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Waterlogging Does Not Have a Lasting Impact on Yield Performance and Micronutrient Status of Oat (*Avena sativa*)

Britta Pitann  | Timo Hoppenheit | Karl H. Mühling 

Institute of Plant Nutrition and Soil Science, Kiel University, Kiel, Germany

Correspondence: Britta Pitann (bpitann@plantnutrition.uni-kiel.de)**Received:** 22 July 2024 | **Revised:** 27 January 2025 | **Accepted:** 28 January 2025**Funding:** The authors received no specific funding for this work.**Keywords:** copper | iron | manganese | micronutrients | oat | waterlogging | zinc

ABSTRACT

Waterlogging increasingly threatens global crop production, particularly affecting major crops like wheat, barley, and maize at all growth stages. Although research on oat tolerance to waterlogging is limited, there is evidence that oat may be a suitable alternative crop due to its resilience and ability to maintain yields despite nutrient imbalances caused by waterlogging. However, it remains uncertain how oat responds to changes in soil micronutrient availability during periods of waterlogging. Therefore, this study aims to investigate whether (1) micronutrient toxicities or deficiencies are induced during waterlogging, (2) the timing of the flooding event is relevant for the expression of a possible nutrient imbalance, and (3) micronutrient toxicities/deficiencies affect yield performance. In order not to exclude possible varietal differences, three oat varieties were grown in large-scale containers and exposed to 14 days of waterlogging at either BBCH 31 or BBCH 51. Although early but not late waterlogging was effective in reducing dry weights, especially in white oat, yield performance, as reflected by the harvest index, was not affected at all. While early waterlogging increased Mn and Fe concentrations in all oat varieties, they were well below toxic level. In contrast, Cu concentrations in white oat dropped below the deficiency threshold levels. Zinc status, however, remained completely unaffected in all oat varieties. After late waterlogging, only Mn accumulated to concentration in the toxicity range, but only in white and yellow oat; all other micronutrients remained in a sufficient range. From these results we conclude, that although micronutrient imbalances occurred under waterlogging regardless from its timing, which may explain the transient reduction in dry weight of white oat, the yield of all tested oat varieties was ultimately unaffected. It can therefore be assumed that at least the oat varieties tested have a high regeneration potential and also show a high tolerance to transient micronutrient imbalances.

1 | Introduction

Waterlogging is an environmental constraint affecting agricultural ecosystems worldwide (Aderonmu 2015). Heavy rainfall events are expected to increase in the coming years, especially as climate change continues (Kreienkamp et al. 2016). To date, 10%–12% of the world's arable land is at risk of flooding and thus waterlogging events (Kaur et al. 2020b), with approximately 3700 flood events being already recorded between 1985 and 2010 (<http://floodobservatory.colorado.edu/>). In Germany, such

heavy rainfall events have become more frequent in the last 15 years, resulting in enormous yield losses of the major crops (Ploschuk et al. 2018; Winterrath et al. 2017). The effect of increased precipitation is further exacerbated when soil structure is poor due to high clay content, (anthropogenic) compaction, or poor drainage (Alifu et al. 2022; Najeeb et al. 2015).

From a soil perspective, waterlogging is defined as a condition in which the critical threshold level of less than 10% air-filled pore space is reached (Kramer and Boyer 1995). As O₂ levels decline,

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Summary

- Varietal differences exist regarding micronutrient imbalances in oat after early and late waterlogging.
- Micronutrients accumulate in vegetative tissues but not grains after waterlogging.
- Micronutrient imbalances are only of transient nature in oat.
- Micronutrient imbalances are not yield effective in oat.
- Oats shows a high recovery potential and tolerance to waterlogging.

the concentrations of other gases, such as CO₂ or ethylene, increase (Ponnamperuma 1972, 1984).

Furthermore, soil anoxia has been demonstrated to facilitate additional alterations in soil chemistry, consequently affecting rhizosphere conditions. When plants are exposed to oxygen deficiency in soil, as is the case under waterlogging, the plant roots are first confronted with a severe energy deficit as a consequence of a reduction in oxidative phosphorylation (Colmer and Voesenek 2009). This, in turn, results in impaired water and nutrient uptake, which leads to a reduction in shoot and root dry mass (Malik et al. 2002). As a consequence, root death becomes inevitable as waterlogging persists (Gibbs and Greenway 2003). Secondly, this condition may be further exacerbated by a shift in the soil redox potential (Eh) and pH towards more reducing and acidic conditions. This, in turn, affects the solubility of (micro)nutrients in the soil, thereby affecting their availability to plants. This can result in deficiencies or toxicities of (micro)nutrient.

While denitrification processes are dominant under conditions of high soil moisture, plants are at risk of nitrogen (N) deficiency due to N volatilization as nitrous oxide, which further contributes to climate change (Ponnamperuma 1972). Similarly, waterlogging induced N deficiency has also been reported for other crops, including oat (Arduini, Baldanzi, and Pampana 2019), maize (Ren et al. 2017), oilseed rape (Zhou, Zhao, and Lin 1997), and wheat (Wollmer, Pitann, and Mühling 2018). In contrast, micronutrients such as manganese (Mn²⁺) or iron (Fe²⁺) are directly affected by changes in the redox potential, leading to an accumulation in the soil solution and, thus, resulting in an increased plant uptake and probable toxicity (Ponnamperuma 1984). A number of studies have already reported the presence of toxic concentrations of Mn and Fe in a variety of crops, including wheat (Khabaz-Saberi, Setter, and Waters 2006; Setter et al. 2009; Stieger and Feller 1994), maize (Ashraf and Rehman 1999), and oilseed rape (Ashraf and Mehmood 1990). However, the lack of comparability among these studies is due to differences in experimental design, specifically the duration or timing of the waterlogging event, which has resulted in varying levels of toxicity and sites of toxicity (root vs. shoot). Conversely, there is also evidence that waterlogging does not inevitably result in micronutrient toxicity. Instead, it may lead to an increased uptake of certain micronutrients, such as Mn, in wheat and

barley (Steffens et al. 2005). To date, only Wollmer, Pitann, and Mühling (2019) have investigated the impact of different time points of waterlogging stress (BBCH 31 vs. BBCH 51), including a recovery phase, that is, not harvesting immediately after the end of the stress, on the micronutrient status of two winter wheat cultivars and oilseed rape.

While there is a plethora of in planta data on Fe and Mn after waterlogging or flooding are manyfold, studies on other micronutrients are still scarce or contradictory (e.g. Kee and Bloomfield 1962; Setter et al. 2009; Steffens et al. 2005). In particular, the data regarding Zn are inconsistent. For instance, submerged paddy rice soils have been shown to result in the formation of zinc sulfides (Alloway 2008), which render the Zn unavailable and thus deficient (Scharpenseel et al. 1983). This finding contradicts the results of Pavanassivam and Axley (1980), who reported an increase in Zn availability and thus tissue concentration upon flooding, due to the decrease in Eh and pH.

