Global Change Biology Bioenergy

RESEARCH ARTICLE OPEN ACCESS

Moderate Drought Constrains Crop Growth Without Altering Soil Organic Carbon Dynamics in Perennial Cup-Plant and Silage Maize

Khatab Abdalla^{1,2} 💿 | Hannah Uther¹ | Valentin B. Kurbel¹ 💿 | Andreas J. Wild¹ 💿 | Marianne Lauerer³ 💿 | Johanna Pausch¹ 💿

¹Agroecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany | ²Environment, Natural Resources and Desertification Research Institute, National Centre for Research, Khartoum, Sudan | ³Ecological Botanical Gardens, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany

Correspondence: Khatab Abdalla (khatab.abdalla@uni-bayreuth.de)

Received: 8 May 2024 | Revised: 20 September 2024 | Accepted: 27 September 2024

Funding: This work was supported by the Bavarian State Ministry of the Environment and the Water Management Department of the Government of Upper Franconia within the project "Demonstrationsprojekt Silphie-Anbau im Projektgebiet Nördliche Frankenalb."

Keywords: bioenergy crops | carbon sequestration | climate change | dissolved organic carbon | soil nitrogen | soil respiration

ABSTRACT

Silage maize (Zea mays L.) intensification to maximise biomass production increases greenhouse gas emissions, accelerates climate change and intensifies the search for alternative bioenergy crops with high carbon (C) sequestration capacity. The perennial cup-plant (Silphium perfoliatum L.) not only serves as a viable bioenergy source but may also be a promising soil C conservator. However, the dynamics of soil organic C (SOC) under the C3 cup-plant, exposed to moderate drought conditions, that reduces growth rate without causing crop failure, compared with the drought-tolerant C4 maize, remains unexplored. Here, we investigated in a lysimeter experiment the effects of moderate drought stress on crop growth and soil CO₂ efflux under cup-plant and silage maize compared with well-watered conditions. Soil CO₂ efflux along with root and shoot biomass, soil moisture and temperature as well as SOC and nitrogen (N) were measured over three consecutive years. Irrespective of the watering regime, cup-plant induced a greater soil CO₂ efflux (16% and 23% for 2020 and 2021, respectively), which was associated with higher root and shoot biomass compared with silage maize suggesting a substantial contribution of the roots to total soil CO₂ efflux. In addition, soil CO₂ efflux correlated negatively with soil dissolved N and positively with microbial C:N imbalance suggesting that low soil N availability influences soil CO2 efflux through processes related to N-limitation such as N-mining. Strikingly, moderate drought had no effect on soil CO₂ efflux and C content and microbial biomass C, but increased dissolved organic C and microbial biomass N in both crops suggesting a complex interplay between C availability, N-limitation and microbial adaptation under these conditions. Although cup-plant increased soil CO₂ efflux, the observed higher root and shoot biomass even under moderate drought conditions suggests a similar soil C management as silage maize; however, this still requires longer-term investigation.

1 | Introduction

Approximately 84% of the global energy production is derived from fossil fuels leading to 35 billion Mg (10^6 g) of carbon dioxide

 (CO_2) emissions per year (Friedlingstein et al. 2023; IEA 2023). The CO₂ emissions are projected to exceed 43 billion Mg by 2050 (IEA 2023), potentially resulting in a global temperature rise of about 2°C-3°C unless proactive measures are implemented.

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Therefore, minimising greenhouse gas emissions and maximising the net removal of CO_2 from the atmosphere is necessary for environmental sustainability.

Finding suitable bioenergy crops and management practices can enhance atmospheric CO₂ removal and soil carbon (C) storage (El Akkari et al. 2018; Wu et al. 2018). Europe, particularly Germany dominates global bioenergy crop cultivation, with maize (Zea mays L.) being the most widely used crop (de Schutter and Giljum 2014; Szarka et al. 2021). However, recent drought and heat stress have reduced maize productivity in Germany (Peichl et al. 2019), leading to further agricultural intensification, which exacerbates environmental issues such as soil fertility losses by erosion or nitrate leaching to groundwater (Müller, Kayser, and Isselstein 2011; Peichl et al. 2019; Ruf et al. 2021). The aggravated environmental problems associated with low maize productivity in Germany (e.g., Lower Saxony), accelerate the search for alternative crops with high yields and low environmental drawbacks (Gansberger, Montgomery, and Liebhard 2015; von Cossel et al. 2020). The search centred on large-scale C sequestration and storage through the cultivation of perennial crops as a promising option to increase biomass production, soil C storage and thereby soil fertility.

