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Phenotypic traits of sunflower varieties depend on the composition of cover crops

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ABSTRACT

Context: Introducing cover crop (CC) mixtures is a promising approach to enhance the multifunctionality of ecosystem services provided by CCs. However, CC mixtures have contrasting effects on subsequent crop yield, depending on multiple factors such as the type of subsequent crop and the mixture composition. In the context of climate change, sunflower (*Helianthus annuus* L.), which is adapted to environments with low nitrogen (N) and water requirements, has multiple varieties with different drought-tolerance strategies. However, little is known about how drought-tolerant sunflower varieties differ in their response to CCs in low-input systems.

Objective: This study aimed to characterize CC ecosystem services related mainly to N and water and to investigate how CC ecosystem services influence the responses of sunflower varieties that differ in drought sensitivity.

Methods: CCs and sunflower varieties were organized in a randomized non-complete block design with a split-plot arrangement in 2021–2022 and 2022–2023. CC treatments consisted of a pure grass CC (rye), a mixture of legume CCs (purple vetch/fodder pea), three mixtures of legume and non-legume CCs (faba bean/Indian mustard/phacelia; fodder pea/rye/purple vetch and fodder radish/hairy vetch/white mustard) and a relay CC treatment (fodder sorghum then faba bean). Sunflower varieties exhibited different drought-tolerance strategies for leaf expansion and transpiration. Establishment, development, growth, N status and productivity were evaluated for the sunflower varieties preceded by CCs through low- and high-throughput phenotyping. Multiple variables of growth and development were assessed by applying image-processing tools to unmanned aerial vehicle (UAV) RGB images.

Results: The results indicate that CCs influenced early and late N-release uptake by sunflower, thereby extending the seed-filling period. Optimizing the CC chosen allows for yields equivalent to those of intensively tilled bare soil, while increasing the amount of carbon returned to the soil and weed control in low-input cropping systems. Furthermore, in addition to the CC chosen, optimizing the sunflower varieties chosen can improve sunflower growth during dry years.

Implications: These results can inform decisions about CCs, sunflower variety and management in low-input systems to better match the nitrogen released from CC residues to subsequent cash crop responses during vegetative and post-flowering phases.

1. Introduction

Sunflower (*Helianthus annuus* L.), generally considered as a drought-tolerant crop, is cultivated mainly without irrigation in temperate climates due to its greater ability to extract water and preferential development of roots under water-deficit conditions (Maury et al., 2011; Garcia-Vila and Fereres, 2012; Debaeke and Izquierdo, 2021). However, water and heat stresses caused by climate change impact sunflower, generally advancing its flowering, shortening its growing season and decreasing its growth, which may decrease its yield in western Europe

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by up to 20–30 % by 2100 when drought occurs during its growing season (Moriondo et al., 2011; Debaeke et al., 2017b). Under water-deficit conditions, sunflower can maintain its water content using several adaptive processes, such as decreasing the leaf-expansion rate before flowering and decreasing transpiration by closing stomata, thereby decreasing photosynthesis and accelerating leaf senescence (Connor and Hall, 1997; Maury et al., 2011). Water deficit first decreases leaf expansion and then stomatal conductance when the fraction of transpirable soil water (FTSW) falls below 0.60 and 0.40, respectively (Sadras et al., 1993; Casadebaig et al., 2008; Garcia-Vila and Fereres, 2012). FTSW quantifies the degree of leaf-expansion and transpiration responses to water deficit (Sinclair, 2005), which depends on the genotype (Mojayad and Planchon, 1994; Pereyra-Irujo et al., 2008). Two main drought-tolerance strategies have been identified for sunflower (Casadebaig et al., 2008; Rengel et al., 2012; Duruflé et al., 2023). In the conservative strategy, sunflower decreases leaf expansion and transpiration when FTSW is relatively high, which decreases available soil water less; genotypes with this strategy may be better suited to environments with severe water deficit. In the productive strategy, sunflower maintains leaf expansion and transpiration despite a high water deficit. The net effect of these strategies on productivity depends on the intensity and frequency of water deficits. Similarly, the degree of water deficit can increase the harvest index and water-use efficiency (Flenet et al., 1996). Studies have highlighted that too few environmental conditions (e.g. soil, weather, crop management) are tested when assessing the performance of varieties before and after commercial use (Debaeke et al., 2011; Casadebaig et al., 2016). Indeed, varieties are rarely tested under stressful abiotic conditions, which are increasingly observed in the context of climate change, water restrictions and diverse cropping systems, such as low-input systems or systems with cover crops (CCs).

Moreover, when testing varieties, the physical environment, constraints perceived by plants (e.g. water and nitrogen (N) stresses) and key traits (e.g. drought tolerance) are rarely characterized routinely. Sunflower ideotypes must be designed to adapt to new environments and cropping systems (Debaeke et al., 2021). An ideotype was initially defined as a "biological model which is expected to perform or behave in a predictable manner within a defined environment" (Donald, 1968). In crop breeding, an ideotype can be extended to the crop phenotype that best meets a given objective. Plant breeders and agricultural advisors have recommended and ranked certain sunflower traits for water-limited environments and low-input systems, such as the ability to efficiently use nutrients from the soil or fertilizers to produce near maximum yields by improving root systems and the harvest index, which increases water-use efficiency (Debaeke et al., 2021). Moreover, low-input systems (*i.e.* lower N fertilization rate and plant density) could help decrease water use after flowering by decreasing leaf area and evapotranspiration and mitigating the risk of sunflower diseases compared to those of conventional systems (Sadras et al., 1991; Debaeke et al., 2014). In addition to the choice of cultivar, management decisions such as optimal sowing dates, N-fertilization practices and the introduction of CCs to mitigate impacts of crop water stress could help adapt sunflower to water-limited environments (Allinne et al., 2008; García-López et al., 2016; Souques et al., 2024).

CCs are known to provide supporting services such as reducing soil erosion; improving water quality and soil physical, biological and chemical fertility and regulating services such as control weeds and plant pathogens (Van Eerd et al., 2023). Introducing CC mixtures is a promising approach to increase the multifunctionality of the ecosystem services provided by CCs (Tribouillois et al., 2016; Couëdel, 2018). Thus, the CCs chosen influence potential ecosystem services or disservices (i.e. negative effects) and can influence the yield of the following cash crop. In the literature, CC mixtures have contrasting effects on the yield of the subsequent crop, since their influence on yield depends on the type and management of CCs, the type of cash crop, fertilizer application to the cash crop (or not) and soil and climate conditions (Bourgeois et al., 2022; Wojciechowski et al., 2023). For sunflower, most legume CCs (in a monocrop or mixture) increased or did not influence yield (Wortman et al., 2012; Rosner et al., 2018; Ait Kaci Ahmed et al., 2022), while non-legume CCs could decrease it (Adeux et al., 2021; Ait Kaci Ahmed et al., 2022; Meyer et al., 2022). The yield could decrease due to depletion of water caused by CCs terminated late and/or spring drought, both of which increase the water stress of sunflower (Meyer et al., 2022), or by N immobilization caused mainly by non-legume CCs (in a monocrop or mixture) (Adeux et al., 2021; Ait Kaci Ahmed et al., 2022; Meyer et al., 2022). Non-legume CCs take up large amounts of mineral N from the soil, decrease nitrate leaching effectively and release less N than legume CCs, as reflected in their higher C:N ratio (20−30), which also leads to lower and slower mineralization of CC residues (Thorup-Kristensen et al., 2003; Couëdel, 2018). A moderate C:N ratio ($>$ 25) can lead to N immobilization by micro-organisms that assimilate soil mineral N (SMN) to meet their N requirements (Nicolardot et al., 2001). Matching the N released from CC residues to the N demand of the subsequent cash crop is crucial to optimize the cash crop's N status and N uptake (Lara Cabezas et al., 2004; Raimondi et al., 2021). Improving the timing of mineralization of N from CCs to the N uptake of the subsequent crop could depend on the amount of N released by CCs (Raimondi et al., 2023). This could be critical for sunflower, whose N requirements peak between floral initiation and anthesis (ca. 120 kg N. ha^{-1}), according to its critical N-dilution curve (Debaeke et al., 2012). Nevertheless, maintaining an optimal N supply during seed filling can delay leaf senescence after flowering, which is generally accelerated by water deficit (Goswami and Srivastava, 1988; Moschen et al., 2017). Water and N influence the growth, physiology and productivity (e.g. grain yield, oil concentration) of sunflower (Debaeke and Izquierdo, 2021). Some studies have addressed effects of the interaction between water deficit and N supply on sunflower (Gonzalez-Dugo et al., 2010; Ahmad et al., 2014). Water deficit can decrease the amount of SMN available for crops, because water is needed to mineralize N and solubilize N fertilizers, which can be taken up by roots. Water deficit also influences physiological mechanisms such as leaf expansion, which can decrease crop N demand. However, little is known about how sunflower varieties with contrasting drought tolerance respond to different N-release patterns from CC residues (Souques et al., 2024).

In the present study, we studied the field responses of sunflower varieties with differing drought sensitivity to a range of preceding CCs, during two growing seasons, in southwestern France. We characterized CC ecosystem services related mainly to soil water and N dynamics and their impacts on the establishment, development, growth and productivity of different sunflower varieties.

2. Materials and methods

2.1. Experimental site

The field experiment, conducted over 2 years (2021–2022 and 2022–2023), was performed at the INRAE (French National Research Institute for Agriculture, Food and Environment) research station in Auzeville-Tolosane, southwestern France (43° 31' N, 1° 29' E). The experiment was carried out on two adjoining plots with deep clay-loam soil (ca. 1.6–1.8 m). The main characteristics of the soil differed among depths and years (Table A.1). The site has an oceanic climate with both Atlantic and Mediterranean influences. Daily weather data were collected from a weather station located at the experimental site (Fig. 1A, B). Soil water content (SWC) was monitored between sunflower sowing and harvest using capacitance probes, which measured SWC every 5 cm over a depth of 90 cm (Sentek Sensor Technologies, Australia) (Fig. 1C).