Unfortunately, the majority of these studies have been conducted primarily on the major high-yielding crops. However, given the recent resurgence in popularity of oat (*Avena sativa* L.) due to its nutritional benefits and its versatility, particularly in the context of stress conditions (Ruja et al. 2021; Welsh 1995), it is imperative to also study its behaviour in the presence of waterlogging. There is already evidence that oat has a higher agronomic tolerance (Arduini, Baldanzi, and Pampana 2019), enabling more effective adaptation and, consequently, more stable yields when subjected to waterlogging (Cannell et al. 1985; Setter and Waters 2003; Watson, Lapins, and Barron 1976). Although transient nutrient imbalances, especially of nitrogen, are induced by waterlogging, oat has the capacity to completely regenerate during its life cycle when a “post-waterlogging rescue N fertiliser” is applied (Kaur et al. 2020a; Rasaei et al. 2012; Watson, Lapins, and Barron 1976). Nevertheless, it remains unclear whether oat is capable of tolerating (micro)nutrient imbalances or even returning to an optimal state during its growth cycle when subjected to submergence. To date, the only study to report on the effects of waterlogging on micronutrients on oat is that of Bjerre and Schierup (1985) which observed an increased total uptake of Mn and Fe after 21 days of waterlogging, accompanied by a decrease in Zn and Cu.

In the light of the aforementioned data, the present study aims to analyse the micronutrient status of the plants after 14 days of waterlogging, imposed either at BBCH 31 (stem elongation) or BBCH 51 (beginning of heading). To account for genotypic differences, three oat varieties (black oat, white oat and yellow oat) were compared, in order to facilitate cultivar selection on waterlogging-affected sites. It is hypothesized that (1) micronutrient imbalances are more pronounced at earlier growth stages compared to later stages, and (2) waterlogging-induced micronutrient deficiencies or toxicities do not affect yield of oat.

2 | Materials and Methods

2.1 | Plant Material and Experimental Setup

The experiment was set up in the outdoor area of the Experimental Station of the Institute of Plant Nutrition and Soil Science, Kiel University, Germany (54°20′ 50″N, 10°6′

55''E). Three oat (*Avena sativa* L.) varieties (provided by Saaten Union, Germany) were selected for the experiment: Zorro (black oat), Symphony (white oat), and Apollon (yellow oat). Plants were grown to maturity in large containers (volume: 120 L; area: 0.16 m²; see also Hohmann et al. 2016) at a seeding density of 90 seeds per container, arranged in three rows.

Two different soil types were selected: a Cambisol subsoil (sL, pH 5.5; IUSS Working Group WRB 2015) from the experimental farm "Hohenschulen" of Kiel University, Germany, and an arable loamy sand soil (pH 6.1) from the Ost-Holstein (district in Schleswig-Holstein, Germany). To prevent bias resulting from disturbances of the natural soil structure and allow for natural development, the containers were already filled in 2018 as follows (from bottom to top): (1) 20 kg gravel; (2) 100 kg subsoil + sand (1:1, w/w); (3) 30 kg subsoil + topsoil (1:1, w/w); (4) 10 kg topsoil. In the final step, plants were fertilised according to the standard application for field-grown oat (in kg ha⁻¹: 100 N, splitted into N1 [67 kg ha⁻¹] before sowing and N2 [33 kg ha⁻¹] at shooting stage, 55 P, 80 K). Plant protection measures were applied as required.

2.2 | Stress Treatments

Waterlogging (100% water holding capacity [WHC]) was imposed at two different time points during the growing season: (1) at BBCH 31 (W1, early WL) and (2) at BBCH 51 (W2, late WL). The stress treatment was implemented for 14 consecutive days and the soil was allowed to dry to 60% WHC after water drainage. Control plants were grown at 60% WHC throughout the growing season. To maintain the intended WHC, water supply was monitored every 2 days and rewatering was performed if necessary, based on weight loss.

2.3 | Plant Sampling and Analysis

One week after the cessation of each waterlogging treatment (W1 and W2), 30 samples were randomly collected and the aboveground plant biomass was quantified. At seed maturity, the remaining plants were harvested, separated into panicles and straw, and the biomass was weighed. Dry weights were recorded after samples were oven dried at 60°C to constant weight. The samples were then milled to a fine powder (Cyclotec 1093, Foss Tecator, Höganäs, Sweden) for further analysis.

Micronutrient analysis (Mn, Fe, Zn and Cu) was conducted in accordance with the method delineated by Jezek et al. (2015). In brief, 200 mg of finely ground plant material was treated with 10 mL of 69% HNO₃ for microwave digestion (1800 W, MARS 6, Xpress, CEM, Matthews, MC, USA) at 190°C for 45 min. Subsequently, the nutrient concentrations were then analysed by inductively coupled plasma-mass spectrometry (ICP-MS; Agilent Technologies 7700 Series, Böblingen, Germany).

A combustion analysis of total S was performed using a CNS elemental analyser (Flash EA 1112 NCS, Thermo Fisher Scientific,

Waltham, USA). Approximately 5 mg of finely ground plant material were weighed into tin capsules. A certified wheat flour standard (Isotopenstandard Weizenmehl, IVA Analysentechnik, Meerbusch, Germany) was employed as a reference material for data validation.

2.4 | Statistical Analysis

The statistical analysis was conducted using the statistical software package SPSS (version 25.0). Data analysis was based on four replicate containers per treatment, with the experiment set up as a completely randomised design (CRD). The treatment effect per cultivar was tested using one-way ANOVA according to Duncan's multiple range test (for homogeneous variances) or the Games-Howell test (for heterogeneous variances) at a significance level of $p \leq 0.05$. Significant differences are indicated by different letters. The significance of the correlations was tested using a two-tailed Pearson's correlation coefficient at a significance level of $p \leq 1\%$.

3 | Results

3.1 | Dry Weights and Harvest Index

When waterlogged for 14 days at BBCH 31 (W1), plant height (Figure 1) and fresh weight (data not shown) were reduced across all oat varieties. However, the impact of waterlogging was most pronounced in white oat, with a reduction in dry weight by approx. 43%. In contrast, black and yellow oat retained dry weights comparable to the respective control (Figure 3A).

One week after cessation of late waterlogging stress at BBCH 51, both white and yellow oat showed a reduction in dry weight production at W1 (Figure 3B), whereas no difference was observed for black oat compared to the respective control. In contrast to W1, late waterlogged (W2) white oat neither showed a reduction in plant height (Figure 2) and fresh weight (data not shown) nor dry weight (Figure 3B), remaining at the level of the respective control. Notably, black and yellow oat showed a marked increase in dry weight of approx. +48% and +31%, respectively, following late waterlogging compared to their respective controls (Figure 3B). This contrasts with the observation that plant height (Figure 2) and fresh weight (data not shown) were not affected.

These results were largely confirmed in mature oat plants at harvest (Figure 3C). In black oat, no change in dry weight was measured in early waterlogged plants (W1), neither in straw nor in grain (Figure 3C,D). In contrast, the total dry weight (grain + straw) of W2 plants increased by +50%, driven by a significant increase in grain dry weight (Figure 3D), while straw dry weight remained unaltered (Figure 3C). Similar to the results observed in waterlogging at BBCH 31 (Figure 3A), white oat (W1) could not recover dry weight until maturity in both in straw and grain (Figure 3C,D), but maintained dry weight to the level of control treatment in W2 plants in both fractions. For yellow oat no differences in straw and grain in both W1 and W2 plants were measured (Figure 3C,D).

