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Root herbivory controls the effects of water availability on the partitioning between above- and below-ground grass biomass

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Abstract

1. The fraction of primary productivity allocated below-ground accounts for a larger flow of carbon than above-ground productivity in most grassland ecosystems. Here, we addressed the question of how root herbivory affects below-ground allocation of a dominant shortgrass prairie grass in response to water availability. We predicted that high levels of root herbivory by nematodes, as seen under extreme drought in sub-humid grasslands, would prevent the high allocation to root biomass normally expected in response to low water availability.
2. We exposed blue grama *Bouteloua gracilis*, which accounts for most of the net primary productivity in the shortgrass steppe of the central and southern Great Plains, to three levels of water availability from extreme low to intermediate and extreme high crossed with a gradient of rootherbivore per cent abundance relative to the total nematode community in soil microcosms.
3. As hypothesized, the effect of water availability on below-ground biomass allocation was contingent on the proportion of root herbivores in the nematode community. The relationship between below-ground biomass allocation and water availability was negative in the absence of root herbivory, but tended to reverse with increasing abundance of root feeders. Increasing abundance of root-feeding nematodes prevented grasses from adjusting their allocation patterns towards root mass that would, in turn, increase water uptake under dry conditions. Therefore, below-ground trophic interactions weakened plant responses and increased the negative effects of drought on plants.
4. Our work suggests that plant responses to changes in precipitation result from complex interactions between the direct effect of precipitation and indirect effects through changes in the below-ground trophic web. Such complex responses challenge current predictions of increasing plant biomass allocation below-ground

in water-stressed grasslands, and deserve further investigation across ecosystems and in field conditions.

KEYWORDS
climate change, ecosystem functioning, grassland, nematodes, plant biomass allocation, precipitation, primary production, soil fauna

1 | INTRODUCTION

Below-ground net primary production (BNPP) accounts for a larger flow of carbon than above-ground net primary production (ANPP) in most water-limited ecosystems (Potter et al., 1993). Yet, current understanding of BNPP patterns and controls is narrower than that for ANPP (Lauenroth, 2000; Wilcox et al., 2017). The fraction of ecosystem NPP allocated below-ground (f_{BNPP} = BNPP/ANPP + BNPP) is not fixed but may vary over time as plant species with flexible allocation strategies adapt to changes in their environment that affect resource availability (Hui & Jackson, 2006; Song et al., 2019). According to the concept of a 'functional equilibrium' of biomass allocation, plants will allocate relatively more biomass to roots if below-ground resources (e.g. water, nutrients) become the limiting factor for growth, whereas they will allocate relatively more biomass to shoots if above-ground resources (e.g. CO_2, light) are limiting (Brouwer, 1962). This concept has largely been supported by empirical data for abiotic drivers such as light, nutrients and water (Bloom, Chapin, & Mooney, 1985; Poorter & Nagel, 2000). However, reductions in soil-water availability may disproportionally affect higher trophic levels such as below-ground predators of root herbivores, with consequences that cascade down and affect plant responses (De Sassi, Tylianakis, & Wright, 2012; Preisser & Strong, 2004; Tylianakis, Didham, Bascompte, & Wardle, 2008). The influence of such responses and interactions across multiple trophic levels on plant biomass allocation patterns remains unexplored. A quantitative understanding of the mechanisms controlling biomass allocation patterns is of fundamental importance to global-change ecology, as these patterns set limits on carbon assimilation and biomass production.

