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**Title: Resistance and change in a High Arctic ecosystem, NW Greenland:
Differential sensitivity of ecosystem metrics to 15 years of experimental
warming and wetting**

Running head: Mixed High Arctic responses to climate change

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Abstract

Dramatic increases in air temperature and precipitation are occurring in the High Arctic ($>70^{\circ}\text{N}$), yet few studies have characterized the long-term responses of High Arctic ecosystems to the interactive effects of

experimental warming and increased rain. Beginning in 2003, we applied a factorial summer warming and wetting experiment to a polar semidesert in northwest Greenland. In summer 2018, we assessed several metrics of ecosystem structure and function, including plant cover, greenness, ecosystem CO₂ exchange, aboveground (leaf, stem) and belowground (litter, root, soil) carbon (C) and nitrogen (N) concentrations (%) and pools, as well as leaf and soil stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Wetting induced the most pronounced changes in ecosystem structure, accelerating the expansion of *S. arctica* cover by 370% and increasing aboveground C, N, and biomass pools by 94–101% and root C, N, and biomass pools by 60–122%, increases which coincided with enhanced net ecosystem CO₂ uptake. Further, wetting combined with warming enhanced plot-level greenness, whereas in isolation neither wetting nor warming had an effect. At the plant level the effects of warming and wetting differed among species and included warming-linked decreases in leaf N and $\delta^{15}\text{N}$ in *Salix arctica*, whereas leaf N and $\delta^{15}\text{N}$ in *Dryas integrifolia* did not respond to the climate treatments. Finally, neither plant- nor plot-level C and N allocation patterns nor soil C, N, $\delta^{13}\text{C}$, or $\delta^{15}\text{N}$ concentrations changed in response to our manipulations, indicating that these ecosystem metrics may resist climate change, even in the longer term. In sum, our results highlight the importance of summer precipitation in regulating ecosystem structure and function in arid parts of the High Arctic, but they do not completely refute previous findings of resistance in some High Arctic ecosystem properties to climate change.

Keywords

CO₂ flux, ecosystem, carbon, vegetation change, stable isotopes, tundra, polar semi-desert

Introduction

Profound recent climate change in the High Arctic (>70 °N) is expected to continue and accelerate in the 21st century (Bintanja, 2018; Bintanja & Selten, 2014; Blunden & Arndt, 2019; Hanna et al., 2012; IPCC, 2014; NASA, 2020). High Arctic terrestrial ecosystems, being very cold, arid, and often sparsely vegetated contrast significantly with the lower latitude Arctic, yet there are only a few long-term (>10 years) ecological and biogeochemical research efforts in the region, hindering our ability to forecast vegetation and soil responses, greenhouse gas feedbacks and carbon (C) sequestration (Hudson & Henry, 2010; Lamb et al., 2011; Lupascu et al., 2014, 2018; Robinson et al., 1995; Schaeffer et al., 2013; Schmidt et al., 2012; Sharp et al., 2013; Walker et al., 2008; Wookey et al., 1993). Given recently accelerated Arctic warming and the concomitant loss of sea

ice (AMAP, 2017; Box et al., 2019; NSIDC, 2020; Overland et al., 2019), it is critical to understand High Arctic ecosystem structure and function under realistic future climate regimes.

At larger, synoptic scales, increases in near-surface air temperature and precipitation are well underway across the broader High Arctic, but substantial local spatial heterogeneity in these trends complicates ecological inference for the broader region (AMAP, 2017; Bintanja, 2018; Bintanja & Selten, 2014; Box et al., 2019). For example, in Greenland, fourfold regional disparities in the strength of air temperature increases combined with regional differences in the directionality of precipitation change have developed (Bintanja, 2018; Bintanja & Selten, 2014; Hanna et al., 2012; Mernild et al., 2015). How these synoptic- and regional-scale climate phenomena manifest as ecologically relevant local climates remains somewhat uncertain, as the temperature and moisture regimes High Arctic plants and soil microbiota experience also depend on a variety of site factors, including thaw depth and soil texture and drainage. However, recent shrub-ring evidence from different Arctic sites indicates that larger-scale Arctic climate trends are relevant to local biological processes (Buchwal et al., 2020). Thus, ongoing broad-scale multivariate climate change and regional idiosyncrasies in the High Arctic highlight the need for ecological studies that analyze the individual and interactive effects of experimental warming and wetting.

Inconsistent responses to experimental warming and wetting have been observed previously in polar semidesert ecosystems (Rogers et al., 2011; Schaeffer et al., 2013; Sharp et al., 2013; Welker et al., 1993; Wookey et al., 1993, 1995). On Svalbard, five years of combined warming and wetting reduced vascular plant cover, whereas when applied individually warming and wetting had little effect (Robinson et al., 1998). Previous work at our site in northwest Greenland found non-linearities in the response of net ecosystem carbon exchange (NEE) to two levels of experimental summer warming and two levels of experimentally increased snow depth, but little evidence of vegetation change (Rogers et al., 2011; Sharp et al., 2013). However, these studies were relatively short-term (7 years or less); few experimental studies have been maintained in the High Arctic for a similar duration to the longer-term efforts in the Low Arctic (e.g. Chapin et al., 1995; DeMarco et al., 2014; Leffler et al., 2016).

Of the few longer-term climate change experiments that have been performed in the High Arctic, many have addressed the temperature component of climate change, with mixed results (Elmendorf et al., 2012; Hudson et al., 2010; Welker et al., 2004). In Alexandra Fiord, 1-2 °C experimental warming triggered sustained increases in plant height at a densely vegetated polar oasis, but little vegetation response in an evergreen

shrub heath (Hudson et al., 2011; Hudson & Henry, 2010), and site-dependent changes in annual net CO₂ uptake (Welker et al., 2004). On the other hand, the long-term (14 years) augmentation of summer precipitation stimulated soil CO₂ efflux but did not affect SOM pools at Zackenberg (Christiansen et al., 2012). In one of the only long-term (15 years) studies from the High Arctic that used a multivariate approach to simulate different climate change scenarios, fertilization alone increased vegetation height and cover, warming alone increased vegetation cover, but warming, fertilization, and irrigation had few main effects and no interactive effects on soil microbial communities or ecosystem greenhouse gas exchange (Lamb et al., 2011).

Such apparent discrepancies in High Arctic ecosystem responses to experimental climate manipulations are likely underpinned by the species-specific ecophysiology of Arctic plants (Chapin & Shaver, 1985; Jespersen et al., 2018; Leffler et al., 2016; Pattison & Welker, 2014). For example, enhanced CO₂ sink strength has been tentatively linked to the expansion of the deciduous shrub *Salix arctica* (Sharp et al., 2013); this relatively fast-growing species has repeatedly demonstrated ecophysiological plasticity, for example by increasing leaf nitrogen (N) and photosynthetic capacity with deeper snow (Leffler & Welker, 2013; Rogers et al., 2011), or by increasing leaf size and plant height with warming (Hudson et al., 2011). Likewise, in a polar semidesert on Svalbard, vegetation cover change was largely attributed to shifts in leaf-level ecophysiological traits in *Dryas octopetala* (Robinson et al., 1998; Welker et al., 1993; Wookey et al., 1995). Alternatively, if a community is dominated by slow-growing, less ecophysiotogically responsive evergreen species, warming may not induce vegetation change (i.e. Hudson & Henry, 2010). Yet, as with ecosystem-level metrics, few longer-term leaf- or tissue-level responses to climate manipulations have been obtained in the High Arctic.

In this study we examine how vegetation (community cover, greenness, and tissue chemistry), summer ecosystem CO₂ fluxes, and ecosystem C and N pools have changed in a High Arctic semidesert following 15 years of experimental climate manipulations. We used the factorial application of summer warming (+60 W m⁻², hereafter referred to as warming) and increased summer precipitation (hereafter referred to as wetting) to answer: i) what are the longer-term responses of plants, CO₂ exchange, and soils to experimental warming and wetting, alone and in combination? and ii) have the climate manipulations driven changes in ecosystem C and N sequestration? This study is part of a long-term research program (Sharp et al., 2013; Sullivan et al., 2008), and we compare our findings with previous findings from this site and other High Arctic sites to highlight examples of ecosystem resistance and change.

Methods

Site description

The experimental site is in northwest Greenland on the Pituffik Peninsula (76° 33' N, 68° 34' W; elevation 180 m a. s. l.), adjacent to Thule Air Base. The landscape is polar semidesert, characterized by patterned ground features and a mixture of barren and vegetated ground. The maximum height of vegetation is c. 15 cm. The main vascular plant species are *Dryas integrifolia* (an evergreen dwarf shrub), *Salix arctica* (a deciduous shrub) and *Carex rupestris* (a graminoid), that together comprise 93% of the vascular vegetative cover (Sharp and Sullivan, unpublished data). The soils are 54–64% sand, 33–38% silt and 3–7% clay (Sullivan et al., 2008).

The climate is typical of the arid High Arctic and changing rapidly; from 1971 to 2019, the mean annual temperature was -10.6 °C and rising 0.6 °C decade⁻¹ (Figure 1, NOAA/NCDC, 2020). From 1952 to 2019, annual precipitation averaged 120 mm yr⁻¹, and has recently become more variable, as precipitation variance from 1986 to 2019 was 1.5 times higher than from 1952 to 1985. Half of the annual precipitation falls during June, July, and August, when the mean temperature is 4.9 °C (1952–2019).

Experimental design

The experimental design is detailed in Sullivan et al. (2008) and Sharp et al. (2013). Briefly, in 2003, twenty-four 0.8 × 2 m experimental plots including both vegetated (0.8 × 1 m) and bare ground (0.8 × 1 m) in equal proportions were established in three homogenous 70 m × 60 m areas. Plots were assigned to one of four different climate treatments: warming (+T), wetting (+W), combined warming and wetting (+T+W), and unmanipulated control (CTL). All treatments were replicated six times but in 2009 replication was reduced for logistical reasons (post reduction: +T, n = 5; +T+W, n = 5). The experimental design also included another level of warming (+30 W m⁻²), which was excluded from this study (see e.g. Sharp et al., 2013).

Experimental plots were warmed using infrared heaters (1.6 x 0.12 m, Kalglo Electronics Co. Inc., Bethlehem, PA) during the growing seasons 2004–2018 (typically June 5 (± 3 days) through August 20 (± 3 days)). In the +T and +T+W treatment, infrared heating was +60 W m⁻². Increased growing season wetting was simulated with weekly hand watering using deionized water that had been left to equilibrate with ambient air temperature for 24 hours. In 2018, watering was started after all experimental plots had become snow free (late June) and carried out five times, July 3–4, 13, 19 and 27–30, and August 10.

Microclimate effects of the treatments have been documented previously (Sharp et al., 2013; Sullivan et al., 2008). During the 2018 growing season, the continued effects of the treatments on the soil microclimate were verified by recordings of soil temperature (°C, 10 cm depth), and soil moisture (%; 0–12 cm depth, TDR Campbell Scientific Logan, UT). TDR probes were not calibrated on site; values are presented for treatment comparison only. In total, six measurement campaigns were conducted (June 26–28; July 8, 17, 26–31; August 2 and 8) and during each campaign, all experimental plots were measured once. The dates of microclimate measurements were usually staggered by several days from the dates with experimental watering. Throughout the duration of the experiment (2004–2018), the warming treatments (+T, +T+W) increased summer soil temperatures by 2 °C whereas wetting decreased them on average by 0.3 °C in comparison to control (Supporting Information Table S1). During year 2018, the wetting treatments (+W, +T+W) increased annual precipitation by c. 40% from baseline and increased soil moisture from 15.7% to 17.3% (Supporting Information Table S1).

