total annual precipitation alone is not a good indicator for the feasibility of catch and cover cropping in dryland farming. Other factors need to be taken into consideration. One important factor is rainfall distribution throughout the year. If precipitation is distributed evenly and there is a constant recharge of soil water, catch and

cover cropping might be feasible depending on soil type and management. For example, cash crop yields on Vertisols in dryland areas were shown to decrease after CCC cultivation on average by 30% due to a severe reduction of SWC and N_{\min} (Garba et al., 2022). Similarly, SWC and N_{\min} were significantly lower after CCC cultivation in comparison to a bare fallow on Chernozems, resulting in a cash crop yield reduction of approximately 7.5% in dryland cropping systems (Garba et al., 2022). This is in agreement with other studies which found a reduction in cash crop yields after the cultivation of CCC in water-limited regions (*i.e.*, Blanco-Canqui et al., 2015).

While total annual precipitation in central Europe is not expected to change, periods without rainfall will become increasingly longer and more precipitation will fall in single, extreme precipitation events (Trenberth, 2011). If there is no even distribution of rainfall throughout the year, water conservation through water-smart management might not be possible and farmers should refrain from catch and cover cropping in (semi-)arid and drought regions as it is neither agronomically nor economically feasible.

Humid regions / wet years

Similar to arid regions, CCC also reduce SWC in humid regions (Garba et al., 2022). However, contrary to arid regions, (a) precipitation is generally sufficient to replenish soil water losses (Dabney et al., 2001), (b) a reduction of SWC in humid regions can provide desirable ecosystem services (Garba et al., 2022), and (c) catch and cover cropping either has a positive or neutral effect on the yield of a succeeding crop in these regions (Blanco-Canqui et al., 2015; Bourgeois et al., 2022), which means that they do not lead to economic losses for farmers. Ecosystem services linked to the reduction of SWC in humid regions with excessive rainfall include the reduction of runoff through improvements of drainage and water infiltration (Blanco-Canqui et al., 2015). Furthermore, reduced SWC in these regions allows earlier use of heavy machinery on the fields without the risk of soil compaction. Therefore, in humid regions / in years with very high precipitation, late termination or the cultivation of winter-hardy CCC is advisable to increase transpiration losses and reduce SWC before seedbed preparation for a succeeding cash crop (Gentsch et al., 2022; Selzer and Schubert, accepted). In these regions, ecosystem services provided by CCC (*e.g.*, enhanced nutrient cycling efficiency, increased soil organic carbon, reduction of runoff, reduction of erosion, and weed suppression) exceed the disservices (*e.g.*, risk of increased pest populations or diseases) making CCC cultivation not only agronomically but also economically feasible.

4.2.1.4 Implications for the legislative framework in Germany

The termination date has been identified as one of the most important management practices for water conservation in CCC cultivation (Alonso-Ayuso et al., 2014; Gentsch et al., 2022; Kaye and Quemada, 2017; Selzer and Schubert, accepted). In Germany, current legislation mandates farmers to sow their winter CCC until 1 October and leave them on the field until 15 February of the following year in order to receive Greening subsidies (LLH, 2020). During this four-months period, farmers cannot terminate CCC growth mechanically but rely on frost-sensitive CCC to form a natural mulch for water conservation (Figure 4.2). In a warm and dry spring, this could mean that CCC are not terminated in time to prevent ET losses if (a) winter-hardy CCC are used or (b) the frost events are not severe enough to kill frost-sensitive CCC in winter. The necessity of a more economic water management in our agroecosystems questions the period set by the German government. In fact, in January and February 2022 temperatures at the experimental station of the Institute of Plant Nutrition in Giessen, Germany (50°35'53.30"N, 8°40'1.56"E), rose to > 10°C while humidity decreased to values < 70% at the same time on several occasions (Appendix D.1). As a consequence, ET of ryegrass increased significantly (Appendix D.2), leading to a reduction of SWC (Selzer and Schubert, accepted).

Although current legislation was not put in place with the aim of optimizing SWC for a succeeding crop but rather for an overall improvement of ecosystem services provided by the agroecosystems (European Commission, 2017; European Parliament; Council of the European Union, 2013), the depletion of soil water by CCC in combination with an increasing frequency of drought events (Samaniego et al., 2018; UFZ, 2022) necessitates a thorough evaluation of the legislative framework. Legislation should reflect the different aims of catch and cover cropping based on the climatic conditions. While a year-round soil cover is desirable in regions with a high risk of nutrient leaching (*e.g.*, regions with high precipitation and high nutrient inputs in combination with sandy soils) or soil erosion (*e.g.*, regions with high precipitation in combination with a steep slope), the focus of catch and cover cropping in dry regions should be on the conservation of soil water. In the same way as farmers need to make site-specific management decisions, the legislative framework should reflect recent advances in CCC research instead of using a 'one-size-fits-all' approach. For dry regions this would mean that (a) catch and cover cropping should not be made mandatory and (b) farmers should be allowed to mechanically terminate CCC growth before 15 February if the SWC falls below a

certain threshold. On the other hand, in regions with excessive precipitation the current legislative framework for the period of CCC cultivation will aid in reducing leaching losses and should even be made mandatory to increase the nutrient cycling efficiency (Klages et al., 2022).

Challenges which need to be addressed in creating such climate-tailored and water-smart frame conditions for CCC cultivation include (a) determining the threshold SWC at which mechanical termination of CCC is advisable, (b) distinguishing between regions in which catch and cover cropping should be made mandatory and regions in which it stays a voluntary option, (c) tailoring subsidies so that neither farmers in dry nor in humid regions face economic disadvantages, and (d) providing simple and easy-to-access tools for farmers to support them in their decision-making process concerning CCC cultivation.