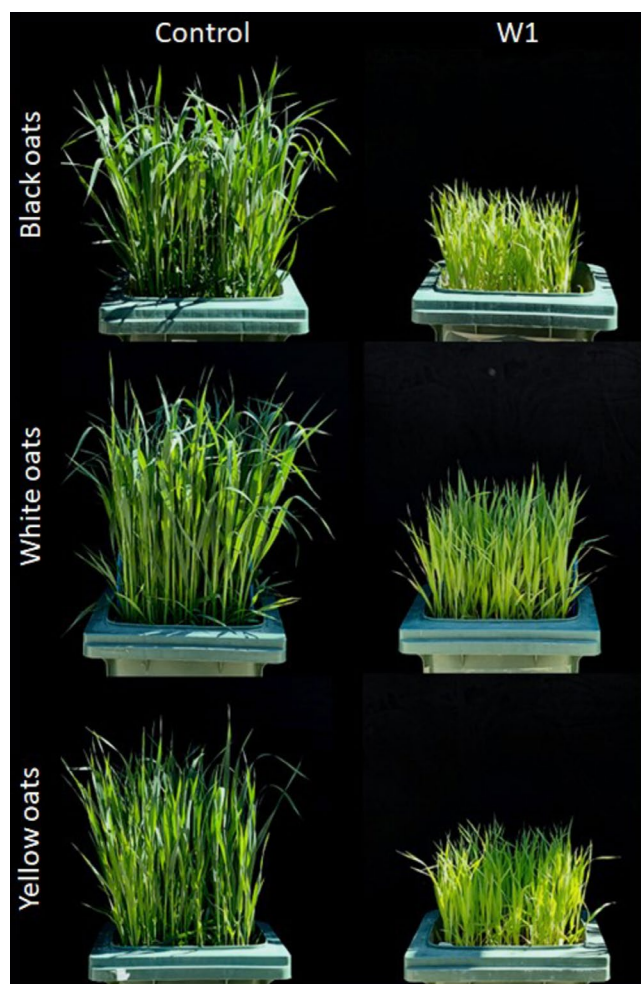


FIGURE 1 | Effect of waterlogging at BBCH 31 (W1) on shoot growth of three different oat varieties compared to well-drained conditions (control).

Although changes in dry weight occurred in response to early and late waterlogging, at with the greatest effects observed in white oat (Figure 3), this was not the case for in HI (Figure 4). All oat varieties showed a comparable HI to their respective control, indicating that waterlogging did not affect yield.

3.2 | Micronutrient Concentration After Early and Late Waterlogging

Following a 14-day period of waterlogging at BBCH 31, Mn concentration in shoots significantly increased in all three oat varieties (Figure 5A). Similarly, Fe concentration increased, but only in black and white oat. (Figure 5B). In contrast, Zn concentration in aboveground biomass remained unaffected at the level of the respective controls (Figure 5C). Copper concentration decreased significantly, reaching a level below the minimum threshold level for optimum growth, only in white oat upon early waterlogging, but not in black and yellow oat (Figure 5D).

Following the cessation of early waterlogging, a second sampling date was conducted was after a period of 6 weeks. At this point, a change was observed in the micronutrient status. Manganese

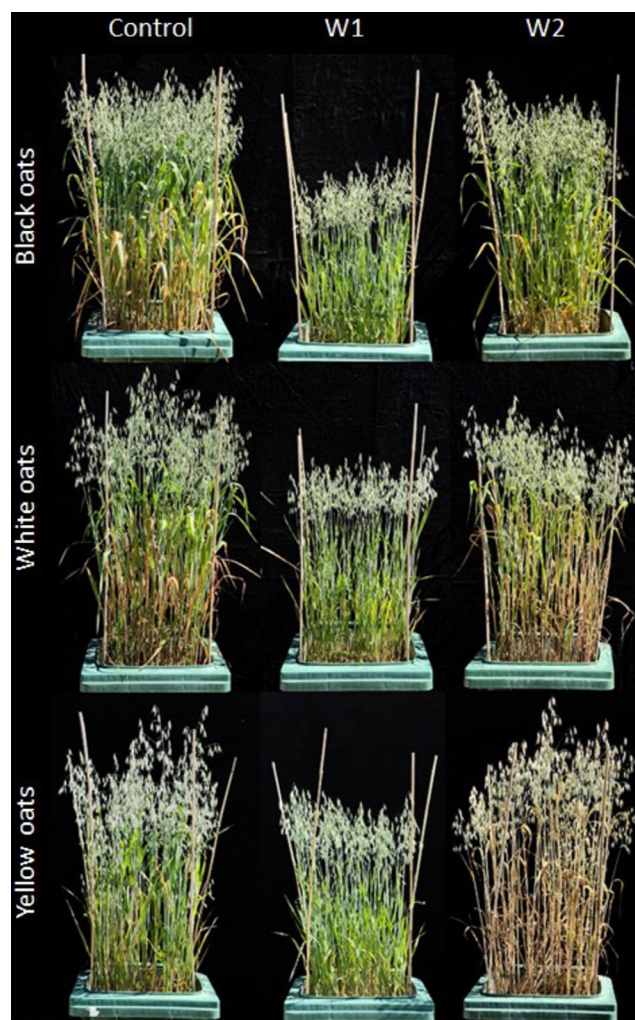


FIGURE 2 | Effect of waterlogging at BBCH 51 (W2) on shoot growth of three different oat varieties compared to well-drained conditions (control) and early waterlogged plants (W1).

concentration of black oat in W1 was no longer statistically different from the respective control (Figure 6A), a result that was also observed for W2 plants. In white oat, the initial increase in Mn diminished and reached the level of the control, while late waterlogging (W2) resulted in an increase in Mn (+57%). In yellow oat, however, Mn remained significantly increased in W1 plants, while late waterlogging (W2) resulted in an even higher Mn concentration (Figure 6A). For both white and yellow oat, the Mn concentration exceeded the maximum threshold level for optimal growth. With regard to Fe, only in yellow oat did late waterlogging results in a notable increase, which nevertheless remained in the range conducive for optimal growth (Figure 6B). Zinc was the only micronutrient that remained unaffected by both early and late waterlogging in all three oat varieties (Figure 6C). As for Cu in black oat, its concentrations exhibited a similar pattern to that of Zn, being non-responsive in shoot biomass regardless of the waterlogging event (Figure 6D). In white oat, however, the apparent decrease in Cu in W1 plants was neutralised and reached the level of the respective control. Only late waterlogging (W2) resulted in a significant, albeit not growth-affecting decrease in white oat. Similarly, the Cu concentration dropped significantly in yellow oat after late waterlogging (Figure 6D).