Vegetation Cover and Community Greenness

On July 30, 2018, downward looking aerial digital images were taken from the vegetated part (0.8 m x 1 m) of each experimental plot for use in plant community cover analysis and for extracting community greenness. Cover for the three dominant vascular plant species (*D. integrifolia*, *S. arctica*, and *C. rupestris*) was measured retrospectively using an image-based point-frame technique. A digital “point-frame” simulating the 2003 point-frame (1.0 × 0.8m, with 11 rows and 9 columns of evenly spaced intersecting lines, see Sharp (2013) for details) was superimposed on the image, and the plant species under each line intersection was recorded. In 2003 only the first pin hit was recorded, thus the 2018 image-based cover values are directly comparable with the 2003 values and used here to evaluate changes in the contributions of different species to vegetation cover over time, but not to evaluate total abundance. Also, because the 2003 point-framing focused only on the vegetated part of each plot, our measurements were not designed to analyze the proportion of total vegetated cover in relation to non-vegetated cover.

Plot images were also used for assessing community greenness following previously described methods (Peichl et al., 2014; Sonnentag et al., 2012). Images were scaled, corrected for brightness, and an area approximately 25 cm × 45 cm was selected. Green (G), red (R), and blue (B) channels were extracted (software Fiji; Schindelin et al., 2012) and green chromatic coordinate (GCC) was calculated as follows: $GCC = G / (G + R + B)$.

CO₂ Fluxes and Partitioning

We measured NEE continuously June 17–August 20, 2018 using an automated chamber system. Six transparent chambers (model 8100-104C, Li-Cor Inc., Lincoln, NE, USA) were connected through a manifold (model 8150, Li-Cor Inc., Lincoln, NE, USA) to an infrared gas analyzer (IRGA; model 8100 A/81 50, Licor, Inc., Lincoln, NE) that was calibrated weekly. Chambers were attached to 20 cm diameter PVC collars installed in the vegetated part of the experimental plots to 5 cm depth. NEE was measured in two each of the control and +T+W plots, and one each of the +W and +T plots. Measurement cycles were carried out at 30-minute intervals. One measurement cycle consisted of a 30 second pre-purge of the chamber with ambient air, a two-minute measurement interval, followed by a 45 second post-purge of the chamber. NEE was calculated using a curvilinear fit of the relationship between time and CO₂ concentration during chamber closure. The vegetation inside each collar was also imaged July 30 and the vegetation was assessed using the same image-based point-frame technique as above.

We used the CO₂ flux data set in two ways. First, the NEE measurements (hourly means) were decomposed into ecosystem respiration (R_{eco}) and gross ecosystem production (GEP, Figure S2); we used the daily mean CO₂ flux between 0300 and 0400 (when photosynthesis largely ceases due to low light, typically $< 0.06 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) as a proxy for R_{eco} . This R_{eco} value was then used to calculate GEP as the difference between NEE and R_{eco} (Rogers et al., 2011). To calculate the cumulative growing season NEE, we computed a running sum of the hourly mean NEE values.

Second, we examined components of CO₂ flux in the two replicated treatments (CTL, +T+W, $n = 2$) during peak season (approximately July 13- August 3). We restricted this analysis to this time window to limit the effects of leaf expansion or senescence on day-to-day variation in photosynthesis and respiration, and because it overlaps with the vegetation imaging and leaf sampling. For each plot and day, we fit a non-rectangular hyperbolic relationship between NEE and incident PAR (i.e., a light curve):

$$\text{NEE} = (-a * b * \text{PAR}) / (a * \text{PAR} + b) + R_{eco}$$

where a and b are fitted parameters describing the curve and R_{eco} is ecosystem respiration at $\text{PAR} = 0$ (i.e., the intercept) using the quantreg procedure in R (i.e., the median best fit; Koenker, 2021) to avoid influence by outliers. Technical issues prevented sufficient data for light curve fits on one day in two chambers, and these data were removed. From the fitted parameters we extracted R_{eco} and calculated NEE at $\text{PAR} = 1000 \mu\text{mol m}^{-2}$

s⁻¹, producing an estimate of NEE₁₀₀₀ at a realistic full-sunlight value for the High Arctic in mid-summer (Figure S3). We then calculated GEP and GEP₁₀₀₀ as the difference between NEE or NEE₁₀₀₀ and R_{eco} , respectively (Leffler et al., 2019; Rogers et al., 2011).

Plant and Ecosystem C and N

To assess the effects of experimental warming and wetting on leaf chemistry, fully developed green leaves were collected from multiple individuals of *S. arctica* and *D. integrifolia* in the experimental plots July 18, 2018. The samples were dried, ground, and analyzed for N (%), C (%), $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ with an elemental analyzer (model 4010, Costech Analytical, Valencia, CA, USA) linked to a continuous flow isotope ratio mass spectrometer (model DeltaPLUS XP, Thermo-Finnegan Scientific, Waltham, MA) at the University of Alaska-Anchorage. The reference materials used were internal standards of known relation to the international standards of Vienna Pee Dee belemnite (for C) and atmospheric N₂ (for N).

To assess long-term ecosystem responses to the experimental warming and wetting treatments, we sampled above- and belowground biomass and soil at the end of the growing season (August 13-14, 2018). A vegetated turf 25 cm × 45 cm was removed to 2–5 cm depth from each plot's vegetated half. Turfs were air dried, vegetation was clipped, and vascular plants were sorted by species. *S. arctica* and *D. integrifolia* were further separated into leaves and stems. Roots and litter (consisting mostly of intact or fractionated leaves and stems) were not differentiated by species.

Biomass and soil samples were further dried in an oven (48 h, 55 °C), weighed, ground using a ball mill, and analyzed for C and N content with an elemental analyzer (model 4010, Costech Analytical, Valencia, CA, USA). Soil samples were also analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (see text above). To obtain plot-level C and N pools, whole turf dry weights of different above- and belowground ecosystem compartments were multiplied by their measured C or N concentrations, and these were normalized per area (g m⁻²). For vegetation, leaf and stem biomass (*S. arctica*, *D. integrifolia*) as well as total above- (defined henceforth as stems + leaves) and belowground (roots) biomass were also used to calculate indexes about plant resource allocation. Difficulties attaining consistent turf depth during sampling prevented us from obtaining reliable soil bulk density, thus we calculated soil C and N pool estimates and present them for context, but we did not subject them to formal statistical analysis.

Statistical Analyses

For analyses of vegetation cover change, we computed the difference in percent cover for each species in each plot by subtracting the percent cover in 2003 from the cover in 2018 (Fig. S1). We used this to examine, first, overall background change solely in the unmanipulated control treatment and, second, if climate manipulations further affected change over time in comparison to the controls. To compare background change among the species, we used a one-way ANOVA on the control-only data with species as the fixed effect, where a significant species effect would indicate a statistically significant difference in trajectory among the species. These were followed by Tukey post-hoc tests for specific comparisons among species. To examine the singular and interactive effects of warming (+T) and wetting (+W) on cover change in each species, we used a two-way ANOVA with warming and wetting as fixed effects.

For examining CO₂ exchange (not replicated for all treatments), we first visually present cumulative NEE over the growing season in the different treatments (Figure 3). We then examined the relationships between cumulative NEE (at the end of the growing season) and 2018 *S. arctica*, *D. integrifolia*, and *C. rupestris* cover using linear regressions. For the analysis of peak season fluxes in the replicated treatments, Control (n = 2) and +T+W (n = 2), we examined daily NEE differences between treatments for daily mean and light-normalized NEE₁₀₀₀ and GEP₁₀₀₀ as well as daily R_{eco} in a mixed model framework using the lme4 package (Bates et al., 2015) with a fixed treatment effect and a random plot effect. This model was tested against a null model (intercept and random plot effect only) using the likelihood ratio.

The singular and interactive effects of warming and wetting on peak season community greenness, leaf N (%), $\delta^{13}C$, and $\delta^{15}N$ for *S. arctica* and *D. integrifolia* and, at the end of the experiment, for stem and root C (%) and N (%) as well as plant resource allocation (e.g. total leaf C/total stem C for *S. arctica*), were tested with two-way ANOVA models with warming and wetting as fixed effects.

Finally, we examined the singular and interactive effects of warming and wetting on soil C (%), N (%), $\delta^{13}C$, and $\delta^{15}N$, above- and belowground ecosystem C, N, and biomass pool size as well as proportional allocation among species and tissues using ANCOVA models with pre-experiment vegetation attributes as covariates and warming and wetting as fixed effects. For species-specific ANCOVA models a single covariate was included following a priori assumptions (e.g. 2003 *S. arctica* cover is the covariate for *S. arctica* total stem C in 2018). For plot-level response variables (e.g. total aboveground C) we included 2003 cover values for each of the three community dominants as covariates.

All analyses were conducted in R v. 4.0.5 (R Development Core Team, 2021), and plots created using ggplot (Wickham, 2016), cowplot (Wilke, 2020), gt (Iannone et al., 2021), ggpp (Aphalo, 2021), and ggpattern (FC & Davis, 2021). In ANOVA, ANCOVA, and mixed-model analyses data and residuals were assessed for normality, independence, and homogeneity; log transformations were used for ANCOVA tests on *D. integrifolia* biomass and aboveground N as well as *S. arctica* aboveground N. For ANCOVA tests, data were also assessed for interactions among covariates and the climate treatments (none were found). Because the inherent variability in cover and soils is so high at this site, we use $P < 0.1$ as the threshold for statistical significance. There are cases where this significance level is exceeded but the treatment means show great differences that may be of substantial ecological importance, and we point these out when P approaches 0.2 (i.e. Yoccoz, 1991).

Results

Vegetation Cover Change

Between 2003 and 2018, substantial vegetation change occurred at our site in the unmanipulated control plots (i.e. “background” change), but trends differed among species (Figure 2, $F_{2,9} = 6.4$, $P = 0.01$). In the control plots, the mean cover change was negative in *C. rupestris* (90% CI [-17.2, -5.3]), neutral in *D. integrifolia* (90% CI [-3.7, 8.2]), and mostly positive in *S. arctica* (90% CI [-1.6, 10.3]). The background changes observed in *S. arctica* and *D. integrifolia* cover were statistically different from those in *C. rupestris* ($P < 0.05$ for both pairwise comparisons). The climate manipulations did not influence cover change in *D. integrifolia* or *C. rupestris* but wetting amplified the expansion of *S. arctica*—the increase in *S. arctica* cover with wetting was 3.7 times larger than that observed in the non-wetting treatments (Figure 2b).

CO₂ Exchange

At the end of the growing season, all treatments including the control treatment were net CO₂ sinks, although the magnitude appeared to depend on the climate treatment (Fig. 3a). The warming treatments, with and without wetting, were the strongest growing season CO₂ sinks (-70 g m⁻²), whereas the wetting alone and control treatments were slightly weaker sinks (-40.6 g m⁻² and -17.6 g m⁻², respectively). Sink strength was correlated with *S. arctica* cover in the flux chambers ($t_5 = -2.74$, $R^2 = 0.48$, $P = 0.13$, Fig. 3b), but did not correlate with cover of *C. rupestris* ($t_5 = 0.82$, $R^2 = 0.02$, $P = 0.77$) or *D. integrifolia* ($t_5 = -0.33$, $R^2 = 0.01$, $P = 0.86$).

The differences in the C sink between the climate treatments seemed to originate from different proportional contributions of GEP and R_{eco} between treatments (Figure S2). With warming, alone or in combination with wetting, higher levels of peak-season GEP were the primary contributor to CO_2 sink strength; mean July and August GEP was -1.3 to $-1 \mu mol CO_2 m^{-2} s^{-1}$ in those two treatments, whereas control GEP was $-0.63 \mu mol CO_2 m^{-2} s^{-1}$. However, with wetting applied in isolation, consistently low R_{eco} was the main contributor to the treatment's sink strength; mean July and August R_{eco} ($0.32 \mu mol CO_2 m^{-2} s^{-1}$) was 27–108% lower than in any of the other treatments (0.44 – $0.67 \mu mol CO_2 m^{-2} s^{-1}$).

