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Perennial Cup Plant (*Silphium perfoliatum* L.) Outperforms Silage Maize (*Zea mays* L.) in Root Biomass and Nitrate Retention

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ABSTRACT

Achieving European climate neutrality by 2050 will require an increase in energy production from renewable sources. Silage maize (*Zea mays* L.), the most commonly used crop in Germany, is increasingly subject to yield losses associated with soil degradation and nutrient depletion. The perennial cup plant (*Silphium perfoliatum* L.) has emerged as an alternative to reduce nutrient losses, mainly nitrogen (N), while maintaining similar biomass production. A lysimeter experiment was conducted to evaluate N dynamics between plant, soil, and leaching for maize and cup plant under moderate drought and well-watered conditions over 4 years. After the first year of growth, cup plant had higher shoot and root biomass than maize regardless of the watering conditions (e.g., in 2021 mean shoot biomass of maize was 266 g m^{-1} compared to 2696 g m^{-1} of cup plant). Notably, moderate drought did not affect shoot biomass in either crop (except in 2021 and 2022 for the cup plant). The higher biomass production of the cup plant was associated with higher N concentration in the shoot tissue compared to maize, likely due to its more efficient soil N utilization. This result was further supported by the lower soil dissolved N concentration and a reduction of nitrate leaching of 88% in 2021 and by up to 99% in 2022 under cup plant compared to maize. A higher microbial biomass N under cup plant suggests enhanced N immobilization by microorganisms. This is further supported by a higher microbial C/N imbalance under cup plant than maize in 2022, indicating a stronger N relative to C limitation. Our results showed that cup plant can provide high shoot and root biomass and significantly reduced nitrate leaching, indicating its potential as an alternative to maize and thus as a bioenergy crop for environmental sustainability in a changing climate.

1 | Introduction

In line with the European Green Deal proposed in 2019—reaching climate neutrality by 2050—Germany has committed to phase out coal in its energy balance after 2030 (Manowska et al. 2024). Achieving this goal will require a shift to predominantly bioenergy crops with enhanced biomass production as renewable energy sources (Hansen et al. 2019). Currently, maize (*Zea mays* L.) is the most economically important energy crop in Germany and represents the largest share of agricultural materials converted to electricity (Ruf et al. 2021; Szarka et al. 2021). Under optimal conditions, maize can efficiently take up nitrogen (N) from the soil, minimizing N losses to the environment (Schittenhelm et al. 2021). However, due to late sowing, slow biomass development, and usually no subsequent crop after harvest (Di and Cameron 2002; Grunwald et al. 2020), the soil remains

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uncovered for a long period of the year. Exposed soil leads to a higher risk of nutrient leaching (Di and Cameron 2002). This leaching potential, particularly for nitrate, is low during the vegetation period with adequate fertilization but increases with an oversupply of N (Svoboda et al. 2013). Additionally, more frequent extreme weather events, such as heat waves and droughts, have been associated with reduced silage maize yields (Jacob et al. 2014; Sedlmeier et al. 2018; Schmitt et al. 2022). Consequently, the search for more sustainable bioenergy crops with comparable biomass production has expanded, taking into account both the economic and ecological benefits.

The cup plant (*Silphium perfoliatum* L.), from the Asteraceae family, was suggested as a promising alternative to maize for bioenergy production (Schittenhelm et al. 2021). It is a perennial C3 crop, native to North America, that occurs naturally in areas with high air humidity and soil moisture content (Gansberger et al. 2015). In the year of sowing, cup plant forms a rosette and can only be harvested profitably the following year for 10–15 years (Ende and Lauerer 2022; Gansberger et al. 2015). The growth height, and by that the yield, varies between 1.8 and 3 m, depending on sowing density, fertilization, soil type, water availability, harvest time, and climate (Gansberger et al. 2015). Under high water supply conditions, the biomass yields are comparable to those of maize (Schoo, Schroetter, et al. 2017). In contrast, under dry conditions, the yield of the cup plant (C3 crop) is assumed to be lower compared to maize (C4 crop) due to different photosynthetic pathways resulting in a lower water use efficiency of cup plant (Cumplido-Marin et al. 2020; Schoo, Wittich, et al. 2017). As a deep-rooting species, cup plant may cope with moderate drought stress but is likely to suffer a yield penalty under intensive and/or prolonged drought (Ende et al. 2021; Ruf and Emmerling 2022). Prolonged heat and drought stress over consecutive years is due to climate change a possible climate scenario for the near future (Suarez-Gutierrez et al. 2023). Moderate drought stress is the most common form of drought leading to reduced growth rates rather than total crop failure (Vadez et al. 2024). However, adaptation to moderate drought remains insufficiently understood at a mechanistic level, and plant responses may differ compared to those under extreme drought.

The extensive root system of cup plant has been shown to reduce soil dissolved N compared to maize (Abdalla et al. 2024; Grunwald et al. 2020). Its perennial nature minimizes soil disturbance by eliminating the need for annual tillage under field conditions (Bury et al. 2020; Kantar et al. 2016; Ryan et al. 2018). Over time, this enhances soil organic matter and alters greenhouse gas emissions (e.g., CO_2 and N_2O). Additionally, the root system of cup plant is partly renewed every year, which also contributes to an increase in SOC over time (Cumplido-Marin et al. 2020). Furthermore, Ruf et al. (2018) found that SOC was higher under perennial crops than under annual crops, and that this higher SOC correlated positively with microbial biomass C (MBC). Similarly, Abdalla et al. (2024) and Emmerling et al. (2017) reported higher MBC under cup plant than maize, though Ruf and Emmerling (2020) found the opposite. To balance their stoichiometric demands, microbes may immobilize soil mineral N. Thus, high root N uptake together with high rates of microbial N immobilization may cause lower N availability in soils under perennials, leading to reduced nitrate leaching (Schlautman et al. 2021). The latter can additionally be explained by a lower nitrification activity under perennial plants compared to annual plants (Pinay et al. 2007). These effects lead to lower soil mineral N levels which in turn leads to reduced N leaching in perennial cup plant compared to annual maize (Grunwald et al. 2020). This disadvantage in N leaching under maize monoculture can be partly compensated by agricultural practices like intercropping (Manevski et al. 2015) or crop rotation (Zong et al. 2024). The cup plant seems to be a promising alternative to silage maize without changing the agricultural practices, especially for sites where groundwater nitrate levels surpass limits, necessitating reduced leaching.

Despite the recognized benefits of cup plant as a perennial biomass crop, there is limited research on its growth under moderate drought conditions and how this affects N dynamics compared to annual crops such as maize. In particular, the impact of moderate drought on N uptake by the plant and loss via leaching in cup plant has not been studied over multiple years, despite this being an increasingly relevant scenario in the context of future climate change. Our study addresses this knowledge gap by investigating N dynamics over four consecutive years under well-watered and moderate drought conditions. This approach enables us to evaluate how perennial growth and moderate drought stress interact to influence N dynamics in cup plant compared to maize.