2.2. Treatments

The conventional cropping system in southwestern France consists of

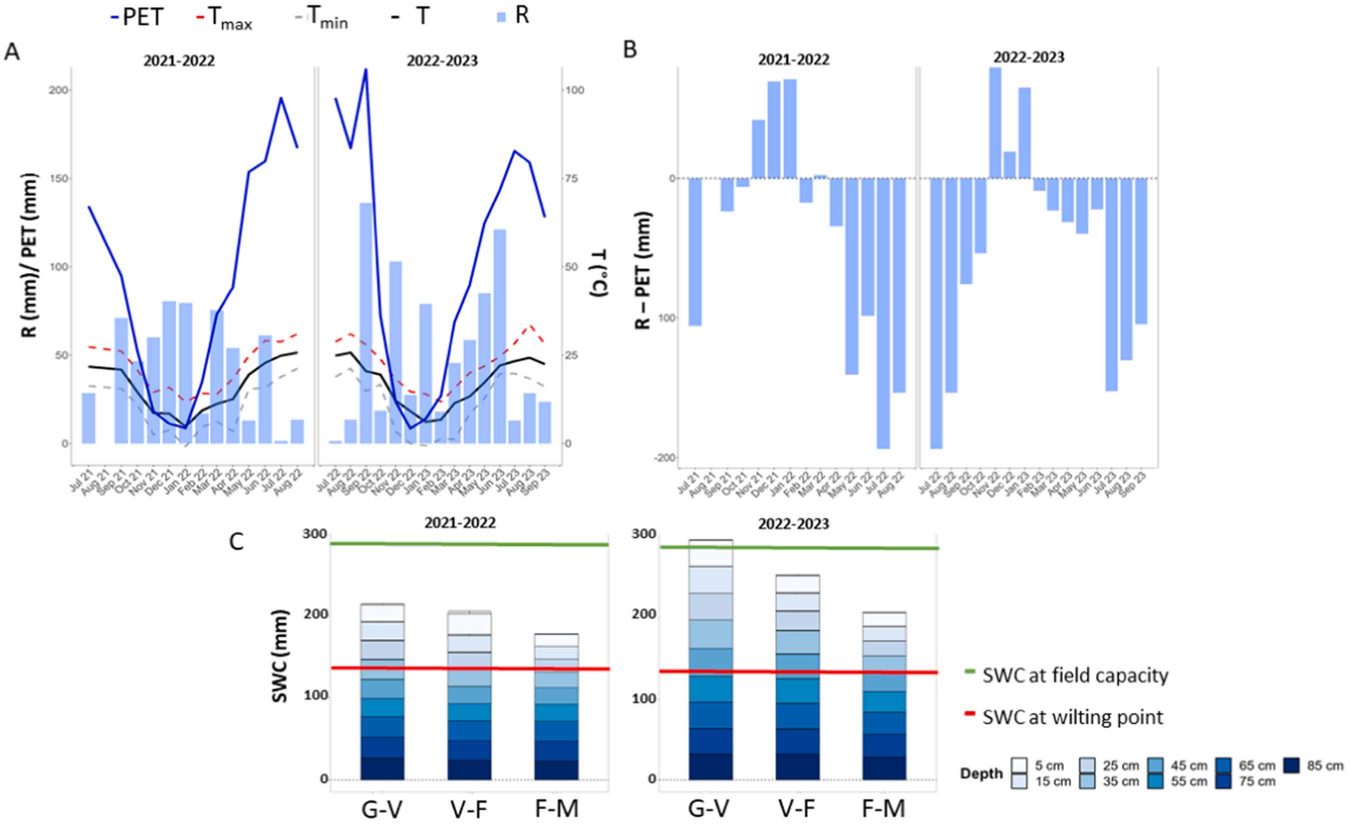


Fig. 1. Weather characteristics in Auzeville (INRAE research station), France, during 2021–2022 and 2022–2023 agricultural sampling campaigns. **A** Monthly rainfall (R) (mm), potential evapotranspiration (PET) (mm), mean temperature (T) (°C), mean minimum temperature (T_{min}) (°C) and mean maximum temperature (T_{max}) (°C). **B** Effective rainfall (R – PET) (mm) calculated as the sum of daily measurements. **C** Mean soil water content (SWC) (mm) measured with a soil moisture sensor every 5 cm over a depth of 90 cm during three periods (G-V: germination to vegetative stages; V-F: vegetative to flowering stages; F-M: flowering to maturity stages).

a short rotation of durum wheat (*Triticum turgidum* L. subsp. *durum* Desf.) and sunflower. In this study, the long fallow period between durum wheat and sunflower was used to study six CC treatments and one bare soil treatment. The weather conditions and cropping operations varied during the experiments (Table 1). In both years, durum wheat was harvested at the end of June or beginning of July.

Six CC treatments were selected to represent the CC mainly used in France by farmers before sunflower (mixture of grass and legume, crucifers (pure or mixture) and mixture of legume and phacelia) (Agreste, 2017; Terres Inovia, 2021) and different dynamics of N mineralized by CCs.

The six CC treatments consisted of the following:

-a "relay" CC treatment with fodder sorghum (*Sorghum bicolor* L. cv “Piper”) sown immediately after wheat harvest, followed by faba bean CC (*Vicia faba* L. cv “Irena”) sown in the fodder sorghum in autumn (on 19 October in both years). The fodder sorghum was grinded a few days after faba bean sowing, and the first frosts killed the sorghum plants, while the faba bean developed over the winter and spring.

-five CC treatments sown with a cereal seed drill around mid-September after seedbed preparation using a rotary harrow. These treatments consisted of (i) a pure rye CC (*Secale cereale* L. cv “Wastauro”), (ii) a mixture of fodder pea/purple vetch CC (*Pisum sativum* L. cv “Arkta”/*Vicia bengalensis* L. cv “Titane”), (iii) a mixture of rye/fodder pea/purple vetch CC, (iv) a mixture of faba bean/Indian mustard/phacelia CC (*V. faba* L. cv “Irena”/*Brassica juncea* L. cv “Vitasso”/*Phacelia tanacetifolia* Benth. cv “Maja”), and (v) a mixture of fodder radish/hairy vetch/white mustard CC (*Raphanus sativus* L. var. oleiformis Pers. cv “Terranova”/*Vicia villosa* Roth. cv “Savane”/*Sinapsis alba* L. cv “Abraham”).

A bare soil treatment was also included. Although keeping soils bare and untilled during the long fallow period is the most common practice that farmers use, the soil in this study was kept weed-free mechanically, using two passes of a cultivator (working depth: 12–15 cm), and by hand. Farmers would probably use a single application of glyphosate, but this herbicide is no longer authorized on INRAE research stations. The two cultivator passes also improved the seedbed structure.

The experimental design was a randomized non-complete block design with a split-plot arrangement including CC treatments in main plots (288 m^2: 48 m x 6 m) and sunflower varieties in subplots (27 m^2: 4.5 m x 6 m), with four replicates in 2021–2022 and three replicates in 2022–2023. CC treatments were irrigated at sowing in 2022–2023, due to a particularly dry summer in 2022. The proportion of species in CC mixtures was calculated as the recommended density of each sole crop divided by the number of species (Table A.2). CC was terminated in mid-April using a flail mower and quickly incorporated into the soil using a disc cultivator twice (working depth: 10–12 cm). A rotatory cultivator was used to refine the coarse seedbed between CC termination and sunflower sowing.

Sunflower was sown with 50 cm spacing between plant rows using an experimental seed drill at the end of April, once CC treatments had been terminated. A roller-crimper was used to ensure good seed-soil contact in 2022 due to sowing in wet furrows. The subplot factor consisted of sunflower cultivars with different drought tolerance strategies for leaf expansion (LE) and transpiration (TR): a conservative strategy for LE and TR (MAS 86OL), a conservative strategy for LE but a productive strategy for TR (MAS 89 M), a productive strategy for LE but a conservative strategy for TR (CARRERA) and a productive strategy for LE and TR (MAS 98 K) (Table 2). The subplot factor also included a bare soil plot (*i.e.* without sunflower) in which weeds were controlled with a rotary cultivator or manually to estimate the decomposition of CC

Table 1
Climate characteristics, cover crops and sunflower management. The fallow period corresponds to the duration between harvest of the preceding crop and sunflower sowing. The sunflower growing season (GS) starts at sowing and stops at maturity. R: Rainfall, SGDD: Sum of growing degree days, Tb: Base temperature, T: Temperature, PET: Potential evapotranspiration, DAS: Days after sowing.

Category	Characteristic	2021–2022	2022–2023
Climate	Cumulative R(mm) during the fallow period	527	383
	SGDD (°C.d) during the fallow period (Tb = 0°C)	3828	2620
	Mean T (°C) during the fallow period	12	12
	Mean PET (mm) during the fallow period	615	345
	Cumulative R (mm) during the sunflower GS	87	242
	SGDD (°C.d) during the sunflower GS (Tb = 4.8°C)	2202	2016
	Mean T (°C) during the sunflower GS	23	21
	Mean PET (mm) during the sunflower GS	663	573
CC cycle	**Sowing date**		
	Fodder sorghum/Faba bean	9 July 21/19 Oct 21	30 Jun 22/19 Oct 22
	Other CC treatments	13 Sept 21	12 Sept 22
	Irrigation (mm)		
	Fodder sorghum/Faba bean	0/0	60/30
	Other CC treatments	0	20
	Termination date		
	Fodder sorghum	20 Oct 21	24 Oct 22
	Other CC treatments	7 Apr 22	18 Apr 23
Sunflower cycle	**Sowing date**	28 Apr 22	24 Apr 23
	Fertilization (kg N.ha^{-1})	0	0
	Irrigation (mm)	20 (13 DAS)	0
	Weed management	chemical	chemical and mechanical

residues after termination. To focus on the drought strategies of sunflower cultivars, all cultivars had high resistance to fungal diseases. The sowing sunflower density was 88,000 seeds.ha^{-1}. Wireworm (both years) and slug controls (only in 2022–2023) were applied at sowing, and a net was set up at sowing and maturity to protect seeds from birds. Irrigation was applied only once, 13 days after sowing (20 mm) in 2022, because a crust had formed, which could have decreased sunflower emergence. Weeds were managed with herbicides in both years (S-Metolachlore, 1.04 L.ha^{-1}) and with an inter-row cultivator in 2023 due to high weed pressure. No N fertilizer was applied in order to reveal the CC green-manure effect on sunflower growth.

2.3. Measurements

2.3.1. Cover crop and soil sampling

Before CC termination, shoot samples of each species in CC treatments were collected from 0.5 m^2 quadrats in each plot. Additionally, the shoots and roots of 10 plants of each species in CC treatments were collected to estimate root biomass and calculate the root:shoot ratio of CC species. Roots were extracted to a depth of 30 cm using a spade fork, which allowed the majority of roots to be collected for the species studied. The soil blocks were then immersed for 24 hours in the laboratory and gently washed with water. When weeds were associated with the CCs, they were removed after rinsing so as not to be counted in the biomass of the species sown as CCs. Fresh shoots and roots of each species were weighed. A sample of shoots and roots of each species in CC treatments was dried at 80°C for 48 h, then weighed and ground to measure total carbon (C) and N concentrations via elemental analyses using the Dumas method (MicroVario Cube, Elementar, Langenselbold, Germany) and to measure cellulose, hemicellulose and lignin concentrations using the Van Soest method (Van Soest et al., 1991). N acquired by CCs results from soil N uptake and biological N fixation in legumes and was calculated as N concentration multiplied by CC biomass.

At CC sowing and termination, five soil cores were randomly extracted from 0–30, 30–60 and 60–90 cm layers with a hydraulic core drill in each block (at CC sowing) and in each plot (at CC termination) and pooled by depth. Fresh and dry soil cores were weighed to evaluate the amount of soil water (mm). SMN (kg N.ha^{-1}) was calculated by measuring mineral N concentrations (i.e. nitrate and ammonium) in the pooled soil cores using a continuous flow auto-analyzer (Skylar 51,000, Skalar Analytic, Breda, Netherlands) (standard NF ISO 14256–2). The decrease in SMN due to N acquisition by CCs was assessed by comparing the SMN of tilled bare soil and to that of CCs at termination.

2.3.2. Sunflower establishment and development

Unmanned aerial vehicle (UAV) flights were operated each week from sunflower emergence to 28 July in 2022 and 11 September in 2023. A multispectral camera with a 5.7 mm focal length lens (acquiring 1600 ×1300 pixel images) was mounted on a quadcopter drone (Phantom 4, DJI). The drone flew at a controlled altitude of 20 m and a constant speed of 2.2 m.s^{-1} for ca. 20 min per flight, with images captured at 1 s intervals. Flights were performed during clear and cloudless days from 8:00–12:00. An automatic image-processing pipeline was applied to the images (Hiphen, Avignon, France) to count the emerged plants (BBCH stages 11–12) and flowering capitula (BBCH stages 61–65) detected by a deep-learning-based object-detection algorithm (Fast R-CNN) (Ren et al., 2017) in each plot each year. The stage of sunflower maturity was assessed through manual monitoring each week using the scale of Terres Inovia (Martin-Monjaret, 2019).