All modeled flux values showed an amplified response in the combined warming and wetting treatment relative to control conditions (Figure S3). The mixed model analysis on the CO_2 fluxes showed that observed peak-season NEE ($\chi^2 = 1.79$, $P = 0.18$), GEP ($\chi^2 = 2.41$, $P = 0.12$), and R_{eco} ($\chi^2 = 3.49$, $P = 0.06$), as well as estimated NEE₁₀₀₀ ($\chi^2 = 2.25$, $P = 0.13$) and GEP₁₀₀₀ ($\chi^2 = 2.4$, $P = 0.12$) tended to be much higher (51–250%) with combined warming and wetting than in the control plots.

Plant Community Greenness and Tissue Chemistry

Warming, wetting, and their interaction all influenced plant community greenness, but this was mostly driven by the combined warming and wetting treatment, which was 5.8–7.3% greener than the other treatments (Figure 4a).

The effects of the climate treatments on leaf chemistry were species-specific. In *D. integrifolia*, the climate treatments did not affect leaf N or $\delta^{15}N$ (Figures 4b and S4), but warming increased leaf $\delta^{13}C$, whereas wetting decreased leaf $\delta^{13}C$. Warming also increased stem N concentrations 14% in *D. integrifolia*, whereas wetting triggered 4% increases in stem C concentrations (Figure S5). There were no interactive effects of warming and wetting on any of the tissue chemistry variables in *D. integrifolia*.

In *S. arctica* warming decreased peak season leaf N by 11%, but neither wetting nor its interaction with warming affected leaf N levels (Figure 4b). Leaf $\delta^{13}C$ values did not respond to the climate treatments in this species, whereas wetting decreased leaf $\delta^{15}N$ values from 1.2‰ to -1.2‰ (Figure S4), and the interaction of warming and wetting lowered values a further 0.6‰. Wetting triggered slight increases in *S. arctica* stem C concentrations, but not stem N (Figure S5).

The climate treatments had few effects on root and litter chemistry. Warming increased root C concentrations 4% and wetting increased litter N concentrations 11%, but we did not find other effects of warming, wetting, or their interaction on root or litter C or N concentrations (Figures S6-S7).

Soil Chemistry

After accounting for pre-experiment vegetation, the climate treatments did not influence soil C or N concentrations or $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values (Figure 5, Table S2). Soil C, N, and $\delta^{13}\text{C}$ were controlled by pre-experiment *D. integrifolia* cover ($P < 0.1$ for each), being positively correlated with soil C and N and negatively correlated with soil $\delta^{13}\text{C}$.

Ecosystem Pools and Allocation Patterns

After accounting for pre-experiment vegetation, wetting had the most pronounced effect on ecosystem pools, increasing total aboveground C, N, and biomass by 94–101% as well as total root C, N, and biomass by 60–122% (Table 1, Figure 6), whereas warming tended to decrease total root C but for the most part had less impact on C, N, or biomass pools. Neither warming, wetting, nor their interaction affected litter pools; total litter N was explained by pre-experiment *D. integrifolia* cover (Figure 6, Table 1). In general, the climate manipulations did not influence the plot-level allocation of C, N, or biomass among different ecosystem components (Table 1, Figure 6), these were well explained by pre-experiment vegetation composition.

Warming and wetting had significant main (not interactive) effects on plot-level leaf and stem C, N, and biomass pools in the two shrub species. Total aboveground C and biomass in *S. arctica* tissues decreased with warming but responded positively to wetting, driven by a significant increase in leaf C, N, and biomass (Table 2, Figure S8). Warming decreased stem biomass in *D. integrifolia* but warming and wetting had no other significant effects on total aboveground C, N, and biomass in *D. integrifolia* or *C. rupestris* tissues—these were explained well by each species' respective pre-experiment abundance. Neither warming, wetting, or their interaction affected allocation patterns in *S. arctica* or *D. integrifolia*.

Discussion

This High Arctic polar semidesert ecosystem showed mixed responses to the long-term (15 years) factorial application of experimental warming and wetting. Wetting led to 94–101% higher total aboveground C, N, and biomass as well as 60–122% higher total root C, N, and biomass (Figure 6, Table 1). Further, wetting

enhanced *S. arctica* cover, which appeared to be linked with increased growing season CO₂ sink strength and, when combined with warming (the most likely 2050 High Arctic analogue of our climate treatments (AMAP, 2017)), increased community greenness (Figures 3 and 4). Given the consistency with earlier findings at this site (Sharp et al., 2013), these results validate the critical role of summer moisture in co-regulating ecosystem function in some of the driest, coldest habitats in the Arctic and globally. On the contrary, many of the other ecosystem metrics assessed, including soil chemistry (Figure 5), some C, N, and biomass pools and allocation patterns (Tables 1 and 2, Figures 6 and S8) showed little or no response to the climate manipulations. Thus, while our data do suggest a direction for some near-future ecosystem changes in a wetter and/or warmer future High Arctic, including wetting-enhanced above- and belowground C and N storage, they do not fully repudiate previous reports of “resistance” to climate change in some High Arctic ecosystem attributes (Hudson & Henry, 2010; Lamb et al., 2011).

Salix Cover and CO₂ Fluxes Interacting and Responding to Warming and Wetting

Set amid marked local air temperature increases and shifts in precipitation patterns (Figure 1), *S. arctica* cover increased by a factor of 2.4 in the control plots between 2003 and 2018 (Figures 2 and S1), suggesting that deciduous shrub expansion is underway at this site, analogous to that observed at other Low and High Arctic sites (Buchwal et al., 2020; Elmendorf et al., 2012; Weijers & Myers-Smith, 2018). Beyond this background change, both *S. arctica* cover and leaf biomass responded positively to wetting—a pattern that was driven by a particularly dramatic increase in the combined warming and wetting treatment (Figure 2), where it was also accompanied by increased plant community greenness (Figure 4). Collectively, these responses indicate that the coupled increases in air temperature and summer precipitation forecasted for the High Arctic (AMAP, 2017) will favor the expansion of this shrub and concomitant greening. However, most of the *S. arctica* expansion at our site occurred between 2003 and 2011 (see values in Sharp et al., 2013). Although this period was the warmest and wettest of our study (1.7 °C warmer and 67% wetter than the pre-study years for which data are available), the latter part of our study (2012-2018) was also warmer and wetter (1.1 °C and 32%, respectively) than the pre-study years, suggesting that the longer-term shrub growth response to warmer and wetter High Arctic climates may be co-moderated by other factors (e.g. nutrient limitation, Arens et al., 2008).

Our data also indicate that expanding *S. arctica* cover may be a significant driver of net growing season CO₂ fluxes in the arid High Arctic. The slope (-2.7) of the relationship between *S. arctica* cover and cumulative NEE

suggests that even minor gains in *S. arctica* cover can lead to substantial increases in the growing season CO₂ sink. The strongest cumulative CO₂ sinks (Figure 3), the warming and warming combined with wetting treatments, also demonstrated the highest levels of GEP (Figure S2). Since warming decreased leaf N concentration in *S. arctica* it seems more likely that increased leaf area—wetting increased *S. arctica* leaf biomass—drove GEP in these treatments (Figure 4, see also discussion below). Although the limited sample size in our flux dataset warrants caution, the link between CO₂ sink strength and *S. arctica* leaf area is consistent with previous data from this site (Sharp et al., 2013) and from Zackenberg (Soegaard et al., 2000). Thus, if deciduous shrub expansion accompanies warming and wetting the future High Arctic may be capable of enhanced C sequestration in the summer.

Vegetation chemistry and resource allocation mostly resisting change

The plant-level responses to the climate treatments were subtle and differed between the two dominant species, *S. arctica* and *D. integrifolia*. The main beneficiary (in terms of cover) of experimental wetting, *S. arctica*, did not show increased leaf N concentrations (Figure 4)—perhaps due to a dilution effect, given that its expansion was most prominent with wetting (Figure 2)—but it did show reduced leaf $\delta^{15}\text{N}$ values. On the other hand, warming reduced leaf N by 15% in this species and, when combined with wetting, further reduced leaf $\delta^{15}\text{N}$ values (Figure S4). Thus, while *S. arctica* leaf N concentration may largely resist a wetter climate, with increasing temperatures decreased *S. arctica* N uptake and shifts in N sources (as revealed by N isotopic composition) may result. These joint shifts in N and $\delta^{15}\text{N}$ may be caused by changes in the role of the fungal partner—in *S. arctica* ectomycorrhizae (Iversen et al., 2015)—in assisting N uptake. Usually, mycorrhizal tundra plants have negative leaf $\delta^{15}\text{N}$ values (e.g. Michelsen et al., 1998) because the mycorrhizae, while providing the host plant with N, accumulate the heavier ^{15}N (Hobbie & Colpaert, 2003).

In contrast, warming increased leaf $\delta^{13}\text{C}$ in *D. integrifolia*, likely indicating sensitivity to decreased water availability rather than increased photosynthesis, given that we did not observe increasing *D. integrifolia* leaf biomass in this treatment. This differs from previous observations in Svalbard following short-term environmental manipulations (Welker et al., 1993), highlighting the importance of longer-term experiments in the High Arctic. Overall, though, the responses in both species were small relative to those found in other manipulative experiments (particularly those involving deeper snow) at this and other Arctic sites (Jespersen et al., 2018; Leffler & Welker, 2013; Rogers et al., 2011; Semenchuk et al., 2015; Welker et al., 1993, 2005). Also, warming and wetting did not induce any substantial species-level shifts in C or N allocation among

leaves and stems (Table 2, Figure S8), contrasting with observations from other Arctic sites (Chapin & Shaver, 1985; DeMarco et al., 2014; Mack et al., 2004; Oberbauer & Dawson, 1992; Parsons et al., 1994; Shaver et al., 2001). Thus, leaf-level properties and species-level nutrient allocation patterns are tightly regulated in this system and either largely resistant to summer climate perturbations or very slow to change.

Surface soils show resistance to warming and wetting

Results from our soil dataset differ somewhat from our current understanding of High Arctic soil processes. We did not find soil C or N depletion (based on concentrations) associated with warming or wetting (Figure 5, Table S2); several other groups have found warming-linked SOC losses after 8-9 treatment years in the Arctic (Blok et al., 2018; Jung et al., 2020; Semenchuk et al., 2019), although at least one group has also reported no changes with long-term wetting (Christiansen et al., 2012). In our experiment two mechanisms may have buffered soil against respiratory C losses. First, we found that warming increased root C concentrations (Figure S5) whereas wetting increased the total root C pool; root litter is one of the largest contributors to tundra SOM (Loya et al., 2004). Second, GEP was higher with warming throughout much of the summer; over longer time scales this heightened productivity could help stabilize the SOM pool via litter deposition, thus offsetting most of the amplified early- and late-season respiratory CO₂ losses we observed with warming. Given earlier findings of reduced SOC after eight years of warming at this site (Schaeffer et al., 2013), our finding could be interpreted as a degree of ecosystem “resistance”, as reported in Alexandra Fiord in multiple ecosystem metrics (Hudson & Henry, 2010; Lamb et al., 2011). On the other hand, some of the discrepancy with Schaeffer et al.’s (2013) earlier findings could be due to the shallower sampling we conducted (< 5 cm); treatment effects may be present deeper in the soil profile, where substantial quantities of soil C are known to be sequestered at this site (Horwath Burnham & Sletten, 2010).