Water availability is credited as the major control of ANPP in grassland ecosystems (Huxman et al., 2004; Sala, Gherardi, Reichmann, Jobbagy, & Peters, 2012). However, the effect of water availability on BNPP and f_{BNPP} is less established, with equivocal evidence showing that, as precipitation increases, below-ground biomass allocation can decrease (Frank, 2007), increase (Bai et al., 2010) or remain unaffected (Li, Lin, Taube, Pan, & Dittert, 2011; Wilcox, von Fischer, Muscha, Petersen, & Knapp, 2015; Xu, Sherry, Niu, Li, & Luo, 2013). These inconsistences suggest multiple controls determining the effect of water availability on BNPP and f_{BNPP}. Following the 'functional equilibrium' concept, a negative precipitation–f_{BNPP} relationship may be expected as a result of plant responses that reduce leaf area relative to root area during a drought, consequently reducing water loss and increasing water uptake. There is evidence showing increases in root-system investment at the expense of shoot mass with drought (Eziz et al., 2017). Nevertheless, drought has been shown to reduce predator control and increase herbivore pests in grassland ecosystems (De Sassi et al., 2012; Preisser & Strong, 2004; Tylianakis et al., 2008). Below-ground, drought can disrupt the balance between populations of root-feeding nematodes and their predators in a manner that increases the population of root feeders, which are major constraints of ecosystem NPP (Franco et al., 2019). Increases in root herbivory may in turn reduce root biomass, and ultimately affect the direction of the precipitation–f_{BNPP} relationship. However, to date the interactive effects of water availability and root herbivory on plant biomass production and allocation have not been established.

The level of root herbivory by soil nematodes can be an important factor controlling ecosystem NPP in grasslands (Ingham & Detling, 1990). Low levels of root herbivory by soil nematodes may promote soil nutrient flux and root growth in grasses (Bardgett, Denton, & Cook, 1999; Gebremikael, Steel, Buchan, Bert, & De Neve, 2016), whereas increased populations of root-feeding nematodes can lead to high levels of plant infestation and plant damage that reduce below-ground biomass (Scott, French, & Leetham, 1979). As much as 25%–59% plant biomass increases have been reported with nematode control (Ingham et al., 1986; Ingham & Detling, 1990; Smolik & Rogers, 1976; Stanton, 1983; Stanton, Allen, & Campion, 1981). Therefore, increased abundance of root-feeding nematodes under drought may overwhelm the plastic plant responses that increase root allocation relative to leaves in water-stressed plants.

We manipulated both water availability and root-feeding nematode abundance in greenhouse microcosms to investigate how these factors interact to determine the direction of the water availability–f_{BNPP} relationship. In the absence and low abundance of root feeders, we expected a negative slope in the water availability–f_{BNPP} relationship, that is, lower allocation below-ground as water availability increases. This would support the plant-response mechanism which is based on flexible allocation patterns of grasses that reduce leaf mass relative to root mass under drought conditions. However, we predicted the water availability–f_{BNPP} slope to switch from negative to positive as we increased the abundance of root-feeding nematodes. This would support the below-ground herbivory mechanism, which is based on a previous field study showing that drought weakens predation pressure below-ground and increases populations of root-feeding nematodes (Franco et al., 2019). We expected that the increased population of root feeders would lead to reductions in both BNPP and f_{BNPP}, thus impeding plants to increase biomass allocation to roots under drought.

2 | MATERIALS AND METHODS

In a greenhouse setting at Colorado State University's Plant Growth Facilities, we experimentally exposed blue grama *Bouteloua gracilis*, the dominant grass species and accounts for most of the NPP in the Great Plains shortgrass prairie (Lauenroth & Burke, 2008), to a gradient of root-feeder abundance relative to the total nematode community, which also includes bacterivores, fungivores, predators and omnivores (Yeates, Bongers, De Goede, Freckman, & Georgieva, 1993). Bacterivores and fungivores graze microbes in the rhizosphere, releasing part of the nutrients that were immobilized in the microbial biomass into the soil solution in plant-available forms (Pausch et al., 2016). Omnivores and predators feed on other nematodes, and this top-down force is an important regulator of the nematode community composition in soils (Yeates & Wardle, 1996).