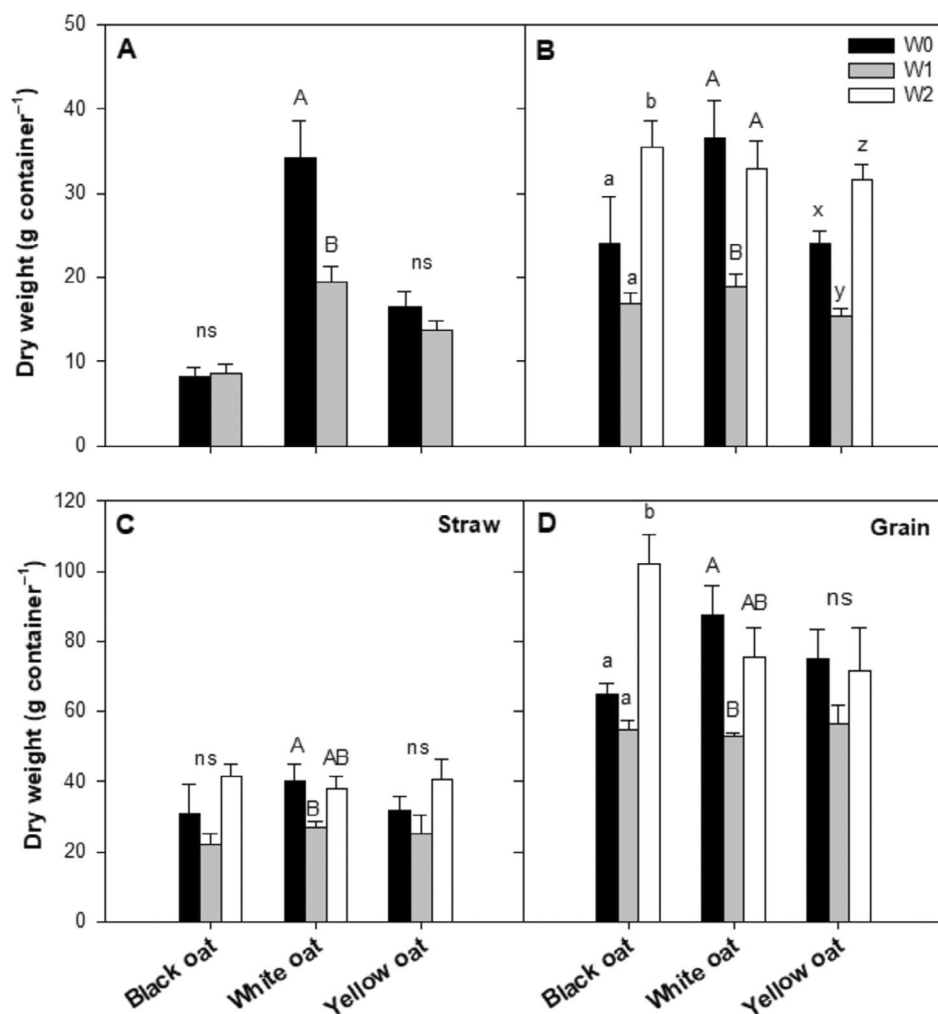


FIGURE 3 | Dry weight of the whole aboveground plant material after 14 days of waterlogging (A) at BBCH 31, (B) at BBCH 51, and in (C) straw and (D) grain at harvest after maturity. Bars represent means + standard errors ($n=4$). Different letters refer to significant differences ($p \leq 0.05$; ns, non-significant) between waterlogging treatments always within one oat variety. W0, control; W1, waterlogging at BBCH 31; W2, waterlogging at BBCH 51.

3.3 | Micronutrient Concentration at Seed Maturity

At seed maturity, wheat plants were harvested and separated into straw and grains. In black oat, the concentration of Mn in straw was not statistically different from the respective control, whereas it was significantly increased in grains (Figure 7A). In white oat, Mn concentration in straw was approx. 3-times higher than in the control in W1 and W2 plants, while in grains it was only 1.4 and 2.2 times higher in W1 and W2 plants, respectively (Figure 7A). The highest Mn concentration was observed in straw of yellow oat, which was 3.4-times higher than its control. Additionally, only late waterlogging resulted in a significant increase in Mn in the grains of yellow oat (Figure 7A).

Analysis of Fe concentrations revealed no significant differences in the straw and grains of the three oat varieties after early waterlogging (W1; Figure 7B). However, a significant threefold increase was observed after W2 compared to the non-waterlogged control. Similarly, grain Fe concentrations

were not affected by early waterlogging, whereas late waterlogging significantly increased Fe in black (118%) and yellow (155%) oat (Figure 7B).

In the straw of all oat varieties, there was no significant difference between the control and W1 treatment, however, late waterlogging resulted in a significant increase in straw (Figure 7C, right). In contrast, both waterlogging scenarios were not significantly affecting Zn concentration in oat grain (Figure 7C, left).

Although Cu concentration in the total shoot biomass decreased in white and yellow oat after late waterlogging (Figure 6D), this situation was reversed at maturity, with no further differences occurring in the straw and grains (Figure 7D). In black oat, however, the straw Cu concentration increased twofold in W2 plants, a difference that was not reflected in the grain Cu concentration (Figure 7D).

Regression analysis indicated that there was no correlation between yield and micronutrients for all three oat varieties, with all coefficients of determination being insignificant (Figure S1).

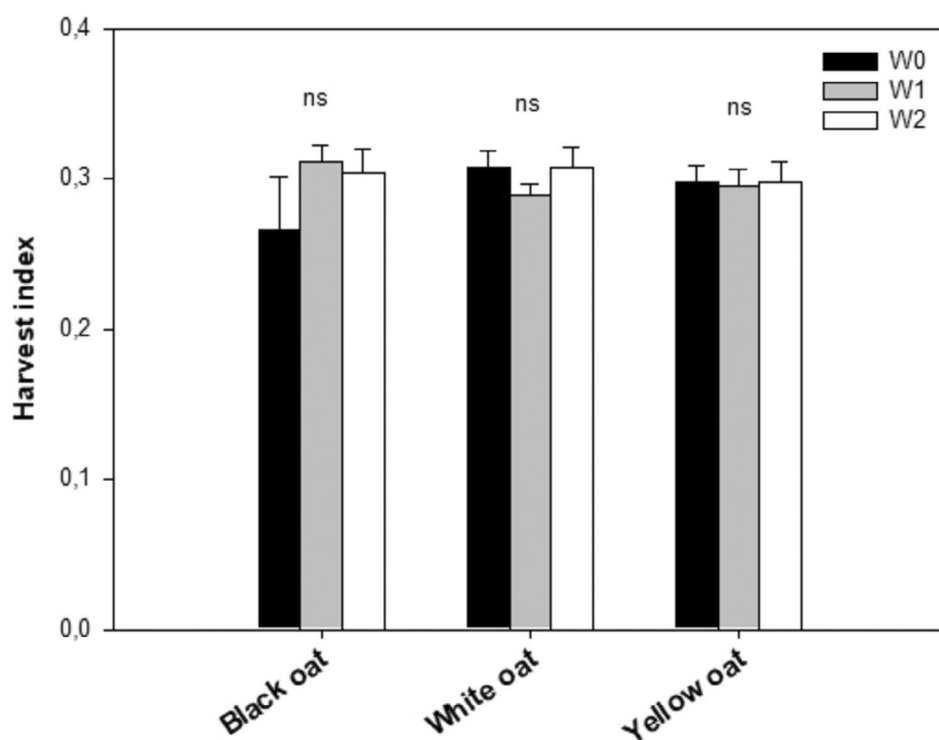


FIGURE 4 | Harvest index after 14 days of waterlogging at BBCH 31 and BBCH 51 at maturity. Bars represent means + standard errors ($n=4$). Different letters refer to significant differences ($p \leq 0.05$; ns, non-significant) between waterlogging treatments always within one oat variety. W0, control; W1, waterlogging at BBCH 31; W2, waterlogging at BBCH 51.

4 | Discussion

The primary factors affecting crop production are climate, namely radiation, temperature and precipitation. However, human activities are accelerating climate change and increasing the risk of extreme weather events (Rosenzweig et al. 2001). In particular, excessive rainfall can result in waterlogging, which can have a detrimental effect on crop productivity. For example, yield losses of up to 50% annually have been attributed to waterlogging in major crops such as wheat, maize, rice, and soybean (Borgomeo et al. 2020; Ding et al. 2020; Hossain and Uddin 2011; Ploschuk et al. 2018; Tian et al. 2021). Despite oat being a crop with a high tolerance level to climatic changes throughout its life cycle (Welsh 1995), little attention has been paid to its response to waterlogging and associated soil anoxia (Mustroph 2018; Setter and Waters 2003). Specifically, with regard to nutrient status, the focus has been solely on the macronutrients nitrogen (N), phosphorus (P) and potassium (K) (Cannell et al. 1985; Watson, Lapins, and Barron 1976), but not on micronutrient status. To address this research gap, this study was conducted to investigate the response of three different oat varieties to temporal waterlogging in terms of growth performance and (micro)nutritional status. To further differentiate the effects of the timing of submergence during the growth cycle, two different developmental stages: shooting and panicle emergence. As small pot experiments are hardly transferable due to limitations in root growth and thus nutrient behaviour in the soil and uptake dynamics, field-like conditions were simulated by using large-scale containers (Hohmann et al. 2016).