2 | Materials and Methods

2.1 | Experimental Site and Set Up

The experiment was conducted at the Ecological-Botanical Garden (49°55′19″ N, 11°34′55″ E, 365 m a.s.l.) of the University of Bayreuth, Germany. The facility consists of a total of 28 built-in lysimeters (20 were utilized for the current study), each with a volume of 1.69 m^3 (length, width: 1.3 m each and 1 m depth), of which 20 were used in this study. The lysimeter basins are funnel-shaped at the bottom. The funnel-shaped part was filled with a layer of gravel, which was covered with a water-permeable drainage fleece to prevent soil loss with the leachate. The leachate water was channeled through the gravel layer to an underground 60 L water tank. Each lysimeter was filled with grassland soil obtained from the floodplain of the Red Main River (near Bayreuth). The soil was classified as *Fluvisol* (IUSS Working Group WRB 2022) with a pH value of 6.5 ± 0.03. The texture was sandy loam with a clay content of 7%, a silt content of 21%, and a sand content of 72%. The soil organic carbon (SOC) and nitrogen (N) contents were 2.08% SOC and 0.17% N, respectively, resulting in a C/N ratio of 12.49 (Abdalla et al. 2024).

Two crops (maize; *Zea mays* L. cv. PM Paolo and cup plant; *Silphium perfoliatum* L.) were subjected to moderate drought stress or well-watered conditions, replicated five times each (Figure S1). A formal blocking design was not possible due to the constraints in the layout of the facility (Figure S1). Nevertheless, we believe that spatial variability is low because: (I) the area is relatively small, (II) all lysimeters were filled with the same soil, and (III) there is no horizontal interaction between the built-in lysimeters. All lysimeters were equipped with an irrigation system and soil moisture sensors (TEROS-13, METER GROUP AG, Munich, Germany) at three depths (25, 50 and 75 cm) to regulate the soil water content based on the watering regime (well-watered or moderate drought stress). The watering conditions were defined based on the initial soil water retention curve, where the volumetric water content in the topsoil (0–25 cm) was maintained at 100% of the soil field capacity (i.e., 25%) for the well-watered and 50% (i.e., 12.5%) for moderate drought. To account for the moisture fluctuations under field conditions, we consider a water content range of 23%–25% as optimal water supply for plant growth, that is, watered treatment, and 13%–15% as conditions causing moderate stress due to water limitation, that is, moderate drought (Abdalla et al. 2024). To ensure proper crop establishment, moderate drought conditions were applied to maize starting 3 weeks after sowing each year. For cup plant, no drought was applied in the establishment year (i.e., 2019); from 2020 onwards, moderate drought treatment was implemented at the same time as for maize.

2.2 | Crop Cultivation

The maize lysimeters were planted in May each year (May 14, 2019; May 4, 2020; May 17, 2021; and May 12, 2022). Three seeds were sown in each of 14 staggered holes. This resulted in four rows, alternating between three and four holes per row (Figure S2). In the following year, the row was maintained, but the positions were changed so that the plants did not grow in the same place in the soil. After germination, the plants were thinned out so that only the best developed plant remained in each hole. At the end of germination, each of the maize lysimeters contained 14 plants, which results in a planting density of approximately 80,000 plants ha^{-1}. The perennial cup plant was planted once on the May 5, 2019, by planting 5 pre-germinated seeds per hole. As with the maize, the plants were thinned out after germination, keeping only the strongest plants. Due to the expected size of the developed cup plant, a distance of 55 cm between each plant was maintained. This resulted in 6 plants per cup plant lysimeter (2 plants per row for a total of 3 rows, Figure S2), corresponding to a planting density of 40,000 plants ha^{-1}. Due to the perennial growth, the vegetation phase of the cup plant starts earlier than that of maize, reaching a height of approximately 15–20 cm (field observation) when the maize is sown.

In 2019, no additional fertiliser was applied due to the high initial levels of N and phosphorus levels (Table 1). From the second year onwards, fertiliser was applied to prevent nutrient deficiencies in the plants during the course of the experiment. The NPK(S) fertiliser 15/15/15 (Complex 15 EC fertiliser) consists of 15% N (6% NO_3^-, 9% NH_4^+), 15% P_2O_5, 15% K_2O, 7.5% SO_3 and 0.01% Zn. The total amount of fertiliser calculated to reach 190 kg N ha^{-1} as recommended for silage maize, was divided into three doses (Table S1). The first dose was added during the preparation of the seedbed before sowing (depth 5 cm), but on the same day. The second dose was added to the soil approx. 3–4 weeks after sowing when the maize had already grown 5–10 cm. The third application was made approx. 3–4 weeks after the second application. The planting densities and fertilizations of both crops 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.

2.3 | Plant Sampling and Analysis

The harvest took place in late September or early October (September 25, 2019; September 30, 2020; October 7, 2021; and September 20, 2022). The total aboveground biomass of the individual plant was cut into pieces and placed in a paper bag. The aboveground biomass of maize was separated into cobs and shoots (stems with leaves). The cobs were excluded from further analysis (C and N content) because our comparison focuses on the environmental benefits and shoot biomass production of the cup plant versus silage maize, for which mature cobs are not considered. The roots were separated from the soil samples taken with a soil auger (see Section 2.4). The roots were washed and, like the shoot biomass, dried at 60°C for at least 3 days to obtain the total dry biomass.

The shoot biomass was first determined as dry weight per lysimeter and expressed in g m^{-2}. Root biomass (g $\mathrm{lysimeter}^{-1}$) was calculated per depth (10 cm increments up to 90 cm) using the dry weight of the roots (m_{root}, g) and the soil (m_{soil}, g) and summed over the area of the lysimeter ($130 \times 130\ \mathrm{cm}^2$) using the soil bulk density (ρ, $\mathrm{g\,cm}^{-1}$) (Equation 1). The bulk density (ρ) was determined based on the 2020 data for each depth and used for all years and all lysimeters.

$$\text{Root biomass}\ \left[\mathrm{g\ lysimeter}^{-1}\right] = \left(\frac{m_{\mathrm{root}}}{m_{\mathrm{soil}}} \times \rho\right) \times 10 \times 130 \times 130 \quad (1)$$

For the C and N content of the plant material sampled in 2019, the entire collected aboveground biomass (rosette) was used for the cup plant lysimeters and mixed. In this year, the maize lysimeters were represented by a randomly selected plant. In the following years, the method was optimized by selecting randomly two plants per lysimeter. Both the shoot- and root biomass were dried, chopped, a subsample milled, and the C and N concentrations were measured using elemental analysis (Euro Vector EA3100, Tecnologico di Pavia, Italy).

TABLE 1 | Nutrient composition of the bulk soil at the beginning of the experiment.

Depth [m]	P [$\mathrm{mg\,kg}^{-1}$]	K [$\mathrm{mg\,kg}^{-1}$]	DN [$\mathrm{mg\,kg}^{-1}$]	NH_4^+ [$\mathrm{mg\,kg}^{-1}$]	NO_3^- [$\mathrm{mg\,kg}^{-1}$]
0–0.1	121.64 ± 6.61	70.11 ± 2.31	70.70 ± 6.25	53.85 ± 14.12	16.84 ± 19.37
0.1–0.3	119.98 ± 3.35	68.35 ± 3.90	80.73 ± 13.75	12.90 ± 6.58	67.83 ± 11.75
0.3–1	122.10 ± 7.64	65.26 ± 2.32	110.02 ± 52.49	2.44 ± 0.65	107.58 ± 51.85

Note: Dissolved N (DN) was determined with a 0.05 M K_2SO_4 extraction method (ratio of 1 g soil: 2 mL solution). Phosphorus (P) and potassium (K) were determined with the calcium acetate lactate CAL-extraction method.

To determine the N content of the shoot and the root biomass, the biomass per lysimeter was multiplied by the N concentration. The N contents of the root biomass were summed up for the individual layers.