The cup-plant (Silphium perfoliatum L.), a C3 perennial from the Asteraceae family, introduced to Europe in the 18th century (Gansberger, Montgomery, and Liebhard 2015; Stanford 1990), has been proposed as an alternative bioenergy crop to silage maize in Germany due to its ecological benefits (Gansberger, Montgomery, and Liebhard 2015; Karpenstein-Machan 2013; von Cossel et al. 2020). Studies on its potential for bioenergy production in Germany began in 2005 (Ruppert, Kappas, and Ibendorf 2013). Cup-plant can be harvested profitably for up to 15 years without replanting and it suppresses weeds after the first year, eliminating the need for tillage and weed control or pesticides (Gansberger, Montgomery, and Liebhard 2015; Hartmann and Lunenberg 2016; Ruppert, Kappas, and Ibendorf 2013; von Cossel et al. 2020). Its high ground cover enhances biodiversity (e.g., insect diversity) and reduces soil erosion and nutrient leaching compared with maize (Gansberger, Montgomery, and Liebhard 2015; Grunwald et al. 2020; Häfner et al. 2023; Mueller et al. 2020). Although its dense and deep root system suggests a drought tolerance potential (Bauböck, Karpenstein-Machan, and Kappas 2014; Franzaring et al. 2014, 2015), a 2-year experiment found it had 34% lower water use efficiency than maize indicating less drought tolerance (Schoo, Schroetter et al. 2017; Schoo, Wittich et al. 2017). Nevertheless, long-term cup-plant cultivation may increase soil water holding capacity due to increased C inputs to the soil from its root systems (Schoo, Wittich et al. 2017).

Although intensive research focuses on the applicability of cupplant to replace silage maize for bioenergy production, less attention has been paid to soil nutrient dynamics, particularly C and N. Among the few existing studies, Kemmann et al. (2023) reported that cup-plant reduced biomass production per hectare (-34%) and consequently per unit of applied N (-32%) compared with silage maize suggesting lower N requirements under cupplant. Grunwald et al. (2020) found lower soil mineral N under established cup-plant due to extended N uptake phase caused by early seasonal growth and regrowth after harvest. The low soil

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Therefore, the aim of this study was to evaluate the effects of well-watered and moderate drought conditions on plant growth and soil C dynamics under cup-plant compared with silage maize. It was hypothesised that (i) cup-plant increases the total soil CO₂ efflux compared with silage maize, due to its large and dense root system and thus higher contribution of root respiration. Additionally, the expected rapid depletion of soil available N as a result of the prolonged N uptake phase of cup-plant may further lead to microbial N-mining, accelerating the organic matter decomposition and contributing to higher total CO₂ efflux. However, the losses of C as CO₂ could potentially be offset by an increased C input from cup-plant into the soil. We further hypothesise that (ii) moderate drought stress limits the growth and activity of roots and soil microorganism, thereby reducing soil CO₂ efflux in both crops compared with well-watered conditions.

2 | Materials and Methods

2.1 | Experimental Set-Up

For this experiment, an existing built-in lysimeter facility (28 lysimeters) at the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55'19" N, 11°34'55" E, 365 m a.s.l.) was used (Zul et al. 2007). The lysimeters were constructed with concrete walls and sealed with a coating material (Inertol 49 W) to prevent horizontal water movement. The upper part (main part) of the lysimeter had an internal volume of $1.69 \,\mathrm{m^3}$ (i.e., width: $1.3 \,\mathrm{m} \times \text{length}$: $1.3 \,\mathrm{m} \times \text{depth}$: 1 m). The lower part is a funnel shape, filled with gravel and covered at the top with drainage fleece to prevent soil loss with the leachate. The leachate was collected from a 100-L tank connected to the bottom of the lysimeter by a polyethylene pipe. However, leachate results were not included in this study.

The main part of the lysimeter (i.e., 1.69 m^3) was filled with soil collected from the floodplain of the Red Main River (near Bayreuth, Germany) and classified as *Fluvisol* based on its diagnostic fluvic material (IIUS-WRB 2022). The soil has slightly acidic reaction (pH_{H20} = 6.5 ± 0.03) with relatively low SOC content and sandy loam texture (Table 1). Out of 28 lysimeters, 20 lysimeters were used for the current study with two crops, that is, maize (*Zea mays* L.) and cup-plant (*Silphium perfoliatum* L.) subjected to moderate drought stress and well-watered conditions (Figure S1).

2.2 | Crops Cultivation and Watering Regimes

The crops (maize and cup-plant) and watering regimes (wellwatered and moderate drought) were arranged in a randomised design with five replicates each while the drought plots were kept close to each other. Ten lysimeters were planted with 14 hybrid maize (Zea mays L. cv. PM Paolo) plants per lysimeter (1.69 m²), with a 32.5 cm spacing between plants and 28 cm between rows. Another 10 lysimeters were planted with six cupplants (Silphium perfoliatum L. a cultivar from the USA) each with 55 and 40 cm between plants and rows, respectively. We used plant density of four plants per m² for cup-plant (approx. 40,000 ha⁻¹ plants) and eight plants per m² for silage maize (approx. 80,000 plants ha⁻¹). These planting densities are in accordance with common practices in the Bavarian farming system as published by the Bavarian State Research Center for Agriculture (LfL) and the Technology and Support Center (TFZ), Bavaria, Germany. The perennial cup-plant was planted once on the 5th of May 2019 and maintained until the end of the experiment in

TABLE 1 | Baseline properties of the soil used in the lysimeter given as mean \pm SE (n = 5).