4.1 | Initial Growth Reduction Is Not Affecting Harvest Index of Oat Under Temporal Waterlogging

As observed in other crops (e.g. Arduini, Baldanzi, and Pampana 2019; de San Celedonio, Abeledo, and Miralles 2014; Hussain et al. 2022; Ploschuk et al. 2018), oat also demonstrates an initial reduction in shoot growth following early, but not late waterlogging (Figures 1 and 2). Similarly, Watson, Lapins, and Barron (1976) described a reduction growth during the early developmental stage, which they attributed to a damage of the root system. Also, Ploschuk et al. (2018) reported a reduction in root mass density in barley, wheat and oilseed rape after early waterlogging, as a consequence of O_2 deprivation and ethylene formation. As fresh weights decline after early waterlogging, it can be anticipated that dry weights will also be adversely affected, this hypothesis has been supported by empirical evidence from studies conducted on four *Brassica* species by Ashraf and Mehmood (1990) and on wheat by Malik et al. (2002). However, it is not inevitable that reductions in shoot growth will be accompanied by a decrease in dry weights. In this study, only white oat showed a reduction in dry weight by 43% (Figure 3A), which coincides with the results of Watson, Lapins, and Barron (1976) and Cannell et al. (1985). These authors also demonstrated a comparable decrease of shoot dry weight, which they attributed to a 50% decline in root dry weight in oat. However, neither black nor yellow oat were responsive immediately after the cessation of the early stress (W1; Figure 3A). The development of dry weight in yellow oat was subject to change over time. Following an initial lack phase, dry weights declined by 36%, a trend that was also observed in white

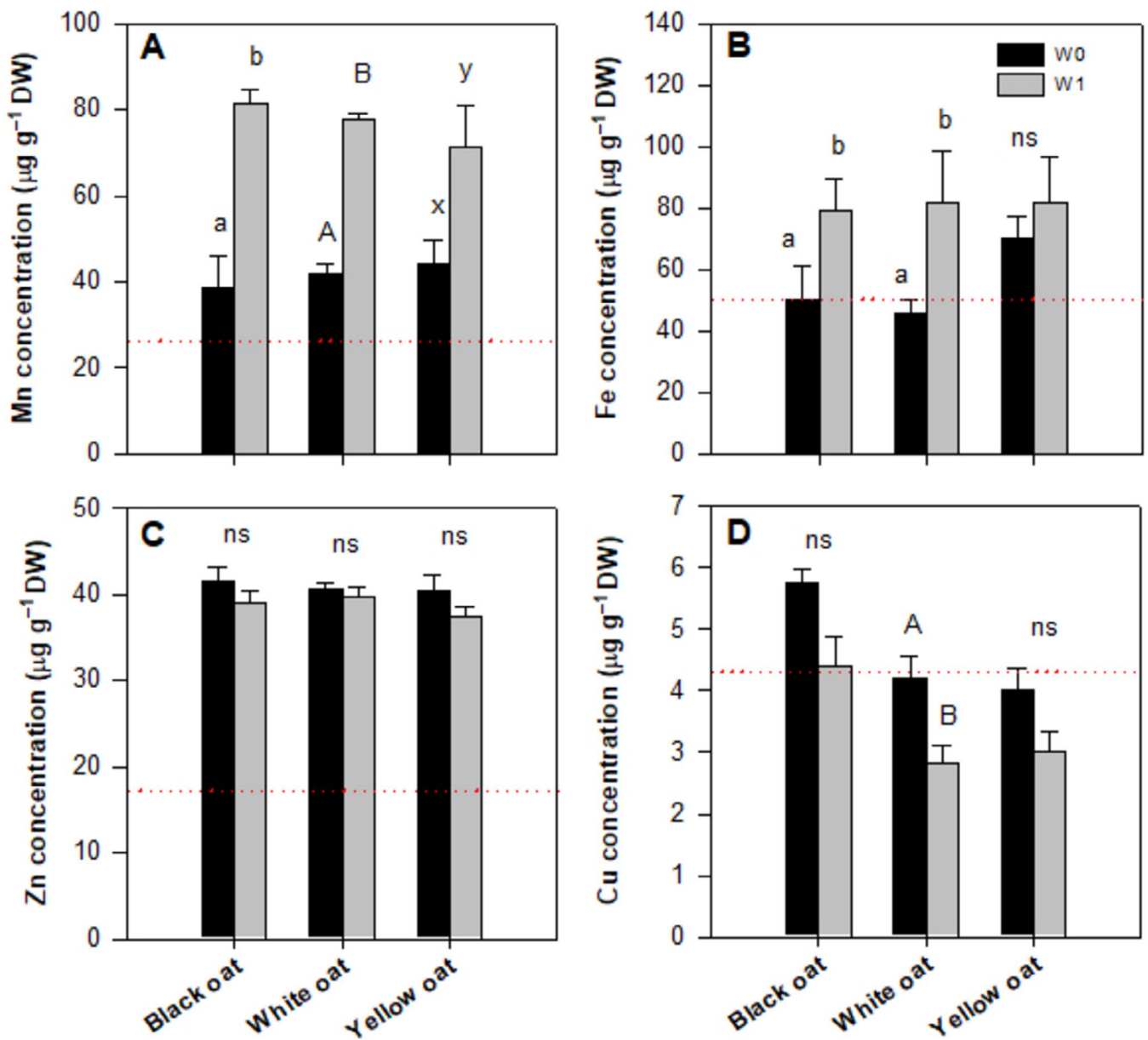


FIGURE 5 | (A) Manganese, (B) iron, (C) zinc, and (D) copper concentration of the whole aboveground plant material after 14 days of waterlogging at BBCH 31. Bars represent means + standard errors ($n=4$). Different letters refer to significant differences ($p \leq 0.05$) between waterlogging treatments within one oat variety. Red dotted line represents the minimum threshold level for optimal growth according to Bergmann (1993). W0, control; W1, waterlogging at BBCH 31.

oat (W1; Figure 1B). In contrast, late waterlogging (BBCH 51) did not have a negative effect on shoot dry weights across all oat varieties (W2; Figure 3B), but rather increasing in yellow oat. While the reduction in dry weight of W1 stressed plants persisted in white oat until maturity (Figure 3C,D), and was also expressed in straw and grains, late waterlogging had no effect on the straw or grain of black and yellow oat. The initial changes in dry weight can be attributed to N deficiencies in the vegetative shoot tissue, a correlation that has also been described for oat and other crops (Arduini, Baldanzi, and Pampana 2019; Ren et al. 2017; Wollmer, Pitann, and Mühling 2018; Zhou, Zhao, and Lin 1997). Transient nitrogen deficiency in oat upon early waterlogging (Pitann and Mühling 2024) coincides with an immediate drop of soil nitrate concentration together with onset of waterlogging at W1 (Table S1). Such a loss in nitrate-N can be

attributed to a number of processes, including nutrient transformation in waterlogged soils (e.g. denitrification) or leaching (Patrick, Mikkelsen, and Wells 1985; Rasaei et al. 2012), loss of root biomass (Herzog et al. 2016) or impaired nutrient uptake (Colmer and Greenway 2010; Elzenga and Veen 2010).