2.4 | Soil Sampling and Analysis

The soil was sampled at the harvest using a soil auger with a core diameter of 4.7 cm. There was one sampling point per lysimeter from 0 to 90 cm with 10 cm intervals, resulting in nine samples. One sampling point between three plants was drilled per lysimeter for cup plant and maize (Figure S2). The position of the drill hole remained at the same distance from the plants every year. In the laboratory, the roots were extracted from the soil samples by hand-picking with tweezers. The remaining soil was sieved to < 2 mm for further analysis and stored accordingly.

To determine the total C and N contents of the soil, a homogenous subsample was dried at 60°C to constant weight, milled, and analysed using elemental analysis (Euro Vector EA3100, Tecnologico di Pavia, Italy). For the microbial biomass analysis, two fresh composite samples representing the upper 0–50 cm and the lower 50–90 cm were prepared. The soil samples were stored in a refrigerator at 4°C until extraction. Microbial biomass C and N were determined using the chloroform fumigation extraction (CFE) method adapted from Vance et al. (1987). A 0.05 M K_2SO_4 solution was added to 15 g of fresh soil at a ratio of 1:4, shaken vertically for 60 min, and filtered through a 110 mm filter paper to obtain the extractable soil organic C and N. Another 15 g of fresh soil from the same samples were fumigated with 75 mL of ethanol-free chloroform (ethanol-free, LiChrosolv VWR). The C and N in the samples were then extracted with 0.05 M K_2SO_4 as described above. The C and N in both extractions were measured with the multiC/N analyzer (Analytik Jena GmbH, Jena, Germany). The C and N of the unfumigated samples represent the extractable C (referred to as dissolved organic C; DOC) and extractable N (dissolved N; DN) through a 0.05 M K_2SO_4 solution in the soil, whereas the C and N in the fumigated samples represent the total C and N.

The amount of C and N in the microbial biomass (mg kg^{-1} soil) was calculated according to Equation (2), where $N_{\text{fumigated}}$ and $N_{\text{unfumigated}}$ are the values obtained from the analyses. k_{EN} is the extraction factor for N of 0.54. Equation (2) is shown as an example for MBN but can be used analogously for MBC, with a k_{EC} of 0.45 (Joergensen 1996; Joergensen and Mueller 1996). A C/N imbalance is calculated according to Mooshammer et al. (2014), by dividing the DOC/DN ratio by the MBC/MBN ratio.

$$\text{MBN} = \frac{N_{\text{fumigated}} - N_{\text{unfumigated}}}{k_{\text{EN}}} \tag{2}$$

The DN from the unfumigated samples was related to the weighed sample quantity and extrapolated to the respective lysimeter basin for the relative N distribution (Section 2.6) using the bulk density of the soil (ρ). The same was done to calculate N of the microbial biomass.

2.5 | Leachate Sampling and Analysis

The leachate from the lysimeters was collected in 60 L canisters and sampled regularly from July 2019 onwards. The volume of the leachate was recorded, and a homogeneous subsample of 250 mL was taken. The canisters were emptied after each sampling. Sampling was carried out until a few weeks after the harvest in order to determine the leaching of nitrate even after aboveground biomass removal. If the canisters contained < 250 mL, as much sample as possible was taken and the volume recorded. Volume below 1 L was rounded to 1 L. During the experiment, there were five instances in 2020 due to the lockdown during the Coronavirus pandemic and three in 2021 due to heavy rainfall in which all of the canisters overflowed. A volume of 60 L was assumed for these samples, which might have resulted in an underestimation of nitrate leaching during this time. The leachate was filtered through a 0.45 μm filter to ensure that no particles remained in the liquid. The nitrate concentrations in the leachate were determined in the BayCEER Central Laboratory for Analytics using ion exchange chromatography analysis (Metrohm 881 Compact IC pro) and then converted to the N concentration. To determine the total $N\text{-}NO_3^-$ load in the leachate, the nitrate concentrations were related to the total volume of the respective leachate sample (N leaching).

2.6 | Relative N Distribution Calculations

The relative N distribution was calculated based on the previously obtained data for each year separately. This consists of the following pools: N in shoot and root biomass, N in microbial biomass, DN in soil, cumulative N leaching as nitrate, and total N in the soil. The latter was calculated based on %N in soil and bulk density (ρ) for each soil layer and summed for the relative N distribution. Microbial N and DN were subtracted from the total soil N before calculating the relative N distribution.

For the relative N distribution per lysimeter, the N content of each pool was summed and set to 100%. The N proportion of each pool to the total N in the system was then calculated.

2.7 | Statistical Analysis

All statistical analysis and figure generation were carried out using R software (version 4.2.0; R Core Team 2022). Outliers were identified and removed from the dataset before the statistical analysis using the interquartile range (IQR) criterion and tested with the boxplot.stats() function. The data was preceded by checking the residuals of the used model (ANOVA) for normal distribution and variance homogeneity (*shapiro.test()* and *leveneTest ()*; package *car*; with a limit p value ≥ 0.05). If the data did not show normal distribution and variance homogeneity, two times data transformations (i.e., log- or square root-transformation) were applied. The normally distributed data was then analyzed using either one- or two-way analysis of variance (ANOVA).

For the year 2019, a one-way ANOVA was used to determine statistical differences due to a missing moderate drought treatment for cup plant (function *aov ()*, limit value of ≤ 0.05). From 2020 to 2022, a two-way ANOVA was used to test the effect of plant (i.e., cup plant, maize) and watering-regime (i.e., moderate drought, well-watered conditions) and their interaction (limit value of ≤ 0.05). When the interaction was not significant, we interpreted the main effects directly from the ANOVA results without further analysis. In case of a significant interaction between crop type and watering regime, post hoc comparisons among the four treatment combinations (maize–drought, maize–watered, cup plant–drought, cup plant–watered) using Tukey's HSD test (functions *TukeyHSD()* and *HSD.test()*; package *agricolae*), which allowed us to identify specific group differences while controlling for multiple comparisons.

In the case of the N-leaching in 2022 and shoot biomass in 2020, transformation was insufficient to achieve normal distribution. In this case, a Scheirer-Ray-Hare test (scheirerRayHare(), package rcompanion) was conducted for the two factors and their interaction effect. If a significant interaction effect was detected, post hoc comparisons were performed using Dunn's test with Bonferroni correction (dunnTest(), FSA package).