Soil properties	Mean±SE
pH (1:5, water)	6.5 ± 0.03
Total nitrogen (g kg ⁻¹)	1.24 ± 0.01
Soil organic carbon (gkg ⁻¹)	14.88 ± 0.05
Carbon: Nitrogen ratio	12.51 ± 0.23
Soil bulk density (g cm ⁻³)	$1.46 \pm 0.0.$
Soil organic carbon stocks (kg m^{-2})	2.43 ± 0.03
Soil nitrogen stocks (kg m ⁻²)	1.83 ± 0.01
Available phosphorus (mg kg ⁻¹)	121.21 ± 5.87
Available potassium (mg kg ⁻¹)	67.91 ± 2.81
Clay content (%)	7.0 ± 0.16
Silt content (%)	21.3 ± 0.34
Sand content (%)	71.7 ± 0.03
Soil texture class	Sandy loam

2021 with annual harvesting of the aboveground biomass in the last week of September every year. The silage maize was sown in the first week of May each year and harvested at the same time as the cup-plant.

All lysimeters were equipped with automatic drip irrigation and soil moisture and temperature sensors at three soil depths: 25, 50 and 75 cm to provide supplemental irrigation as needed for each watering regime. Based on the initial soil water retention curve, the soil has 25% and 6% volumetric water content at the field capacity and permanent wilting point, respectively (Figure S2). Given that the experiment was conducted on repacked sandy loam soil, making it susceptible to moisture fluctuations, we defined well-watered and moderate drought conditions as a volumetric water content equal to 100% (i.e., 25%) and 50% (i.e., 12.5%) of the volumetric water content at the field capacity in the topsoil (0-25 cm), respectively. To account for the moisture fluctuations under field conditions, we considered a water content ranges of 23%-25% for well-watered and 13%-15%, for moderate drought stress. To ensure the survival of the crops, moderate drought stress was initiated 4 weeks after maize sowing for both maize and cup-plant. No drought stress was applied to the cup-plant during its establishment year (2019), when it only forms a rosette.

No fertiliser was added in 2019 because of high nutrient availability in the soils. In 2020 and 2021, both crops were fertilised three times per growing season with NPK(S) fertiliser (Complex 15 EG-fertiliser) containing 15% N (6% NO_3^- , 9% NH_4^+), 15% P_2O_5 , 15% K_2O , 7,5% SO₃, 0.01% Zn (Table S1).

2.3 | Weather Data, Soil Temperature and Moisture Content

The study site has 8.2°C and 741mm long-term mean annual (1980-2019) temperature and precipitation, respectively (Zsolnay, Walentowitz, and Aas 2023). During the experimental period, the weather data (i.e., precipitation and air temperature) were obtained from a weather station (49°55'45"N, 11°35'10" E) located approximately 200 m from the experimental site. Data were automatically recorded and logged every minute and provided as 10-min averages or sums. In the current study, we derived daily values of air temperature and precipitation for the years 2019, 2020 and 2021 (Figure S4). Continuous soil moisture and soil temperature were obtained from automatic sensors (TEROS 13 and 21, METER GROUP AG, Munich, Germany) installed at 25, 50 and 75 cm depths allowing real-time measurements of soil temperature and moisture content. The real-time measurements of soil moisture across the depths allowed the implementation of well-watered and drought-stressed moisture content conditions, which were maintained remotely by adjusting the water supply by the irrigation system based on the soil moisture reading.

2.4 | In Situ Soil CO₂ Measurements

In situ CO_2 fluxes were measured over three consecutive years, two to three times per month over the growing seasons. In addition, few measurements were taken once a month

after harvest and before snow to further investigate respiration trends in the absence of crops. Soil CO₂ efflux was measured using the LI-COR 6400 gas exchange system equipped with the LI-COR 6400-09 soil respiration chamber (LI-COR, Biosciences, Lincoln, NE, USA). Measurements were taken from two PVC collars (4.4 cm high and 10 cm diameter) inserted 2.4 cm (leaving 2 cm above the soil surface) permanently into the soil, in the middle between three plants in each lysimeter (10 collars per treatment). During the measurements, the soil chamber was inserted 1.5 cm into the PVC collar, leaving 0.5 cm between the bottom edge of the chamber and the soil surface. The first CO₂ flux measurement was done 2 weeks after the collars were installed to eliminate the effect of soil disturbance on soil CO₂ fluxes. Soil CO₂ efflux was measured between 9 am and 1 pm, which was found to be approximately equal to the daily average based on a 24 h measurement cycles every 3 h at the experimental site (Figure S3). Cumulative soil CO₂ flux was calculated using linear interpolation between two measurement dates.

2.5 | Shoot, Root Biomass and Soil Sampling

The shoot biomass (cut 5 cm above the soil surface) was harvested at the end of each growing season. Plants inside each lysimeter were harvested separately. Dry weight was measured after 4 days of oven-drying at 60°C, and the total shoot dry biomass was calculated for each lysimeter (kg per m²). On the day of harvest, soil and roots were sampled using a soil auger with a core diameter of 4.7 cm. Samples were taken at 10 cm intervals starting from the soil surface to a depth of 90 cm from a sampling point located between three plants. From each 10 cm depth, roots were separated from the soil by sieving (< 2 mm) and further handpicking, washed and oven-dried at 60°C for 4 days to calculate root dry mass. Root dry mass was expressed in g per unit soil volume and extrapolated to the whole lysimeter area and expressed as kg per m² to allow calculation of the root-to-shoot ratio.