Wetting drives increases in some above- and belowground pools

We found that experimental wetting increased total aboveground C, N, and biomass and total root C, N, and biomass (Figure 6), indicating that increased summer precipitation may enhance total ecosystem C and N storage in the arid High Arctic. Given the predicted and observed increases in Arctic precipitation as sea ice loss leads to greater open water in the Arctic (AMAP, 2017; Bintanja et al., 2020; Førland et al., 2020; Min et al., 2008), this finding merits broader testing. Also, the divergence in aboveground and root pools we observed between the wetting and the warming treatments suggests that regional differences in climate change could lead to critical differences in ecosystem structure. Finally, the absence of strong treatment

effects in other components of ecosystem C or N storage or plot-level allocation could again be interpreted as examples of resistance (Table 1), suggesting some ecosystem properties are more strongly conserved and, without the alleviation of other constraints (e.g. nutrient limitation), may require multiple decades to change.

Conclusions

As the Arctic warms and moistens and regional climate idiosyncrasies are amplified, meaningful projections for extant and newly exposed land surfaces in the future High Arctic rely on field data from relatively few sites. For such efforts, our multifaceted dataset, collected in one of the most spatially extensive ecosystem types in the High Arctic during a period of rapid climate change, paints a complex picture of resistance and change after fifteen years of simulated future Arctic climates. In several ecosystem metrics we found strong evidence of climate-induced change, while in others we did not. In contrast to the relatively well-established effects of climate warming (Elmendorf et al., 2012; Hudson et al., 2011; Hudson & Henry, 2010; Welker et al., 2000), our findings highlight the crucial role of summer moisture in regulating High Arctic ecosystem function. Our warming treatment induced relatively weak responses in most of the ecosystem metrics assessed, whereas wetting drove substantial changes in several metrics. Most critically, our results suggest increased summer moisture, one likely facet of broader Arctic 'moistening' (Bintanja, 2018), will drive arid High Arctic landscapes toward enhanced ecosystem C and N storage through above- and belowground processes, whereas increased air temperature alone may not.

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Author Contributions

JMW conceived the original experiment. JMW and AJL developed the 2018 research questions. AJL, MV, and RGJ collected the data. RGJ, AJL, and MV conducted analyses. RGJ, AJL, MV, and JMW wrote the manuscript.

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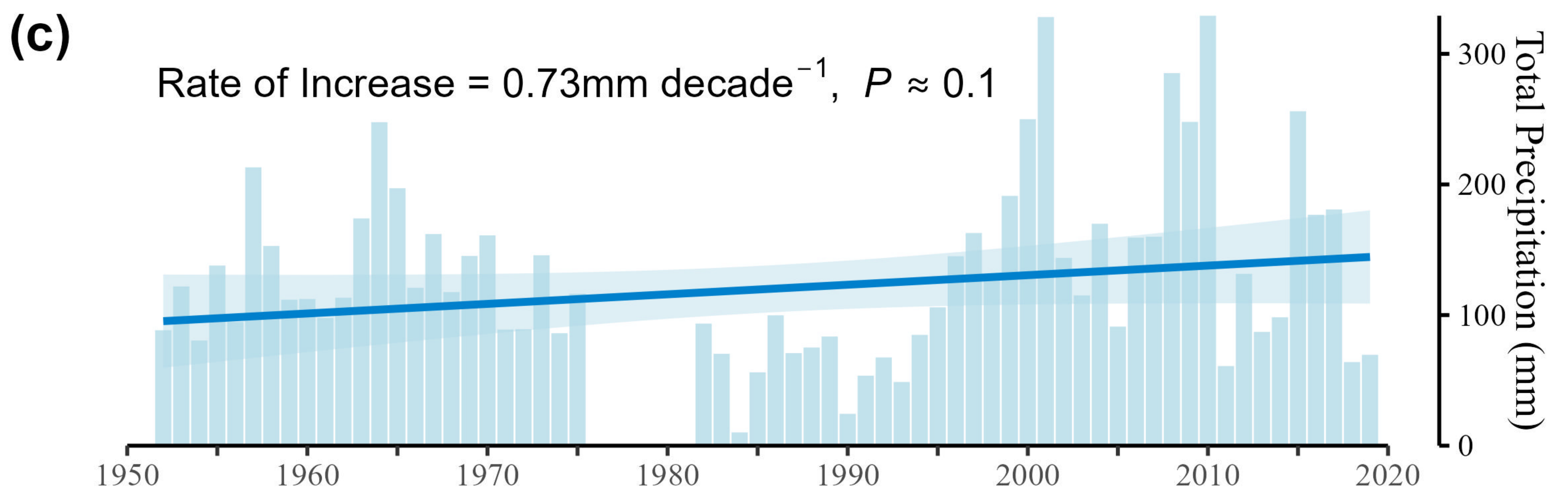
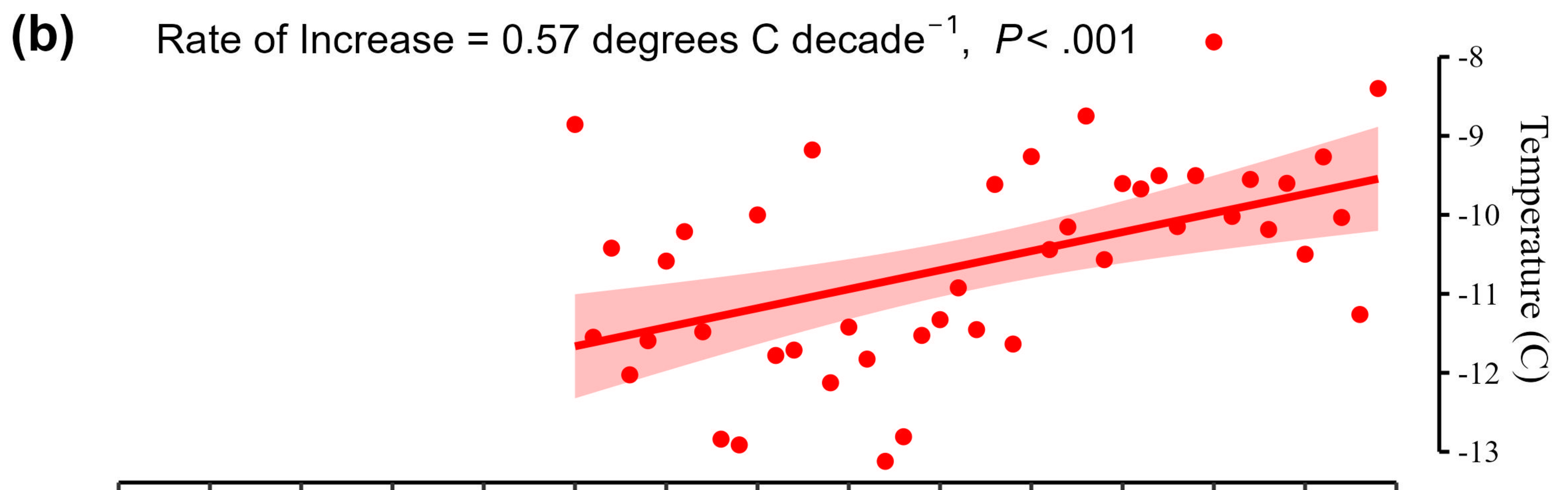
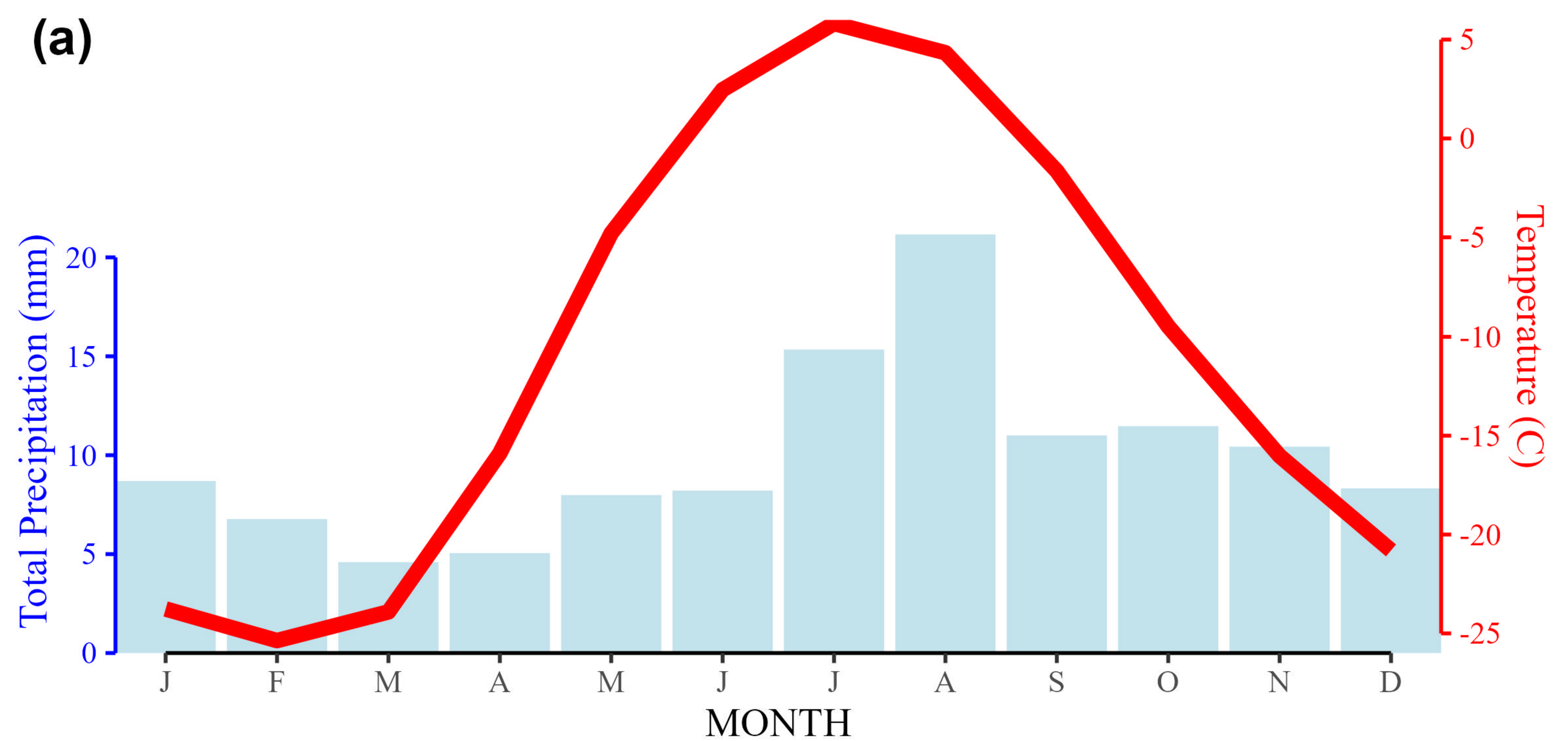
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Dependent variable	Model term	Carbon			Nitrogen			Biomass		
		Est.	<i>F</i>	<i>P</i>	Est.	<i>F</i>	<i>P</i>	Est.	<i>F</i>	<i>P</i>
Aboveground Pool	Pre-Experiment Salix Cover	-0.46	0	0.974	0	0.12	0.73	-2.53	0.08	0.788
	Pre-Experiment Dryas Cover	-1.87	1.38	0.259	-0.02	2.69	0.123	-4.72	1.19	0.293
	Pre-Experiment Carex Cover	-2.4	0.83	0.376	-0.04	0.77	0.395	-5.91	1.03	0.327
	Temperature	4.38	2.88	0.112	0.08	2.58	0.13	9.77	2.89	0.111
	Wetting	96.49	5.68	0.032	1.69	6.37	0.024	222.94	5.39	0.036
	Temperature * Wetting	-74.4	2.82	0.115	-1.2	2.38	0.145	-175.33	2.86	0.113
Litter Pool	Pre-Experiment Salix Cover	-0.53	1.52	0.237	0.07	0.95	0.347	-7.03	2.53	0.134
	Pre-Experiment Dryas Cover	3.91	2.77	0.118	0.18	6.45	0.024	10.87	0.95	0.346
	Pre-Experiment Carex Cover	2.14	1.25	0.282	0.09	2.25	0.156	5.58	0.44	0.516
	Temperature	16.92	0.02	0.89	0.05	0	0.975	-25.93	0.03	0.86
	Wetting	23.19	0.17	0.682	0.27	0.12	0.731	-71.09	0.02	0.897
	Temperature * Wetting	-13.96	0.04	0.845	0.18	0.01	0.927	100.13	0.17	0.684
Root Pool	Pre-Experiment Salix Cover	4.37	14.18	0.002	0.03	6.97	0.019	8.22	10.28	0.006
	Pre-Experiment Dryas Cover	-4.13	1.43	0.252	-0.04	1.33	0.268	-7.98	2.13	0.166
	Pre-Experiment Carex Cover	-2.4	1.08	0.316	-0.02	0.86	0.369	-3.49	0.37	0.551
	Temperature	-41.16	3.87	0.069	-0.25	1.56	0.232	-74.43	2.66	0.125
	Wetting	62.87	7.1	0.018	0.62	3.32	0.09	106.31	4.22	0.059
	Temperature * Wetting	5.28	0.01	0.911	-0.1	0.03	0.866	6.11	0	0.952
Leaf/Stem	Pre-Experiment Salix Cover	-0.05	2.74	0.12	-0.04	1.52	0.238	-0.04	1.24	0.284
	Pre-Experiment Dryas Cover	-0.01	0.1	0.751	-0.01	0.3	0.594	-0.02	0.01	0.904
	Pre-Experiment Carex Cover	0	0.13	0.721	-0.01	0.41	0.53	-0.01	0.79	0.389
	Temperature	0.33	0.92	0.354	0.26	0.17	0.689	0.31	0.05	0.831
	Wetting	0.22	0.47	0.502	0.41	2.6	0.129	0.46	1.36	0.264