3 | Results

3.1 | Shoot- and Root Biomass

Shoot biomass dry weight (DW) varied markedly between crops and watering regimes over the study period (Figure 1). In the establishment year (i.e., 2019; Figure 1A) no significant effect of the treatments was detected. Starting from 2020, cup plant produced significantly higher shoot biomass compared to maize ($p < 0.001$), regardless of the watering regimes (Figure 1B,C). In this year, both crop type and watering regime significantly influenced shoot biomass ($p < 0.001$ and $p = 0.0017$, respectively), and a significant crop × watering interaction was observed ($p = 0.005$). Drought reduced shoot biomass in cup plant but had little additional effect on maize, which showed consistently low biomass under both watering regimes. Otherwise, the differences between the plants under moderate drought stress and watered plants are not significant but show a tendency towards lower shoot biomass during moderate drought. Root biomass dynamics closely followed the shoot biomass trends over the study period (Figure 2). The root biomass was generally not affected by the drought treatment, apart from lower values in cup plant in 2020 and 2021

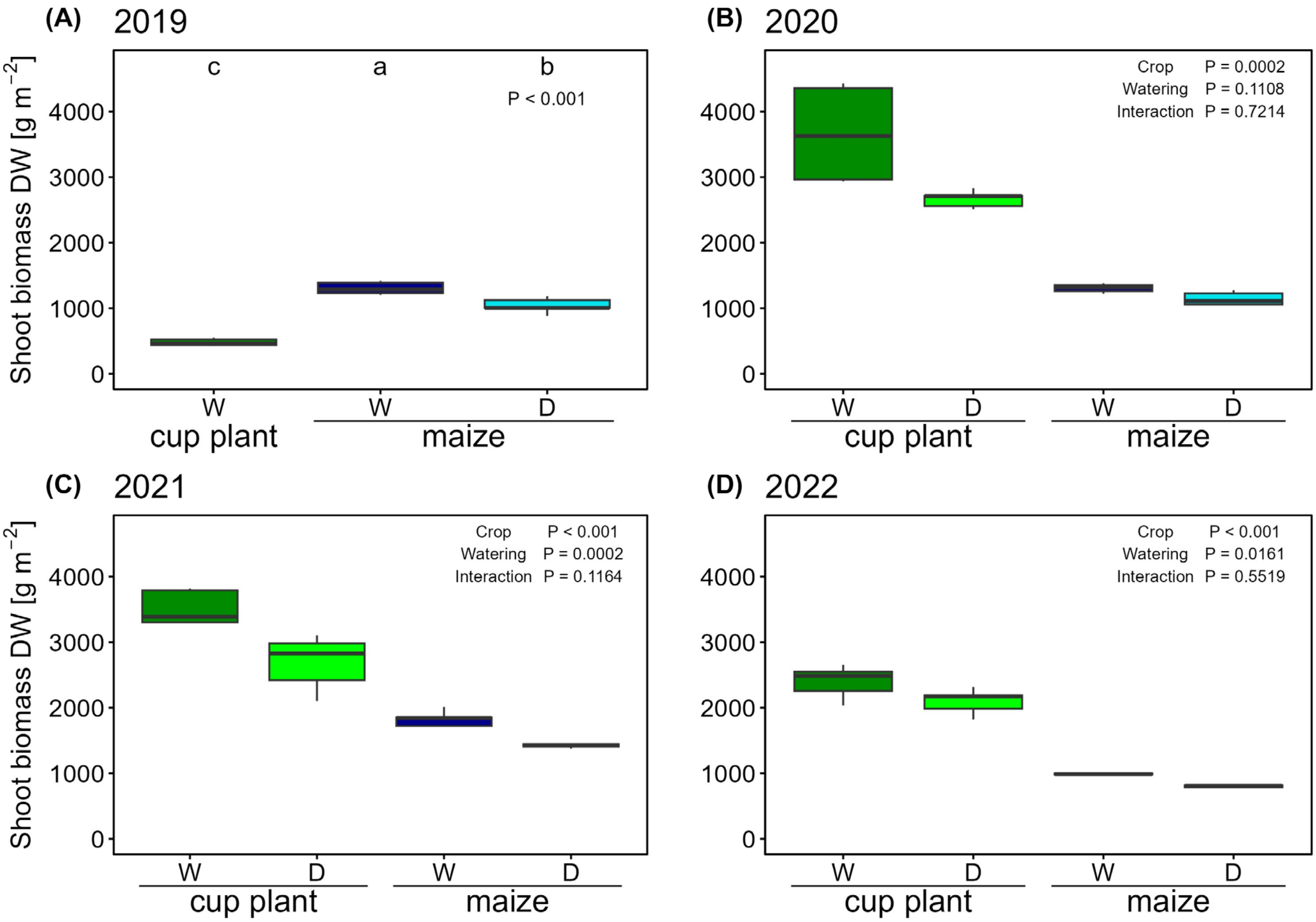

FIGURE 1 | Dry weight (DW) of the shoot biomass (without the cobs) harvested at the end of each growing season (A. September 25, 2019; B. September 30, 2020; C. October 7, 2021; and D. September 20, 2022). No moderate drought stress was applied to the cup plant in its establishment year (2019). Different letters indicate significant differences ($p \leq 0.05$) among the crop × water regime (W = well-watered; D = moderate drought) combinations (maize–drought, maize–watered, cup plant– drought, and cup plant–watered) for the respective year.