2.6 | Soil Analysis

The sieved, root-free soil samples from each 10 cm depth were divided into two portions; one portion was stored in a refrigerator at 4°C for further analysis of dissolved C, N and microbial biomass, and the other portion was dried at 60°C for 3 days and ground in a ball mill (MM 400, Retsch GmbH, Hann, Germany) for total soil C and N analysis. Total soil C and N content were analysed using an Elemental Analyzer (EA3100, EuroVector, Tecnologico di Pavia, Italy). Since there was no reaction with HCl (1 M), the total soil C was considered to be equivalent to the soil organic C. The SOC stock was calculated as the product of soil bulk density (g cm⁻³), depth (cm) and SOC concentration (%) following the equation by Batjes (2014).

For the dissolved organic C (DOC) and dissolved N (DN) analysis, two composite samples representing the topsoil (0-50 cm) and subsoil (50-100 cm) were used from each lysimeter. Briefly, a fresh subsample equivalent to 30g of dry soil was dissolved in 60 mL of $K_2 \text{SO}_4$ (0.05 M) solution, mechanically shaken at 200 rpm for 1 h and filtered through 0.45 µm filter paper. The filtrates were analysed for C and N



using the multi N/C 2100s analyzer (Analytik Jena GmbH, Jena, Germany). For the analysis of microbial biomass C and N (MBC and MBN; only carried out in 2021), another set of samples was fumigated with ethanol-free chloroform for 2 h in an airtight desiccator. After the chloroform fumigation, the desiccator was flushed with air 10 times to ensure that any residual chloroform had evaporated. The fumigated samples were extracted with K_2SO_4 and the extract was measured for total C and N as described above. Finally, MBC and MBN were calculated as the difference between the fumigated and unfumigated samples using conversion factors of 0.45 and 0.54 for MBC and MBN, respectively (Beck et al. 1997; Brookes et al. 1985). The C:N imbalance for soil microbes was calculated by dividing the resources (DOC:DN) by the microbial biomass (MBC:MBN) (Mooshammer et al. 2014).

2.7 | Statistics Analysis

The data were found to be normally distributed based on the Shapiro–Wilk test (p > 0.05). Plant and soil parameters, i.e., root biomass, shoot biomass, root-shoot ratio, SOC, N, DOC, DN, MBC, MBN and C:N imbalance affected by crop type (i.e., maize and cup-plant), watering regime (i.e., well-watered and moderate drought) and their interactions were analysed using two-way analysis of variance (two-way ANOVA). As soil CO₂ efflux was measured repeatedly over time from the same PVC collar, a three-way repeated ANOVA was used, with crop and watering regime as fixed effects and the date as random effect. A significance threshold of $p \le 0.05$ was used for comparisons of means using Tukey HSD post hoc test, unless otherwise indicated. As Bartlett's sphericity test was significant (p < 0.001), the data of 2021 was scaled (z-scored) and a principal component analysis (PCA) was performed. In this data set, values were measured at the end of the growing season, but the cumulative CO₂ was used to reflect the overall changes rather than short-term fluctuations. Subsequent ADONIS test and Pairwise PERMANOVA were used to further investigate the drivers of soil CO₂ efflux. Statistical analysis and figure generation were performed using SigmaPlot (version 14.5, Systat Software Inc., Richmond, California, USA) and R Studio (R Core Team 2021) with ggplot2 (Wickham 2016).

3 | Results

3.1 | Weather and Soil Conditions

During the study period, the total annual precipitation was 607, 635 and 699 mm for 2019, 2020 and 2021, respectively (Figure S3). The mean annual air temperature was lowest in 2021 at 8°C compared with 10°C for both 2020 and 2019. The mean soil moisture content at 25 cm depth over the growing seasons for the moderate drought maize ranged from $12.29 \pm 0.18\%$ in 2019 to 15.93 ± 0.19 in 2020 (Table 2). However, the overall mean for well-watered maize reached up to $23.76\% \pm 0.08\%$ in 2021. Similar variations in soil moisture content were also observed between moderate drought and well-watered cup-plants, for example, the overall mean of soil moisture content at 25 cm under moderate drought maize was 12.25 ± 0.23 compared with 23.25% $\pm 0.07\%$ for the well-watered maize in 2021. Low