Additionally, to understand how CC influenced sunflower senescence, the area under the cover (AUC) of green cover (%.°C.d) and of normalized green cover (°C.d) based on the sum of degree days were determined from images acquired weekly after flowering (from 26 July) until maturity of the earliest treatments (23 August) in 2022–2023. Green cover (%) detection and quantification were achieved by determining the percentage of green pixels in each plot using the XGBoost method (Chen and Guestrin, 2016). This approach assesses the likelihood of a pixel being green by analyzing its values across various RGB and LAB color channels. The AUC of green cover, which equaled the green cover at each sum of degree days, was used as a proxy of the duration of photosynthetically active leaf area after flowering. In addition, normalized green cover, which equaled the green cover at each

Table 2
Oil type, flowering and maturity earliness, and varietal parameters for the ecophysiological response of sunflower to soil water deficit as implemented in the SUNFLO crop model for the four varieties studied (Gosseau et al., 2019; Casadebaig et al., 2008; Souques et al., 2024). Values correspond to model parameters that describe the shape of the response of the physiological processes (leaf expansion and transpiration) to the fraction of transpirable soil water. The terms in parentheses indicate how early or late the process responds to water deficit (i.e., at lower or higher water deficit, respectively). TKW: thousand-kernel weight.

Variety	Oil type	Flowering	Maturity	TKW (g)	Leaf expansion rate	Transpiration rate
MAS 86OL	oleic	mid-early	mid-late	70	−2.40 (**mid-early**)	−7.64 (**mid-early**)
MAS 89 M	linoleic	mid-late	mid-late	57	−2.15 (**early**)	−13.98 (**late**)
MAS 98 K	linoleic	mid-early	mid-late	63	−3.68 (**mid-late**)	−8.68 (**mid-late**)
CARRERA CLP	linoleic	late	late	76	−4.55 (**late**)	−5.40 (**early**)

sum of degree days divided by the maximum green cover, was used to estimate a proxy of the leaf senescence ratio. The leaf senescence ratio equaled the number of senescent leaves (*i.e.* with < 50 % green area) divided by the total number of leaves at flowering, on 27 July, 8 and 22 August 2023.

2.3.3. *Sunflower growth and N status*

To calculate plant height and biovolume, we used 3D point-cloud data generated from photogrammetric processing using Agisoft Photoscan software (v1.91) on UAV RGB images for each plot. To our knowledge, no publications have been published on the use of biovolume for sunflower, but it has been used to estimate the above-ground biomass of forage crops (Sangjan et al., 2022) and olive trees (Safonova et al., 2021), with good correlations ($r > 0.8$). For each plot, the soil baseline was determined as the lowest point in an expanded area (i.e. the soil buffer, including the plot area with soil) (Fig. A.3.A). The maximum height of vegetation was calculated as the vertical distance between the soil baseline and the 99th percentile of the height distribution across the entire plot inside (i.e. the height exceeded by only 1% of all points measured in the plot). Plant height heterogeneity was computed using sections of 30 cm within the plot limits (Fig. A.3.B). The maximum height of each section was identified, and a coefficient of variation (CV) of the plot was calculated. Similarly, the biovolume, which approximates biomass well, was calculated using a regular grid whose cell size was set as the resolution of the point-cloud data (i.e. 0.025 m) (Fig. A.3. C and D). Biovolume is defined as the sum of the maximum height in each grid cell multiplied by the cell's area:

$$Biovolume_{plot} = \sum_{1}^{n} Max\ height_{n} \quad \times cell\ area \tag{1}$$

The biovolume rate ($m^3.^{\circ}C^{-1}.d^{-1}$), used as a proxy for growth rate, equaled the slope of the biovolume from plant emergence to 5 July in 2022 and 3 July in 2023.

Leaf area index (LAI) was estimated by measuring the total leaf number, area and position of the largest leaf at flowering for 10 sunflowers on MAS 98 K subplots in 2021–2022 and for subplots of all varieties in 2022–2023. LAI was estimated as a function of these plant-architecture descriptors in the SUNFLO crop model (Casadebaig et al., 2008).

To assess the N status of sunflower at vegetative and flowering stages, the shoots of five sunflower plants (variety MAS 98 K) were sampled from 0.5 m^2 quadrats in each subplot. Fresh shoots were weighed and oven dried at 80°C for 48 h. The dried shoots were weighed and ground to measure total C and N concentrations via elemental analyses using the Dumas method (MicroVario Cube, Elementar, Langenselbold, Germany). The N uptake by sunflower plants (kg $N.ha^{-1}$) equaled shoot N concentration multiplied by shoot biomass. The N Nutrition Index (NNI), an indicator of the N status of plants, was calculated for sunflower using the critical N-dilution curve during vegetative growth developed by Debaeke et al. (2012):

$$NNI = \frac{Nm}{Nc} \tag{2}$$

$$Nc = 4.53 \times DM^{-0.42} \tag{3}$$

where Nm is the shoot N concentration (%), Nc is the critical shoot N concentration (%) (*i.e.* minimum shoot N concentration needed to maximize crop growth), which was calculated using the critical N-dilution curve for sunflower and DM is the dry aboveground biomass. The vegetative and flowering stages corresponded to sunflower stages E1 and F1, respectively, of the scale used by Terres Inovia (Martin-Monjaret, 2019).

2.3.4. *Sunflower productivity*

Aboveground biomass (shoot) ($t.ha^{-1}$), seed number, thousand-kernel weight (TKW, g) and yield ($t.ha^{-1}$) were measured by collecting 10 plants in each subplot at maturity. For one variety (MAS 98 K), the shoots and roots of five plants were collected to estimate the root: shoot ratio and root biomass. Roots were extracted to a depth of 30 cm using a spade fork, which allowed the majority of roots to be collected for the species studied. The soil blocks were then immersed for 24 hours in the laboratory and gently washed with water. Dry shoot, seed and root biomass were ground to measure the total N concentration via elemental analyses using the Dumas method (MicroVario Cube) and to estimate the amount of N in shoots, seeds and roots as N concentration multiplied by its biomass per ha. The seed protein concentration was calculated as the seed N concentration multiplied by 5.3. Seed oil concentration (as a percentage of dry weight) was measured using a nuclear magnetic resonance analyzer (minispec MQ10, Bruker, Billerica, Massachusetts, USA). The amount of oil in seeds was calculated as the oil seed concentration multiplied by its grain yield.

The harvest index was calculated as the seed yield divided by total aboveground biomass at harvest. Water-use efficiency for total aboveground biomass ($kg.ha^{-1}.mm^{-1}$) was calculated as sunflower total aboveground biomass divided by rainfall, irrigation from sowing until maturity plus variation of soil water content from sowing to harvest.

2.3.5. *Sunflower soil sampling*

Five soil cores were taken at three depths (i.e. 0–30, 30–60 and 60–90 cm) in each subplot using a hydraulic core drill during the sunflower growing season. Soil cores were also collected from a bare soil plot without sunflower plants during the growing season on 20 June 2022 and 22 June 2023, 6 July 2022 and 13 July 2023, and 20 September 2022 and 2023, which corresponded to the vegetative, flowering and maturity stages of the sunflower in the other plots, respectively. These dates were chosen to estimate the soil N available for sunflower during the growing season, including N mineralized by humus and CCs.

2.4. *Statistical analysis*

All data were analyzed using R software (R Core Team, 2023). The linear mixed model included four factors – CC treatment ($\beta\mathbf{1}$), sunflower variety ($\beta\mathbf{2}$), year ($\beta\mathbf{3}$) and block ($\beta\mathbf{4}$) – their interactions – the random effect with CC treatment nested within block (u) and the residual error (ϵ), using the *lmerTest* package:

$$Y_{ijkl} = \mu + \beta\mathbf{1}_i + \beta\mathbf{2}_j + \beta\mathbf{3}_k + \beta\mathbf{4}_l + (\beta\mathbf{1}\ \beta\mathbf{2})_{ij} + (\beta\mathbf{1}\ \beta\mathbf{3})_{ik} + (\beta\mathbf{2}\ \beta\mathbf{3})_{jk} + (\beta\mathbf{1}\ \beta\mathbf{2}\ \beta\mathbf{3})_{ijk} + u_{li} + \epsilon_{ijk}$$

First, analysis of variance was performed to test effects of treatments on sunflower establishment, development, N status, growth and productivity measured in 2021–2022 and 2022–2023. Then, analyses of variance were carried out separately for each sunflower variety in order to study the effects of the fallow period management method and the year on the variables studied and for each CC treatments in order to study the effects of the sunflower varieties and the year on the variables.

Post-hoc multiple comparisons (Tukey's test) were performed to compare treatments within a factor. Correlation and regression models were used to assess relationships between variables for all sunflower varieties and then for each variety individually. Differences among treatments were considered significant at $\alpha = 0.05$.

The phenotypic plasticity method of Finlay and Wilkinson (1963) was used to study the variability in sunflower final aboveground biomass (shoot) as a function of CC treatment across all sunflower varieties and to analyze the response of drought tolerance strategy for each variety over both years. The environmental mean of final aboveground biomass was determined as the mean of biomass over all varieties for each CC treatment. The slope of the regression defined the plasticity of aboveground biomass for each variety.

3. Results

3.1. Cover crop functions

The mean total biomass of CCs at CC termination varied from 2.7 t.ha^{-1} for the Pea+Vetch mixture in 2021–2022–17.3 t.ha^{-1} for the Sorghum→Faba bean in 2022–2023 (Table 3). CCs had higher mean total biomass over the fallow period of 2022–2023 than over that of 2021–2022.

Over the two years, the C concentration of the CCs varied from 42.3 % for Rye to 46.1 % for Faba bean+Mustard+Phacelia, which resulted in a total acquisition of C of 1.2–7.4 t C.ha^{-1}. Faba bean+Mustard+Phacelia, Radish+Vetch+Mustard and Sorghum→Faba bean acquired the most C in both years (Fig. 2).

The mean total N acquired by CCs was 50 % higher in 2022–2023 than in 2021–2022 ($p < 0.001$), due to higher biomass and N concentration. Total N acquired by CCs ranged from 38 kg N.ha^{-1} for Rye to 250 kg N.ha^{-1} for Sorghum→Faba bean (Table 3). The percentage of total N acquired by belowground biomass of CCs ranged from 3 % for Pea+Vetch to 22 % for Rye (Table A.4).

CCs decreased SMN by a mean of 19 kg N.ha^{-1} in 2021–2022 and 66 kg N.ha^{-1} in 2022–2023, resulting in low SMN at CC termination (mean of 20 kg N.ha^{-1} both years) (Table A.5) (both $p < 0.001$).

SWC at CC termination (60 % and 100 % of available soil water in 2021–2022 and 2022–2023 for tilled bare soil) did not differ among CC treatments and tilled bare soil in 2021–2022. Conversely, at CC termination in 2022–2023, SWC was higher for tilled bare soil than for all CC treatments ($p < 0.001$) (Table A.4). CC mixture Pea+Vetch in 2022–2023 had the lowest SWC among CC treatments (20 % lower than that in bare soil).

Two indicators were used to assess N mineralization dynamics as a function of CC treatment: the C:N ratio of CCs (shoots + roots) and SMN in a bare soil (during the sunflower growing season) vs. that with decomposing CC residues 65 and 84 days after termination (DAT) (in 2022 and 2023, respectively), 102 and 106 DAT (2022 and 2023, respectively), and 176 DAT, corresponding to vegetative, flowering stage and maturity stages of sunflower, respectively. The total C:N ratio ranged from 18 to 41, with differences observed among CC treatments and between years (Table 3). The lowest total C:N ratio was measured for Pea+Vetch (18) and Rye+Pea+Vetch (20) compared to other CC treatments in 2021–2022 (mean C:N ratio of 36) ($p < 0.001$) and Faba bean+Mustard+Phacelia (19) compared to Radish+Vetch+Mustard (40) in 2022–2023 ($p < 0.001$). Moreover, SMN (in a bare soil) at vegetative and flowering stages was higher in 2021–2022 than in 2022–2023. N mineralization dynamics varied among CCs, with some CC residues releasing N early at sunflower's vegetative stage (e.g. Pea+Vetch in 2021–2022, Sorghum→Faba bean and Faba bean+Mustard+Phacelia in 2022–2023), while others released N later (Rye+Pea+Vetch in 2022–2023) or immobilized soil N during the vegetative stage (Rye and Radish+Vetch+Mustard) (Fig. A6).