	Temperature * Wetting	-0.14	0.13	0.728	-0.14	0.13	0.72	-0.4	1	0.333
Shoot/Root	Pre-Experiment Salix Cover	-0.03	4.57	0.051	0.01	1.27	0.279	-0.11	1.53	0.236
	Pre-Experiment Dryas Cover	0.03	2.73	0.121	0.03	3.58	0.079	-0.03	1.11	0.31
	Pre-Experiment Carex Cover	0	0	0.968	0	0.01	0.91	-0.06	1.07	0.318
	Temperature	0.33	0.2	0.664	-0.08	0.21	0.655	0.93	0.01	0.906
	Wetting	0	0.74	0.403	0.07	0.01	0.919	1.61	0.55	0.472
	Temperature * Wetting	-0.5	0.73	0.408	-0.2	0.1	0.751	-1.84	1.39	0.258
Aboveground Salix/ Total Aboveground	Pre-Experiment Salix Cover	0.03	20.36	<0.001	0.02	21.38	<0.001	0.03	21.39	<0.001
	Pre-Experiment Dryas Cover	0	0	0.975	0	0.01	0.92	0	0	0.948
	Pre-Experiment Carex Cover	0	0	0.964	0	0.02	0.893	0	0.02	0.886
	Temperature	-0.09	1.04	0.326	-0.07	1	0.334	-0.08	1.05	0.324
	Wetting	0.1	2	0.179	0.13	3.44	0.085	0.1	2.31	0.151
	Temperature * Wetting	0.04	0.06	0.811	0.03	0.05	0.83	0.03	0.05	0.822
Aboveground Dryas/ Total Aboveground	Pre-Experiment Salix Cover	-0.02	21.18	<0.001	-0.02	22.7	<0.001	-0.02	23.06	<0.001
	Pre-Experiment Dryas Cover	0	0.65	0.435	0.01	0.7	0.417	0.01	1.09	0.315
	Pre-Experiment Carex Cover	0	0.24	0.63	0	0.36	0.557	0	0.26	0.619
	Temperature	0.07	0.66	0.429	0.05	0.72	0.41	0.06	0.63	0.44
	Wetting	-0.09	2.11	0.169	-0.12	3.75	0.073	-0.09	2.47	0.139
	Temperature * Wetting	-0.05	0.11	0.75	-0.04	0.08	0.781	-0.05	0.11	0.744

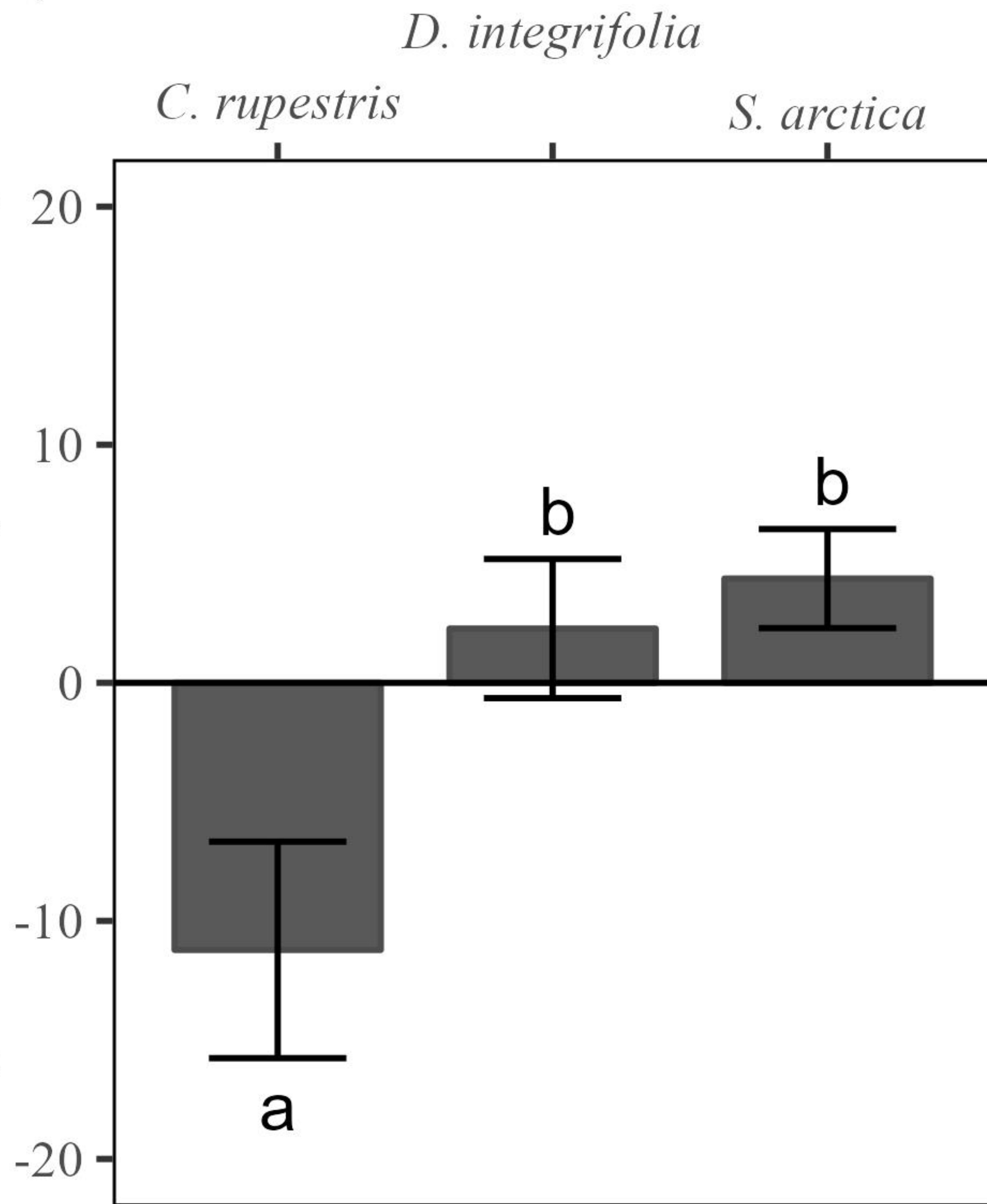
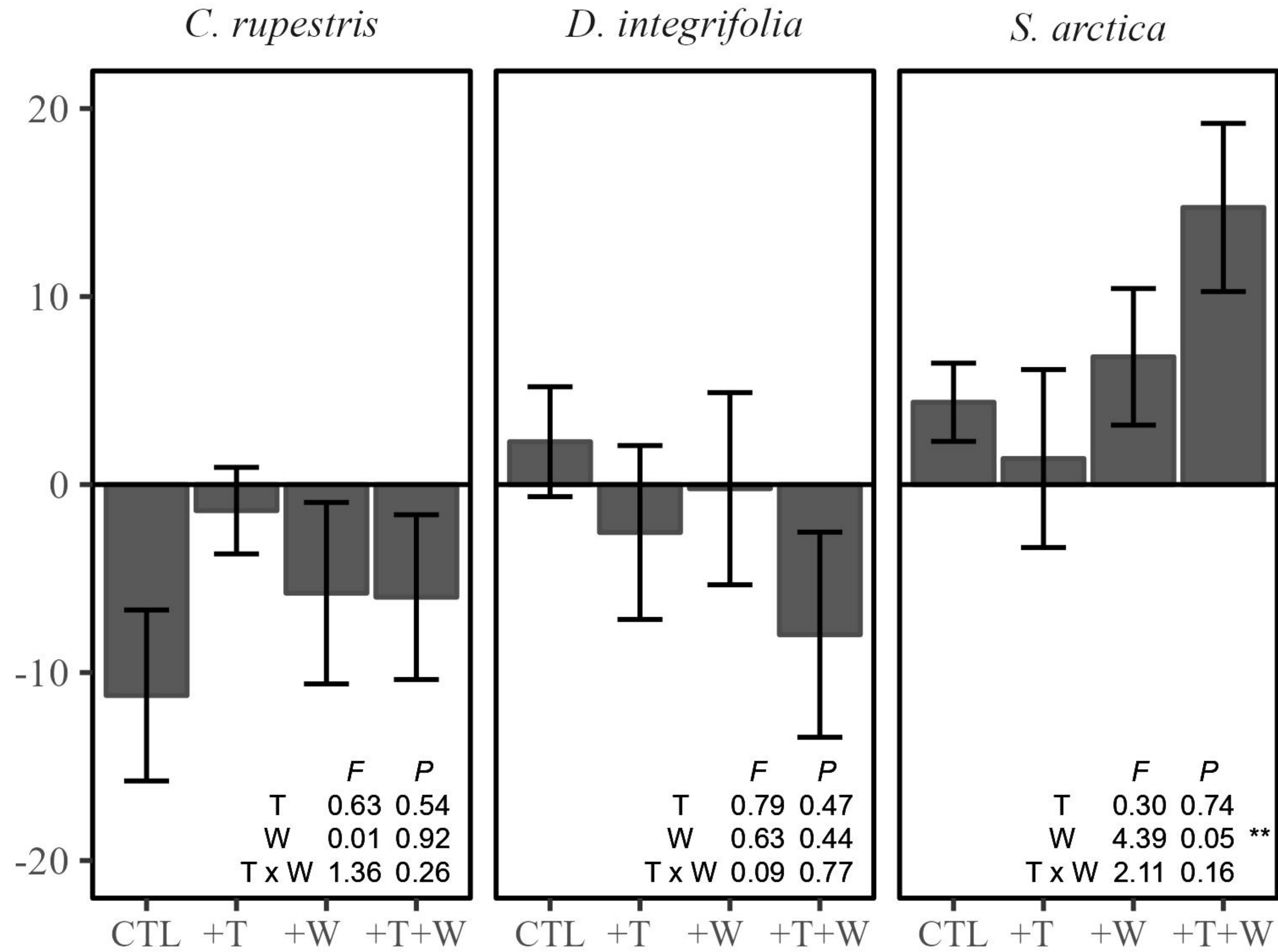
Dependent variable	Model term	Carbon			Nitrogen			Biomass		
		Est.	F	P	Est.	F	P	Est.	F	P
<i>Salix arctica</i>										
Aboveground Pool	Pre-experiment Salix cover	6.82	10.17	0.009	0.18	6.95	0.023	14.37	10.78	0.007
	Temperature	-49.93	3.5	0.088	-1	0.59	0.46	-103.96	3.49	0.089
	Wetting	19.71	2.39	0.151	0.39	0.99	0.341	40.78	2.45	0.146
	Temperature * Wetting	14.09	0.15	0.703	0.57	0.16	0.699	30.46	0.17	0.69
Leaves Pool	Pre-experiment Salix cover	1.49	13.96	0.003	0.04	10.2	0.009	3.47	14.02	0.003
	Temperature	-10.79	2.1	0.176	-0.29	1.86	0.2	-25.37	2.15	0.171
	Wetting	6.32	7.19	0.021	0.19	6.44	0.028	14.26	6.93	0.023
	Temperature * Wetting	7.18	0.85	0.375	0.18	0.63	0.444	16.7	0.85	0.375
Stems Pool	Pre-experiment Salix cover	5.33	6.88	0.025	0.09	7.95	0.018	10.89	8.62	0.014
	Temperature	-39.07	3.22	0.103	-0.61	3.51	0.09	-78.59	3.49	0.088
	Wetting	13.48	1.23	0.293	0.25	1.5	0.249	26.51	1.31	0.277
	Temperature * Wetting	6.83	0.05	0.833	0.08	0.02	0.878	13.76	0.05	0.824
Leaf/Stem	Temperature	1.66	0.7	0.421	4.06	0.66	0.434	1.61	0.35	0.563
	Wetting	0.12	0.67	0.431	0.61	0.7	0.42	0.35	0.38	0.55
	Temperature * Wetting	-1.58	0.91	0.359	-4.23	1.38	0.263	-1.79	1.12	0.309
<i>Dryas integrifolia</i>										
Aboveground Pool	Pre-experiment Dryas cover	1.37	5.86	0.028	0.03	12.67	0.003	0.03	10.21	0.006
	Temperature	3.13	1.94	0.183	-0.09	1.79	0.199	-0.18	2.76	0.116
	Wetting	44.37	0.32	0.577	0.12	0.19	0.669	0.13	0.18	0.678
	Temperature * Wetting	-62.51	2.33	0.146	-0.41	0.82	0.378	-0.43	0.76	0.398
Leaves Pool	Pre-experiment Dryas cover	0.57	2.89	0.108	0.02	4.15	0.058	1.25	2.43	0.138
	Temperature	5.07	1.01	0.331	0.09	0.77	0.392	11.23	1.09	0.312
	Wetting	28.3	0.31	0.587	0.57	0.51	0.487	79.23	0.4	0.536
	Temperature * Wetting	-38.85	1.82	0.196	-0.7	1.42	0.251	-104.06	1.75	0.204