	Maize				Cup-plant			
	Moderate drought		Well-watered		Moderate drought		Well-watered	
	MC (%)	ST (°C)	MC (%)	ST (°C)	MC (%)	ST (°C)	MC (%)	ST (°C)
2019								
Max.	16.92	24.68	23.01	24.22	21.08	23.14	26.68	23.75
Mean	12.29	19.86	17.85	19.86	18.58	19.76	22.20	19.66
Median	11.34	20.81	19.58	20.75	19.13	21.27	22.10	20.16
Min.	9.17	14.91	8.64	15.53	15.31	13.91	18.22	14.91
SD	2.18	3.43	4.22	3.05	1.72	3.36	1.76	3.13
SE	0.24	0.63	0.46	0.56	0.19	0.61	0.19	0.57
CV	0.18	0.17	0.24	0.15	0.09	0.17	0.08	0.16
2020								
Max.	20.12	24.4	25.61	23.82	20.59	22.21	25.72	21.46
Mean	15.93	18.65	23.34	18.9	15.25	17.49	22.50	17.38
Median	17.17	20.12	23.77	20.75	16.44	18.79	22.47	18.66
Min.	8.77	13.36	18.52	12.88	8.84	11.56	18.61	13.11
SD	3.07	3.36	1.41	3.88	4.19	3.36	1.97	3.11
SE	0.33	0.40	0.15	0.46	0.46	0.41	0.21	0.37
CV	0.19	0.18	0.06	0.21	0.27	0.19	0.09	0.18
2021								
Max.	18.51	22.3	26.62	23.38	18.61	21.57	25.25	23.46
Mean	12.69	19.01	23.76	18.95	12.25	18.42	23.25	18.46
Median	12.09	19.51	24.53	19.37	11.78	18.93	23.60	18.66
Min.	8.43	14.50	18.67	15.7	8.54	1.83	20.25	15.1
SD	2.94	1.84	1.82	1.81	2.77	1.83	1.31	1.86
SE	0.32	0.21	0.20	0.21	0.30	0.20	0.14	0.21
CV	0.23	0.12	0.08	0.12	0.23	0.10	0.07	0.10

TABLE 2 | Summary statistics of the soil moisture content (MC) and soil temperature (ST) over the growing seasons at the 25 cm soil depth (*n* = 5).

Abbreviations: CV, coefficient of variation; SD; standard deviation; SE, standard error.

soil moisture content was observed in the well-watered treatments, as indicated by a coefficient of variation of < 0.1, while in the moderate drought treatments, the coefficient of variation reaches up to 0.28, reflecting moderate variability in moisture distribution. This pattern is obvious in Figure S5, where the well-watered treatments show less variation in soil moisture content, while the drought treatments show a wider range of variability across the soil depths.

3.2 | Root and Shoot Biomass

The shoot and root biomass of maize and cup-plant under moderate drought and well-watered conditions varied significantly over the three growing seasons (Figure 1). In 2019, the wellwatered maize produced the greatest shoot biomass compared to the moderate drought-stressed maize and the watered cup-plant (no drought-stressed cup-plant in 2019) (Figure 1a). Irrespective of the watering conditions, cup-plant produced significantly more shoot biomass in the following seasons (e.g., 165% in 2020% and 93% in 2021) compared to silage maize (Figure 1b,c). The watered cup-plant produced 37% and 23% more shoot biomass than the drought-stressed cup-plant in 2020 and 2021, respectively. But the maize did not respond to the watering regime in either year. In 2020, root biomass followed a similar pattern to that of shoot biomass, with the watered cup-plant inducing the greatest biomass, followed by the moderate drought-stressed cup-plant and maize being the lowest (Figure 3e). Interestingly, the moderate drought-stressed cup-plant produced similar root biomass to the watered cup-plant in 2021. The root/shoot ratio was higher in cup-plant than in maize in all 3 years (Figure 1g-i). Both moderate drought-stressed crops had a higher root/shoot ratio than the well-watered crops, but the difference was not significant in the case of cup-plant.



FIGURE 1 | Mean ± SE of the shoot biomass (a–c), root biomass (d–f) and the root/shoot ratio (root/shoot) (g-i) of maize and cup-plant under moderate drought (D) and well-watered (W) conditions over three consecutive years (2019, 2020 and 2021). There was no drought cup-plant treatment in 2019. Means followed by different letters within 1 year are significantly different at $p \le 0.05$; (n = 5). p values in each graph are the results of one-way ANOVA in 2019 and two-way ANOVA in 2020 and 2021.

3.3 | Soil CO₂ Efflux

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Soil CO₂ efflux varied significantly between crops (i.e., maize and cup-plant), watering regime (i.e., well-watered and drought-stressed) and sampling date over the three growing seasons (Table S2 and Figure 2). In 2019, well-watered maize induced greater soil CO₂ efflux than the moderate drought-stressed maize in five sampling events, out of the seven events measured over the growing season (Figure 2a). The final cumulative CO₂ was greatest in the well-watered maize $(420.14 \pm 12.11 \text{ g CO}_2 \text{ m}^{-2})$ compared with the moderate drought-stressed maize and the well-watered cup-plant (Figure 2a). During the first year, when the cup-plant was in its establishment phase, CO₂ was higher in maize, as the cupplant adopts a rosette growth form during this period. In 2020, regardless of the watering regimes cup-plant tends to emit more soil CO₂ compared with maize in most of the measurement events during the growing season and also in the first two events postharvest (Figure 2c). Irrespective to the water regime, cup-plant induced on average 16% greater CO₂ flux than maize (Figure 2d). Similarly, in 2021, the well-watered cup-plant exhibited the highest soil CO₂ efflux for most of the sampling events, followed by the moderate drought-stressed cup-plant, with the drought-stressed maize showing the lowest soil CO_2 efflux (Figure 2e,f). As the first measurements in the 2021 growing season were only taken 6 weeks after planting, the cumulative soil CO_2 efflux was lower than in previous years.