The biochemical composition of CC residues did not differ significantly between years, except for higher lignin concentration in 2022–2023 ($p < 0.001$) (Table 3). Rye grown alone had lower lignin and higher hemicellulose concentrations than other CCs did ($p < 0.001$). Total cellulose concentration was higher for mixtures of Faba bean+Mustard+Phacelia and Radish+Vetch+Mustard in 2021–2022 and for Radish+Vetch+Mustard in 2022–2023 than for other CC treatments, due mainly to a higher cellulose concentration in mustard residues ($p < 0.001$).

The higher SMN at CC sowing in 2022–2023 stimulated weed growth, leading to higher weed biomass compared to that in 2021–2022 for certain CC mixtures ($p < 0.001$) (Table 3 and A.1). Weed-control levels by CCs varied, with more control by certain mixtures (*e.g.* Sorghum→Faba bean and Faba bean+Mustard+Phacelia) and less control for others composed of less weed-competitive legumes (e.g. Pea+Vetch and Rye+Pea+Vetch) (Table 3).

3.2. Impact of cover crops on varietal traits of sunflower

The experimental design enabled study of effects of CCs on the establishment, growth, development and productivity of sunflower varieties, as well as effects of interactions between CC treatment and

Table 3
Mean total cover crop (CC) (and standard error) biomass (t.ha^{-1}), carbon (C) acquired (t.ha^{-1}), nitrogen (N) acquired (kg N.ha^{-1}), C:N ratio for aboveground and belowground biomass of CC species, percentage of weeds in aboveground biomass and biochemical composition of CCs aboveground biomass (i.e., lignin, hemicellulose and cellulose percentages) without weeds at CC termination in 2021–2022 and 2022–2023. For Sorghum→Faba bean, biomass and C acquired were determined using total sorghum biomass at sorghum termination in October; N acquired and C:N ratio were calculated using sorghum mulch at CC termination, as indicated by highlighted data (unpublished data from previous INRAE studies). Composition was not measured for sorghum in Sorghum→Faba bean mixture. Different letters indicate significant ($p < 0.05$) differences between CC treatments using Tukey's test. NS: not significant.

	Aboveground + Belowground Aboveground							
Cover crop treatment	**Biomass** t.ha^{-1}	**C acquired** t C.ha^{-1}	**N acquired** kg N.ha^{-}	**C:N ratio**	**Weed percentage** 1 %	**Lignin** %	**Hemicellulose** %	**Cellulose** %
2021–2022								
Rye	3.3 (0.1) a	1.2 (0.1) a	38.3 (1.3) a	34.0 (2.2) bc	13.4 (3.3) ab	3.2 (0.7) a	22.7 (0.5) c	16.7 (0.2) a
Pea+Vetch	2.7 (0.2) a	1.2 (0.1) a	71.2 (2.6) b	18.1 (1.8) a	40.6 (4.9) c	9.0 (0.7) b	12.1 (0.4) ab	17.5 (0.6) a
Rye+Pea+Vetch	3.2 (0.1) a	1.4 (0.1) a	77.2 (3.4) b	20.4 (0.5) a	19.9 (4.1) b	9.6 (0.3) b	16.6 (0.5) b	18.0 (0.2) a
Faba bean+Mustard+Phacelia	7.3 (0.4) b	3.1 (0.1) b	106.5 (9.3) cd	39.5 (2.4) c	5.8 (1.1) a	9.5 (0.3) b	11.8 (0.4) ab	23.0 (0.7) b
Sorghum→Faba bean	6.5 (0.4) b	2.9 (0.2) b	126.7 (9.2) d	31.0 (0.1) b	4.1 (0.9) a	5.2 (0.7) a	9.6 (2.7) a	14.3 (0.6) a
Radish+Vetch+Mustard	7.6 (0.2) b	3.0 (0.4) b	99.63 (3.7) c	40.5 (0.9) c	11.0 (2.5) ab	8.7 (0.3) b	11.6 (0.2) ab	24.7 (0.8) b
Year	5.1 (0.2) a	2.1 (0.2) a	86.5 (4.3) a	30.4 (1.3)	15.8 (2.8) a	7.5 (0.9) a	14.1 (0.3)	19.03 (0.5)
p CC	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
2022–2023								
Rye	4.0 (0.4) a	1.8 (0.2) a	68.1 (7.4) a	28.1 (0.9) ab	44.3 (5.9) bc	4.3 (0.5) a	19.9 (0.2) c	19.4 (0.2) a
Pea+Vetch	5.2 (0.6) a	2.4 (0.2) a	109.7 (3.2) b	27.0 (3.7) ab	71.3 (4.7) d	11.3 (1.3) b	13.9 (0.8) b	17.6 (0.4) a
Rye+Pea+Vetch	4.1 (0.3) a	1.9 (0.2) a	96.8 (7.5) b	25.9 (2.0) ab	55.7 (4.7) cd	10.2 (0.1) b	14.3 (0.2) b	19.6 (0.2) a
Faba bean+Mustard+Phacelia	6.1 (0.5) a	2.8 (0.3) a	185.1 (15.5) c	18.7 (3.2) a	5.1 (1.7) a	10.3 (0.4) b	11 (0.6) ab	18.6 (1.0) a
Sorghum→Faba bean	17.3 (1.3) b	7.4 (0.3) b	250.4 (9.5) d	31.4 (4.6) ab	1.1 (0.5) a	7.9 (0.7) ab	9.0 (0.3) a	14 (0.5) a
Radish+Vetch+Mustard	4.7 (0.9) a	2.1 (0.4) a	67.5 (9.8) a	39.9 (1.5) b	29.6 (1.7) b	13.6 (0.9) b	14.2 (0.3) b	32.5 (1.0) b
Year	6.9 (0.7) b	3.1 (0.2) b	130.0 (8.0) b	28.7 (2.6)	34.5 (3.1) b	9.2 (0.7) b	13.7 (0.4)	20.3 (0.5)
p CC	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.01	< 0.001	< 0.001
2021–2022 and 2022–2023								
p CC	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
p year	< 0.001	< 0.001	< 0.001	NS	< 0.001	< 0.001	NS	NS
p CC * year	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	NS	NS	< 0.001

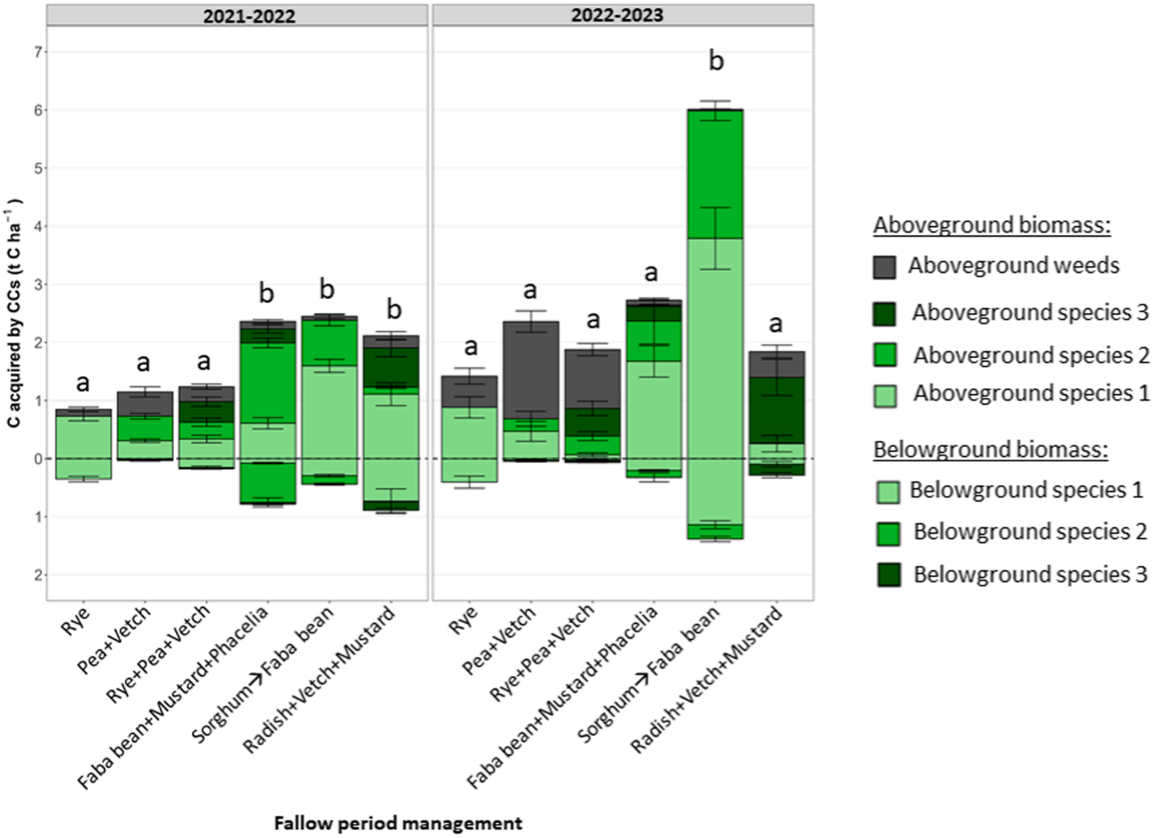


Fig. 2. Mean carbon (C) acquired by cover crops (CCs) (t C.ha^{-1}) and standard errors by CC treatment in 2021–2022 and 2022–2023. Species 1 and 2 for bispecific mixtures and Sorghum→Faba bean refer to the species listed in the name of the species composition. Species 1, 2 and 3 for trispecific mixtures refer to the species listed in the name of the species composition.

sunflower variety, and among CC treatment, sunflower variety and year. Sunflower traits varied among the varieties (Tables A.18 and A.19).

3.2.1. *Establishment of sunflower varieties*

The final emergence rate of sunflower was higher in 2022–2023 (7.1 plants.m^2) than in 2021–2022 (5.7 plants.m^2), as a reminder, the sowing density was 8.8 plants.m^{-2}. The effects of CCs on sunflower emergence varied among CC treatments and between years. In 2022, sunflower emergence in plots with CCs was at best equivalent to that in bare soil (≈ 6.6 plants.m^2), but often lower, particularly after Pea+Vetch and Rye. In 2023, however, sunflower emergence after Pea+Vetch (5.7 plants.m^2) remained lower than that in bare soil (7.4 plants.m^2), but was equivalent to or higher than that in bare soil for other CC treatments, particularly after Faba bean+Mustard+Phacelia (7.5 plants.m^2) (Table A.7). No interaction between CC treatment and sunflower variety on sunflower emergence was identified.

3.2.2. *Nitrogen status of sunflower varieties*

NNI and N uptake were significantly higher in 2021–2022 than in 2022–2023 at both stages ($p < 0.001$) (Fig. 3 and Table A.8). NNI was higher for tilled bare soil and Sorghum→Faba bean (mean of 0.8 and 0.7 at the vegetative and flowering stage, respectively) and lower for Rye (0.5 and 0.4, respectively) in both years ($p < 0.001$) (Table A.8). Concerning N uptake, sunflower took up more N and did so earlier, beginning with the vegetative stage after tilled bare soil, Pea+Vetch in 2021–2022, Faba bean+Mustard+Phacelia and Sorghum→Faba bean in both 2021–2022 and 2022–2023, compared to Rye in both years. Sunflower also took up N after flowering, particularly after Rye+Pea+Vetch in 2022–2023, as indicated by the significant increase in N uptake between flowering and maturity (Fig. 3). The N uptake by sunflower at maturity was correlated with SMN in a bare soil at maturity ($r = 0.58$, $p < 0.001$ in 2021–2022 and $r = 0.49$, $p = 0.04$ in 2022–2023) (Fig. A.9).