Stems Pool	Pre-experiment Dryas cover	0.8	9.63	0.007	0.02	11.01	0.004	1.85	9.72	0.007
	Temperature	-1.94	3.02	0.101	0.02	1.31	0.269	-11.32	3.69	0.073
	Wetting	16.06	0.21	0.657	0.13	0.1	0.759	25.63	0.04	0.853
	Temperature * Wetting	-23.67	2.15	0.162	-0.31	1.57	0.228	-42.52	1.49	0.239
Leaf/Stem	Temperature	0.11	0.23	0.636	0.11	0.61	0.446	0.14	0.35	0.56
	Wetting	0.24	0.36	0.558	0.5	1.54	0.231	0.37	0.81	0.38
	Temperature * Wetting	-0.36	1.83	0.193	-0.55	1.77	0.2	-0.48	2.13	0.161
<i>Carex rupestris</i>										
Aboveground Pool	Pre-experiment Carex cover	0.29	15.4	0.001	0	12.37	0.003	0.78	17.02	0.001
	Temperature	0.33	0.02	0.9	0.01	0.31	0.583	0.59	0.04	0.849
	Wetting	0.81	0.26	0.617	0.02	1.17	0.295	1.59	0.26	0.62
	Temperature * Wetting	-0.18	0	0.952	0.01	0.03	0.864	0.51	0	0.945
Leaves Pool	Pre-experiment Carex cover	0.29	15.4	0.001	0	12.37	0.003	0.78	17.02	0.001
	Temperature	0.33	0.02	0.9	0.01	0.31	0.583	0.59	0.04	0.849
	Wetting	0.81	0.26	0.617	0.02	1.17	0.295	1.59	0.26	0.62
	Temperature * Wetting	-0.18	0	0.952	0.01	0.03	0.864	0.51	0	0.945

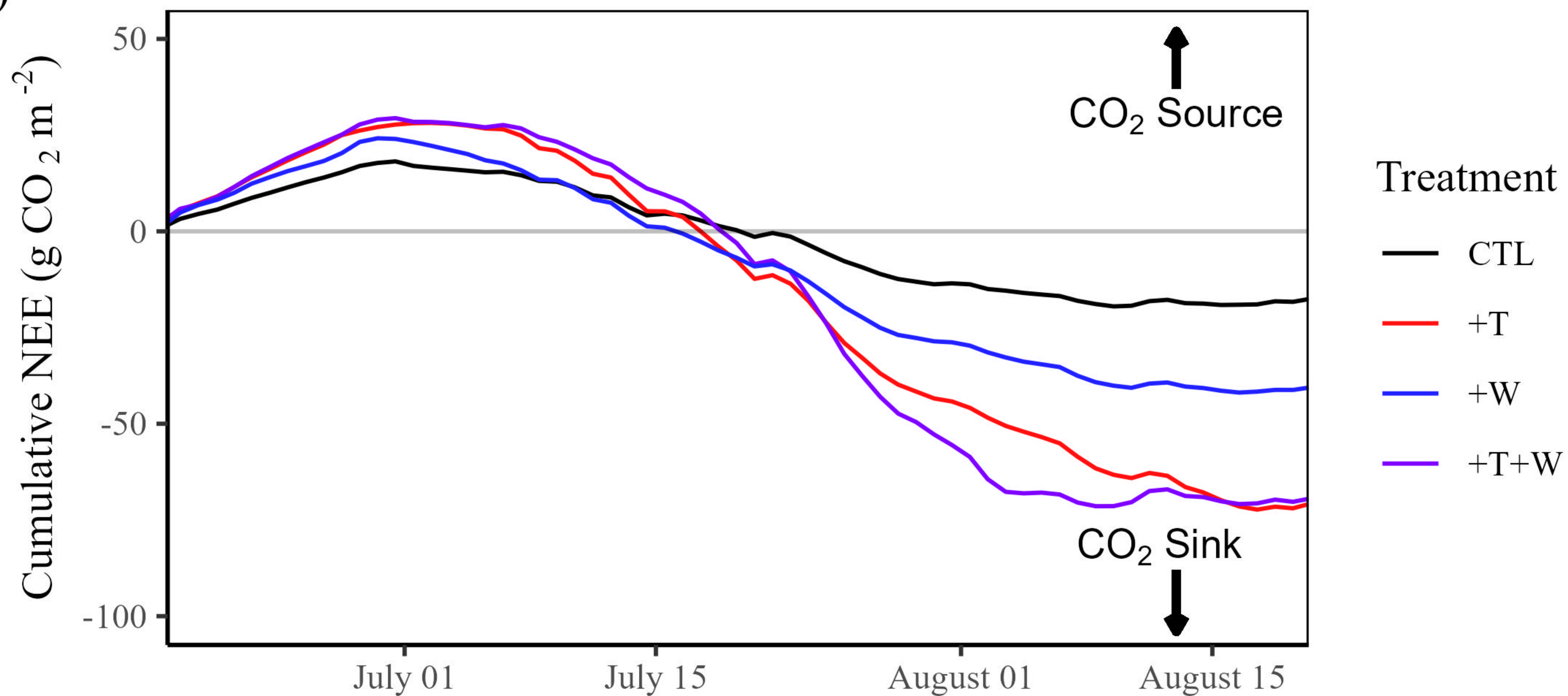


(a)

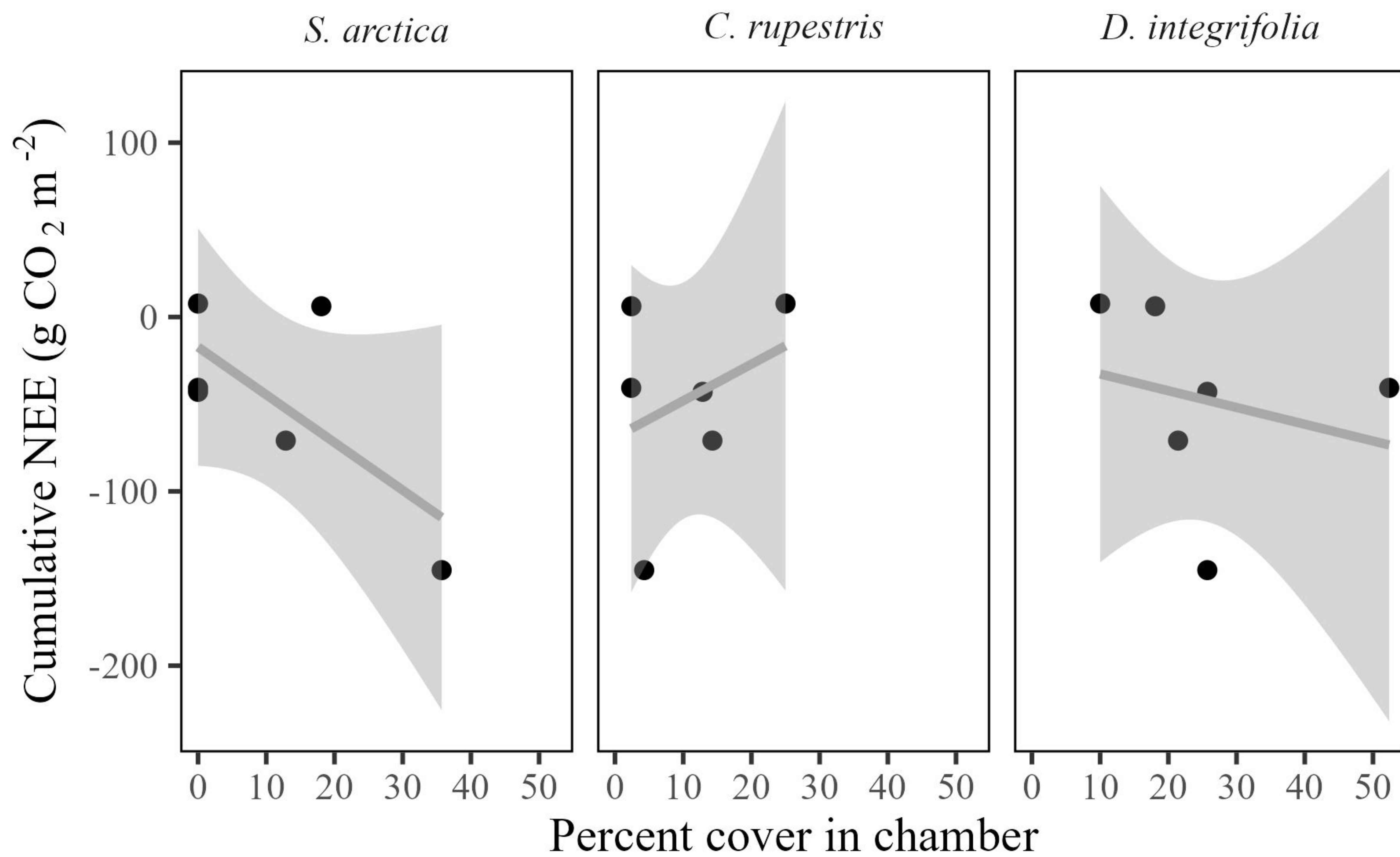
Change in Percent Cover (2003 - 2018)