3.4 | Soil Organic Carbon and Nitrogen

After 3 years of crops cultivation, no significant change was observed in SOC content and stocks (Figure 3). However, soil DOC and DN between maize and cup-plant under different watering regimes changed significantly over the three growing seasons, with more pronounced differences in 2021 (Figure 4). In 2019, drought-stressed maize had the highest DOC than both watered maize and cup-plant (Figure 4a). In 2020, moderate drought-stressed plants had significantly higher soil DOC than the well-watered plants, corresponding to 18% higher DOC for maize and 8% for cup-plant (Figure 4b). In 2021, the differences between moderate drought and wellwatered maize reached 62%, compared to 66% difference between drought and watered cup-plant (Figure 4c). In contrast to DOC, DN was rather affected by crop type than watering



FIGURE 2 | Mean ± SE of the soil CO₂ efflux, and the final cumulative CO₂ efflux of maize and cup-plant under moderate drought (D) and wellwatered (W) conditions over the growing seasons of 2019 (a and b), 2020 (c and d) and 2021 (e and f). The red dashed line indicates the harvest time of each year. Means followed by different letters within one year are significantly different at $p \le 0.05$; (n = 5). p values in the cumulative CO₂ graphs are the results of one-way ANOVA in 2019 and two-way ANOVA in 2020 and 2021.

regime, with maize exhibiting significantly higher soil DN values than cup-plant in all three growing seasons (Figure 4d–f). Regardless of the watering regime, the soil cultivated with maize had on average about 2.6 times greater DN than cupplant in both 2020 and 2021.

3.5 | Microbial Biomass Carbon and Nitrogen

The soil MBC was affected by crop type, with cup-plant inducing a greater microbial biomass than maize (Figure 5a). However, MBN was mostly altered by the watering regime, where the well-watered maize induced 14% greater MBN than the moderately drought-stressed one and the well-watered cupplant induced 16% greater MBN than the drought-stressed cupplant (Figure 5b). In addition, the DOC:DN and C:N imbalance followed the same pattern by being greater in cup-plant than in maize (Figure 5c,d). Within each crop, the drought-stressed treatments had higher DOC:DN and C:N imbalance than the watered crop.

3.6 | Drivers of Soil CO₂ Flux

The relationships between all the studied variables affected by crop types and watering regimes were further investigated using principal component analysis (PCA; Figure 6 and Table S3) and correlation coefficients (Table 3). The PCA showed overall significance (Adonis test, p < 0.05) and significantly different clustering between crop types (pairwise ANOVA, p < 0.05) (Figure 6). Principal components (PC) 1 and 2 explained 77.84% of the variance with 53% of the total variance represented by PC1. Crop type was explained by the *x*-axis (PC1). The factors C:N imbalance, root biomass and soil DN were among the factors



FIGURE 3 | Mean ± SE of the soil organic carbon (SOC) content (a–c) and stocks (d–f) of the soil cultivated with maize and cup-plant under moderate drought (D) and well-watered (W) conditions over the growing seasons of 2019, 2020 and 2021. Means followed by different letters within 1 year are significantly different at $p \le 0.05$; (n = 30).



FIGURE 4 | Dissolved organic carbon (DOC; a-c) and dissolved nitrogen (DN; d-f) extracted from soil samples from maize and cup-plant under moderate drought (D) and well-watered (W) conditions over three consecutive seasons (2019, 2020 and 2021). Red short-dashed line represents the mean values. Means followed by different letters within 1 year are significantly different at $p \le 0.05$; (n = 30). p values in each graph are the results of one-way ANOVA in 2019 and two-way ANOVA in 2020 and 2021.

contributing the highest to this axis (Table S3). Water treatment was explained by the *y*-axis (PC2), to which predominantly MBC:MBN, MBN and DOC contributed (Table S3). Overall soil

 CO_2 efflux increased significantly with the increase in shoot biomass, root biomass, root/shoot ratio and C:N imbalance and decrease with the increase in DN (Figure 3 and Table S3).



FIGURE 5 | Soil microbial biomass carbon (a), microbial biomass nitrogen (b) dissolved organic carbon: Dissolved nitrogen (c) and carbon: Nitrogen imbalance (d) in 2021 from maize and cup-plant under moderate drought (D) and well-watered (W) conditions. Red short dashed line represents the mean values. Means followed by different letters are significantly different at $p \le 0.05$; (n = 30). p values in each graph are the results of two-way ANOVA.



FIGURE 6 | Principal components analysis (PCA) bi-plot showing the relations between cumulative soil CO_2 efflux (CO_2) and driving factors: RB, root biomass; SB, shoot biomass; R:S, root/shoot ratio; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBC:MBN; DOC, dissolved organic carbon; DN, dissolved organic nitrogen; and C:N imbalance of crop type and watering regime (maize and cup-plant subjected to moderate drought and well-watered conditions).

TABLE 3 | Correlation coefficient (r) of the studied parameters; cumulative soil CO₂ efflux (CO₂) and driving factors.

Parameters	CO ₂	RB	SB	R:S	DOC	DN	MBC	MBN
RB	0.71**							
SB	0.71**	0.82***						
R:S	0.60**	0.94***	0.58*					
DOC	0.07	0.28	0.10	0.34				
DN	-0.66**	-0.74	-0.69**	-0.67*	-0.11			
MBC	0.29	0.41	0.50*	0.30	-0.06	-0.65**		
MBN	0.22	0.23	0.42	0.06	-0.52*	-0.43*	0.72**	
C:N imbalance	0.70**	0.96***	0.81***	0.89**	0.32	-0.79**	0.44*	0.21

Abbreviations: C:N imbalance, carbon:Nitrogen imbalance; DN, dissolved nitrogen; DOC, dissolved organic carbon; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; R:S, root/shoot ratio; RB, root biomass; SB, shoot biomass.