The root-feeder gradient had four treatments (0%, 35%, 50% and 100%) that were crossed with three levels of irrigation from extreme low to intermediate and extreme high, in a full factorial, completely randomized design with six replicates per treatment. Two of the root-feeder treatments (35% and 50%) also included members of other nematode trophic groups (see Table 1), thus accounting for ecological interactions within the nematode community. Further details on the nematode and water treatments are given in the following sections.

2.1 | Preparation of soil microcosms and irrigation system

We used a bucket-loader tractor to collect approximately 400 kg of topsoil (5-cm depth) from a shortgrass prairie at the Semi-Arid Grassland Research Center, Nunn-CO. Following soil collection, we stored a small portion of the soil (~20 kg) in a cold chamber at 4°C to provide nematode inoculum for the experimental treatments. The remaining soil was defaunated using a thermal treatment described in Franco et al. (2017) that kills 99% of nematodes and prevents their recolonization for a minimum of 8 weeks while avoiding major disturbances to soil structure.

The experimental units consisted of PVC tubes of 10 cm diameter by 30 cm height filled with 600 g of nematode-free sand at the bottom, and 2 kg of defaunated soil on top of the sand. The bottom sand layer had the function of facilitating water drainage through the microcosms. We attached a plastic end cap to the bottom of each microcosm and made a single small hole at the centre of each end cap to allow water drainage. A total of 72 microcosms were set in the greenhouse benches (inside two large plastic bathtubs required by USDA regulations to avoid water spills and nematode dispersion), and placed in a way to form three rows over the bench where we assembled a drip irrigation system. That system consisted of three sub-main water lines made of PVC pipes that branched off the main water line (that connected to the water source) and ran the length of the microcosms rows. These sub-main lines had equal water application rates, and irrigation times controlled individually, thus allowing the application of three separated water treatments. Water feed lines consisted of spaghetti plastic tubing that had one end attached to the sub-main lines and the other end attached to the soil surface of microcosms.

We evenly watered soils in all microcosms (all sub-main lines), then planted 15 commercial seeds of blue grama (obtained from Pawnee Buttes Seed Inc.) in the well-watered soils in each microcosm. Two weeks after germination started, we removed all but five seedlings from each microcosm. During that period, we evenly and daily watered the microcosms until germination, and every other day until germinated seedlings had two pairs of leaves, at which point we applied the water and nematode experimental treatments.

2.2 | Water treatments

We applied three levels of irrigation from extreme low- to intermediate- and extreme high-water amounts. The intermediate irrigation treatment consisted of water pulses equivalent to 4.4 mm of water. For the extreme irrigation levels, we reduced and increased the amount of water per pulse by 80%. This manipulation rate mimics extreme precipitation manipulation levels that we applied in a previous field experiment in the shortgrass steppe, which corresponded to the first and 99th percentile of long-term precipitation for the rainfall reduction and addition treatments, respectively (Franco et al., 2019). Therefore, the extreme low irrigation treatment consisted of 0.9-mm water pulses, whereas the extreme high irrigation treatment applied 8.02 mm per pulse. Total amount of

TABLE 1 Mean abundance and standard deviation ($n = 10$ 1-ml aliquots of the prepared inocula) of inoculated nematode trophic groups in each treatment. Relative abundances are presented under parentheses

Treatment	Bacterial feeders	Fungal feeders	Root feeders	Omnivores	Predators
Defaunated	0	0	0	0	0
Native community	882 ± 207 (49%)	76 ± 57 (4%)	661 ± 149 (36%)	134 ± 68 (7%)	73 ± 30 (4%)
Native community + root feeders	882 ± 207 (41%)	76 ± 57 (3%)	1,001 ± 239 (47%)	134 ± 68 (6%)	73 ± 30 (3%)
Root feeders	0	0	995 ± 260 (100%)	0	0