**(b)**

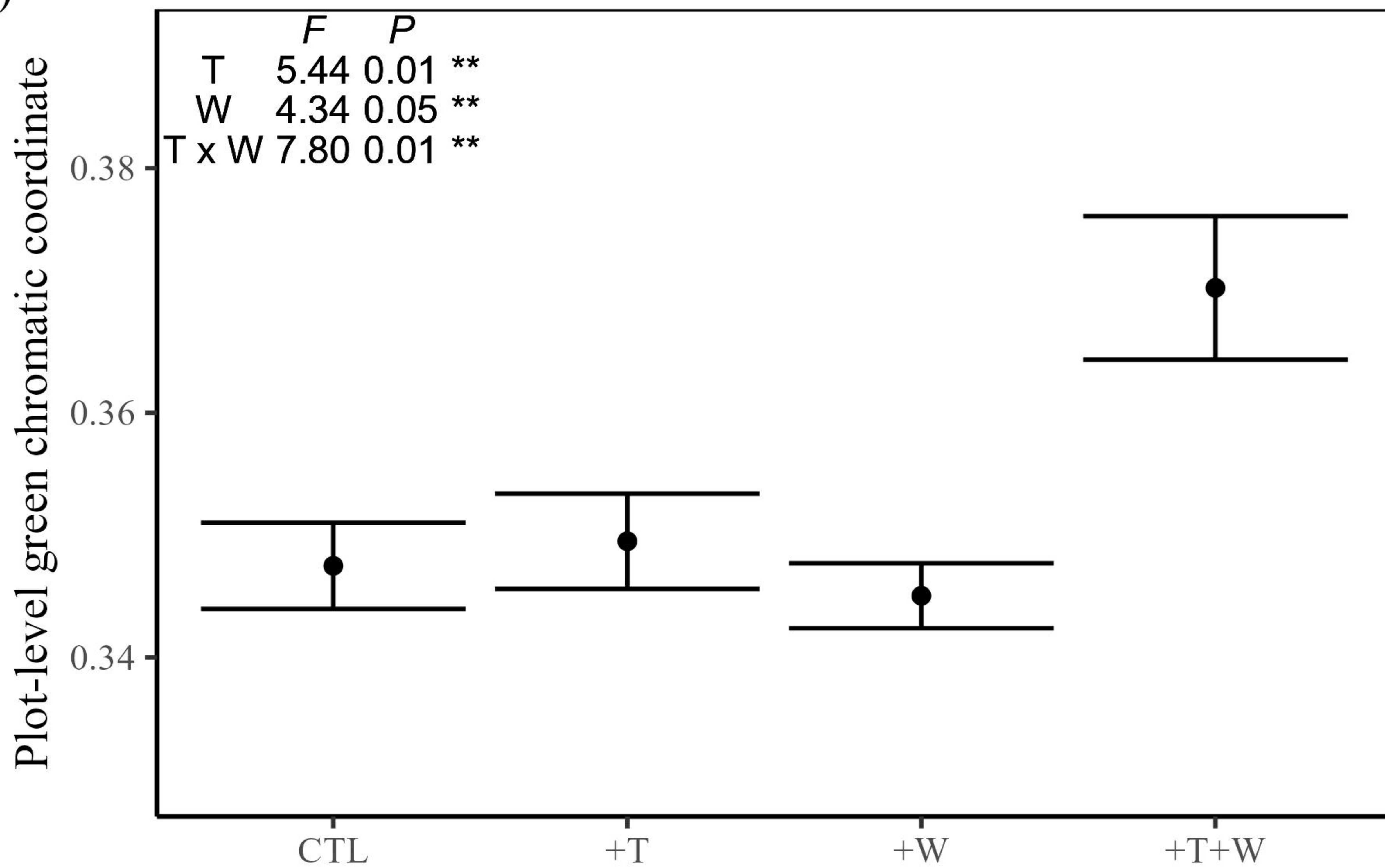
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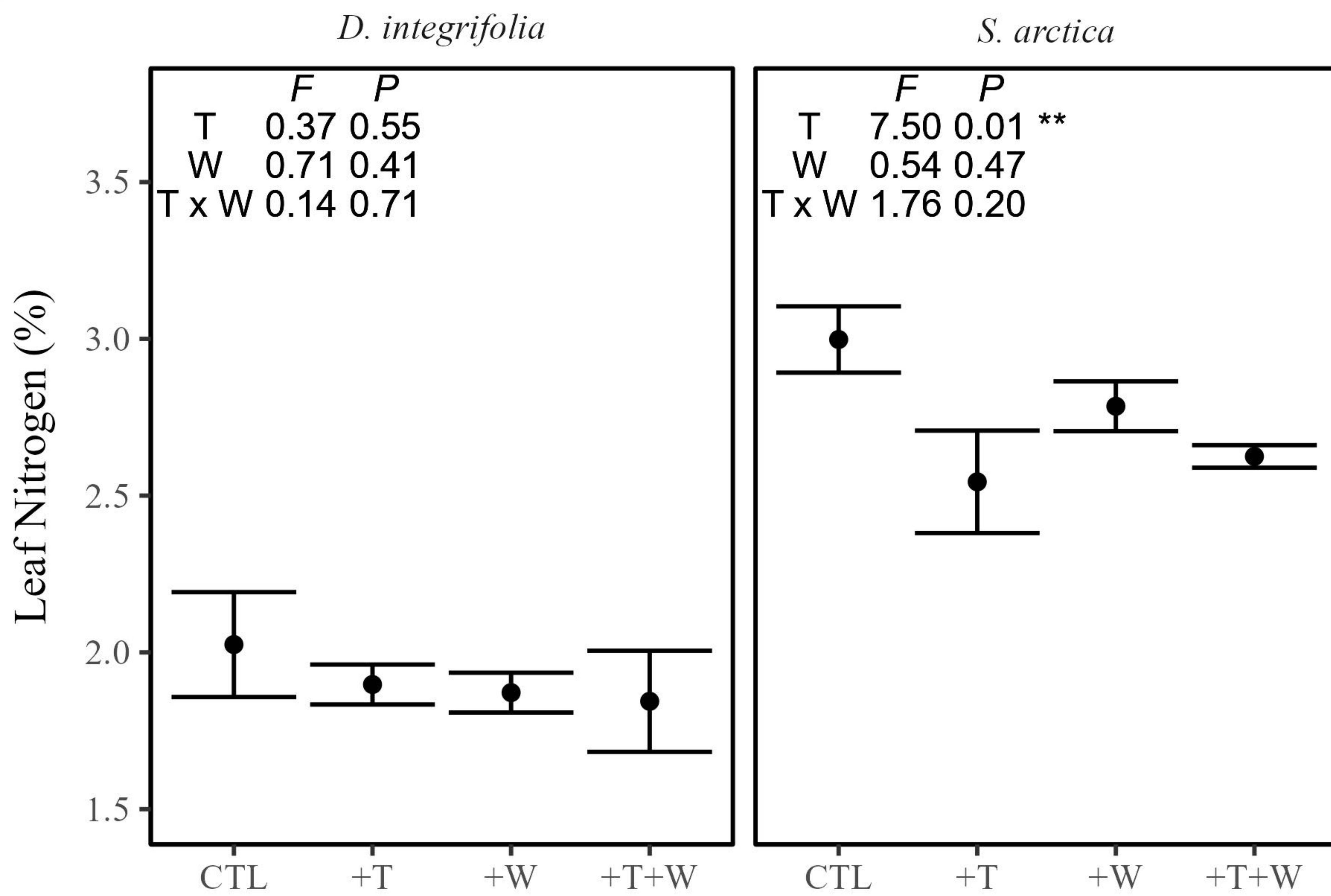
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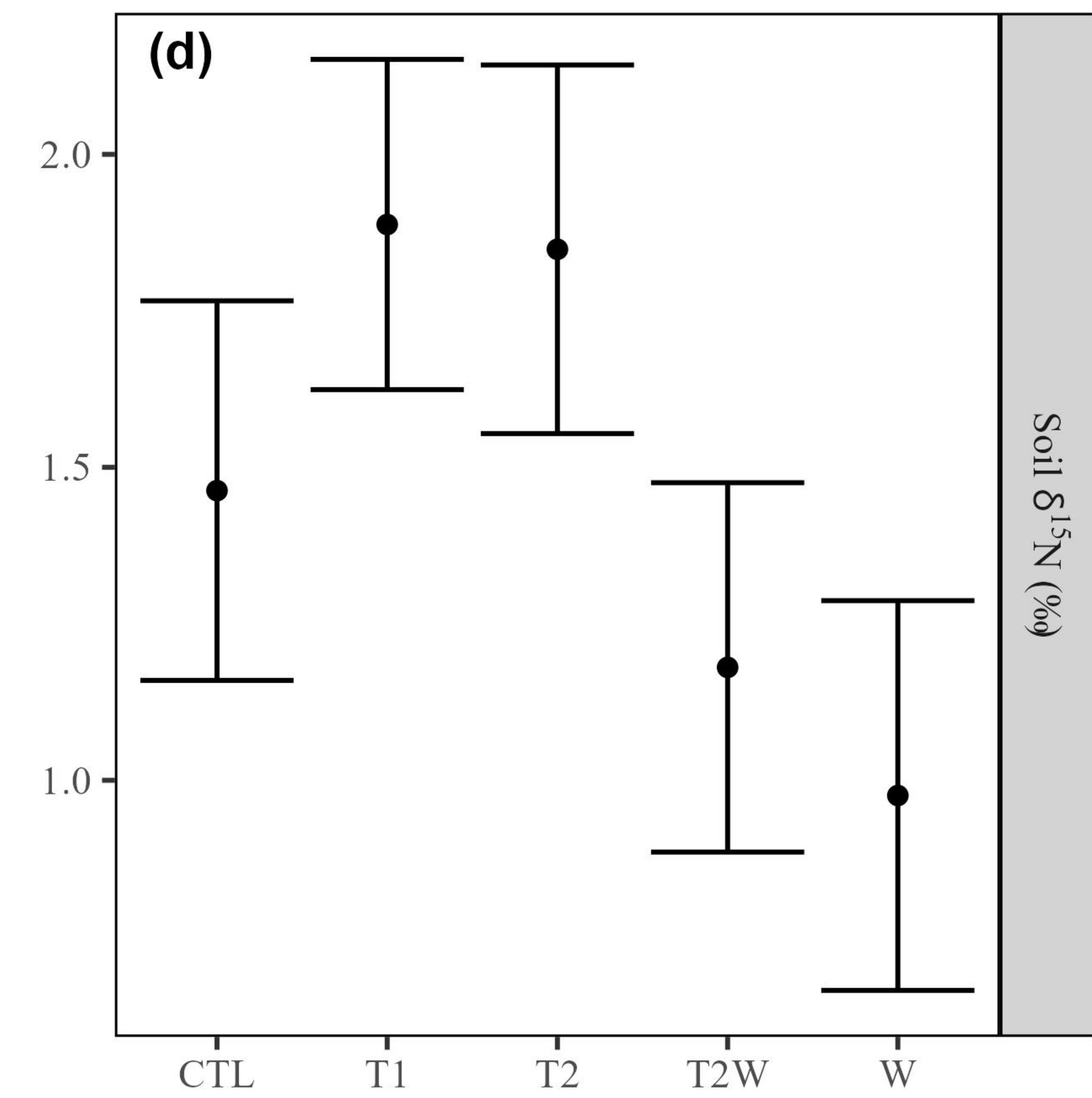