However, that oat does indeed have a high recovery potential compared to other crops (e.g. wheat, barley and legumes; Pitann and Mühling 2024; Setter and Waters 2003; Solaiman et al. 2007; Watson, Lapins, and Barron 1976), was also shown in this study: The harvest index of all oat varieties remained unchanged compared to its respective control despite being waterlogged at either tillering (W1) or heading (W2) (Figure 4). Watson, Lapins, and Barron (1976) showed that the greatest reduction in grain yield of oat occurred when the plants were

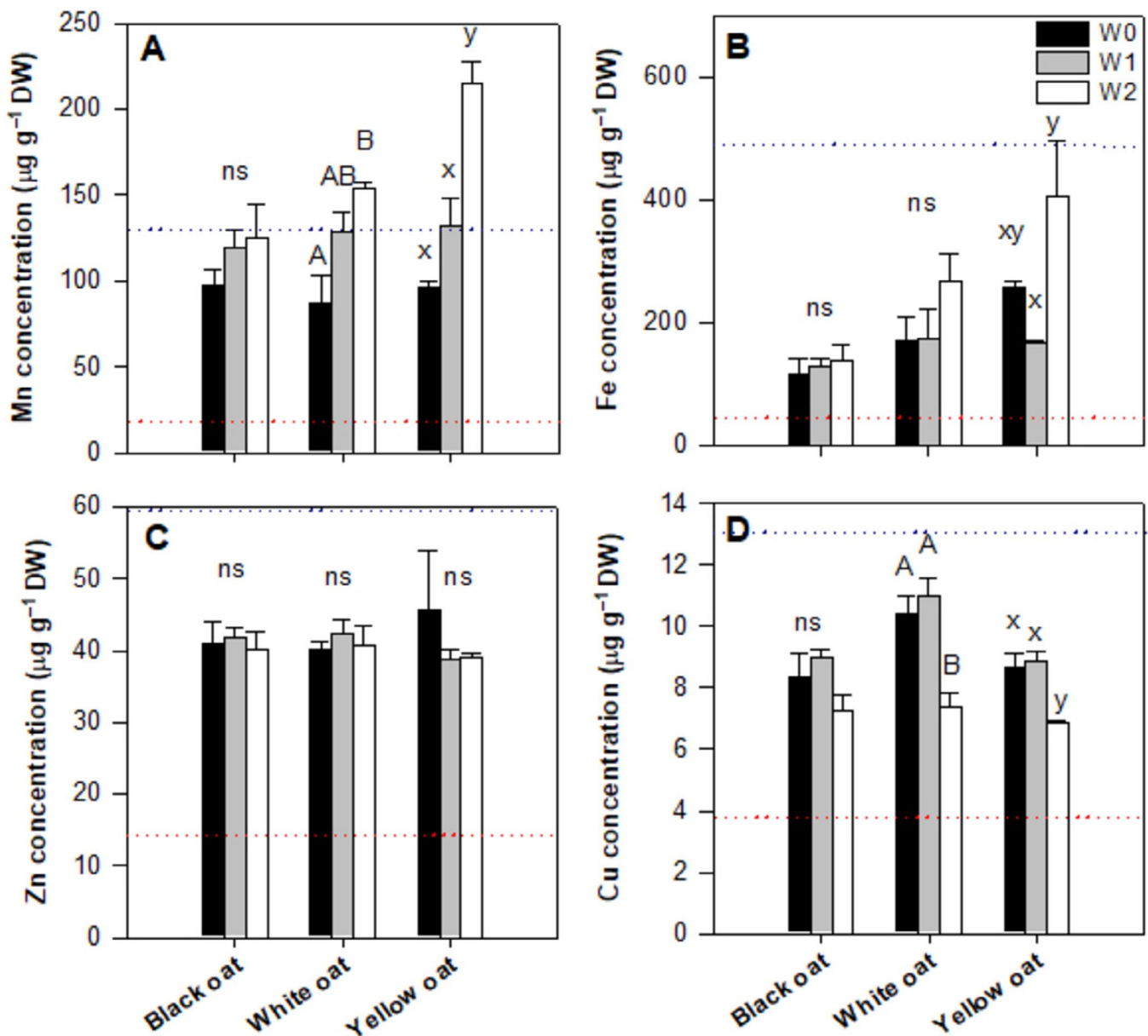


FIGURE 6 | (A) Manganese, (B) iron, (C) zinc, and (D) copper concentration of the whole aboveground plant material after 14 days of waterlogging at BBCH 51. Bars represent means + standard errors ($n = 4$). Different letters refer to significant differences ($p \leq 0.05$; ns, non-significant) between waterlogging treatments within one oat variety. Red/blue dotted lines represent the minimum/maximum threshold levels for optimal growth according to Bergmann (1993). W0, control; W1, waterlogging at BBCH 31; W2, waterlogging at BBCH 51.

subjected to waterlogging at the tillering stage. However, this reduction could be completely reversed by the application of N immediately following drainage. Similarly, the negative effect of waterlogging on tillering and, consequently, the yield of winter oat was reported to be mitigated after the application of N (Cannell et al. 1985). Moreover, Arduini, Baldanzi, and Pampana (2019) and Pitann and Mühling (2024) have also demonstrated that additional N in the recovery phase can mitigate the detrimental effect of waterlogging on the grain yield of oat. This finding is consistent with the results of the present study; immediately after the drainage of W1 plants, N fertilisation was performed (see Materials & Methods 2.1), serving as a “post-waterlogging rescue N fertiliser” and resulting in a regeneration of the N status until maturity (Pitann and Mühling 2024). However, while stabilisation of HI was

achieved after 14 days of waterlogging in the present study (Figure 4), Arduini, Baldanzi, and Pampana (2019) reported an 8% and 10% decline of HI in *A. sativa* and *A. byzantina*, respectively, after 35 days of stress treatment despite additional N application.

4.2 | Imbalances in Micronutrient Status of Oat Under Waterlogging Are Not Yield-Affecting

Soil pH and redox potential have been identified as significant factors that strongly influence the concentration and availability of micronutrients in the soil (Stevenson and Cole 1994). This can result in an imbalance in plant nutrient levels (Khabaz-Saberi, Setter, and Waters 2006; Ponnampetuma 1972). While