water applied for the extreme low, intermediate and extreme high-water treatments was 24.3, 118.8 and 216.5 mm, respectively. To put these water amounts in the context of actual growing-season precipitation at the shortgrass steppe, the average precipitation for a 12-week period (duration of this experiment) during the growing season (May–August) is ~153 mm, given a mean growing-season precipitation of 204 mm (Lauenroth & Burke, 2008). The frequency of irrigation was the same among treatments, and determined through the monitoring of soil moisture tension (or matric potential, i.e. the energy that plants must spend to extract water from the soil) in six extra microcosms (not used for data acquisition) that received the intermediate irrigation treatment. Microcosms were irrigated when soil moisture tension in the extra microcosms dropped below 60–70 kPa to avoid grass stress at the intermediate irrigation level (Allan Andales, pers. comm.). In this way, watering frequency accounted for the continuous increase in evapotranspiration rates with plant growth. The water amount in the intermediate irrigation treatment was determined to bring soil moisture tension >60–70 kPa.

2.3 | Nematode treatments

We added nematodes into the defaunated soil microcosms to build a gradient from low to natural and increased abundance of root-feeding nematodes. Three types of nematode communities were inoculated into the microcosms: (a) native shortgrass-prairie nematode community with 35% of root feeders and (b) native shortgrass-prairie nematode community plus extra root feeders to increase the relative abundance of root feeders to 50%. This increased relative abundance of root feeders mimics that observed under extreme drought in previous field experiments (Franco et al., 2019). Finally, we had a treatment (c) with 100% root-feeding nematodes, and the fourth nematode treatment was a defaunated control. By keeping the native nematode community (native species and abundances) along with root-feeders in treatments (a) and (b), we assured a high degree of ecological realism in our treatments. The abundance of nematode trophic groups in each treatment is shown in Table 1.

The inoculum with native shortgrass-prairie nematode community had an average of 366 ± 87 nematodes per 1 ml, and an average proportion of root feeders of 36 ± 4% ($n = 10$ aliquots of 1 ml). This inoculum was obtained from 24 kg of non-defaunated soil previously stored in a cold chamber at 4°C. This amount of soil corresponded to the sum of soils in the top 5-cm layer of all microcosms to be inoculated. We extracted nematodes in water using Baermann funnels (Hooper, 1970), from which we took 20 ml aliquots daily for 3 days. We combined all extracted solutions in a 2,000-ml flask, allowed 2 hr for nematodes to settle to the bottom of the flask, and finally removed excess supernatant water by decanting the nematode solution to a final volume of 180 ml (calculated to allow the addition of 5 ml of inoculum in a total of 36 microcosms that received native-community treatments). We kept the removed nematode-free excess water to add 5 ml into each of those microcosms not receiving the native nematode inoculum (defaunated and 100% root-feeders treatments) to standardize the inputs of soil nutrients and microbes across all microcosms. No nematodes were found in the nutrient and microbial inoculum. We stored both inocula in a refrigerator at 4°C for 24 hr until we inoculated the microcosms.

For the two treatments with increased abundance of root feeders, we used a plant-parasitic nematode species, *Pratylenchus penetrans*, cultured under laboratory conditions. This nematode species is found in all temperate regions globally (Loof, 1991) and, importantly for this experiment, is a parasite of blue grama roots (Figure S1, picture of stained *P. penetrans* inside blue grama roots). We used *P. penetrans* to prepare two solutions. For the treatment with native community + root feeders, we prepared a solution of 90 ml of water containing 65 ± 18 *P. penetrans* per 1 ml. This volume was calculated to allow the addition of 5 ml (or ~325 root feeders) in each of the 18 microcosms receiving this treatment, increasing the proportion of root feeders in the nematode community from the original 35% to approximately 50% (Table 1). For the treatment receiving 100% of root feeders, we prepared a second solution of 90 ml of water containing 199 ± 52 *P. penetrans* per 1 ml. In this case, our goal was to vary the relative abundance but keep the absolute abundance of root feeders in each microcosm equal as in those receiving 50% of root feeders. To that end, we added 5 ml of this solution (i.e. ~995 root feeders) to each of the 18 microcosms receiving only root feeders. The populations of *P. penetrans* used in this experiment were obtained through culture for 90 days in petri dishes with corn roots and Gamborg's B-5 medium, as described in Saeed, MacGuidwin, and Rouse (1997). We extracted *P. penetrans* from 20 petri dishes by slicing the culture medium and corn roots and placing them on Baermann funnels for 24 hr. Inoculum of *P. penetrans* and native community consisted of all vermiform stages in water.