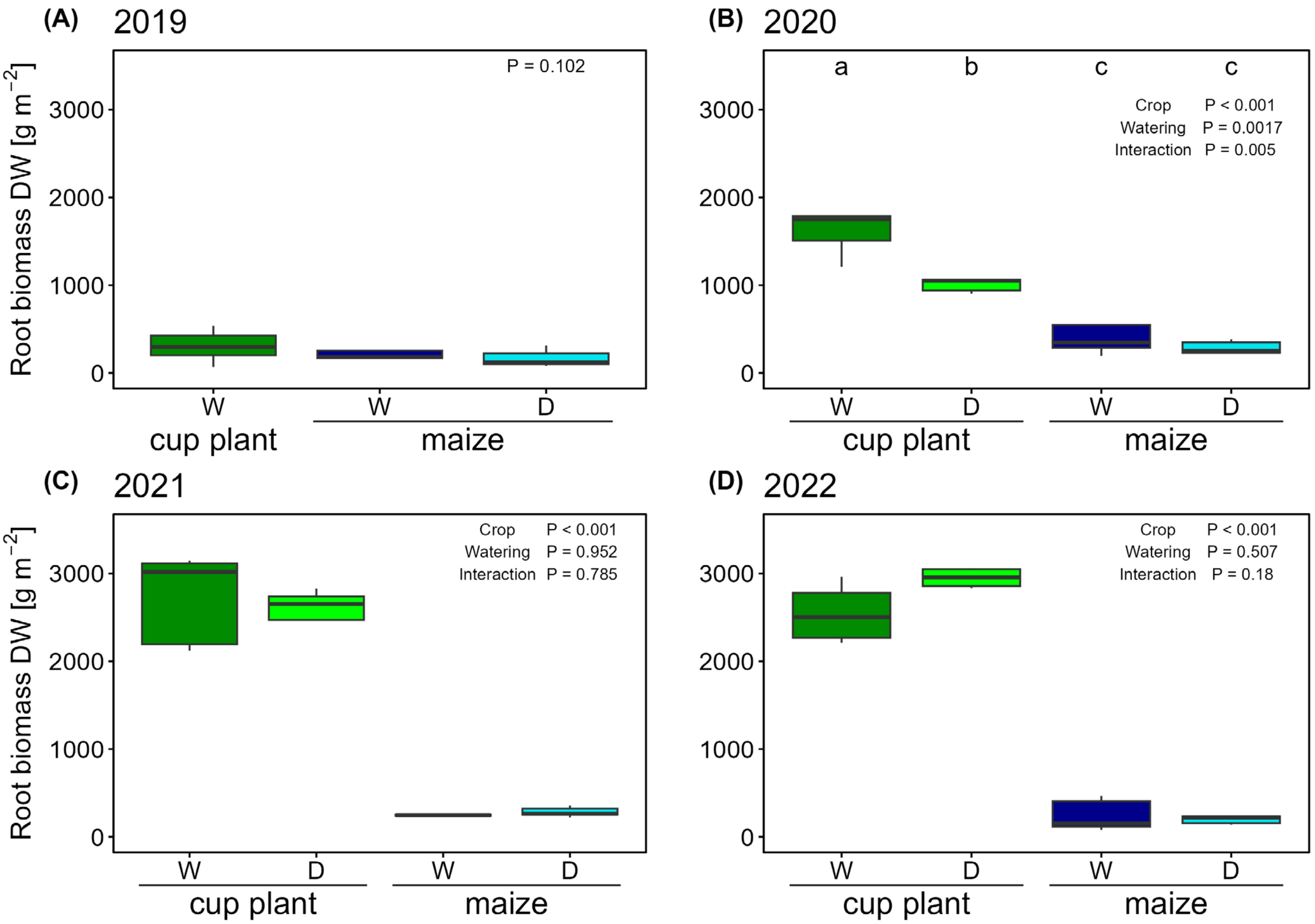

FIGURE 2 | Dry weight (DW) of the root biomass to a 90 cm depth harvested at the end of each growing season (A. September 25, 2019; B. September 30, 2020; C. October 7, 2021; and D. September 20, 2022). No moderate drought stress was applied to the cup plant in its establishment year (2019). Different letters indicate significant differences ($p \leq 0.05$) among the crop × water regime (W = well-watered; D = moderate drought) combinations (maize–drought, maize–watered, cup plant–drought, and cup plant–watered) for the respective year.

(Figure 2). There was a significant interaction of crops and watering regimes in 2020 (Figure 2B). Interestingly, in 2022, cup plant root biomass was higher under drought than under the well-watered treatment (Figure 2B). From 2020 onwards, the cup plant has a higher root biomass compared to maize regardless of the watering regime (e.g., in 2021 mean value of 266 g m^{-1} for maize and 2696 g m^{-1} for cup plant).

3.2 | Soil Dissolved N and Microbial Biomass N

Soil dissolved N (DN) concentrations differed significantly, with a greater effect derived by crop type, and consistently higher values under maize compared to cup plant from 2020 onwards (Figure 3). In the first year of growth (2019), DN did not differ between maize and cup plant. From 2020 to 2022, maize plots exhibited higher DN levels than cup plant, with the largest differences observed in 2022. Notably, in 2022, DN concentrations increased under moderate drought in maize compared to the well-watered treatment, with an observed significant interaction between crops and watering regimes (Figure 3D). A similar interaction trend was observed in 2020 ($p = 0.0786$), when cup plant also showed slightly higher DN under drought compared to watered plots. For microbial biomass N (MBN) moderate drought consistently tended to reduce MBN values compared to well-watered conditions (e.g., maize in 2020 and cup plant in 2021; Figure 4). Significant variation between the crops exists in 2020, with higher MBN under watered maize (Figure 4B) and in 2022, with lower values regardless of the watering regime under maize compared to cup plant (Figure 4D).

3.3 | N Leaching

Cumulative N leaching (as nitrate) was higher under cup plant compared to maize in 2019, the establishment year, when no drought treatment was applied (Figure 5A). However, from 2020 onwards, cup plant has lower N leaching compared to maize. In 2020, the watering regime significantly affected NO_3^- leaching in maize, with higher losses under moderate drought. Similarly, cup plant also exhibited increased leaching under drought compared to the well-watered treatment (Figure 5B).

In 2020, the highest mean nitrate concentrations under both plants were recorded with 81 g L^{-1} for maize (92 g L^{-1} under moderate drought) and 34 g L^{-1} for cup plant (51 g L^{-1} under moderate drought) under watered conditions. This corresponds to a reduction of 58% (44% under moderate drought) by the cup plant (not considering outliers). However, in 2021 and 2022, the mean reduction of nitrate leaching of cup plant compared to maize reached 88% and 99%, respectively. Note, in 2020 and

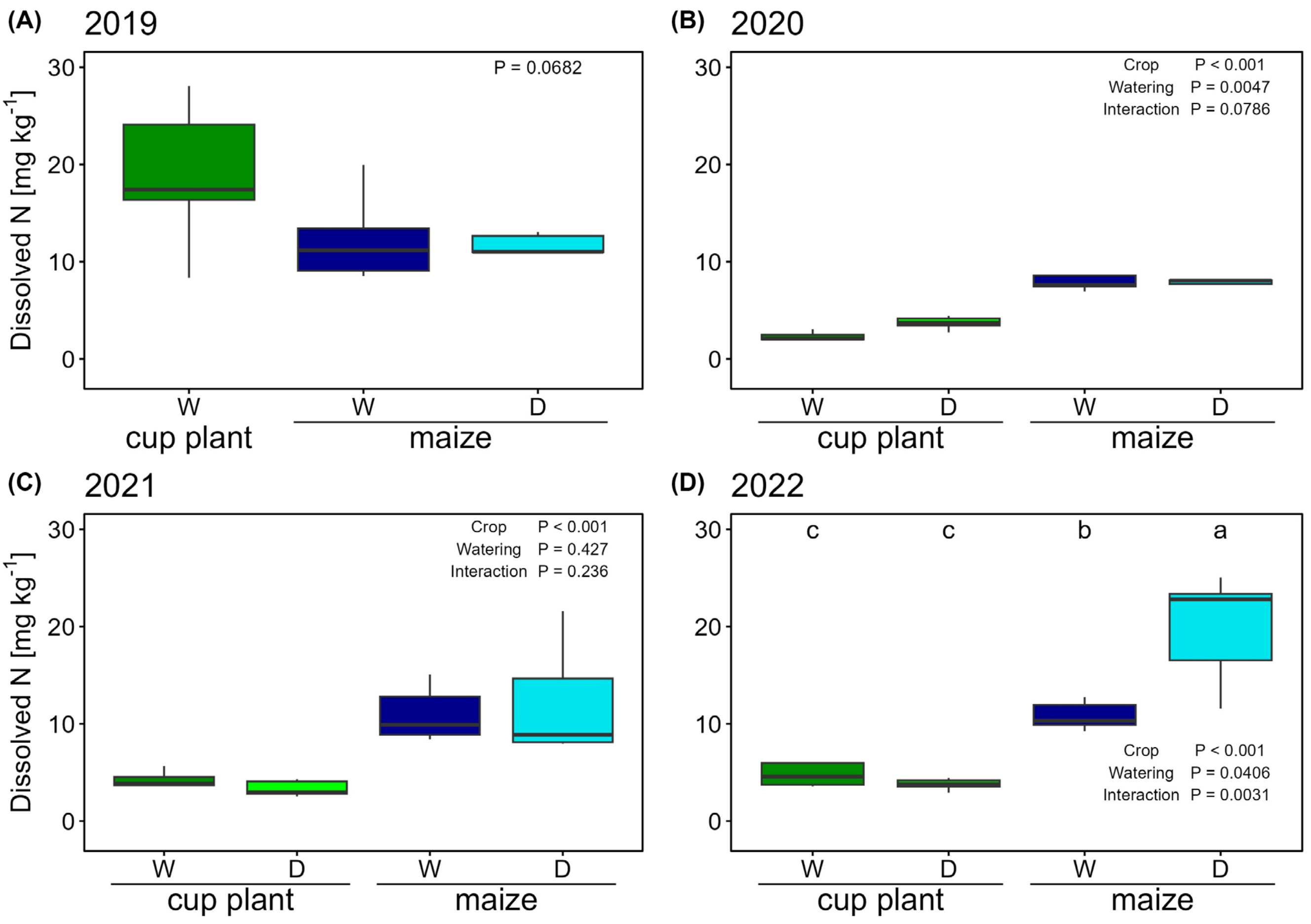

FIGURE 3 | Dissolved nitrogen (N) in the soil sampled with the harvest at the end of each growing season (A. September 25, 2019; B. September 30, 2020; C. October 7, 2021; and D. September 20, 2022). No moderate drought stress was applied to the cup plant in its establishment year (2019). Different letters indicate significant differences ($p \leq 0.05$) among the crop × water regime (W = well-watered; D = moderate drought) combinations (maize–drought, maize–watered, cup plant–drought, and cup plant–watered) for the respective year.