4.2.2 Prediction of water requirement

4.2.2.1 Severe underestimation of ET by AMBAV

At the time of CCC sowing in September it is impossible for farmers to predict the water dynamics of a cover crop which is grown until February of the following year. Therefore, farmers rely on meteorological model predictions to make well-founded management decisions. Particularly the question of water availability at drought-sensitive growth stages of a succeeding cash crop (*e.g.*, flowering) is of interest. It has been shown that CCC use a significant amount of water (Selzer and Schubert, accepted) which could increase the drought stress for a succeeding crop. Hence, accurate simulations of CCC water dynamics are essential for farmers to decide which of the management practices depicted in Figure 4.2 should be applied. The SVAT (soil vegetation atmosphere transfer) model AMBAV by the DWD can be used to calculate the SWC and ET of various crops based on meteorological, crop, and soil specific data (Friesland and Löpmeier, 2007). Due to the relevance of catch and cover cropping for the water availability to a succeeding cash crop, the DWD has started to parametrize CCC for inclusion in AMBAV in recent years and tested the model in two validation trials (Helle, 2021; Kollhorst, 2019). Testing model performance under conditions deviating from those validation trials, it was shown that measured evapotranspiration (ET_m) of the three CCC mustard, oilseed radish, and phacelia grown in container technology was severely underestimated by simulated evapotranspiration (ET_{AMBAV}) (Chapter 3.2). Thus, the sixth hypothesis that ET_{AMBAV} does not differ from ET_m in a container experiment has to be rejected

(Selzer and Schubert, submitted). Possible methodological reasons for the discrepancies were highlighted in Chapter 3.2 (Selzer and Schubert, submitted). Moreover, it was shown that differences in methodology between the container experiments and the validation trials alone cannot explain why variations of ET_m were not recognized by the model (Selzer and Schubert, submitted). Further optimization of the model is needed, especially for irrigated agriculture as it was shown that the water input through irrigation was not recognized and the model was not able to reliably predict ET in times of high irrigation (Selzer and Schubert, submitted).

4.2.2.2 Bottleneck for ET predictions with AMBAV

A sensitivity analysis was conducted to determine the meteorological and crop-specific parameters AMBAV is most sensitive for. Differently than expected, the model was not very sensitive to changes in water supply but more sensitive to changes in humidity and temperature (Selzer and Schubert, submitted). Consequently, the first part of the seventh hypothesis which stated that AMBAV is most sensitive to the meteorological parameter water supply has to be rejected. The second part of the seventh hypothesis – ET_{AMBAV} is most sensitive to the crop-specific parameter LAI – can be accepted as AMBAV showed a higher sensitivity for changes of maximum LAI than changes of maximum crop height (Selzer and Schubert, submitted). This clearly shows that, even in an optimized version of AMBAV, the availability of site-specific meteorological and crop-specific data is the bottleneck for reliable predictions of water fluxes (Selzer and Schubert, submitted).

While meteorological data are available free of charge in the online Climate Data Center (CDC¹) of the DWD which covers 1,195 different locations in Germany, availability of crop and soil specific data are limiting factors. Additionally, although the DWD covers many regions in Germany in its extensive measuring network, it is widely accepted that landscape features such as hedges and trees (Gosme et al., 2016; Sánchez et al., 2010) or differences in elevation can cause differences in micro-climate. As for the crop-specific data, more (field) trials are needed for the parametrization of CCC for AMBAV to reduce the uncertainty of the model. These trials should include different sowing dates and sowing densities. Since measurements of LAI are time-consuming, digital imaging could be an alternative for farmers to non-destructively obtain site-specific LAI-data (Selzer and Schubert, submitted).

¹ Link: https://opendata.dwd.de/climate_environment/CDC

Furthermore, since CCC are often cultivated in mixtures, it is recommended to include at least one of the most common catch and cover crop mixtures (*e.g.*, *Raphanus sativus*, *Avena strigosa*, and *Phacelia tanacetifolia*) in the ongoing parametrization process for the model. Optimization of AMBAV and the parametrization of more CCC species under varying climatic conditions could help to improve overall model performance, making AMBAV a potentially useful tool for farmers. Especially for farmers in regions with increasingly high soil water deficits, *e.g.*, in the federal states Brandenburg, Saxony-Anhalt or Saxony (UFZ, 2022), reliable predictions of the effect of CCC cultivation on SWC would be an asset.

5 Conclusions

There is no doubt that catch and cover cropping can enhance the climate-resilience of agroecosystems and that the crops themselves provide many ecosystem services (*e.g.*, improvements of soil chemical, physical, and biological properties, weed suppression, erosion control, higher biodiversity). However, there are still some agronomic and economic challenges linked to the cultivation of an additional crop. Two of those challenges, namely (1) maximizing the nutrient cycling efficiency and (2) determining the water requirement of CCC, were addressed in this thesis.

While fast-growing CCC with deep roots effectively reduced the nutrient leaching potential for N, P, and K, CCC with high biomass production also depleted soil water in autumn. There was no evidence of the proposed additional water input through occult precipitation. It has been shown that early termination of winter-hardy CCC is an important tool for water conservation. However, the current legislative framework in Germany does not allow mechanical termination of CCC growth before 15 February.

Predictions of water requirements by CCC which are based on simulations with AMBAV are currently not reliable. The model needs further optimization for large-scale application. Farmers should also be aware that the accuracy of the simulations is highly dependent on the availability of site-specific input data.

Overall, it was shown that there is a need for a more differentiated legislative framework for catch and cover cropping which is tailored to various geographic and climatic conditions in Germany and the respective aims of CCC cultivation in those regions: In regions with high precipitation and high nutrient surpluses, CCC cultivation should be made mandatory to reduce nutrient leaching. Furthermore, fertilizer application before CCC cultivation should be restricted or prohibited in these areas. In drier regions, nutrient leaching is not an issue. However, the cultivation of CCC is likely to negatively affect the yield of a succeeding cash crop due to soil water depletion. Therefore, CCC cultivation is neither agronomically nor economically feasible in these regions and should not be compulsory for farmers. Further research is needed to identify in which regions the ecosystem services by catch and cover cropping outweigh the disservices to help realizing such a regionally tailored legislative framework instead of using a 'one-size-fits-all' approach.