3.2.3. *Development of sunflower varieties*

Sunflower flowering was significantly influenced by the use of CC during the previous fallow period. In particular, Rye delayed flowering in both years (32 % and 55 % of flowering plants) compared to other CC treatments and tilled bare soil (mean of 62 % and 80 % of flowering plants) ($p < 0.001$) (Table 4). This effect of the CCs interacted with the sunflower variety: the MAS 98 K variety exhibited less delay in flowering than did CARRERA and MAS 89 M varieties in both years.

Concerning the maturity stage, sunflower matured the latest after Faba bean+Mustard+Phacelia (delay of 194 °C.d) in 2021–2022 and after Rye+Pea+Vetch (delay of 202 °C.d) in 2022–2023 compared to tilled bare soil and Sorghum→Faba bean, as shown by the significant interaction between CC treatment and year ($p < 0.001$). In 2022–2023, the maturation period (from flowering to maturity) was extended by a mean of 342°C.d for the Rye+Pea+Vetch treatment compared to tilled bare soil and Sorghum→Faba bean (Table 4). Maturity date was positively correlated with seed oil concentration in both years, particularly 2022–2023 ($r = 0.58$ for all varieties, $p < 0.001$), and negatively correlated with LAI ($r = -0.61$, $p < 0.001$ for all varieties in 2021–2022 and $r = -0.57$, $p < 0.001$ for all varieties in 2022–2023).

We observed that the AUC of normalized green cover from flowering to maturity was correlated with the leaf senescence ratio on the MAS 98 K variety ($r = -0.53$; $p = 0.01$), with a stronger correlation observed on August ($r = -0.79$; $p < 0.0001$). Using this proxy for leaf senescence, tilled bare soil and Sorghum→Faba bean induced more rapid leaf senescence than did Pea+Vetch, Rye and Rye+Pea+Vetch, which explained the differences observed in the length of the growing season ($p = 0.03$) (Table A.10). Moreover, the AUC of normalized green cover

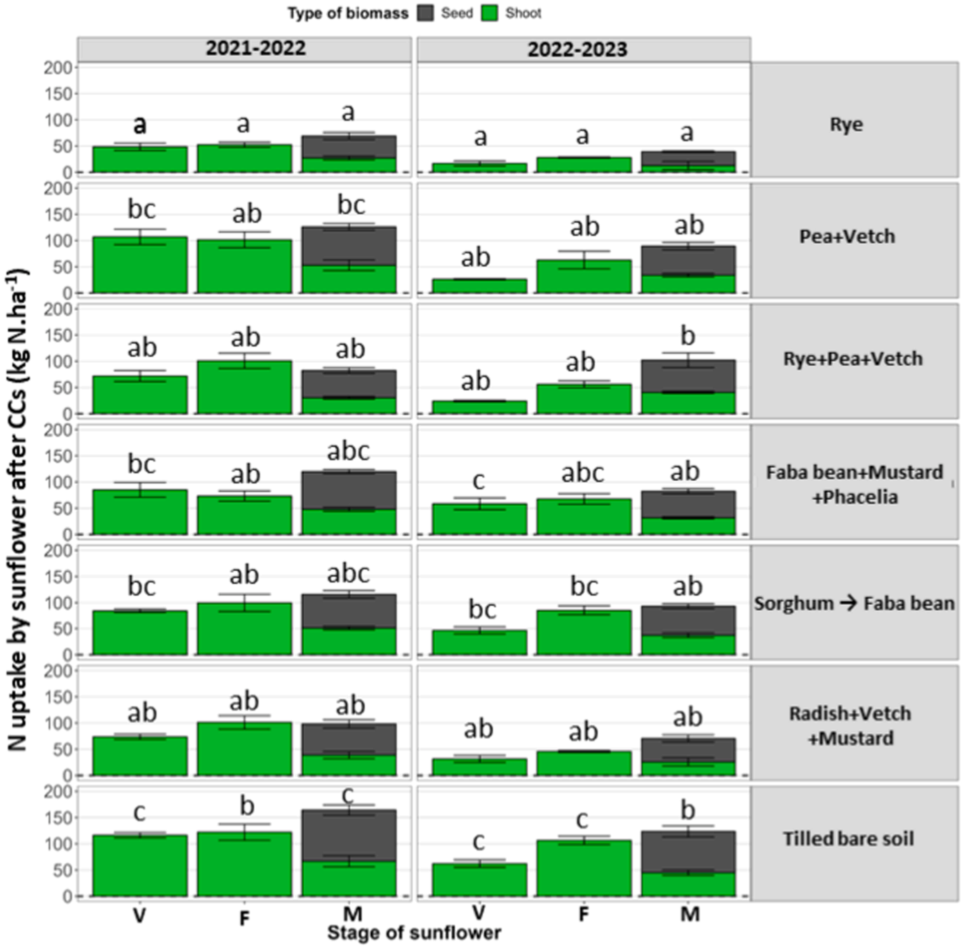


Fig. 3. Mean nitrogen (N) uptake and standard errors by sunflower at vegetative (V), flowering (F) and maturity (M) stages as a function of fallow-period management during the 2021–2022 and 2022–2023 experiments. N uptake at maturity was further categorized into N in seeds or shoots. Different letters indicate significant ($p < 0.05$) differences between fallow-period management for each stage of sunflower using Tukey's test.

during the growing season was correlated with the maturity date of sunflower ($r = 0.70$ for all varieties, $p < 0.001$) and negatively correlated with LAI in 2022–2023 ($r = -0.58$, $p < 0.001$). The AUC of green cover from flowering to maturity was higher for Pea+Vetch tilled bare soil, Rye+Pea+Vetch and Faba bean+Mustard+Phacelia than for Rye ($p < 0.01$) (Table A.10). It was positively correlated with sunflower aboveground biomass at maturity in 2022–2023 ($r = 0.47$, $p < 0.001$) (Fig. A.11.), AUC of normalized green cover ($r = 0.51$, $p < 0.001$) and sunflower yield in 2022–2023 ($r = 0.56$, $p < 0.001$).

3.2.4. *Growth of sunflower varieties*

We observed for the MAS 98 K variety that maximum biovolume was correlated with aboveground biomass at flowering ($r = 0.60$; $p < 0.001$ in 2021–2022 and $r = 0.80$; $p < 0.001$ in 2022–2023) and LAI ($r = 0.80$; $p < 0.001$ in 2021–2022 and $r = 0.70$; $p < 0.001$ in 2022–2023) (Fig. A.11).

The maximum biovolume, biovolume rate and maximum height were greater in 2022–2023 than in 2021–2022 ($p < 0.001$ for all variables) (Fig. 4 and Table A.12). In both years, the maximum biovolume and biovolume rate was higher after tilled bare soil, Faba bean+Mustard+Phacelia and Sorghum→Faba bean than after Rye ($p < 0.001$ for both variables), and the maximum height was higher after tilled bare soil and Faba bean+Mustard+Phacelia than after Rye ($p < 0.001$). No interaction between CC treatment and sunflower variety was observed for the maximum biovolume, biovolume rate or height. Maximum biovolume was strongly correlated with yield ($r = 0.69$, $p < 0.001$ in 2021–2022 and $r = 0.78$, $p < 0.001$ in 2022–2023).

The mean LAI of sunflower measured at flowering was higher in 2022–2023 (2.3) than in 2021–2022 (1.8) ($p < 0.001$). In both years, LAI was significantly higher in the tilled bare soil treatment (3.1) than in the Rye treatment (1.2). The other CCs behaved slightly differently: in 2021–2022, they resulted in similar LAI that was intermediate between the previous treatments, whereas in 2022–2023, LAI after Faba bean+Mustard+Phacelia and Sorghum→Faba bean (mean of 3.2) was equivalent to those under tilled bare soil, and the other CCs had LAI equivalent to those after Rye (mean of 1.6) ($p < 0.001$). In 2022–2023, no interaction between CC treatment and sunflower variety was observed for LAI (assessed only for MAS 98 K in 2021–2022) (Table A.13). LAI was correlated with NNI at the vegetative stage ($r = 0.54$, $p < 0.01$ in 2021–2022 and $r = 0.72$, $p < 0.001$ in 2022–2023), NNI at the flowering stage ($r = 0.54$, $p < 0.001$ in 2021–2022 and $r = 0.69$, $p < 0.001$ in 2022–2023), aboveground biomass at maturity ($r = 0.56$, $p < 0.001$ in 2021–2022 and $r = 0.33$, $p < 0.001$ in 2022–2023) and seed yield ($r = 0.67$, $p < 0.001$ in 2021–2022 and $r = 0.48$, $p = 0.03$ in 2022–2023) (Fig. A.9 and Fig. A.11).

Mean aboveground biomass (shoot) at sunflower maturity was higher in 2022–2023 (4.7 $t.ha^{-1}$) than in 2021–2022 (4.2 $t.ha^{-1}$) ($p = 0.01$). The interaction between CC treatment, sunflower variety or year was significant ($p = 0.02$) (Fig. 5). In 2021–2022 (a dry year), aboveground biomass was significantly higher for CARRERA after tilled bare soil, Pea+Vetch and Faba bean+Mustard+Phacelia treatments (6.2 $t.ha^{-1}$) than for MAS 98 K (5.1 $t.ha^{-1}$) and MAS 86OL (4.3 $t.ha^{-1}$), compared to Rye (mean of 2.4 $t.ha^{-1}$). In 2022–2023, higher biomass

Table 4
Mean percentages of flowering plants on date 1 (5 July 2022 and 3 July 2023) and date 2 (12 July 2022 and 2023) (standard error), sum of growing degree days (SGDD in Tb = 4.8 °C) from sowing to flowering or maturity (°C.d) by cover crop (CC) treatment in 2021–2022 and 2022–2023. Different letters indicate significant ($p < 0.05$) differences between CC treatments each year, using Tukey's test. NS: not significant. N.D: no data.

		Flowering			Maturity
		Proportion of flowering plant at date 1	Proportion of flowering plant at date 2	SGDD from sowing to flowering	SGDD from sowing to maturity
Year	Cover crop treatment	%	%	°C.d	°C.d
2021–2022	Rye	32 (10) a	86 (4)	N.D.	2384 (59) bc
	Pea+Vetch	55 (12) bc	87 (5)	N.D.	2270 (38) abc
	Rye+Pea+Vetch	64 (6) bc	91 (7)	N.D.	2257 (17) abc
	Faba bean+Mustard+Phacelia	67 (7) bc	90 (3)	N.D.	2399 (40) c
	Sorghum→Faba bean	56 (4) b	89 (5)	N.D.	2251 (45) ab
	Radish+Vetch+Mustard	55 (10) b	89 (5)	N.D.	2338 (44) bc
	Tilled bare soil	74 (7) c	90 (5)	N.D.	2159 (34) a
	p CC	$p < 0.001$	NS	N.D.	$p < 0.001$
	p sunflower varieties	$p < 0.001$	0.01	N.D.	0.02
	p CC X sunflower varieties	0.05	NS	N.D.	NS
2022–2023	Rye	0 (0) a	55 (20) a	1231 (22) d	2188 (49) ab
	Pea+Vetch	3 (3) b	78 (10) bc	1173 (23) bc	2208 (57) ab
	Rye+Pea+Vetch	2 (2) ab	79 (10) bc	1178 (29) bc	2330 (53) b
	Faba bean+Mustard+Phacelia	13 (7) c	86 (10) c	1094 (18) a	2153 (69) ab
	Sorghum→Faba bean	0 (0) ab	73 (10) b	1200 (25) cd	2015 (29) a
	Radish+Vetch+Mustard	1 (1) ab	80 (0) bc	1167 (15) bc	2194 (21) ab
	Tilled bare soil	1 (1) ab	83 (0) bc	1152 (32) b	1957 (62) a
	p CC	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.01$
	p sunflower varieties	NS	$p < 0.001$	$p < 0.001$	$p < 0.001$
	p CC X sunflower varieties	$p < 0.001$	$p < 0.001$	NS	NS
	p year	$p < 0.001$	$p < 0.001$	N.D.	$p < 0.001$
	p sunflower varieties	$p < 0.001$	0.02	N.D.	$p < 0.01$
	p CC	$p < 0.001$	$p < 0.001$	N.D.	$p < 0.001$
	p CC X sunflower varieties	NS	0.03	N.D.	NS
	p CC X year	$p < 0.001$	$p < 0.001$	N.D.	$p < 0.001$
	p sunflower varieties X year	$p < 0.001$	$p < 0.001$	N.D.	NS
	p CC X sunflower varieties X year	NS	NS	N.D.	NS

was measured for MAS 86OL after Faba bean+Mustard+Phacelia (8.4 t.ha^{-1}) and tilled bare soil (6.4 t.ha^{-1}) and MAS 89 M after Faba bean+Mustard+Phacelia (7.2 t.ha^{-1}) compared to Rye (2.3 t.ha^{-1}) (Fig. 5). Overall, across all sunflower varieties and both years, aboveground biomass was higher after Faba bean+Mustard+Phacelia and tilled bare soil, intermediate for Pea+Vetch and lower for Rye ($p < 0.001$).