Finally, we prepared a nematode-free solution containing nutrients from culture medium to be added to those microcosms not receiving *P. penetrans* solutions. We set up five extra Baermann funnels to which we added pieces of culture medium and corn roots from petri dishes that were prepared without nematodes. We extracted the solution from funnels after 24 hr, and added 5 ml to microcosms receiving the defaunated and native community treatments, thus avoiding confounding effects of differential nutrient inputs across treatments.

At day 0 of the experiment, we initiated the water treatments and inoculated microcosms with their assigned nematode treatments. In addition to irrigation water, the inoculation represented an input of 10 ml of water equally added to all microcosms. We used 5-ml glass measuring pipettes attached to a pipet controller (Fisherbrand®) to inoculate nematode and nutrient solutions. Those solutions were constantly and gently homogenized during inoculation. At each microcosm, the solutions were poured into previously opened 2-cm deep holes in the soil. The environmental conditions in the greenhouse were kept at 18–21°C, 30%–50%

humidity and photoperiod of 16-hr light/8-hr dark throughout the experiment.

2.4 | Data collection

We harvested the experiment 12 weeks after inoculation. To ensure harvesting prior to root growth becoming constrained by the size of PVC microcosms, we tracked root growth throughout the experimental period by destructively sampling one of the extra microcosms every 2 weeks. At the sampling day, we clipped shoots at the soil level and stored them in paper bags. We then used a compact circular saw to cut each PVC microcosm in half lengthwise, and poured soil columns over separate aluminium trays for hand-picking roots and collecting the entire soil content. Shoots and roots were dried in an oven at 60°C for 48 hr, and weighed. Above-ground and below-ground biomasses were summed to calculate total biomass production per microcosm, which was divided by the surface area of microcosms and expressed as grams of biomass per m^2. Below-ground biomass was divided by total biomass to calculate the fraction of the total biomass allocated below-ground (f_{BNPP}, expressed as percentage).

2.5 | Statistical analyses

We assessed biomass production and allocation responses by regressing all response variables (ANPP, BNPP and f_{BNPP}) against total water amounts as a continuous explanatory variable, discrete nematode treatments and their interactions in linear models. The assumptions of homogeneity and normality were validated. All analyses were performed in R 3.1.3 (R Core Development Team, 2013).

3 | RESULTS

The water-availability and nematode treatments interacted to affect f_{BNPP} (water × nematodes; $p = 0.0084$, $R^2 = 0.30$), revealing that the slope of the water availability–f_{BNPP} relationship became shallower with increasing proportion of root feeders in nematode communities (Figure 1). Plants growing on both defaunated soil and soil with a native nematode community had steep and negative water availability–f_{BNPP} relationships, with a non-significant increase in the slope between the defaunated and native community treatments of 0.04 ± 0.05 ($p = 0.3892$), and f_{BNPP} values higher than 50% at lower water levels for both treatments. Increased abundance of root feeders in the native nematode community increased the f_{BNPP} ~ water availability slope by 0.12 ± 0.05 ($p = 0.0161$) compared to the defaunated treatment, and made f_{BNPP} insensitive to changes in water availability. Finally, when only root feeders were present, the f_{BNPP} ~ water availability slope had its largest increase relative to the defaunated treatment (0.16 ± 0.05; $p = 0.0022$), ultimately making that relationship slightly positive (Figure 1). Notable differences between nematode treatments at the lowest water level drove this interaction, with higher f_{BNPP} in plants growing on defaunated and native-community soils compared to those exposed to the increased abundance of root feeders.