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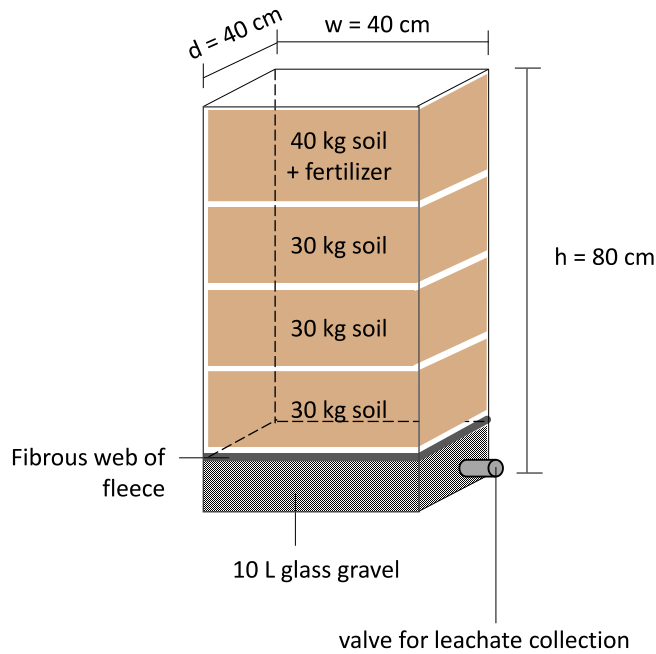
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Appendix

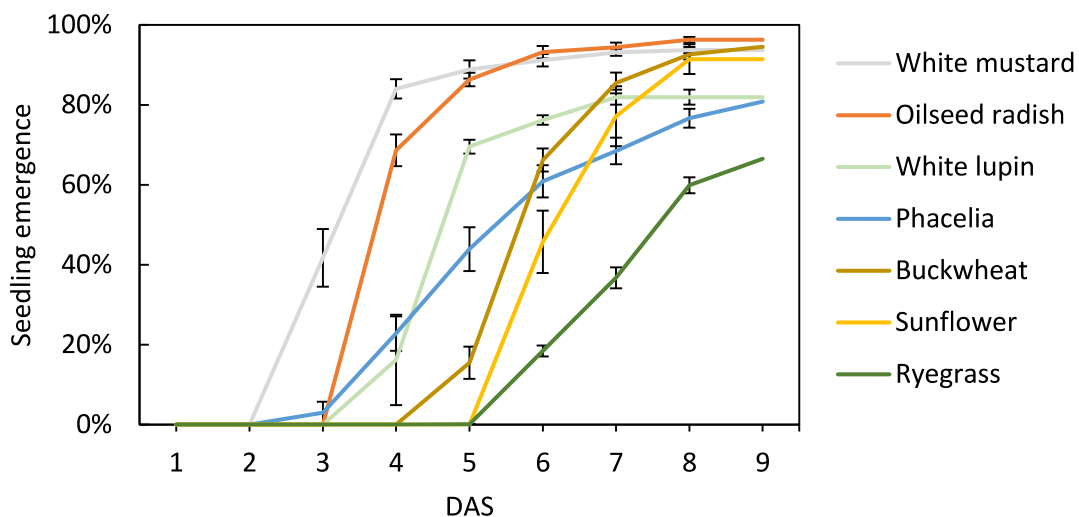
Appendix A: Supplementary material for chapter 2.1

A.1 Container setup



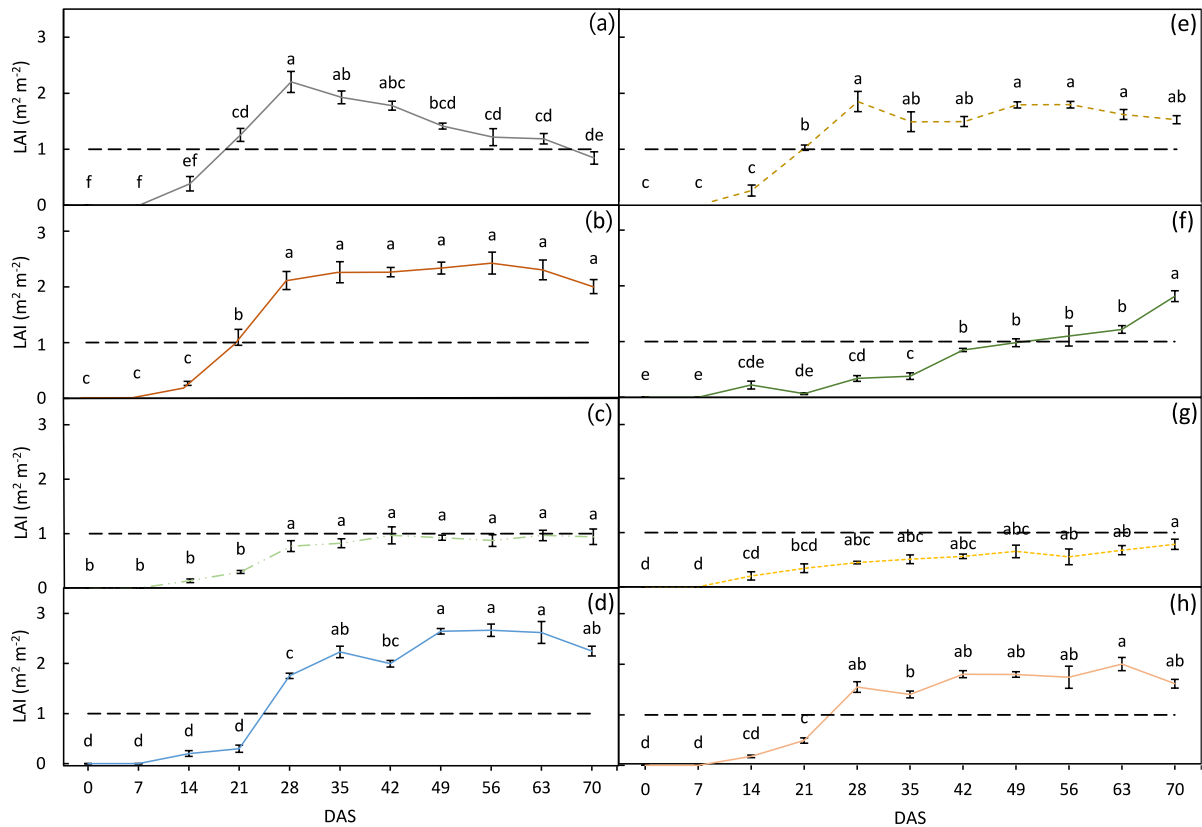
Supplementary information 1 Schematic display of container setup (figure is not to scale). Abbreviations: *d* = depth; *w* = width; *h* = height.