2021, overflow of containers may have led to an underestimation of nitrate leaching at individual sampling events as described in Material and Methods.

3.4 | Relative N Distribution

Across all years and treatments, the highest N amount is in the soil with more than 90% (Figure 6). This is followed by the microbial biomass N with an overall average of 2.2% for all treatments and years (minimum of 1.3% in 2022 for dry maize and maximum of 2.8% for watered cup plant in 2022). The relative N distribution was affected by the crop type rather than the watering regime. The N in the plant pools (belowground and aboveground pools) is higher under cup plant than maize over the 4 years. Within the maize, in percentage terms, there is more N in the aboveground pool (excluding the cobs) compared to the belowground pool. Looking at the N pool in the leachate, the highest proportion is observed in 2020 for both plants compared to all years, with a higher pool under maize compared to the cup plant. In 2021 and 2022, the relative N loss through leaching was less under cup plant (below 0.05%), while maize lost around 0.3% N through leaching. Interestingly, no consistent pattern was observed in the soil DN pool between the crop types and years.

4 | Discussion

4.1 | Biomass Production and Plant N Concentration

Except for the first year (2019), cup plant has always had a higher root- and shoot biomass compared to maize regardless of the watering regimes (Figures 1 and 2), suggesting its potential for sustainable bioenergy production (von Cossel et al. 2020). Partly contradicting our results, lower shoot biomass under cup plant but higher root biomass compared to silage maize were already reported in the literature (Ruf and Emmerling 2022; Schoo, Schroetter, et al. 2017). However, Schittenhelm et al. (2021) reported greater biomass dry matter under cup plant with values similar to our results. Schoo, Wittich, et al. (2017) conclude that, due to its high potential evapotranspiration, the cup plant can attain biomass yields comparable to those of maize only at sites with high water supply. However, during severe drought conditions (i.e., 10% soil water content) a significantly lower biomass yield of both plants can be expected (Ende et al. 2021; Schoo, Wittich, et al. 2017). In our study, moderate drought induced a significantly lower dry shoot biomass production in cup plant in 2021 (Figure 1C), which can be linked to the significantly lower root biomass in the previous year (Figure 2B). This can be attributed to a lower plasticity of root traits under cup plant to

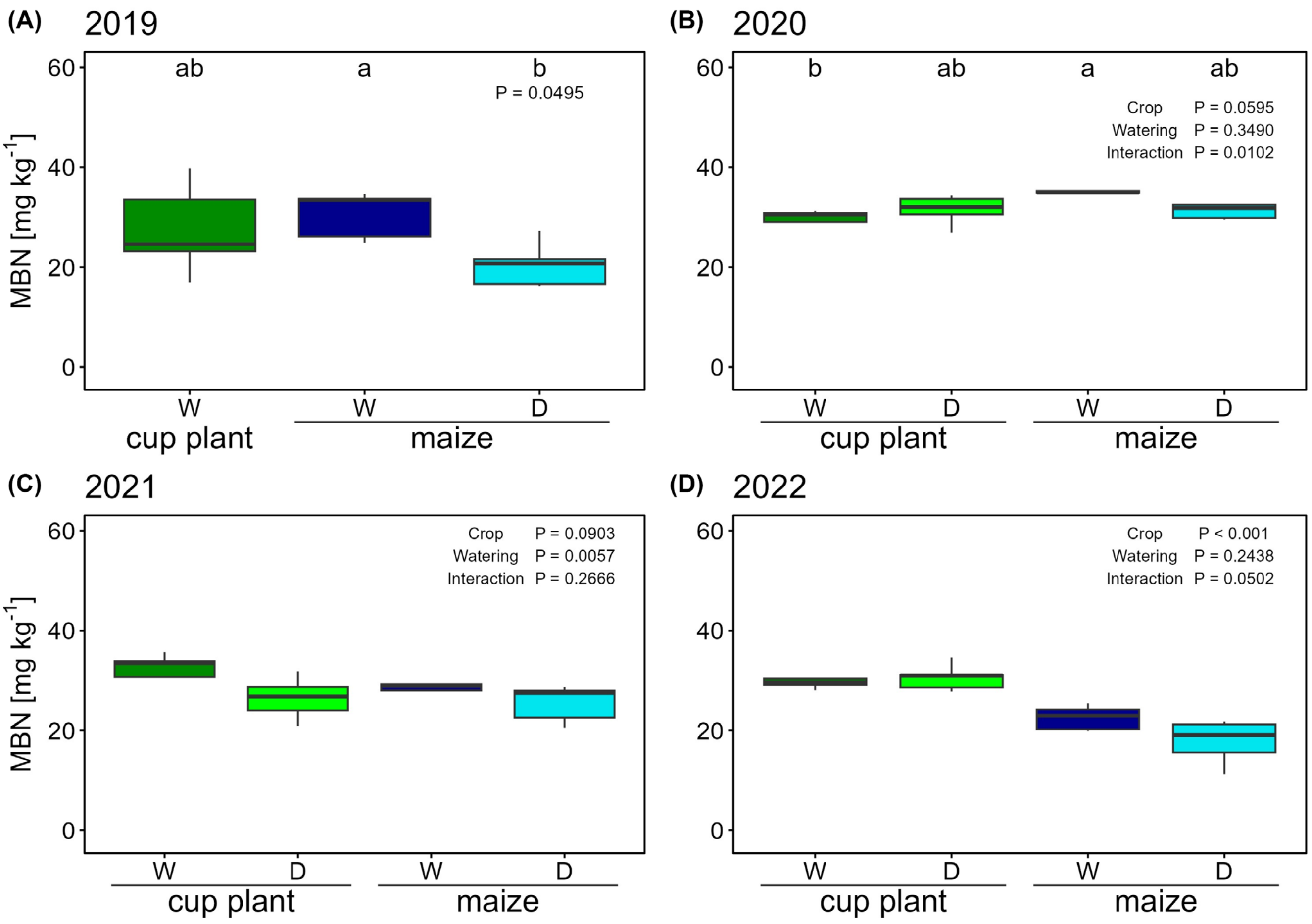

FIGURE 4 | Microbial biomass nitrogen (MBN) in the soil sampled with the harvest at the end of each growing season (A. September 25, 2019; B. September 30, 2020; C. October 7, 2021; and D. September 20, 2022). No moderate drought stress was applied to the cup plant in its establishment year (2019). Different letters indicate significant differences ($p \leq 0.05$) among the crop × water regime (W = well-watered; D = moderate drought) combinations (maize–drought, maize–watered, cup plant–drought, and cup plant–watered) for the respective year.

improve water acquisition under moderate drought conditions compared to maize (Schoo, Schroetter, et al. 2017). Additionally, roots in deep soil layers indicate the potential of cup plant to access deep soil water and nutrient resources compared to maize (Schoo, Schroetter, et al. 2017).