The final root:shoot ratio and root biomass of sunflower was higher in 2021–2022 (0.15, 1 t.ha^{-1}) than in 2022–2023 (0.09, 0.6 t.ha^{-1}) ($p < 0.001$ for root:shoot ratio and $p = 0.01$ for root biomass), with higher root:shoot ratio averaged over both years for Faba bean+Mustard+Phacelia, Sorghum→Faba bean and Rye+Pea+Vetch (mean of 0.14) than Rye (0.08) and higher root biomass for tilled bare soil (1 t.ha^{-1}) and Sorghum→Faba bean (1 t.ha^{-1}) compared to Rye (0.4 t.ha^{-1}) over both years ($p < 0.001$) (Table A.14).

Harvest index and water-use efficiency for total aboveground biomass were higher in 2021–2022 (0.40 and 37 kg.ha^{-1}.mm^{-1}) than in 2022–2023 (0.36 and 23 kg.ha^{-1}.mm^{-1}) ($p < 0.001$) (Table A.19). Harvest index was lower for MAS 89 M (0.38) and CARRERA (0.38) in 2021–2022 and MAS 86OL (0.34) in 2022–2023 compared to MAS 98 K both years (0.44 in 2021–2022 and 0.39 in 2022–2023), corresponding to the interaction between year and varieties ($p < 0.01$). In 2021–2022, the harvest index was higher after Rye (0.44) and Rye+Pea+Vetch (0.43) compared to tilled bare soil (0.37) and Pea+Vetch (0.38) ($p < 0.001$). In 2022–2023, no significant difference between CC modalities was observed for the harvest index. For water-use efficiency, differences between varieties only existed in 2021–2022 for total aboveground biomass with higher water-use efficiency for CARRERA (40.1 kg.ha^{-1}.mm^{-1}) than MAS 86OL (33.7 kg.ha^{-1}.mm^{-1}) ($p < 0.01$) (Table A.12). For both years, water-use efficiencies for total aboveground biomass were higher after Faba bean+Mustard+Phacelia and tilled bare soil (mean of 39 kg.ha^{-1}.mm^{-1}) than Radish+Vetch+Mustard and Rye (mean of 21 kg.ha^{-1}.mm^{-1}) ($p < 0.001$).

3.2.5. *Productivity of sunflower varieties*

Sunflower yield was influenced by the (i) year, with a mean value of 2.8 ± 0.1 t.ha^{-1} in 2022 against 2.5 ± 0.1 t.ha^{-1} in 2023, (ii) CC treatments (Table A.15).

Sunflower yield differed significantly among CC treatments with higher yield after tilled bare soil (3.4 t.ha^{-1}) and Faba bean+Mustard+Phacelia (3.2 t.ha^{-1}) than Radish+Mustard+Vetch (2.3 t.ha^{-1}) and Rye (1.6 t.ha^{-1}) ($p < 0.001$). No difference was significant between sunflower varieties. Yield was correlated with total CC N acquisition ($r = 0.29$, $p < 0.01$ in 2021–2022, and $r = 0.42$, $p < 0.001$ in 2022–2023), total CC N concentration ($r = 0.41$, $p < 0.001$ in 2021–2022 and $r = 0.65$, $p < 0.001$ in 2022–2023) and total CC C:N ratio ($r = -0.20$, $p = 0.05$ in 2021–2022, and $r = -0.37$, $p < 0.01$ in 2022–2023). Yield was also correlated with hemicellulose concentration of CCs ($r = -0.47$, $p < 0.001$ for both years) and lignin concentration of leaves ($r = 0.23$, $p < 0.01$ for both years).

Sunflower seed number and TKW were higher in 2021–2022 (973 and 49 g, respectively) than in 2022–2023 (822 and 41 g, respectively) ($p < 0.001$) (Table A.15). Interaction year X CC treatments was significant for seed number ($p = 0.03$) and for TKW ($p < 0.001$). Higher seed numbers were measured after tilled bare soil and Faba bean+Mustard+Phacelia for both years and Pea+Vetch in 2021–2022 compared to Rye for both years. Higher TKW were observed after Pea+Vetch, Faba bean+Mustard+Phacelia for both years and bare soil only for 2022–2023 compared to Rye for both years.

The mean seed oil concentration of all varieties was higher for Faba bean+Mustard+Phacelia (55 %), Rye (55 %) for both years and Rye+Pea+Vetch (55 %) in 2022–2023 than for tilled bare soil (52 %) for both years, Pea+Vetch (52 %) in 2021–2022 and Sorgho→Faba bean (53 %) in 2022–2023 ($p < 0.01$), according to the interaction year X CCs ($p = 0.03$) (Table A.15). The mean seed oil concentration was significantly higher for CARRERA compared to the others varieties ($p < 0.001$). The amount of oil in seeds averaged over both years,

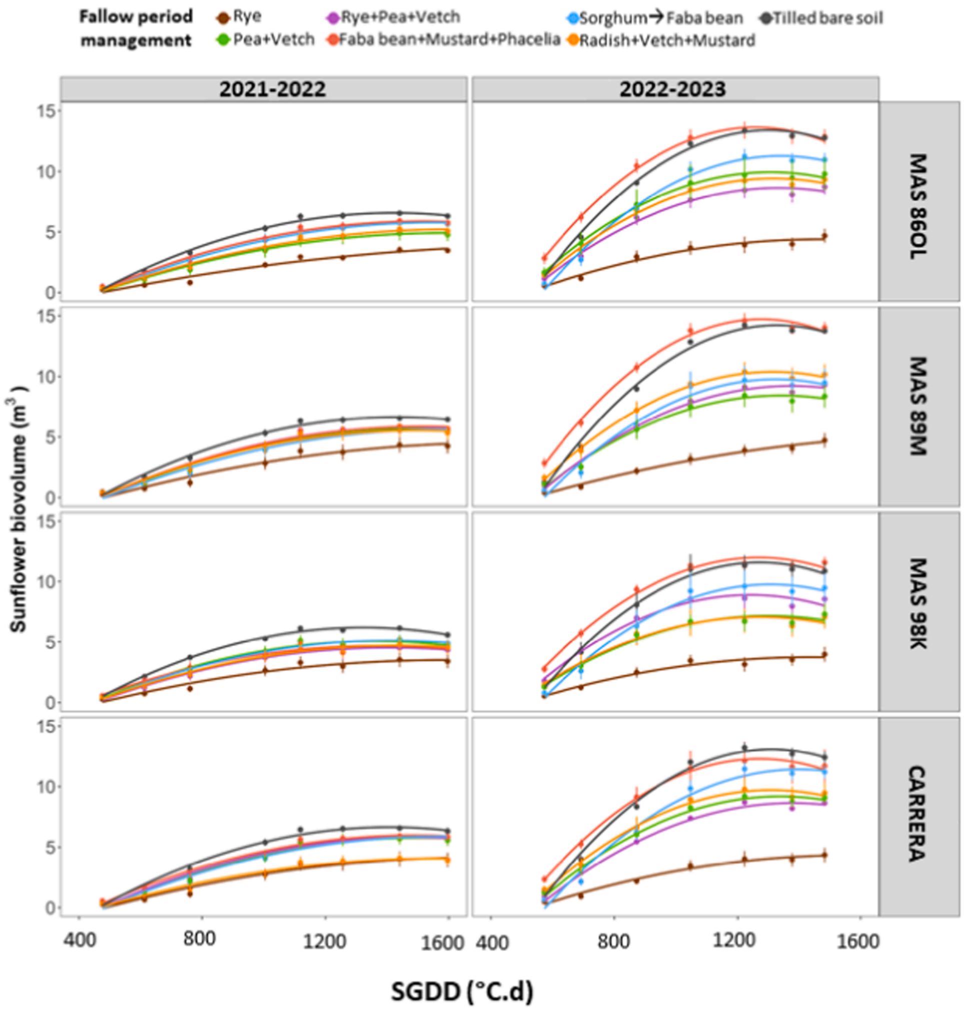


Fig. 4. Dynamics of sunflower biovolume (m^3) over time (expressed as the sum of growing degree days (SGDD)) as a function of fallow-period management and sunflower variety in 2021–2022 and 2022–2023. The curves are second-degree polynomial functions.

strongly related to seed weight, was higher after tilled bare soil (1.8 t.ha^{-1}) and Faba bean+Mustard+Phacelia (1.7 t.ha^{-1}) and lower after Rye (1.1 t.ha^{-1}) ($p < 0.001$) (Fig. 6). The amount of oil in seeds was positively correlated with the amount of protein in seeds, strongly dependent on seed yield of sunflower ($r = 0.91$, $p < 0.001$ in 2021–2022 and $r = 0.93$, $p < 0.001$ in 2022–2023). However, seed oil concentration was negatively correlated with seed protein concentration of sunflower ($r = -0.55$, $p < 0.001$ in 2021–2022 and $r = -0.49$, $p < 0.001$ in 2022–2023) and positively correlated with AUC of normalized green cover from flowering to maturity ($r = 0.59$, $p < 0.001$ in 2022–2023).

The mean seed protein concentration of all varieties was higher after tilled bare soil and Pea+Vetch (12.7 %) for both years, Rye+Pea+Vetch in 2021–2022 (12.7 %) than after Rye (11.1 %) and Radish+Vetch+Mustard (10.6 %) for both years and Rye+Pea+Vetch in 2022–2023 (10.1 %) ($p < 0.001$), according to the interaction year x CCs (Table A.15).