A.2 Seedling emergence



Supplementary information 2 Seedling emergence of different catch crops during the first nine days after sowing (DAS). Mean values ($n = 4$) \pm SE.

A.3 Leaf area index



Supplementary information 3 Leaf area index (LAI) of (a) white mustard, (b) oilseed radish, (c) white lupin, (d) phacelia, (e) buckwheat, (f) ryegrass, (g) sunflower, and (h) a mixture of the seven catch crop species during the vegetation period. Harvest at 74 DAS. Dashed line at $LAI = 1$ indicates point of complete soil coverage. One-way ANOVA and comparison of means adjusted according to FDR. Letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$) \pm SE.

A.4 Rooting depth

Supplementary information 4 Maximum rooting depth of different catch crops at harvest (74 DAS). One-way ANOVA and comparison of means adjusted according to FDR. Letters indicate significant differences ($p < 0.05$). Mean values ($n = 4$) \pm SE.

	Maximum rooting depth (cm)
White mustard	67.50 \pm 0.31 ^a
Oilseed radish	66.13 \pm 0.84 ^a
White lupin	65.88 \pm 0.78 ^a
Phacelia	67.00 \pm 0.25 ^a
Buckwheat	65.88 \pm 0.82 ^a
Ryegrass	67.13 \pm 1.07 ^a
Sunflower	65.50 \pm 1.19 ^a
Mix	65.88 \pm 0.54 ^a

A.5 Catch crops at harvest



Supplementary information 5 Catch crops at harvest (74 DAS).

Appendix B: Supplementary material for chapter 3.1

B.1 Maximum LAI and maximum height

Table S1 Maximum leaf area index (LAI_{max}) and maximum height (h_{max}) of various cover crops for the vegetation periods 2020 and 2021. *DY* = dummy, *WM* = white mustard, *OR* = oilseed radish, *WL* = white lupin, *PH* = phacelia, *BW* = buckwheat, *RG* = ryegrass, *SF* = sunflower. One-way ANOVA and comparison of means adjusted according to FDR. Different superscript letters indicate significant differences ($p < 0.05$) between treatments for that date. Mean values (2020: $n = 4$, 2021: $n = 5$) \pm SE.

	2020		2021	
	LAI_{max} ($m^2 m^{-2}$)	h_{max} (cm)	LAI_{max} ($m^2 m^{-2}$)	h_{max} (cm)
<i>Control</i>				
<i>DY</i>	3.45	73.2	3.49	59.45
<i>Frost-sensitive</i>				
<i>WM</i>	4.58 \pm 0.41 ^c	125.70 \pm 5.90 ^a	4.41 \pm 0.10 ^{bc}	123.07 \pm 1.79 ^a
<i>OR</i>	6.44 \pm 0.43 ^a	69.13 \pm 6.13 ^{bc}	5.91 \pm 0.19 ^a	45.97 \pm 0.97 ^{cd}
<i>WL</i>	2.53 \pm 0.14 ^d	51.09 \pm 1.93 ^{cd}	2.55 \pm 0.19 ^e	42.31 \pm 1.39 ^{cd}
<i>PH</i>	6.32 \pm 0.40 ^{ab}	64.41 \pm 1.41 ^{bcd}	5.40 \pm 0.29 ^{ab}	46.00 \pm 8.15 ^{cd}
<i>BW</i>	4.17 \pm 0.09 ^c	80.13 \pm 2.40 ^{bc}	3.83 \pm 0.20 ^{cd}	77.90 \pm 1.85 ^b
<i>SF</i>	1.97 \pm 0.70 ^d	76.71 \pm 13.14 ^{bc}	2.47 \pm 0.23 ^e	75.87 \pm 0.47 ^b
<i>Mix</i>	4.79 \pm 0.24 ^{bc}	89.34 \pm 12.94 ^b	4.27 \pm 0.28 ^{bc}	56.49 \pm 2.55 ^{bc}
<i>Winter-hardy</i>				
<i>RG</i>	3.5 \pm 0.21 ^{cd}	34.63 \pm 0.29 ^d	2.80 \pm 0.28 ^{de}	33.45 \pm 1.12 ^d

B.2 Dummy



Figure S1 Non-transpiring, artificial plants (*Dummy*) in the container experiment.