These nematode effects on f_{BNPP} (Figure 1) were not apparent when independently analysing the above- and below-ground net primary production (Figure 2). ANPP ($p < 0.0001$, $R^2 = 0.54$) and BNPP ($p < 0.0001$, $R^2 = 0.48$) significantly increased with increasing water availability regardless of the nematode community composition (Figure 2). As a result, the same pattern was observed for total NPP ($p < 0.0001$, $R^2 = 0.55$). It is noteworthy that, under the drought treatment, plants tended to produce more biomass when only root feeders were present (Figure 2). However, we found no statistical support to nematode effects on plant biomass.

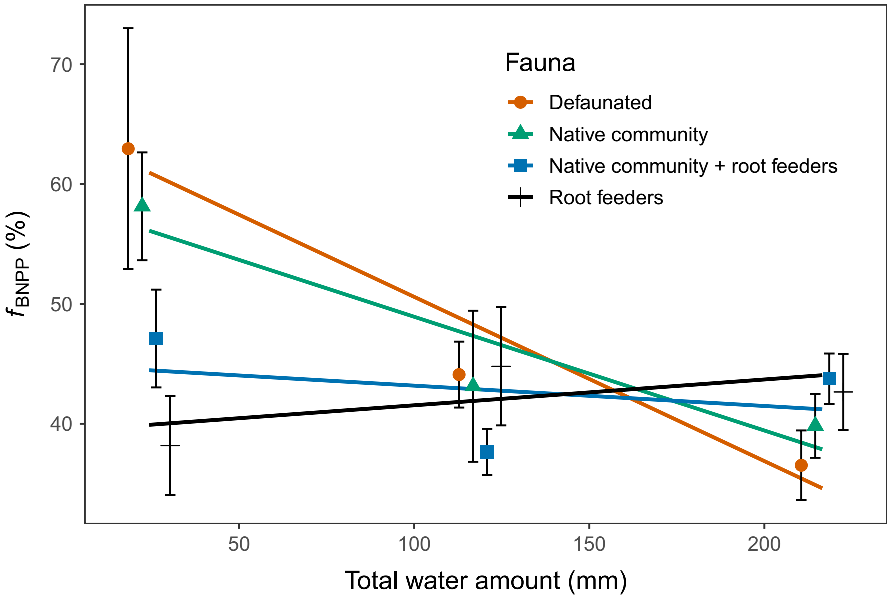

FIGURE 1 Response of the fraction of total plant biomass allocated below-ground (f_{BNPP}) to water treatments and soil-fauna manipulations. Water and soil fauna treatments interacted to affect f_{BNPP} (water × fauna; $p = 0.0084$, $R^2 = 0.30$). Shape-coded points represent means ($n = 6$), and color-coded trend lines represent predictions of a linear regression model. Error bars show standard error of the means