4. Discussion

Growing CCs during a prolonged fallow period can increase CC biomass production but may also deplete soil water and N resources for the subsequent cash crop, thus potentially reducing its yield (Thorup-Kristensen et al., 2003; Alonso-Ayuso et al., 2014). In the present study, soil water content at CC termination was significantly lower under CC treatments compared to tilled bare soil in 2023, with the lowest value after the Pea+Vetch mixture dominated by winter growing ryegrass, but soil water content at CC termination was similar between all treatments in 2022 (Table A.5). However, unlike soil water, late termination of CCs and the low risk of nitrate losses during the fallow period resulted systematically in low SMN at sunflower sowing, regardless of CC species (Meyer et al., 2022) (Table A.5). The reduction in SMN observed in both years may be mitigated by the positive effects of N mineralization from CC residues compared to tilled bare soil on sunflower growth. After CC termination, inorganic N is released through the mineralization of their residues, particularly in legume-dominated mixtures (Tribouillois et al., 2016; Couëdel et al., 2018). This process is facilitated by the lower C:N ratio of legume residues, which accelerates the mineralization of a larger nitrogen pool (Vigil and Kissel, 1991; Justes et al., 2009). Consequently, CC mixtures containing legumes can result in higher net N mineralization from their residues (Tosti et al., 2012; White et al., 2017), thus increasing sunflower yield (Thind et al., 2007; Rosner et al., 2018; Almoussawi et al., 2020; Meyer et al., 2022) compared to that in bare soil. Mixtures with a C:N ratio less than 19, which represented more than 60 % of legume biomass, resulted in higher yields than other CC treatments did but resulted in yields similar to those in tilled bare soil. These results are consistent with those of Ait-Kaci et al. (2022), who observed similar sunflower yields after CC mixtures with legumes and bare soil over a four-year field experiment. However, sunflower yield in the present study was decreased by mixtures dominated by Brassicaceae species, attributed to their high C:N ratio (40) and subsequent N immobilization, which agrees with results

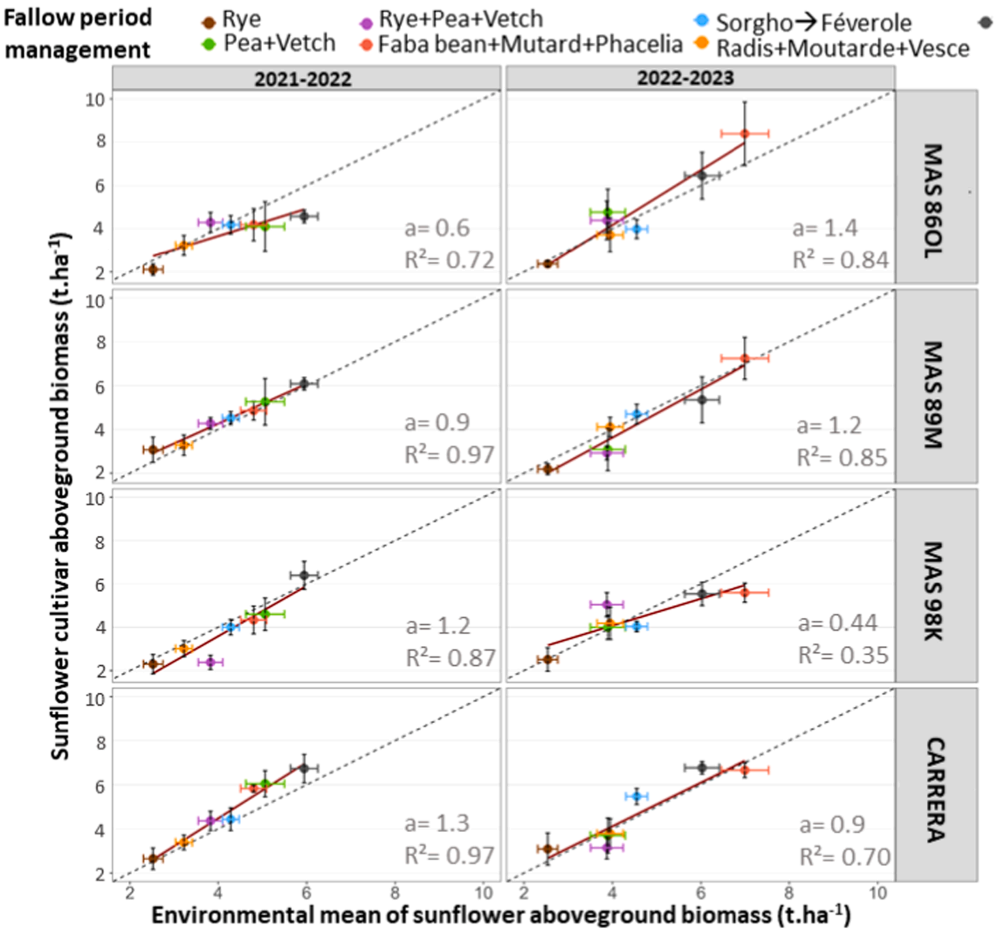


Fig. 5. Relationship between the environmental index and the aerial biomass, excluding seeds, of each variety. The environmental index is the mean value of the aerial biomass of all cultivars for each CC treatment (adapted from Finlay and Wilkinson 1963). The slope of the regression (dark red) corresponds to the plasticity of aboveground biomass of each variety for the range of environmental indices generated by the cover crops. a represents the slope of the regression and R^2 represents the coefficient of determination.

of Adeux et al. (2021) in systems without N fertilization. The variability in sunflower response to CCs may be influenced by other factors, such as the N acquired by CCs, the allelopathic effect and cell-wall components. The high N acquisition by Faba bean+Mustard+Phacelia in 2021–2022 may have helped increase sunflower yield, despite its high C:N ratio (40). Furthermore, the substantial decrease in yield after Rye could be have been due to N immobilization of CC residues, as observed by Rosecrance et al. (2000), along with potential allelopathic effects, which increase when CCs are terminated later (Barnes and Putnam, 1986; Silva and Bagavathiannan, 2023), or the biochemical composition of CC residues. This composition, including soluble compounds, hemicellulose, cellulose and lignin, indirectly influences the C:N ratio of CC residues and N concentration, both of which are related to CC development and species (Nicolardot et al., 2001; Alonso-Ayuso et al., 2014; Pittman et al., 2020; Brockmueller et al., 2023). In the present study, each CC species had specific biochemical concentrations, such as high hemicellulose and low lignin concentrations in rye and high cellulose concentration in mustard (Pittman et al., 2020; Brockmueller et al., 2023). Identifying the relationship between CC composition and N mineralization is challenging due to the complex relationship between N content, morphology, arrangement of biochemical fractions and decomposition of CC residues (Henriksen and Breland, 1999; Nicolardot et al., 2001; Cosgrove and Jarvis, 2012). Overall, CCs provide several functions and have multiple effects on sunflower traits (Fig. 7).

In the present study, the availability of inorganic N emerged as a critical factor that influenced the growth and development of sunflower. The NNI of sunflower, which influences LAI and thus light interception and seed number during vegetative and flowering stages, revealed severe N deficiency, particularly after Rye, which resulted in delayed flowering, consistent with results of Massignam et al. (2009) under low N fertilization (Table 4 and A.8). CC mixtures with legumes (Faba bean+Mustard+Phacelia in 2021–2022 and Rye+Pea+Vetch in 2022–2023) delayed maturity, thereby extending the seed-filling period (Table 4). The larger amount of N released by CCs after flowering helped maintain green leaf area and photosynthesis, which increased oil concentration and yield (Fig. 6 and Table A.17), as observed in previous studies (Steer et al., 1985; Goswami and Srivastava, 1988; Aguirezzabal *et al.*, 2003). To increase productivity, sunflower must efficiently redistribute to seeds nutrients taken up later, a trait observed in the variety MAS 98 K (Tables A.17 and A.19) (Aguirrezábal et al., 2003; Moschen et al., 2017). The selection of sunflower varieties could be pivotal in mitigating potential challenges posed by CCs. An obstacle to using CCs before sunflower could be the latter's demand for optimal sowing quality, which influences its yield (Connor and Hall, 1997; Lecomte and Longueval, 2013). The presence of poorly buried coarse residues, such as grass weeds (especially perennial ryegrass, rye and fodder radish), decreased the sunflower emergence rate (Table A.7). However, choosing varieties with characteristics similar to those of MAS 98 K and MAS 89 M could mitigate the loss of plant density (Table A.18), perhaps due to having smaller seeds than other varieties, thus increasing the germination capacity (Torres et al., 1990).

Sunflower is impacted by climate change but exhibits adaptability to water-restricted conditions due to its drought tolerance and suitability for low-input systems with low N and pesticide requirements

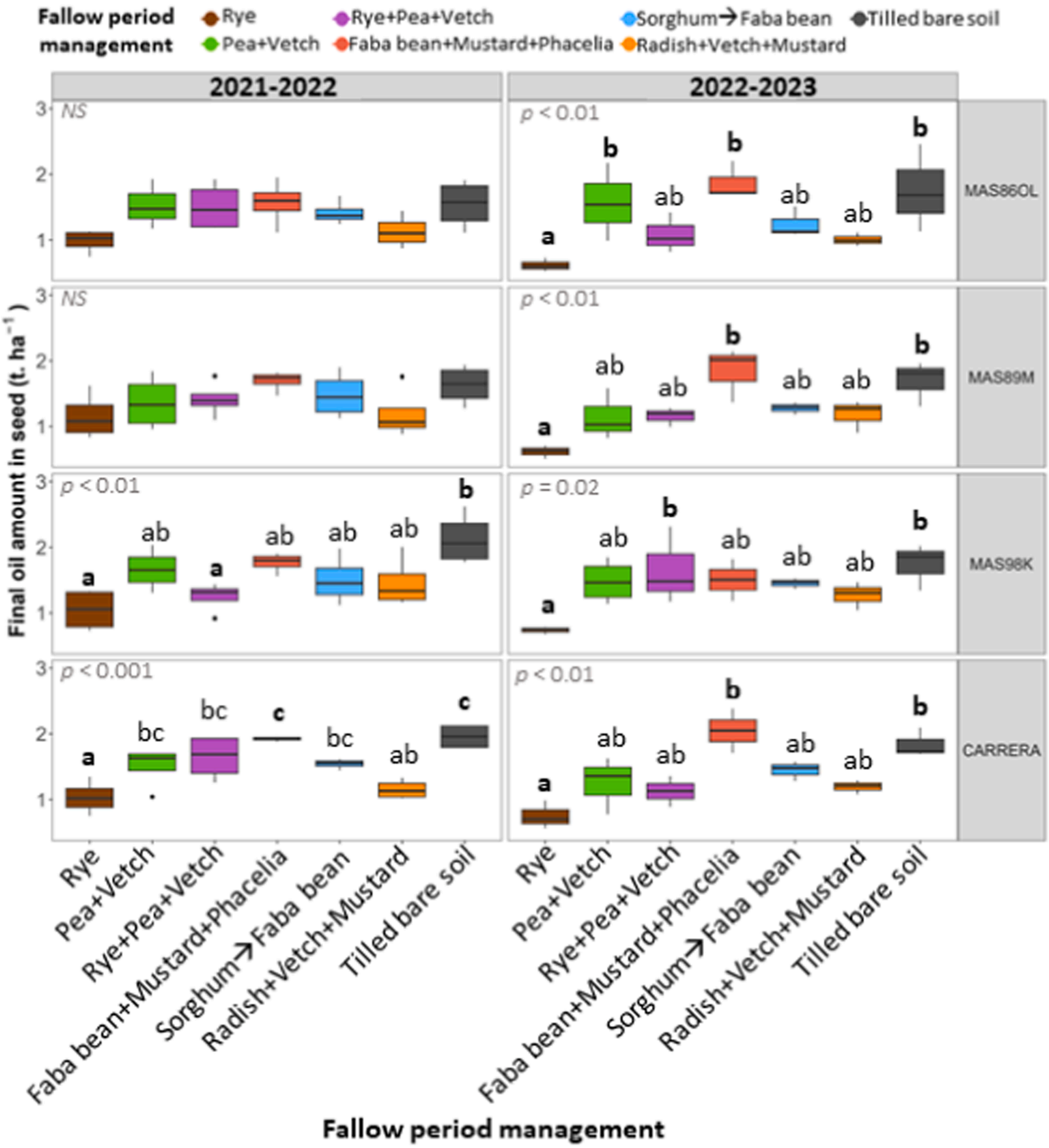
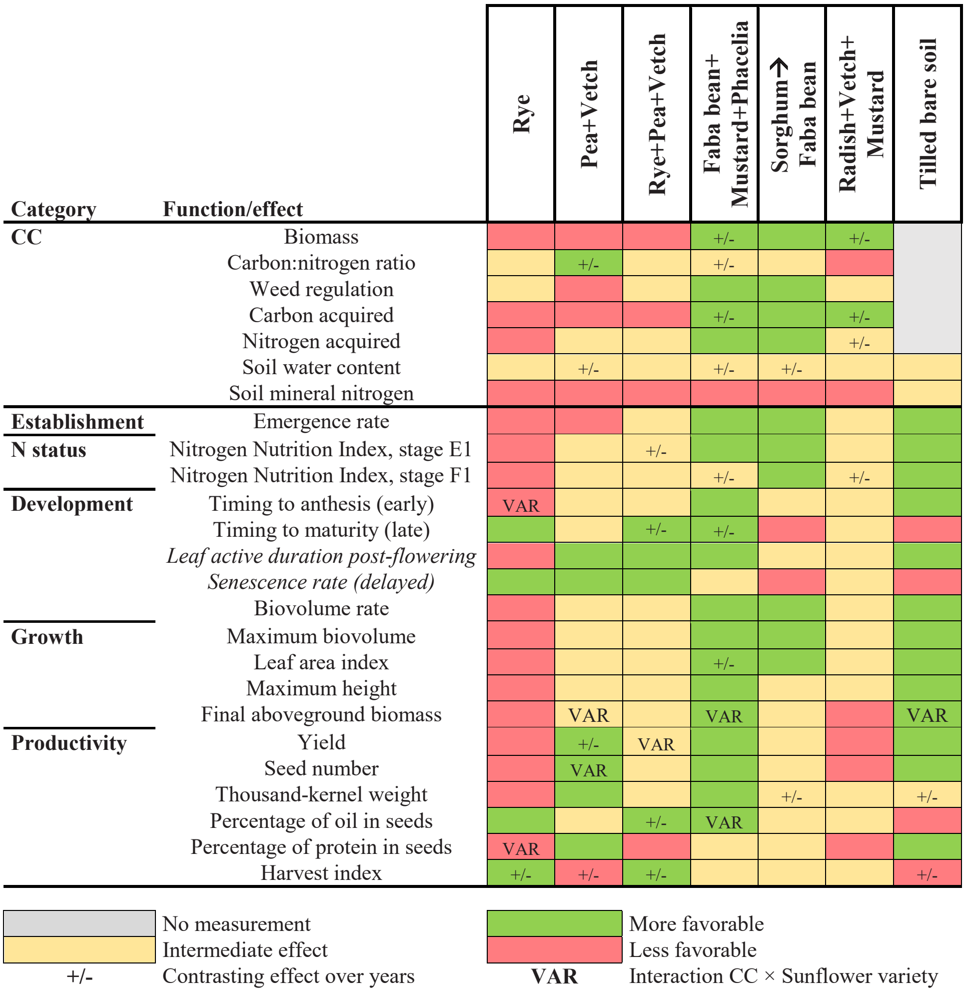