Regardless of the water regime, the higher shoot biomass production under cup plant was associated with higher N allocation in plant tissue than in maize (Figure 6), which indicates higher total N uptake from the soil. Although we did not measure the N uptake rate directly, the N concentration in the shoot and root biomass can be used as a measure for total N uptake (Roumet et al. 2006). The higher N uptake in cup plant can also be supported by the significantly lower C/N ratio in shoot biomass of cup plant compared to maize (Figure S5). The fibrous root architecture of cup plant (Schoo, Schroetter, et al. 2017) allows for a more extensive root system that can efficiently explore the soil for nutrients, particularly N, which is a highly mobile nutrient in the soil (Kiba and Krapp 2016; Li et al. 2016; Sullivan et al. 2000).

4.2 | Soil N Dynamics

Soil dissolved N (DN) is significantly lower under cup plant compared to maize from 2020 onwards (Figures 3 and 6), supporting the assumption of high N uptake through the developed root systems in cup plant. However, within the same crop, moderate drought increased soil DN in some cases compared to the watered crops (i.e., cup plant in 2020 and maize in 2022), which may suggest lower N uptake due to moderate drought stress. Under drought conditions, plant growth is restricted due to reduced water availability; thus, limiting plant N uptake (Dijkstra et al. 2015; He and Dijkstra 2014). Another possible explanation is that reduced water content under moderate drought conditions can concentrate DN in the soil solution through less dilution.

Our general soil DN pattern does align with that of Schittenhelm et al. (2021), who found no significant differences between cup plant (as a cover crop) and maize. They highlighted that 8-year-old cup plant induced a high mineralization rate, resulting in enhanced soil DN. The lower DN under cup plant in our study may be due to N immobilized by soil microbes. This is supported by the fact that cup plant induced a higher microbial C/N imbalance in 2021 and 2022 compared to maize (Abdalla et al. 2024, Figure S10, respectively) indicating a stronger N limitation of microbes under cup plant. This may therefore result in a higher soil organic matter decomposition for nutrient mining under cup plant compared to maize. Nevertheless, the continuous rhizodeposition and root turnover associated with the dense

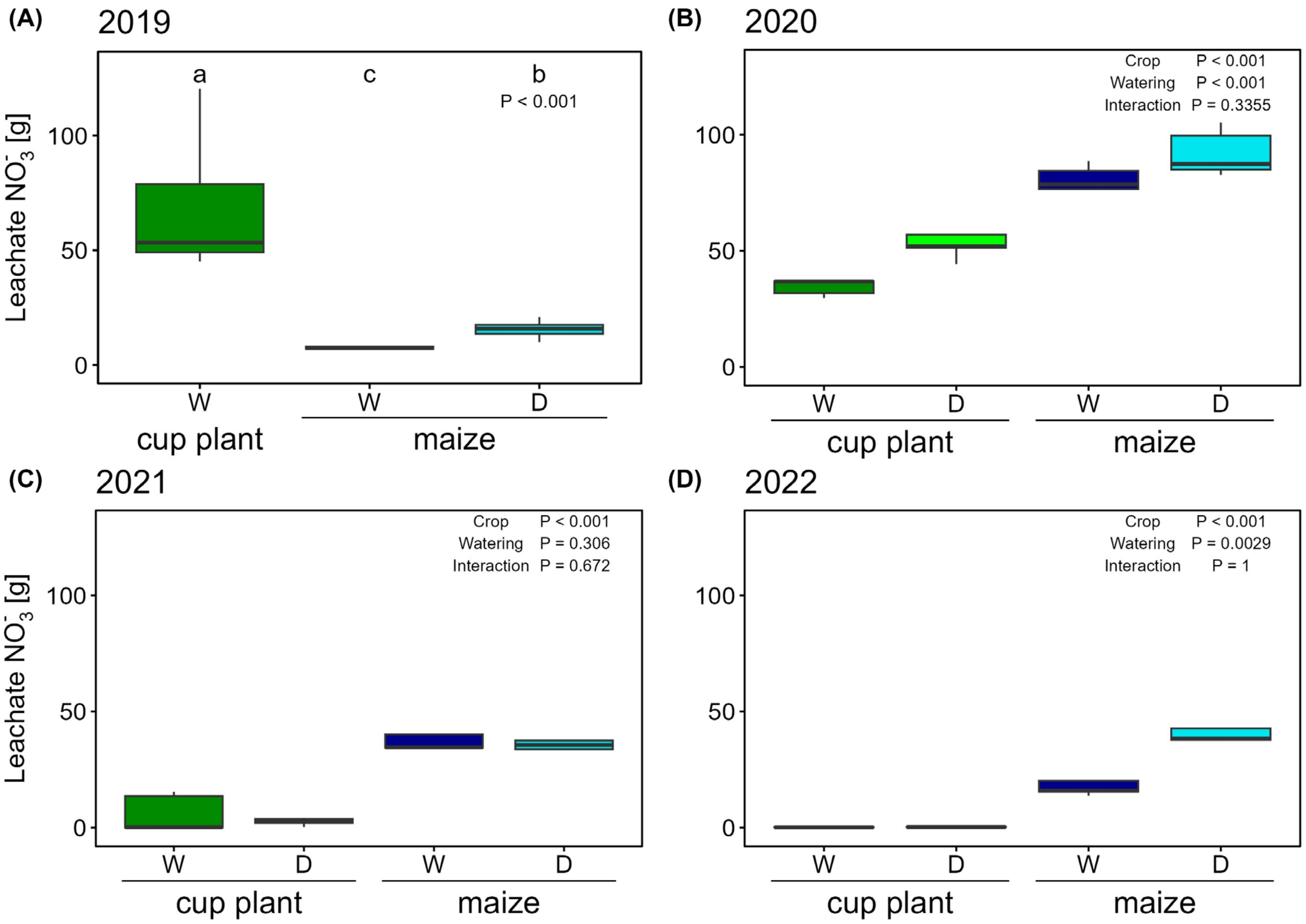

FIGURE 5 | Cumulative nitrate (NO_3^-) leaching per year (A. 2019; B. 2020; C. 2021; and D. 2022), collected on a regular basis (every 2 weeks). No moderate drought stress was applied to the cup plant in its establishment year (2019). Different letters show significant differences ($p \leq 0.05$) between treatments (cup plant, and well-watered (W) maize and moderate drought (D) maize in 2019).

and large cup plant root system may enhance final SOC content compared to the annual maize (Emmerling et al. 2017). In general, perennial crops are thought to enhance soil organic matter quality over time by harnessing the soil microbial growth and activities, which represent the active soil organic matter pool (Culman et al. 2013; Li et al. 2025; Ruf and Emmerling 2020).