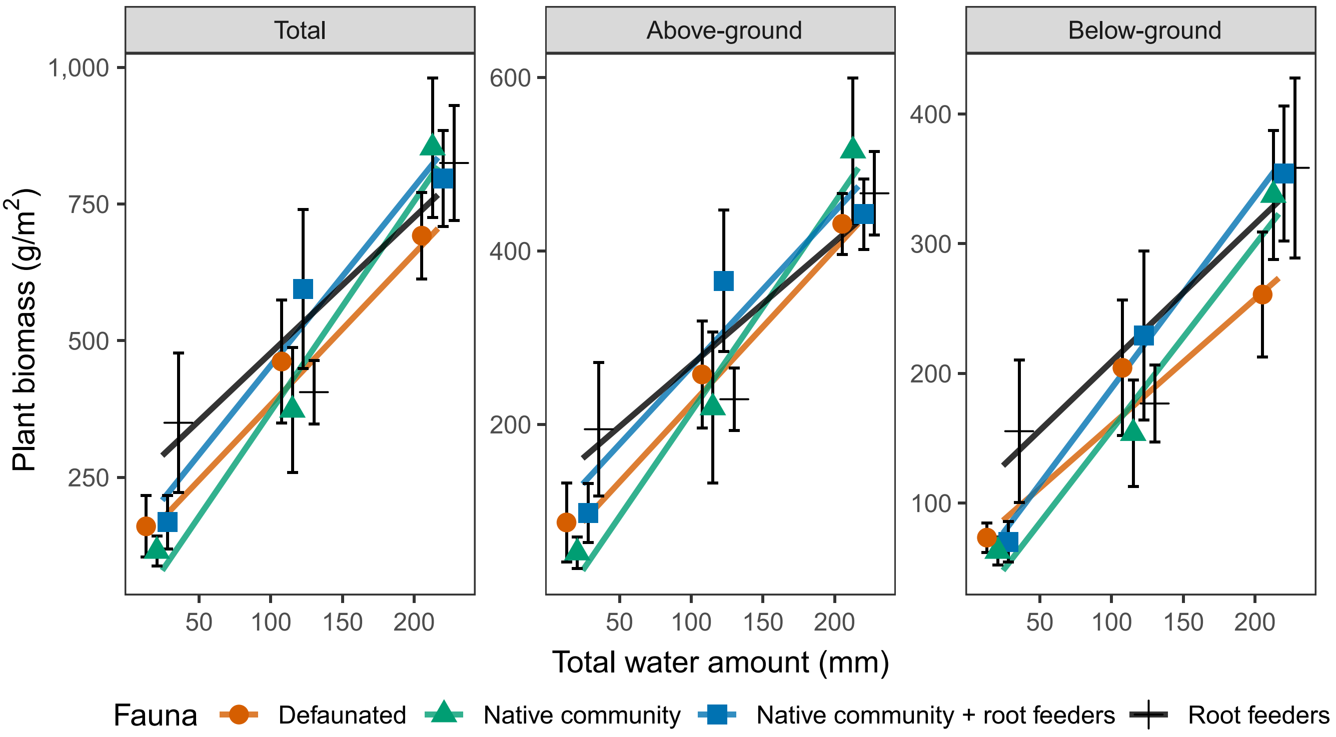

FIGURE 2 Response of the total (NPP), above-ground (ANPP), and below-ground (BNPP) plant biomass to water availability and soil fauna manipulations. Shape-coded points represent means ($n = 6$). Error bars show standard error of the means. Color-coded trend lines represent predictions of a linear regression model for significant water effects (NPP $R^2 = 0.30$; ANPP $R^2 = 0.30$; BNPP $R^2 = 0.30$). $p < 0.0001$. No significant effects of soil fauna treatments were detected ($p > 0.05$)

4 | DISCUSSION

By manipulating both water availability and the abundance of below-ground nematode herbivores in greenhouse microcosms, we found that the effects of changes in water availability on grass biomass allocation are likely to be contingent on the abundance of nematode herbivores. It has been previously shown that drought weakens predation pressure below-ground and increases the abundance of root-feeding nematodes in sub-humid grasslands (Franco et al., 2019). Our findings here indicated that increased abundance of below-ground herbivores can undermine important plant-plastic mechanisms that buffer grass and ecosystem against the effects of drought, and expand our understating on the controls of biomass allocation by highlighting the role of multitrophic interactions.