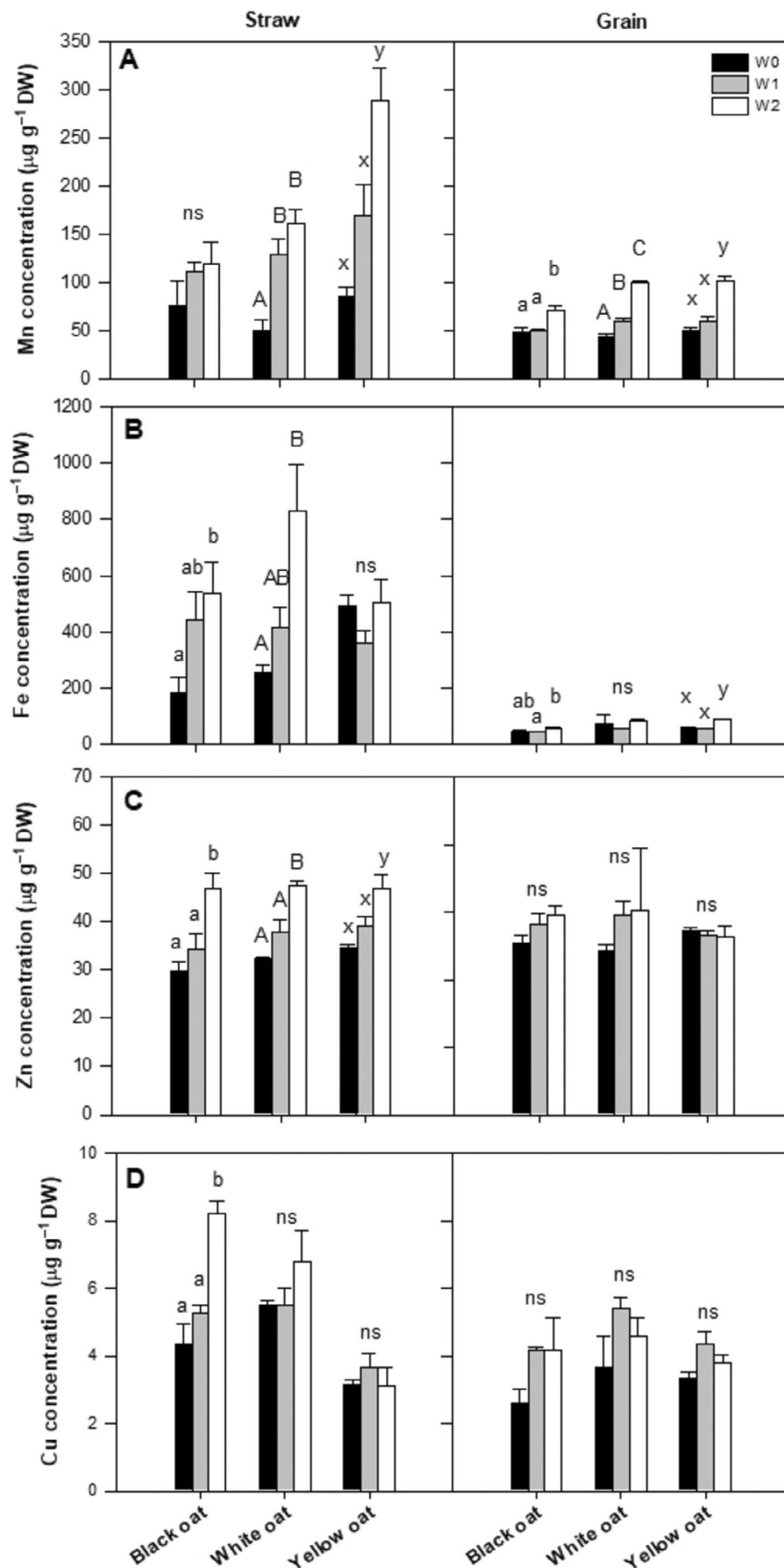


FIGURE 7 | Legend on next page.

FIGURE 7 | (A) Manganese, (B) iron, (C) zinc, and (D) copper concentration after harvest at maturity in straw (left panels) and grain (right panel). Bars represent means + standard errors ($n = 4$). Different letters refer to significant differences ($p \leq 0.05$; ns, non-significant) between waterlogging treatments within one oat variety. W0, control; W1, waterlogging at BBCH 31; W2, waterlogging at BBCH 51.

the majority of studies have focused on the solubility and availability of plant nutrients in soils subjected to submergence (e.g. Husson 2013; Khan et al. 2024; Olomu, Racz, and Cho 1973; Pezeshki and DeLaune 2012; Yaduvanshi et al. 2012), there is a paucity in-planta data. In particular, the relation between temporal waterlogging and micronutrient status has yet to be adequately investigated, particularly for oat such data are completely lacking. As micronutrients are crucial for growth and yield formation, this study aimed to address this gap by determining the effect of temporal waterlogging on Fe, Mn, Cu and Zn in oat, with a special focus on the timepoint of the plant life cycle at which stress occurs.

Variations in climate and moisture can lead to high temporal variability of Eh and pH (Sabienė, Kušlienė, and Zaleckas 2010). Soil pH of well aerated, cultivated soils usually ranges between 5 and 8 (Läuchli and Grattan 2012); however pH is strongly affected by submergence (Zárate-Valdez, Zasoski, and Läuchli 2006), with slightly acidic soils tending to shift pH towards neutrality (Bohrerova et al. 2004; Lu, Watanabe, and Kimura 2004). In this case, the activities of Fe, Mn and Cu in the soil solution decrease significantly per unit increase in pH, which results in a reduced availability and, thus, deficiency (e.g. Fageria, Baligar, and Clark 2002, and references therein). However, there is a negative correlation between soil pH and Eh (Bohrerova et al. 2004). In aerated soils, Eh is between +380 and +400 mV (Brady and Weil 2010), whereas in anaerobic soil conditions, it declines below +350 mV (Pezeshki 2001). For example, Balakhnina et al. (2010) found that the Eh dropped rapidly from +543 to +70 mV in response to flooding, indicative of reducing soil conditions. Similarly, Setter et al. (2009) demonstrated a decline in Eh as low as −200 mV after 50 days of waterlogging in eight Australian soils. As the Eh declines, the solubility and availability of micronutrients to plants increase critically (Pezeshki 2001; Ponnampereuma 1972). For example, Khabaz-Saberi, Setter, and Waters (2006) reported a decrease of wheat growth under waterlogging, which they attributed to the two- to ten-fold increase in Mn and Fe concentration in shoot tissue. Other studies have reported of increased levels of Mn and Fe in wheat and oilseed rape in response to submergence (Khabaz-Saberi, Barker, and Rengel 2012; Setter et al. 2009; Stieger and Feller 1994; Wollmer, Pitann, and Mühling 2019). However, depending on the tolerance level of the varieties and the basic soil characteristics (e.g. micronutrient status, buffer capacity, etc.), the increase did not always exceed the critical concentration for toxicity, especially for Mn (Setter et al. 2009). This finding is in agreement with the results of the present study. Although early waterlogging resulted in an increase of Mn in all three oat varieties and of Fe in black and white oat (Figure 5A,B), this increase was not critically as the concentrations remained well in the range of sufficiency described for oat (Bergmann 1993). Bjerre and Schierup (1985) also showed an increase in Mn and Fe concentrations in waterlogged oat in a neutral soil, reaching levels that could be considered toxic. However, it should be noted that, unlike this study, the waterlogging period was 21 days and

the pH of the soils ranged from 6.2 to 7.5, giving the soil more time for Eh changes and degradation of Mn- and Fe-oxides. The observed increase in Mn uptake is consistent with the increase in available soil Mn (Table S1), while the increase in plant Fe concentrations is inconsistent with soil data, which decreased with waterlogging. However, the results of this study contradict plant data presented by Wollmer, Pitann, and Mühling (2019) who reported no effect on Mn and Fe after early waterlogging in both wheat varieties tested, similar to the results of Steffens et al. (2005) for wheat and barley. As one reason for increased Fe uptake even under lower Fe availability (Table S1), a higher Fe-uptake efficiency of oat in comparison to wheat or barley can be assumed. Due to the capability to release, for example, phytosiderophores into the soil, Fe uptake will be increased even under low Fe availability (Mench and Fargues 1994); however, this needs to be proven for oat under the given stress conditions.