4.3 | Influence of Cup Plant on NO_3^- Leaching

Overall NO_3^- concentration in the leachate was influenced by the crops rather than the watering conditions, with a significant reduction under cup plant compared to maize over the study period (Figure 5). Additionally, a direct relationship between the root system and the NO_3^- leaching can be seen, for example, in 2020, where cup plant under moderate drought induced a reduction in root biomass which resulted in a significantly higher NO_3^- leaching compared to watered conditions (Figure 2B). Our findings are in line with many other studies comparing perennial to annual crops (Huddell et al. 2023; Hussain et al. 2020; Jungers et al. 2019; Pugesgaard et al. 2015). The lower NO_3^- leaching under the perennial cup plant compared to the maize can be attributed to several factors: (i) the developed root system of the perennial cup plant is able to take up soil N efficiently; (ii) its longer growing season prolonged the period of N uptake including early spring and late autumn (Grunwald et al. 2020); (iii) higher evapotranspiration and lower WUE compared to maize (Schoo, Wittich, et al. 2017) reduce the drainage from the root zone. This makes cup plant particularly suited for areas with high water tables or regions vulnerable to groundwater NO_3^- contamination (Grunwald et al. 2020). It should be noted that the magnitude of nutrients leaching from maize will vary depending on the agricultural practices. For instance, the N leaching in maize monocultures, as observed here, can be reduced by crop rotation or intercropping systems if a suitable secondary crop is cultivated (Manevski et al. 2015; Zong et al. 2024). In this context, planting cup plant will reduce NO_3^- leaching and potentially helps keeping the NO_3^- concentration below the European groundwater directive defined limit (e.g., 50 mg L^{-1}) compared to maize.

4.4 | N Distribution in Soil, Plant, and Leachate

The relative distribution of N across soil, plant, and leachate revealed that soil N (including organic, inorganic and microbial N) consistently represented the dominant reservoir (Figure 6), indicating strong N retention in the bulk soil (Wang et al. 2010). As reported in other studies (e.g., Széles et al. 2023), drought reduced plant N uptake, particularly in maize, where both shoot and root

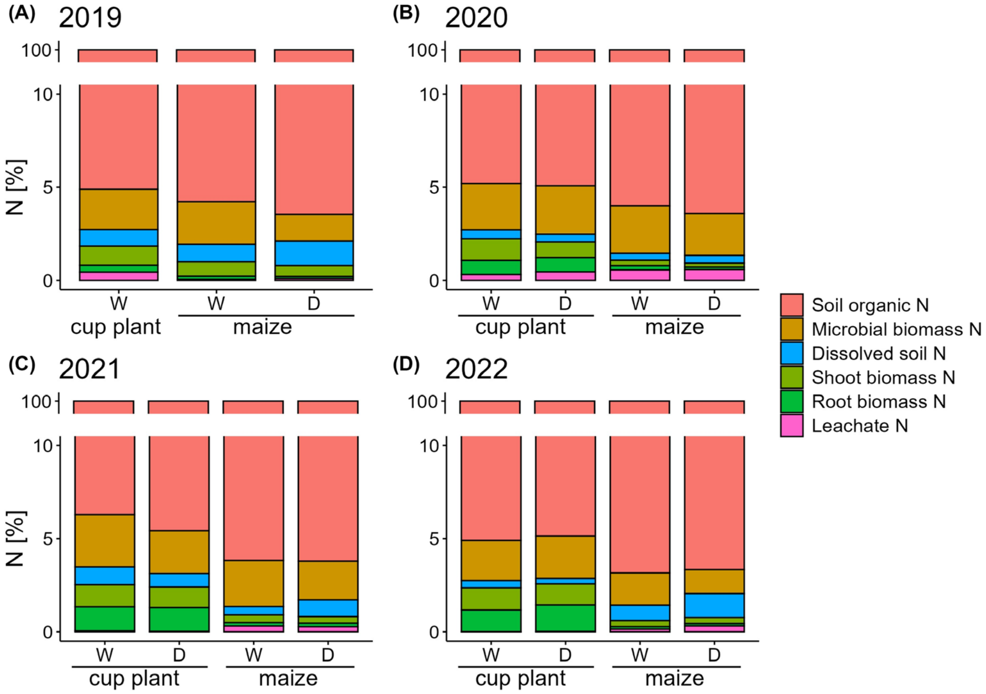

FIGURE 6 | Relative nitrogen (N) distribution of the individual treatments for all 4 years (A. 2019; B. 2020; C. 2021; and D. 2022). No moderate drought stress was applied to the cup plant in its establishment year (2019). Note the interruption of the y-axis to show more clearly the small differences in the other pools compared to soil N. N content in the maize cobs was not analyzed and therefore not considered in the relative N distribution. W = well-watered; D = moderate drought.

biomass N declined under moderate drought conditions in 2021 and 2022 (Figure 6C,D). In contrast, the cup plant showed a more stable or even increased allocation of N to root biomass under moderate drought conditions, reflecting a potentially more resilient root system typical of perennial species (Vico and Brunsell 2018). Microbial biomass N was moderately responsive to drought, with slight reductions observed under dry conditions, especially in maize, suggesting moisture sensitivity in microbial communities or reduced substrate availability (Brockett et al. 2012; Tiemann and Billings 2011). The relative N distribution in the leachate was lowest compared to the plant and soil pools, highlighting the minimal risk of N leaching from the cup plant compared to maize. These patterns highlight fundamental differences in N allocation and retention between annual and perennial cropping systems under variable water availability, with implications for long-term soil fertility and N cycling resilience under cup plant.

Overall, our comparison focused on shoot biomass, excluding cob biomass, as silage maize is typically harvested before reaching full maturity (Schmidt et al. 2023). While including cob biomass (Figure S11) would result in similar total aboveground biomass between maize and cup plant, cup plant demonstrated substantially higher root biomass and markedly lower nitrate leaching. Although N content of the cobs was not analyzed, meaning that the N uptake of maize in our study is underestimated (Ma and Dwyer 2001), the combination of comparable aboveground biomass, greater root biomass, and reduced N losses via leaching suggests that cup plant can sustain biomass production with enhanced environmental performance.

To combine the beneficial effect of intercropping in maize and reduced nitrate leaching under cup plant, an intercropping system maize–cup plant could be implemented in the first year of crop establishment. Although our controlled setting is artificial, it enables us to precisely attribute observed plant–soil responses to drought. This is crucial for modeling the dynamics of future agroecosystems. We acknowledge that validation under variable and naturally occurring drought regimes is essential. Therefore, future research should aim to integrate controlled experiments with long-term field studies to better reflect real ecological conditions and improve the applicability of models.

5 | Conclusion

Our 4-year study demonstrates that, after the first year of growth, cup plant outperforms maize in shoot biomass production, irrespective of the soil water conditions. The increased shoot biomass production was associated with a larger root system, which enabled cup plant to efficiently take up mineral nitrogen, resulting in reduced nitrate leaching compared to maize. Other than a few exceptions (e.g., root biomass in 2020 and nitrate leaching 2021) moderate drought conditions had minimal impact on both crops. Therefore, cup plant has the potential to maintain groundwater protection through reduced nitrate leaching, even under moderate drought stress. The high NO_3^- leaching potential observed in the first year of cup plant cultivation and in general in maize monocultures could be mitigated by intercropping strategies, such as combining maize and cup plant in the first year. Such systems may connect the environmental advantages of cup plant while maintaining high biomass productivity, presenting a sustainable pathway for future agricultural systems that prioritize productivity and environmental protection. Overall, the cup plant presents a compelling alternative to maize for sustainable bioenergy production, offering environmental benefits such as improved groundwater protection, alongside robust biomass yields.

Author Contributions

Anna Hollweg: conceptualization, data curation, methodology, writing – original draft, writing – review and editing. **Johanna Pausch:** conceptualization, funding acquisition, project administration, writing – review and editing. **Finn Zajewski:** field investigation, data curation, methodology. **Marianne Lauerer:** methodology, writing – review and editing. **Khatab Abdalla:** conceptualization, project management, data curation, methodology, writing – original draft, writing – review and editing. All the authors have read and agreed to the published version of the manuscript.

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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.29828939.v1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcbb70074-sup-0001-supinfo.docx.