The slope of the water availability–f_{BNPP} relationship shifted from negative (under natural abundances or absence of root feeders) to null and slightly positive under increased root herbivory (Figure 1). These results contribute to the understanding of how the plant-response and the root-herbivore mechanisms postulated in our hypotheses occur in nature. The negative slope of the water availability–f_{BNPP} relationship under natural herbivore abundance shows that grasses reduce leaf mass relative to root mass during a drought. This observation is consistent with ecological theory (Brouwer, 1962), as well as with previous quantification of the water availability–biomass allocation relationship across spatial gradients (Hui & Jackson, 2006). On the other hand, the positive water availability–f_{BNPP} relationship was driven by herbivore effects at the lowest water level and indicates that root herbivory offsets the physiological plant mechanism when drought is accompanied by increased herbivore populations. When we increased the relative abundance of root herbivores to the level observed under extreme drought in previous field experiments (~50%; Franco et al., 2019), both mechanisms postulated for the plant and herbivory hypotheses seemed to compensate each other yielding a similar proportion of below-ground allocation across the gradient of water availability.

The effect of root feeders reducing f_{BNPP} under low water availability was not accompanied by any root-feeder effect on BNPP (Figure 2). Focusing on the ratio of above-/below-ground productivity allowed us to observe patterns that were not obvious when evaluating the BNPP and ANPP in isolation. Herbivory by root-feeding nematodes overshadowed plastic plant responses that allocated more biomass below-ground under drought conditions and benefit water uptake (Figure 1). These results suggested that increased root herbivory can aggravate the water stress and accelerate grass die-offs under drought, enhancing its negative effect on grasses and ecosystem C fixation. Root-feeding nematodes have previously been reported as a contributing factor to blue grama die-off in the same grassland site studied here (Stanton, Morrison, & Laycock, 1984). A previous study has shown that such increases in the population of root herbivores result from trophic cascade effects that reduce predation control of root feeding nematodes under drought (Franco et al., 2019).

Blue grama *B. gracilis* accounts for 75%–90% of the net primary productivity in the shortgrass steppe of the central and southern

Great Plains (Lauenroth & Burke, 2008). Therefore, changes in blue grama's biomass allocation in response to drought and below-ground herbivory are likely to influence not only grass nutrient and water uptake but also ecosystem-wide responses through plant–plant and plant–soil interactions (Eziz et al., 2017; Jackson et al., 2000; Poorter et al., 2012). Furthermore, herbivory is tightly linked to the local environment and so often occurs in tandem with abiotic stress (e.g. drought; Johnson, Erb, & Hartley, 2016).

The effect of climate change and specifically the effect of changes in precipitation in grassland ecosystems has been widely studied (Sala et al., 2012). In addition, recent advances in above-ground–below-ground ecology have demonstrated the magnitude of soil nematodes potential effects on ecosystem processes, indicating an underestimated influence on soil carbon cycling. For example, the biomass of nematodes in the global topsoil (0.3 gigatonnes) represents ~80% of total human biomass on Earth, and the amount of carbon respired by soil nematodes (0.11 Gt C monthly) is equivalent to roughly 15% of carbon emissions from fossil fuel use (van den Hoogen et al., 2019). Considering this functional relevance of soil nematodes, here we presented novel results testing for the direct and indirect effects of climate change on the functioning of grasslands using native soils, nematodes and plants of a shortgrass steppe prairie. Our work suggests that plant responses to changes in precipitation result from complex interactions between the direct effect of water availability and indirect effects through increased below-ground herbivory. Such complex responses challenge the predictions of increasing plant biomass allocation below-ground in water-stressed grasslands, and deserve further investigation across ecosystems and in field conditions.

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AUTHORS' CONTRIBUTIONS

A.L.C.F., D.H.W., C.M.d.T., O.E.S. and L.A.G. conceived the ideas and designed the study; A.L.C.F., C.M.d.T., W.S.A., K.E.A., E.M.B. and P.G. performed the experiment and collected data; A.L.C.F. led data analysis and drafted the manuscript, and all authors contributed to revisions.

DATA AVAILABILITY STATEMENT

Data are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.12767855 (Franco et al., 2020).

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SUPPORTING INFORMATION

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

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