B.3 Climate chamber experiment

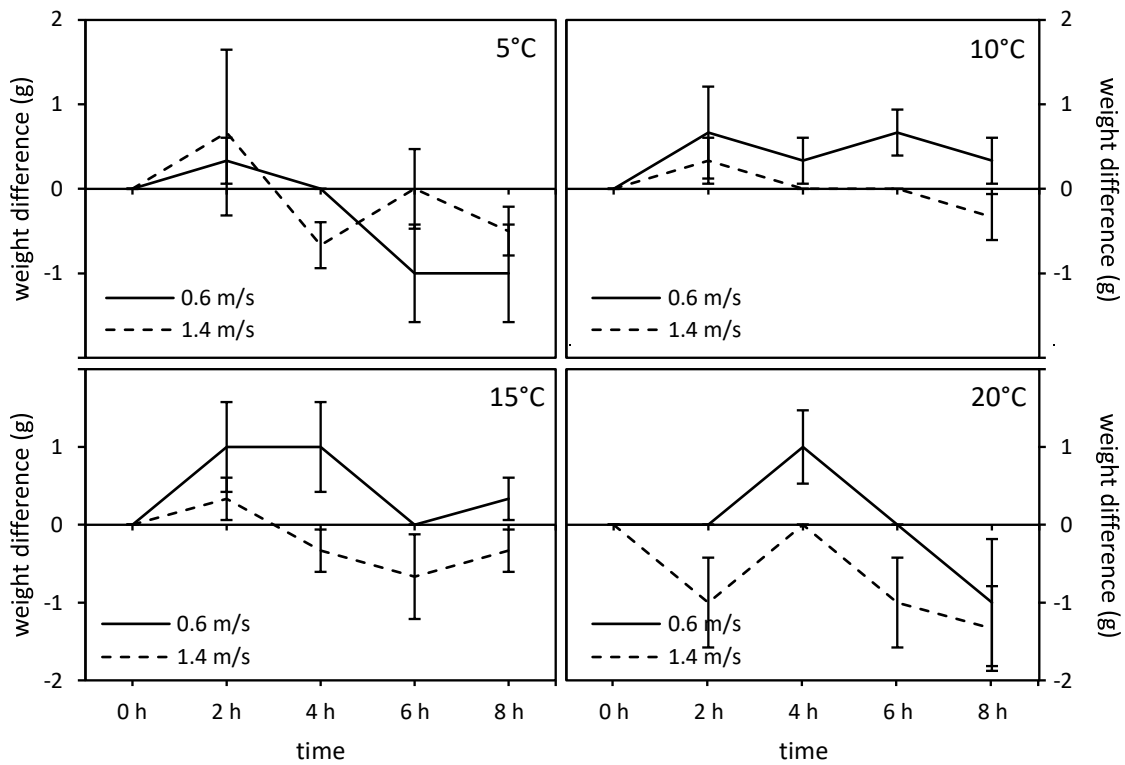


Figure S2 Quantification of occult precipitation in climate chamber experiment. Weight difference of pots in comparison to starting weight to starting weight after 2, 4, 6, and 8 h at 95% relative humidity and a combination of different temperatures (5, 10, 15, and 20°C) and wind speeds (0.6 and 1.4 m s⁻¹). Mean values (n = 3) ± SE.

B.4 Mulch fresh weight

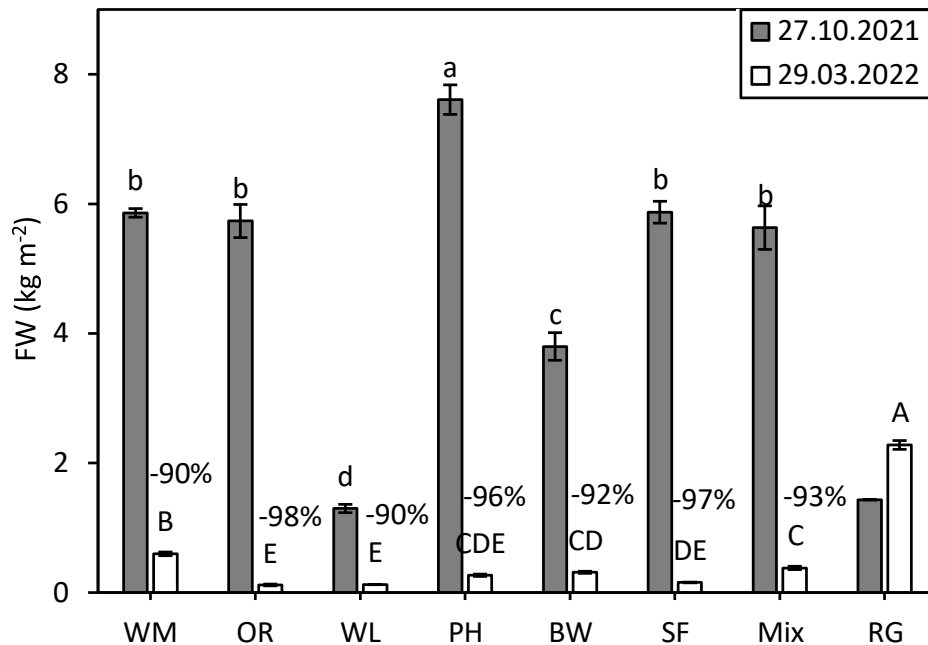


Figure S3 Mulch fresh weight (FW) at the first frost event (27.10.2021) and after termination of the experiment (29.03.2022). BF = bare fallow, DY = dummy, WM = white mustard, OR = oilseed radish, WL = white lupin, PH = phacelia, BW = buckwheat, RG = ryegrass, SF = sunflower. One-way ANOVA and comparison of means adjusted according to FDR. Different letters indicate significant differences ($p < 0.05$) where small and capital letters indicate differences between catch crop species for the first frost event (27.10.2021) and the date of termination (29.03.2022), respectively. Mean values (n = 4) ± SE.