Fig. 6. Amount of oil in seeds (t oil.ha^{-1}) as a function of fallow-period management and sunflower variety in 2021–2022 and 2022–2023. Different letters indicate significant ($p < 0.05$) differences between fallow-period management for each sunflower variety and year, using Tukey's test. NS: not significant.

(Garcia-Vila and Fereres, 2012; Debaeke et al., 2017a). In response to drought conditions during the entire growing season in 2022, sunflower accelerated flowering to escape drought, reduced leaf area to minimize water loss, maintained root growth (perhaps due to allocating more C to roots than to shoots), and increased the harvest index and water-use efficiency, which maintained productivity without irrigation during flowering (Tables A.14, A.18, A.19) (Flenet et al., 1996; Maury et al., 2011). Moreover, lower NNI and N uptake in sunflower in 2023 than in 2022 (Fig. 3 and Table A.8) may have been due to increased weed biomass increasing N and light competition with sunflower, especially in early stages (Reddy et al., 2008; Moreau et al., 2014), and higher density of emerged plants (Marin and Ion, 2022). One strategy for adapting to climate change is to select varieties with drought-tolerance strategies (Casadebaig et al., 2008; Rengel et al., 2012; Duruflé et al., 2023), which could interact with N supply (Raya-Sereno et al., 2023). Although application of N fertilizer under severe drought can increase water deficit due to larger leaf area and water use (Nielsen and Halvorson, 1991; Ashraf et al., 2001), the larger amount of N released by CCs increased aboveground biomass production during the dry year for varieties with a productive strategy for leaf expansion rate (CARRERA) compared to varieties with a conservative strategy (MAS 86OL), without exacerbating the impact of water deficit on yield, by maintaining water-use efficiency (Fig. 5 and Table A.19). Variety MAS 86OL, known to decrease the leaf expansion rate and close stomata when FTSW is relatively high, may have lower N demand and uptake during dry years than other varieties (Ahmad et al., 2014). Morpho-physiological traits can be identified for adapting to new cropping systems and conditions such as drought (Debaeke et al., 2021). Desirable traits for adapting to drought in low-N-input systems with CCs could include greater growth before flowering, thus influencing seed number, the maintenance of active leaf area after flowering and efficient water use, which correspond to traits of variety CARRERA (Tables A.18 and A.19). Other traits conducive to late N release by CCs could include efficient nutrient redistribution, thus influencing TKW, which corresponds to a trait of



Category	Function/effect	Rye	Pea+Vetch	Rye+Pea+Vetch	Faba bean+ Mustard+Phacelia	Sorghum→ Faba bean	Radish+Vetch+ Mustard	Tilled bare soil
CC	Biomass	🟥	🟥	🟥	🟩 +/-	🟩	🟩 +/-	⬜
	Carbon:nitrogen ratio	🟨	🟩 +/-	🟨	🟨 +/-	🟨	🟥	⬜
	Weed regulation	🟨	🟥	🟨	🟩	🟩	🟨	⬜
	Carbon acquired	🟥	🟥	🟥	🟩 +/-	🟩	🟩 +/-	⬜
	Nitrogen acquired	🟥	🟨	🟨	🟩	🟩	🟨 +/-	⬜
	Soil water content	🟨	🟨 +/-	🟨	🟨 +/-	🟨 +/-	🟨	🟨
	Soil mineral nitrogen	🟥	🟥	🟥	🟥	🟥	🟥	🟨
Establishment	Emergence rate	🟥	🟥	🟨	🟩	🟩	🟨	🟩
N status	Nitrogen Nutrition Index, stage E1	🟥	🟨	🟨 +/-	🟩	🟩	🟨	🟩
	Nitrogen Nutrition Index, stage F1	🟥	🟨	🟨	🟨 +/-	🟩	🟨 +/-	🟩
Development	Timing to anthesis (early)	🟥 VAR	🟨	🟨	🟩	🟨	🟨	🟩
	Timing to maturity (late)	🟩	🟨	🟩 +/-	🟩 +/-	🟥	🟨	🟥
	Leaf active duration post-flowering	🟥	🟩	🟩	🟩	🟨	🟨	🟩
	Senescence rate (delayed)	🟩	🟩	🟩	🟨	🟥	🟨	🟥
	Biovolume rate	🟥	🟨	🟨	🟩	🟩	🟨	🟩
Growth	Maximum biovolume	🟥	🟨	🟨	🟩	🟩	🟨	🟩
	Leaf area index	🟥	🟨	🟨	🟩 +/-	🟩	🟨	🟩
	Maximum height	🟥	🟨	🟨	🟩	🟨	🟨	🟩
	Final aboveground biomass	🟥	🟨 VAR	🟨	🟩 VAR	🟨	🟥	🟩 VAR
Productivity	Yield	🟥	🟩 +/-	🟨 VAR	🟩	🟨	🟥	🟩
	Seed number	🟥	🟩 VAR	🟨	🟩	🟨	🟥	🟩
	Thousand-kernel weight	🟥	🟩	🟨	🟩	🟨 +/-	🟨	🟨 +/-
	Percentage of oil in seeds	🟩	🟨	🟩 +/-	🟩 VAR	🟨	🟨	🟥
	Percentage of protein in seeds	🟥 VAR	🟩	🟥	🟨	🟨	🟥	🟩
	Harvest index	🟩 +/-	🟥 +/-	🟩 +/-	🟨	🟨	🟨	🟥 +/-

⬜	No measurement	🟩	More favorable
🟨	Intermediate effect	🟥	Less favorable
+/-	Contrasting effect over years	**VAR**	Interaction CC × Sunflower variety

Fig. 7. Summary of the functions provided by cover crops (CCs) and effects of fallow-period management on the establishment, N status, development, growth and productivity of sunflower. Variables in italics correspond to measurements taken only in 2022–2023.

variety MAS 98 K (Table A. 17). Results of the present study can thus help farmers select sunflower varieties with traits adapted to low-N-input systems that include CCs for a long period, in the context of climate change.

In systems with low N and water inputs, selecting optimal CCs allows for yields equivalent to those of intensively tilled bare soil, regardless of the degree of water deficit, while also providing valuable ecosystem services. For example, incorporating CCs into sunflower-durum wheat rotations, which are common in southwestern France, increases the amount of C returned to the soil (Table 3 and Fig. 2), as demonstrated in the present study, and may increase soil organic C stocks, thereby mitigating climate change compared to intensive tillage of bare soil (Poeplau and Don, 2015; Guardia et al., 2019; Launay et al., 2021; Guidoboni et al., 2023). Another significant ecosystem service provided by CCs in low-input agricultural systems is weed control. In the present study, most weeds were perennial ryegrass, a known nitrophilic species (Moreau et al., 2014). CC treatments that included Poaceae and Brassicaceae species (e.g. Sorghum→Faba bean, Radish+Vetch+Mustard, Faba bean+Mustard+Phacelia and Rye) controlled weeds more at termination than the Pea+Vetch mixture did, mainly due to differences in biomass production and CC species composition (Cordeau and Moreau, 2017; Adeux et al., 2021; Rouge et al., 2022). The significant weed control by Sorghum→Faba bean observed could have been due in particular to the thicker mulch layer of sorghum (Nagabhushana et al., 2001). Therefore, selecting suitable CC species can enhance ecosystem services while maintaining sunflower yield compared to intensively tilled bare soil. In our study with low-N-input systems in South-West of France, the mixture Faba bean+Indian Mustard+Phacelia improved ecosystem services, mitigated disservices and maintained sunflower yield.

5. Conclusion

This study quantified ecosystem functions provided by CCs included for a long period, focusing mainly on N and water dynamics, and their influence on the establishment, development, growth and productivity of several sunflower varieties. Using CCs before sunflower managed without N fertilization or irrigation during flowering revealed little risk of preemptive water competition with sunflower. However, in scenarios with low risk of winter nitrate losses, there was a large decrease in SMN at CC termination, regardless of CC species. Nonetheless, judicious selection of CCs resulted in yields similar to those in intensively tilled bare-soil systems. The increase in sunflower yield was influenced mainly by N mineralization facilitated by CCs, which depended on factors such as CC composition (*e.g.* C:N ratio, N acquisition) and cell-wall components. In systems without N fertilization, inorganic N emerged as the main factor that limited sunflower growth, development and productivity. Sole Rye CC and mixtures with mainly Brassicaceae CC limited the growth and productivity of sunflower. Conversely, CC mixtures with legumes extended the seed-filling period due to later N release, potentially increasing oil concentration and/or yield, enhanced by the selection of a suitable variety. Adopting varieties with drought-tolerance traits could be a strategy for adapting to drought conditions by increasing biomass production in the presence of increased N supply, without exacerbating crop water stress. However, NNI should be sustained at a moderate level to prevent fungal diseases and negative impacts on seed oil concentration (Debaeke et al., 2014; Debaeke and Izquierdo, 2021). In the context of climate change, including CCs in low-input systems is a valuable approach for controlling weeds and increasing the amount of C returned to the soil, while maintaining a yield similar to that in intensively tilled bare-soil systems.

CRediT authorship contribution statement

Camille Tapy: Methodology, Investigation. **Lucie Souques:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Nicolas Langlade:** Writing – original draft, Methodology, Conceptualization. **Lionel Alletto:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Noémie Deschamps:** Methodology, Investigation. **Rachel Lackdari:** Methodology, Investigation. **Philippe Debaeke:** Writing – review & editing, Methodology. **Marc Labadie:** Writing – review & editing, Methodology, Investigation. **Damien Marchand:** Methodology, Investigation. **Eric Lecloux:** Methodology, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2024.109692.

Data Availability

Data will be made available on request.

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