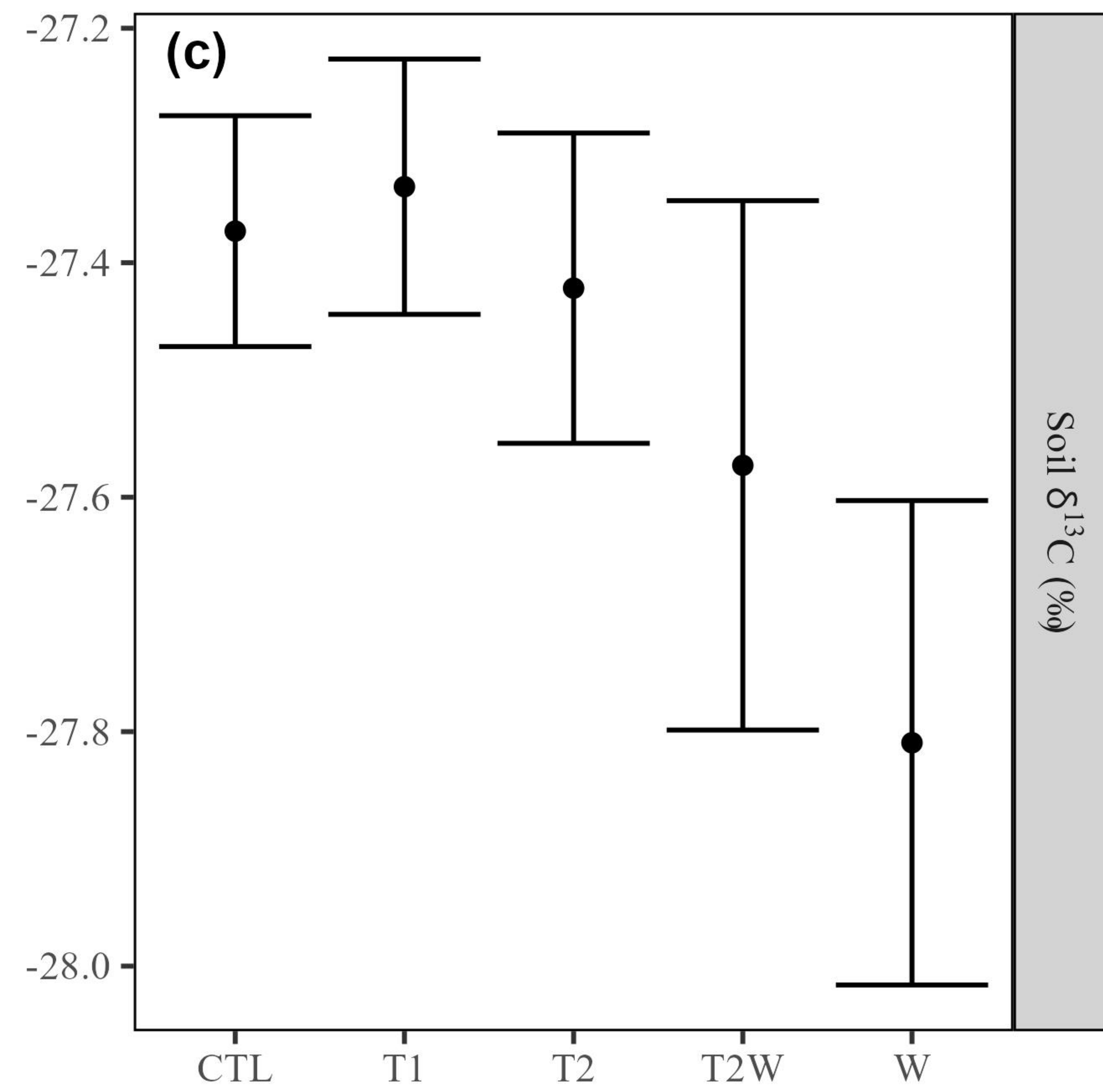
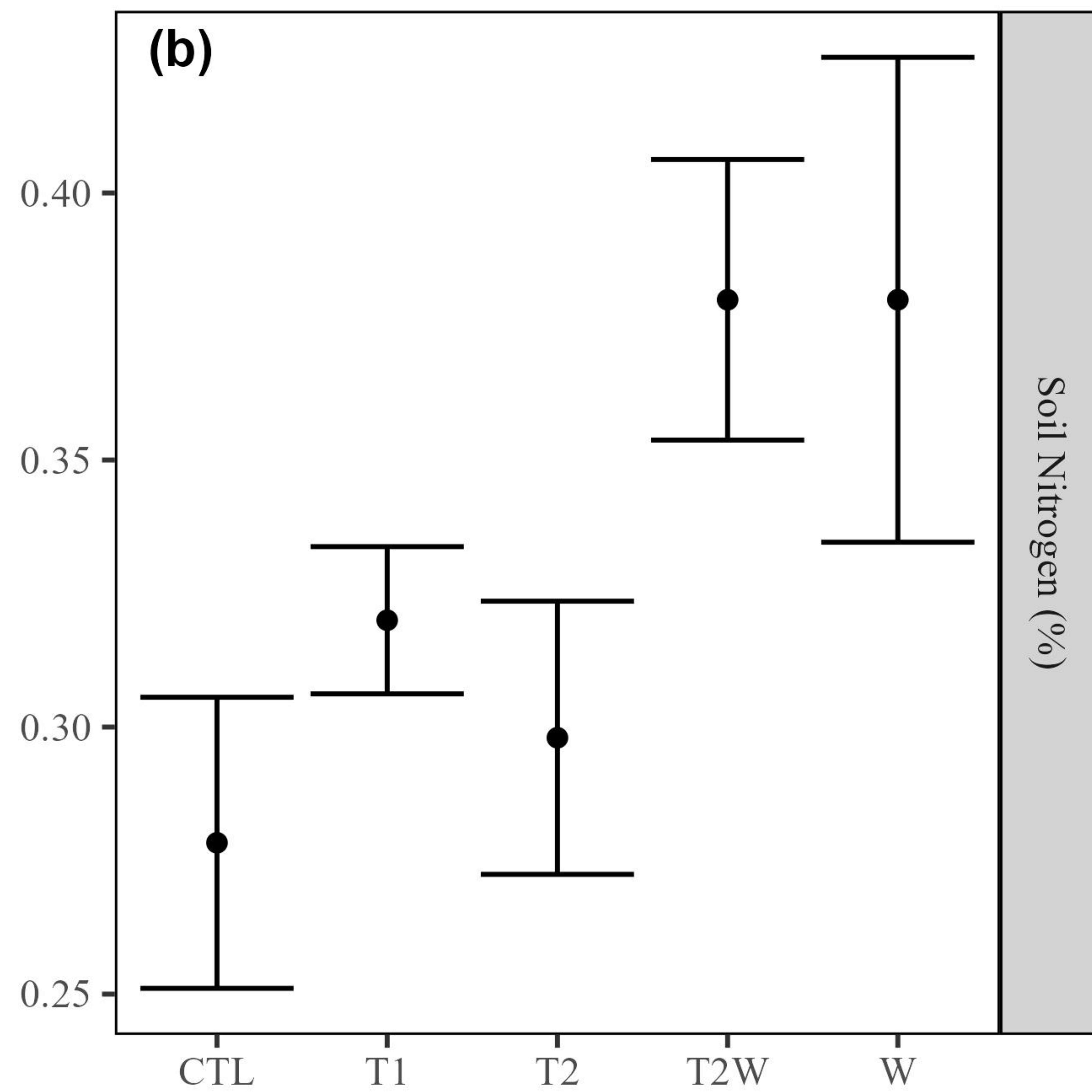
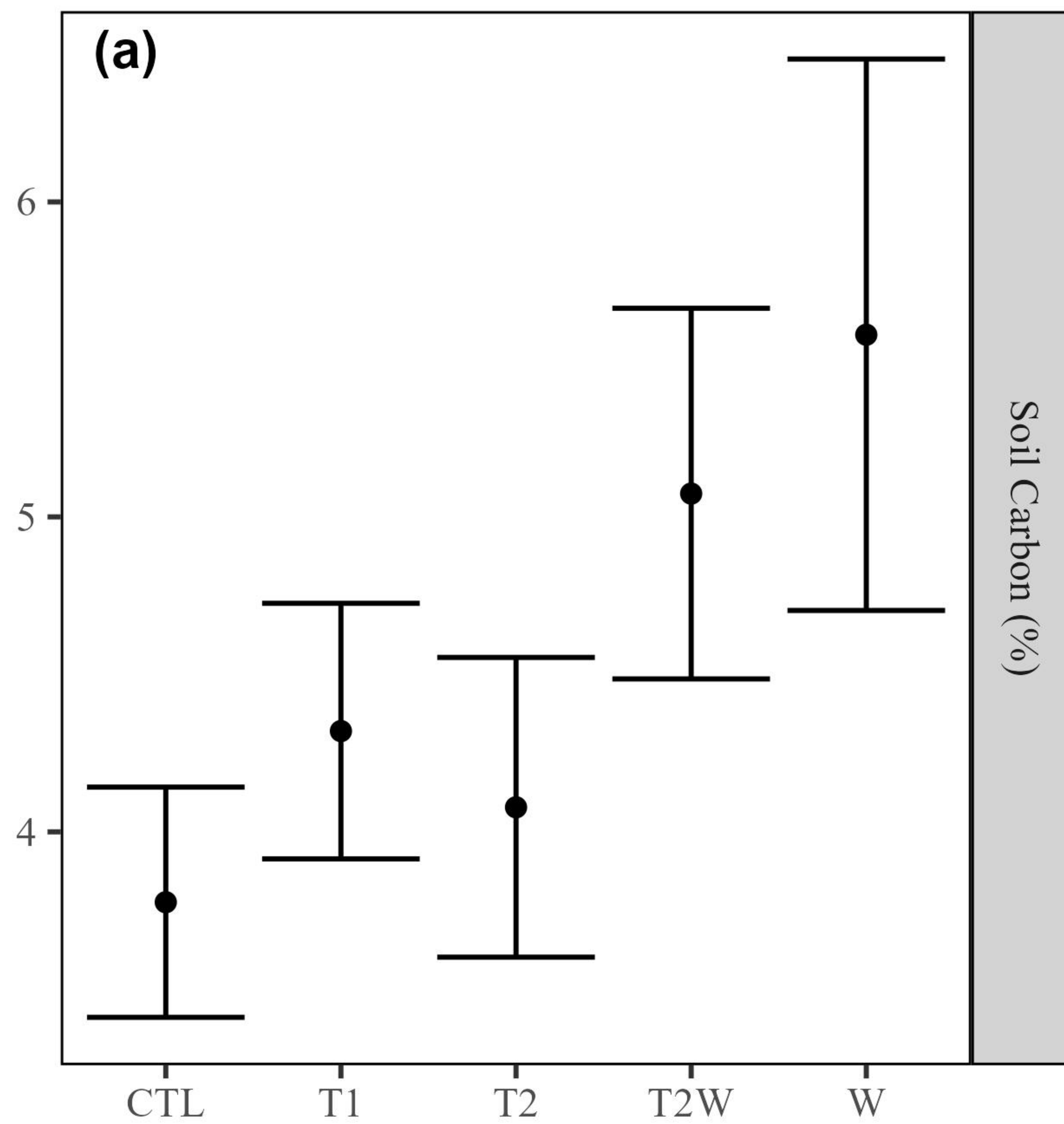


(a)



(b)





Ecosystem Carbon

Ecosystem Nitrogen

Ecosystem Biomass