*Significant at $p \leq 0.05$.

**Significant at $p \le 0.01$.

***Significant at $p \le 0.001$.

4 | Discussion

Regardless of the watering regimes (i.e., moderate droughtstressed and well-watered conditions), cup-plant had a significantly greater biomass (root and shoot) and soil CO₂ efflux compared to silage maize confirming our first hypothesis (Figures 1 and 2). In line with this hypothesis, soil CO₂ efflux was positively correlated with the shoot and root biomass (r=0.71 for each) and the microbial C:N imbalance (r=0.70) in the soils (Table 3). Against our second hypothesis, moderate drought stress had no significant effect on the soil CO₂ efflux (Figure 2), but significantly affected DOC and MBN, as well as the C:N imbalance. Despite these variations in shoot and root biomass and soil CO₂ efflux, no significant differences in the final SOC (content or stocks) were found after three consecutive years of cup-plant cultivation (Figure 3).

4.1 | Moderate Drought Constraints on Crop Biomass

After the establishment year (i.e., 2019), cup-plant had a significantly higher shoot biomass compared with silage maize (Figure 1), which was consistent with other studies (Bauböck, Karpenstein-Machan, and Kappas 2014; Ustak and Munoz 2018). However, this is not a commonly accepted result, as other research suggests that cup-plant may have lower biomass yields than maize (Ruf and Emmerling 2022; Schoo, Schroetter et al. 2017; von Cossel et al. 2020) depending on soil types and water availibilty. Ruf and Emmerling (2022) explained the reduction in shoot biomass of the cup-plant mainly by water limitation, which increased abscission and loss of lower leaves. Given that cup-plant as a C3 plant has a lower drought tolerance and water use efficiency than maize (C4 plant), it is less suitable for areas with limited water supply (Schoo, Schroetter et al. 2017).

Surprisingly, the moderate drought cup-plant still produced more biomass than both well-watered and moderate droughtstressed maize (Figure 1), which could be explained by the low severity of the moderate drought applied in our study, which maintained a certain level of soil moisture throughout the season. It appears that cup-plant may have exhibited better tolerance to moderate drought stress compared with severe drought, with the development of some adaptive strategies (e.g., deep and dense root mass) contributing to its resistance, as in other perennial crops (Volaire 2003; Zwicke et al. 2015). Such an explanation is supported by our results, where after 2 years of adaptation, the root biomass was generally high under cup-plant with similar root biomass between moderately drought-stressed and well-watered cup-plant (Figure 1d-g). Other plant traits, not measured in our study, such as transpiration rate, water use efficiency and leaf interception, have been suggested to contribute to plant adaptation to moderate drought (Vadez et al. 2024). Therefore, despite its lower water use efficiency, cup-plant appears to tolerate moderate drought stress through other traits, such as investing in a high root/shoot ratio, as previously reported by Rummel et al. (2021) in a pot experiment and confirmed by the present study.

4.2 | Effects of Crop Type on Soil CO₂ Efflux

Cup-plant induced a greater soil CO₂ efflux in the second and third year compared to silage maize, regardless of the watering regime (Figure 2). The soil CO₂ efflux was mostly correlated to root and shoot biomass and wider microbial C:N imbalance (Figure 6 and Table 3), confirming the first hypothesis of our study. The fact that both root and shoot biomass were positively correlated with soil CO₂ efflux is not surprising given that root respiration contributes substantially to soil CO₂ fluxes (Pausch et al. 2013; Pausch and Kuzyakov 2012; Wang et al. 2006). In maize, root-derived soil respiration can account for up to 57% of total emissions, while in perennial crops, this contribution can reach up to 73% (Nichols et al. 2016; Pausch et al. 2013; Wang et al. 2006). These findings highlight the important role of root respiration in the total soil CO₂ efflux for both crops, with factors such as soil temperature, moisture and nitrogen fertilisation affecting these contributions.

In addition to root biomass, soil CO2 efflux was negatively correlated with dissolved N and positively correlated with C:N imbalance (Table 3), highlighting the key role of N availability in the increased soil CO₂ efflux observed under cup-plant compared to silage maize. Despite the supplemental fertilisation for both crops, our results showed significantly lower dissolved soil N under cup-plant (Figure 4d-f). The rapid depletion of soil mineral N, previously reported by Grunwald et al. (2020) and Kemmann et al. (2023), appears to be a characteristic of cupplant cultivation. The depletion of soil dissolved N, combined with increased soil microbial biomass C under cup-plant resulted in a higher microbial C:N imbalance compared to silage maize (Figure 5), suggesting that microbial N-mining is a key process driving soil CO₂ fluxes (Huang et al. 2021; Mooshammer et al. 2014). The large root systems of cup-plant (Figure 1) likely contribute to this by increasing C inputs, thereby accelerating the soil organic matter decomposition (Blagodatskaya and Kuzyakov 2011). While consuming the easily decomposable C, the soil microbes seek new N sources by decomposing soil organic matter leading to increased microbial respiration (Abdalla et al. 2022; Meyer et al. 2017). While we did not measure microbial respiration separately or priming effect in this study, it is possible that the fresh C input under N-limitation could enhance microbial activity, potentially leading to a positive priming effect and contributing to SOM decomposition (Chen et al. 2014; Song et al. 2022; Zhou et al. 2022). However, this remains speculative and would require further investigations distinguishing between root respiration and heterotrophic respiration which is critical for a detailed mechanistic understanding of soil respiration processes. Nevertheless, these findings suggest the need for effective soil N management to simultaneously maintain soil fertility and increase soil organic matter accumulation.