In contrast to Mn and Fe, a reduced Cu uptake was measured in white oat after early waterlogging (Figure 5D), resulting in a temporal deficiency. This is in agreement with Steffens et al. (2005) and Bjerre and Schierup (1985), who also reported a decrease in Cu concentration in submerged wheat, barley and oat. Wollmer, Pitann, and Mühling (2019) attributed the reduced Cu uptake of oilseed rape subsequent to early waterlogging to a reduction in Cu availability in soil, which is the case under low Eh (Husson 2013). In addition, it can be argued that the Cu uptake was impaired in this study, triggered by the low internal energy status under O_2 depletion (Colmer and Voeselek 2009). The lack of substrate for the H^+ -ATPase reduces its activity, which in turn leads to plasma membrane depolarization and thus reduced uptake kinetics (Elzenga and Veen 2010; Steffens et al. 2005), but remains to be demonstrated for oat. While there is consensus that waterlogging affects the availability of Zn in plants, there is still some controversy regarding the extent. For example, Scharpenseel et al. (1983) and Sajwan and Lindsay (1986) reported about Zn deficiency in rice grown in paddy fields due to a drop in Eh, while Pavanassivam and Axley (1980) showed increased Zn availability in acidic soils under flooding. However, it is not possible to apply the results of the aforementioned study directly to the present study, as paddy fields are characterised by permanent flooding rather than temporal waterlogging (Sajwan and Lindsay 1986; Scharpenseel et al. 1983). Furthermore, the acidic soils used in the previous study are not comparable to the slightly acidic soil used in this study (Pavanassivam and Axley 1980). More recent findings, however, indicate that waterlogging results in either lower or similar Zn concentrations in shoots (Khabaz-Saberi, Setter, and Waters 2006). In general, pH is considered the most important soil parameter for controlling Zn mobility in soils (Anderson and Christensen 1988). Therefore, it is not surprising that Zn remained unaffected of early waterlogging in all oat varieties as the soil pH also did not significantly change and ranged between 5.0 and 5.8, which is optimal for Zn uptake (Moraghan and Mascagni Jr 1991).

The waterlogging-induced micronutrient imbalances in oat, however, were (1) not critical in terms of toxicity (Mn and Fe)

and (2) not permanent in nature (Mn, Fe and Cu) (Figure 6). Wetland plants, such as rice, possess the ability to elevate the rhizospheric Eh by facilitating the transport of O₂ into the root via the aerenchyma. This mechanism allows plants to protect themselves against highly reductive soil conditions and, thus, micronutrient toxicities (see Husson 2013 and references therein). Given that oat is also capable of extensive aerenchyma formation (Setter and Waters 2003), it can be postulated that Mn and Fe toxicities were similarly circumvented by alterations in the rhizosphere Eh. Furthermore, micronutrient concentrations returned to the control level after waterlogging stress was ceased (Figure 6A,B). As demonstrated by Setter et al. (2009) and Balakhnina et al. (2010), the reaeration of drained soils resulted in an immediate restoration of Eh (> +350 mV) within a few days, allowing for a proper nutrient supply of oat immediately after the waterlogging event (Bjerre and Schierup 1985).

Similar to early waterlogging, late waterlogging resulted in a similar uptake pattern of micronutrients (Figure 6). Manganese was largely increased in white and yellow oat (Figure 6A), reaching concentrations that exceeded the threshold toxicity level of 130 ppm (Bergmann 1993; Figure 6A). In yellow oat, only slight toxic concentration of Fe were observed in the shoot (Bergmann 1993; Figure 6B), a finding that is in line with results reported by Bjerre and Schierup (1985). These results are further consistent with those reported by Wollmer, Pitann, and Mühling (2019) for wheat. The increased uptake of micronutrients, especially at later growth stages, can be attributed to seasonal fluctuations in temperature, because Eh is inversely related to soil temperature (Dorau et al. 2021; Husson 2013). As temperatures increase, the O₂ level in soil is decreasing and so is the Eh (Ponnamperuma 1984). As a results, the release of micronutrients in soils is more rapid in comparison to colder conditions (i.e. at the timepoint of early waterlogging), leading to higher availabilities of, for example, Mn and Fe. However, while Zn concentration in the shoot tissue was unaltered in all three oat varieties when waterlogged at BBCH 51, the Cu concentration dropped in white and yellow oat (Figure 6D). This is most probably due to reduced availability, but remained within a sufficient range.

Even though all plants had time to recover also from W2, at maturity it became evident that total nutrient concentrations (Mn and Fe), irrespective of the variety, were unable to decrease to the level of the corresponding control (Figure 7A,B), as was the case after W1. This effect was also prominent when separating into vegetative (straw) and generative plant parts (grains). However, although all three oat varieties showed a high uptake in Mn and Fe in general, at times reaching toxic levels, it must be noted that the highest concentrations were exclusively measured in vegetative tissues (e.g. shoot and straw; Figures 3–5), while they were comparably low in grains (Figure 7). This phenomenon was also described by Bjerre and Schierup (1985), who noted that waterlogging resulted in higher Mn and Fe concentrations in grains, albeit at a much lower level compared to straw. In contrast to Bjerre and Schierup (1985), Zn concentrations were not higher in grains compared to straw (Figure 7C) but non-significantly different to the control for all oat varieties, while the observed drop of Cu under W2 almost completely levelled off, except for straw in black oat (Figure 7D). The concentrations in the different plant parts allow for reasoning about the ion distribution

patterns in the plant. Nutrient transported from root to shoot is mediated by transpiration through the xylem. Additionally, xylem loading necessitates the presence of ATP as substrate for the H⁺-ATPase (Colmer and Greenway 2010). However, the lack in ATP resulting from the switch to anaerobic respiration together with the reduction in transpiration due to the closure of stomata under waterlogging, inevitably impedes nutrient transport to the shoot (Colmer and Voesenek 2009; Gibbs and Greenway 2003). In particular, when waterlogged occurs late in the growth cycle (e.g. BBCH 51), such limitations in nutrient translocation have a significant impact on grain supply.

5 | Conclusions

Due to a lack in oxygen under waterlogging, the soils' Eh immediately drops to reducing conditions, which in turn results in a higher solubility of micronutrients. Therefore, it is expected that due to the upsurge of micronutrients, also its uptake into the plant increases. This was confirmed for at least Mn and Fe, while Zn was not affected and Cu was reduced. However, varietal differences were observed. Of all the varieties, black oat was least responsive, with no toxicities/deficiencies occurring, followed by white and yellow oat, which were affected by Cu deficiency after early waterlogging and Mn (and Fe) toxicity after late waterlogging. However, these imbalances were only transient. Most importantly, micronutrients (Mn and Fe) mainly accumulate in vegetative tissues, rather than not in grains, with the exception of Zn.

However, since the HI of all oat varieties remained consistent with control conditions, transient reductions in dry weight and imbalances in the micronutrient status, whether after early or late waterlogging, did not affect yield or reduce grain quality in terms of micronutrient composition. The results thus demonstrate the high recovery potential and tolerance to waterlogging of the tested oat varieties. Consequently, oat can be considered a suitable alternative in crop rotation, particularly on sites prone to temporary waterlogging.

Author Contributions

Britta Pitann: conceptualization, investigation, writing – original draft, supervision, writing – review and editing, project administration. **Timo Hoppenheit:** investigation, writing – original draft. **Karl H. Mühling:** conceptualization, writing – review and editing, supervision, resources.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

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Supporting Information

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