B.5 Mulch cover

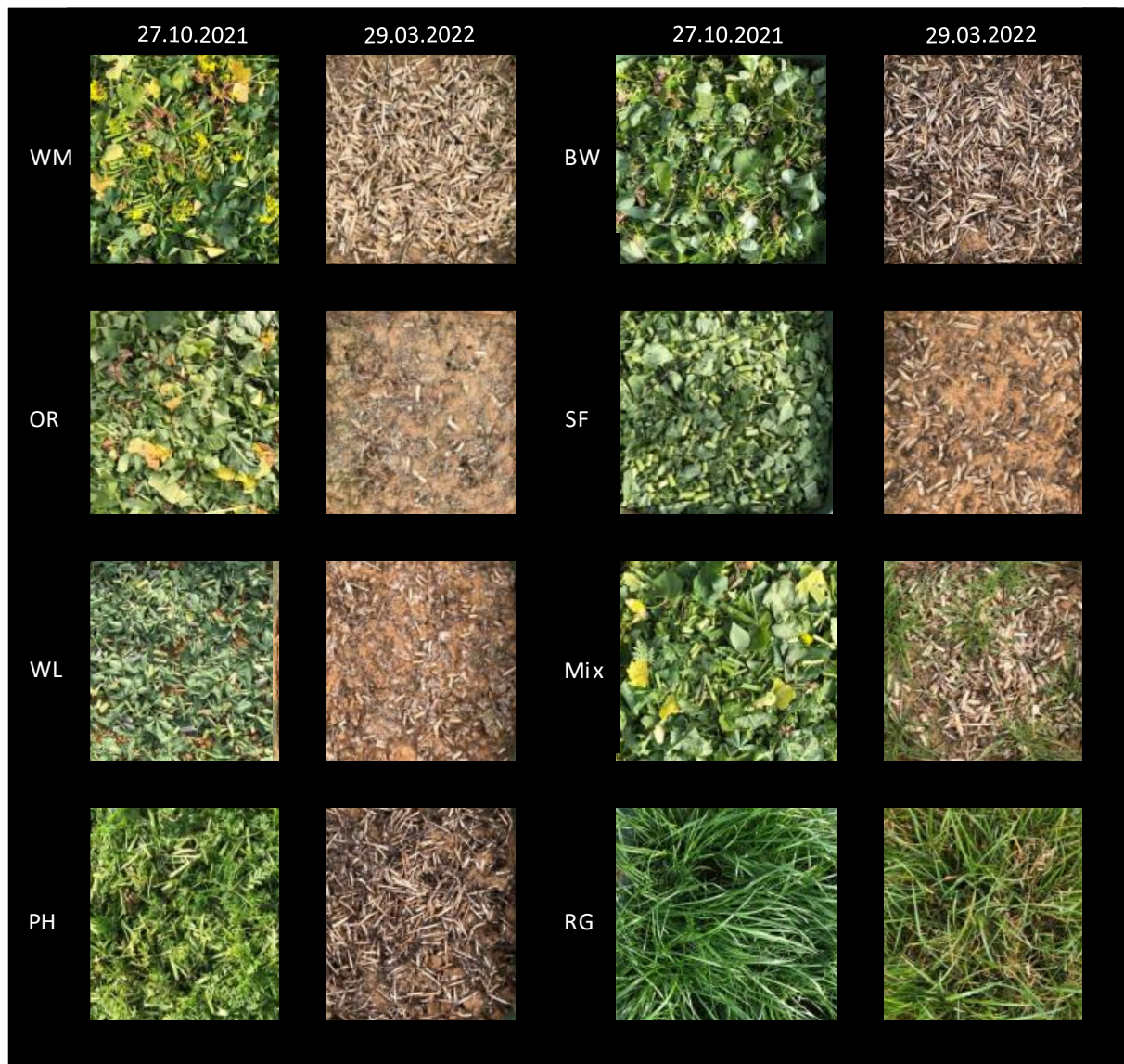


Figure S4 Mulch cover directly after mulching (63 DAS, 27.10.2021) and at the time of termination (216 DAS, 29.03.2022). WM = white mustard, OR = oilseed radish, WL = white lupin, PH = phacelia, BW = buckwheat, RG = ryegrass, SF = sunflower.

Appendix C: Supplementary material for chapter 3.2

C.1 Soil temperature

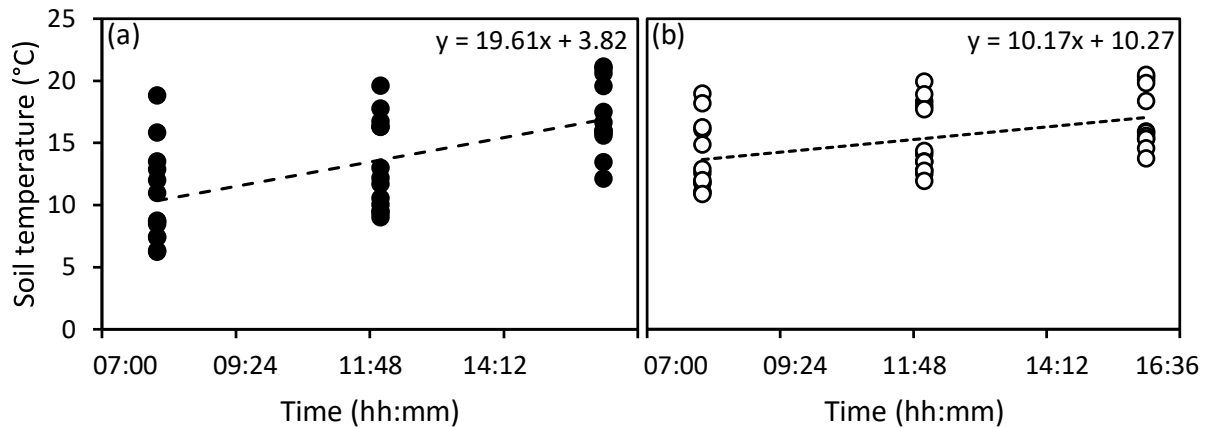


Figure S1 Time course of soil temperature between 8:00 and 16:00 h (a) in a container and (b) under field conditions. Measurements taken over a 13-day period. Mean values ($n = 3$).

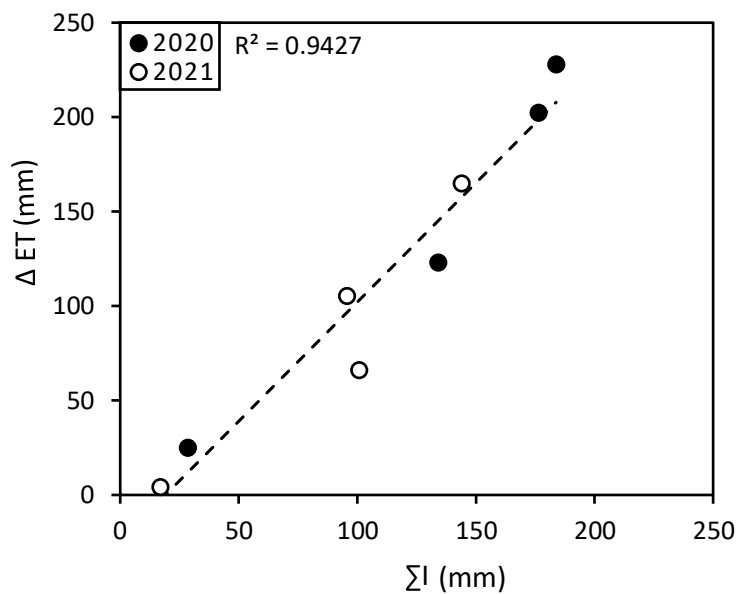
C.2 Irrigation and difference between ET_m and ET_{AMBAV} 

Figure S2 Correlation between cumulative irrigation (ΣI) and the difference between measured and simulated evapotranspiration ($\Delta ET = \Sigma ET_m - \Sigma ET_{AMBAV}$) over the vegetation periods 2020 (●) and 2021 (○).