4.3 | Moderate Drought Constraints on Soil Carbon Dynamics

Contrary to our second hypothesis, we found no significant differences in soil CO_2 efflux between well-watered and moderately drought-stressed crops except for maize in the first year (Figure 2). The lack of differences in soil CO_2 flux between well-watered and moderately drought-stressed crops could be due to several factors. Soil CO_2 flux represents the total soil CO_2 fluxes, that is, root and microbial respiration. Under moderate drought stress root respiration is expected to increase as crops invest more in roots (Figure 1h), while microbes are strongly affected by moderate drought, reducing microbial respiration, resulting in no change in total CO_2 flux. In addition, since the C:N imbalance increases under drought (Figure 5d), which may reduce the need for mining and further decrease microbial respiration.

Another possibility is the fluctuations in the soil moisture content, as seen in our study (Figure S5), could induce drying and wetting cycles which are known to influence the temporal variation of soil CO₂ efflux (Abdalla et al. 2021; Barnard, Blazewicz, and Firestone 2020; Fierer and Schimel 2002). During the rewetting of a dry, carbonate-free soil, as our soil, the biotic processes such as microbial turnover and activities are the main contributors to the soil respiration pulses (Butterly et al. 2009). However, in our study, the microbial biomass C was unaffected by moderate drought (Figure 5a), whereas a decrease in microbial biomass N was observed (Figure 5b). The reduction in soil microbial biomass N under moderate drought stress was explained by the lower mineral N availability as indicated by the higher soil DOC:DN ratio (Figure 5c) and the higher microbial C:N imbalance (Figure 5d).

Overall, the reduced soil moisture content and limited soil mineral N under moderate drought conditions could reduce soil microbial activity, and consequently decrease soil organic matter decomposition. In support of this explanation, several other studies have reported reduced enzyme activity in different agroecosystems exposed to drought stress (Asensio et al. 2024; Homyak et al. 2018; Singh et al. 2021). In addition, the observed higher dissolved organic C under moderately drought-stressed conditions compared with watered crops (Figure 4c) could potentially be due to the lower microbial uptake of dissolved organic C (Singh et al. 2021). These findings may also be supported, by the fact that the low soil mineral N under drought conditions did not increase soil CO₂ efflux due to enhanced soil organic matter mineralisation as it was expected. Therefore, drought stress can strongly affect roots, soil microbial traits and nutrient availability without affecting the overall soil respiration.

5 | Conclusion

The study shows that cup-plant has higher above- and belowground biomass compared with silage maize, even under moderate drought stress conditions. This increased biomass is associated with higher soil CO₂ efflux, which is attributed not only to the greater biomass of cup-plant, but also to a greater microbial carbon: nitrogen imbalance than silage maize. Interestingly, moderate drought stress did not affect soil CO₂ efflux for either crop, despite the higher root biomass in cup-plant compared with well-watered conditions. While soil organic carbon (content and stocks) remained unchanged in the short term (over 3 years), the extensive root system and litter input of cupplant suggest that it may serve as a beneficial future alternative to silage maize. Additionally, the cup-plant ability to rapidly utilize soil nitrogen reduces nitrate leaching, making it an attractive option for regions prioritising water quality. This would also lead to reduced fertiliser requirements and nutrient runoff compared with maize.

Author Contributions

Khatab Abdalla: conceptualization, data curation, formal analysis, methodology, writing – original draft, writing – review and editing. Hannah Uther: data curation, formal analysis, methodology, writing – review and editing. Valentin B. Kurbel: data curation, formal analysis, methodology, writing – review and editing. Andreas J. Wild: formal analysis, investigation, methodology, visualization, writing – review and editing. Marianne Lauerer: funding acquisition, methodology, project administration, writing – review and editing. Johanna Pausch: conceptualization, funding acquisition, project administration, supervision, writing – original draft, writing – review and editing.

Acknowledgements

We would like to acknowledge the financial support of the Bavarian State Ministry of the Environment and the Water Management Department of the Government of Upper Franconia within the project 'Demonstrationsprojekt Silphie-Anbau im Projektgebiet Nördliche Frankenalb'. Special thanks to the technical staff of the chair of Agrecology (Ilse Thaufelder and Angelika Mergner) and the Ecological-Botanical Garden (Guido Arneth and his team) of the University of Bayreuth and the students involved in this research (Friederike Dellmann and Stefanie Hochmuth) for their help and support. *Open access funding*: Funded by the Open Access Publishing Fund of the University of Bayreuth.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.27170211.v1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.