C.3 Leaf area index 2020 and 2021

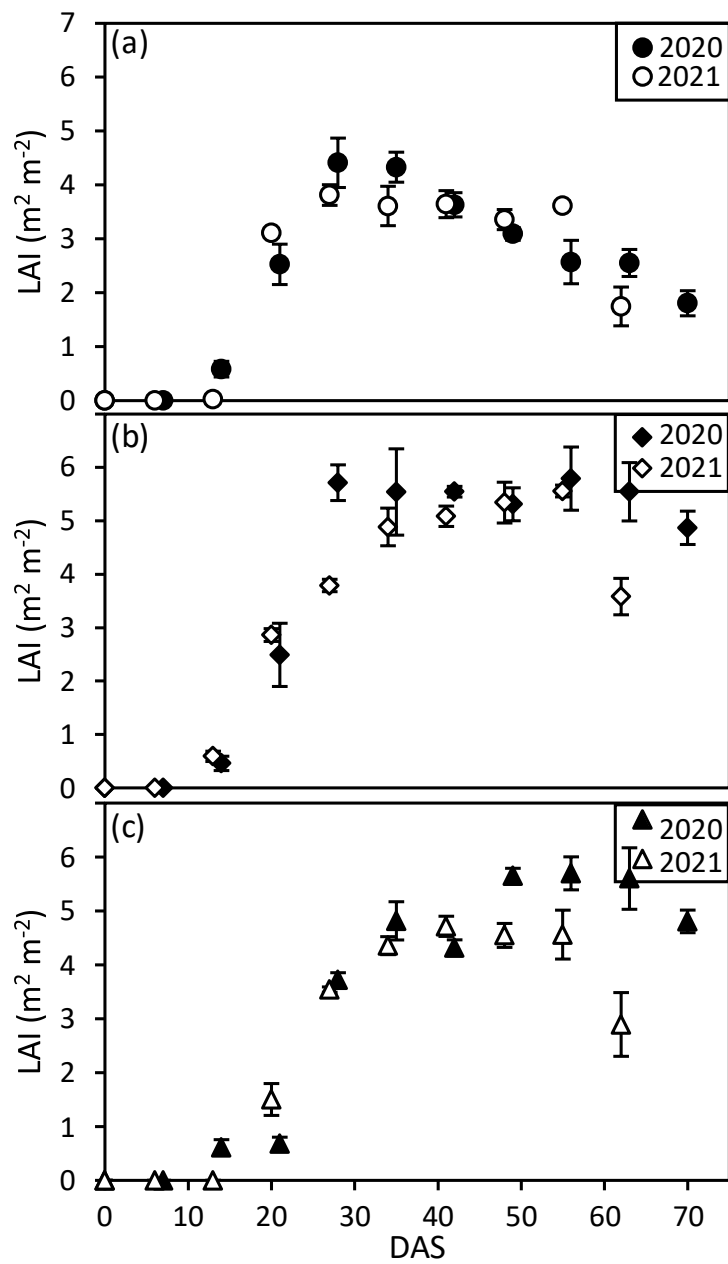


Figure S3 Time course of leaf area index (LAI) of the catch crops (a) white mustard (●), (b) oilseed radish (◆), and (c) phacelia (▲) during the vegetation periods 2020 ($n = 4$) and 2021 ($n = 5$). Mean values \pm SE.

C.1 Stomatal conductance

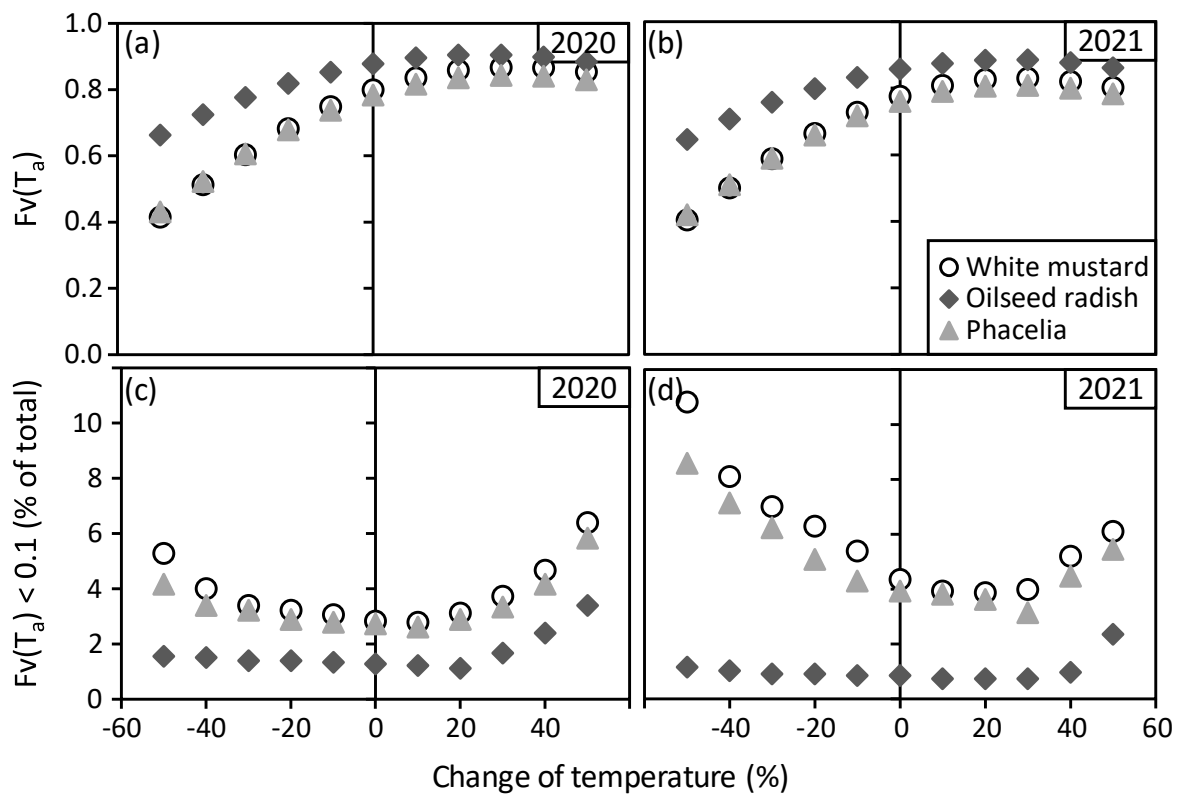


Figure S4 (a, b) Influence of a $\pm 50\%$ change of temperature on the temperature dependent term for the calculation of stomatal conductance ($F_v(T_a)$, $0 \leq F_v(T_a) \leq 1$) for the three catch crops phacelia (\blacktriangle), oilseed radish (\blacklozenge), and white mustard (\circ) based on meteorological data from the vegetation periods (a) 2020 and (b) 2021. (c, d) Percentage of total values with $F_v(T_a) < 0.1$ for the three catch crops phacelia (\blacktriangle), oilseed radish (\blacklozenge), and white mustard (\circ) dependent on $\pm 50\%$ change of measured temperature for the vegetation periods (c) 2020 and (d) 2021.

Appendix D

D.1 Time course of temperature 2021/22

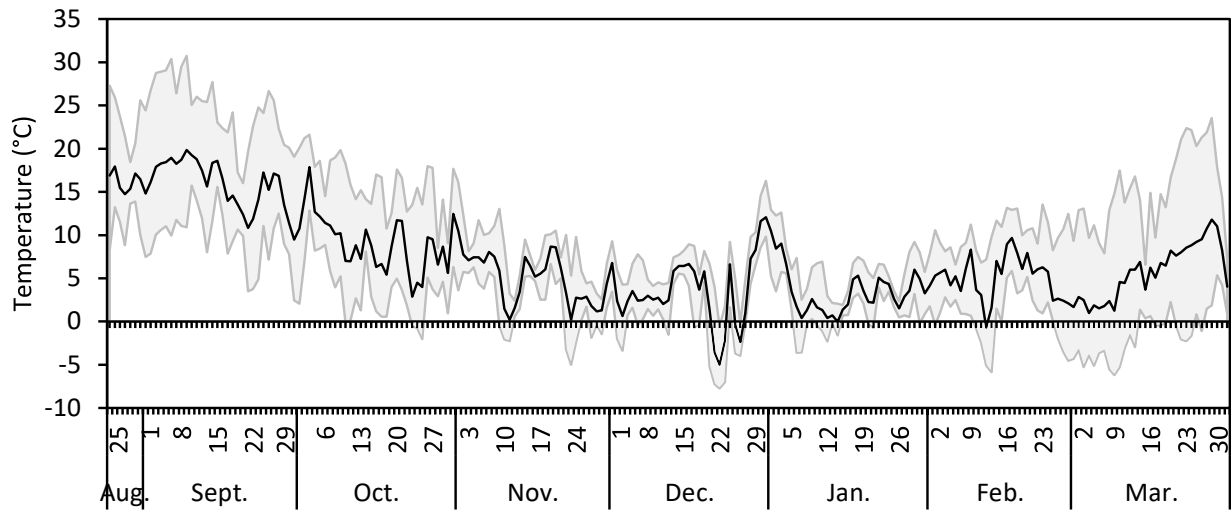


Figure D.1 Time course of temperature for the vegetation period 2021/22 at the experimental station of the Institute of Plant Nutrition in Giessen (50°35'53.30"N, 8°40'1.56"E). Solid black line = mean daily temperature, gray area = temperature range between maximum and minimum daily temperature.

D.2 Weekly evapotranspiration January – March 2022

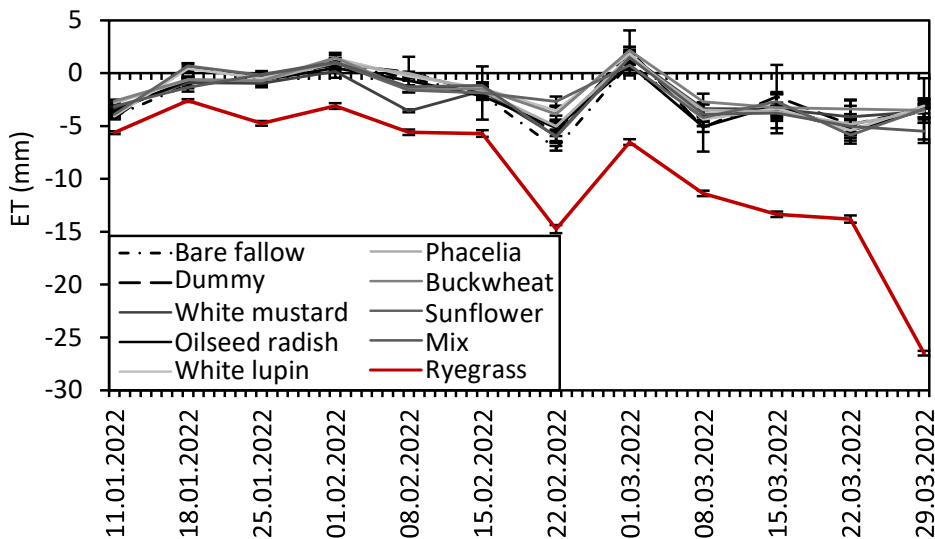


Figure D.2 Weekly evapotranspiration (ET) losses from 11.01.2022 until 29.03.2022 in the different treatments. Mean values ($n = 4$) \pm SE.

Acknowledgments

Conducting research is never a one-person job. Likewise, this PhD thesis is the result of the input of various people who were directly and / or indirectly involved in the process over the past few years.

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Eidesstaatliche Erklärung / Declaration under Oath

Erklärung gemäß der Promotionsordnung des Fachbereichs 09 vom 07. Juli 2004 § 17 (2)

Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angegeben habe.

Alle Textstellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht.

Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der 'Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis' niedergelegt sind, eingehalten.

Declaration according to the PhD regulations of the Faculty 09 as of 7 July 2004 §17 (2)

I declare: This thesis is my own work and was written without any help from others. I only used the sources mentioned in the thesis.

All passages which were quoted verbatim or analogously and all information which was passed verbally is marked as such.

The experiments conducted for this thesis were performed according to the code of best praxis described in the 'Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis'.

Giessen, _____

Tabea Selzer

Curriculum vitæ