Warming of alpine tundra enhances belowground production and shifts community towards resource acquisition traits

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Abstract. Climate warming is expected to stimulate plant growth in high-elevation and high-latitude ecosystems, significantly increasing aboveground net primary production (ANPP). However, the effects of simultaneous changes in temperature, snowmelt timing, and summer water availability on total net primary production (NPP)—and elucidation of both above- and belowground responses—remain an important area in need of further study. In particular, measures of belowground net primary productivity (BNPP) are required to understand whether ANPP changes reflect changes in allocation or are indicative of a whole plant NPP response. Further, plant functional traits provide a key way to scale from the individual plant to the community level and provide insight into drivers of NPP responses to environmental change. We used infrared heaters to warm an alpine plant community at Niwot Ridge, Colorado, and applied supplemental water to compensate for soil water loss induced by warming. We measured ANPP, BNPP, and leaf and root functional traits across treatments after 5 yr of continuous warming. Community-level ANPP and total NPP (ANPP + BNPP) did not respond to heating or watering, but BNPP increased in response to heating. Heating decreased community-level leaf dry matter content and increased total root length, indicating a shift in strategy from resource conservation to acquisition in response to warming. Water use efficiency (WUE) decreased with heating, suggesting alleviation of moisture constraints that may have enabled the plant community to increase productivity. Heating may have decreased WUE by melting snow earlier and creating more days early in the growing season with adequate soil moisture, but stimulated dry mass investment in roots as soils dried down later in the growing season. Overall, this study highlights how ANPP and BNPP responses to climate change can diverge, and encourages a closer examination of belowground processes, especially in alpine systems, where the majority of NPP occurs belowground.

Key words: alpine tundra; belowground plant production; functional traits; Rocky Mountains; soil moisture; warming; water use efficiency.

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INTRODUCTION

Global mean annual temperature is projected to increase 2.6°–4.8°C by 2100 due to ongoing anthropogenic warming, while precipitation is expected to increase at high latitudes and in mid-latitude wet regions and decrease in many mid-latitude and subtropical dry regions (Stocker et al. 2013). Elevation-dependent warming has also been documented, with greater warming at higher elevations (Pepin et al. 2015), a trend that is expected to continue (Palazzi et al. 2019). In the western United States, mean annual temperature is predicted to increase 2.5°–5°C by 2100 (Kumar et al. 2013), with associated advances in the timing of snowmelt (Gergel et al. 2017). Future precipitation change is less certain, but projected to increase in the northwest and decrease in the southwest United States (Dettinger et al. 2015).

Temperature and precipitation both strongly regulate terrestrial ecosystem processes, and increases in temperature alter ecosystem water balance; yet, considerable uncertainty remains over the ecological effects of simultaneous changes in temperature, snowmelt timing, and summer water availability. Experimental warming across biomes reveals stronger positive effects of warming on aboveground net primary production (ANPP) in cooler than in warmer ecosystems (measured as mean annual temperature), and in wetter than drier ecosystems (measured as mean annual precipitation), with the strongest increases in ANPP in tundra systems (Rustad et al. 2001, Natali et al. 2012, Elmendorf et al. 2012a, Demarco et al. 2014, Hufkens et al. 2016). Further, experimentally reduced precipitation generally limits photosynthesis, thereby decreasing ANPP (Wu et al. 2011, Hoeppner and Dukes 2012).

Examining interactions between global change factors is needed to explore more realistic future change scenarios and to identify contexts and mechanisms responsible for ecosystem responses to global change (Klein et al. 2007, Hopping et al. 2018). In field studies, interactions between experimental warming and increased precipitation have been both present (Bai et al. 2010, Xu et al. 2016) and absent (Xu et al. 2013) for a temperate steppe in Inner Mongolia, China, and in a mixed-grass prairie in Oklahoma, USA, respectively. Meta-analyses have reported that warming and altered precipitation counteract one another (Wu et al. 2011) or have no significant interactive effect on plant biomass (Lin et al. 2010, Yang et al. 2018). Additional multifactor experiments across biomes are needed in order to identify patterns. Field studies examining the effects of interactive warming and soil drying on vegetation production, and community composition and structure can help elucidate the overall effects of climate change on net primary productivity, particularly at high elevations.

Additional precipitation during the growing season can alleviate moisture limitations and may compensate for drying effects of warming (Hufkens et al. 2016). Recent work in North America has shown that warming moist alpine tundra in a snowmelt-driven site with variable summer rainfall increases ANPP when water is added, but not otherwise (Winkler et al. 2016). On the Tibetan Plateau, warming decreased ANPP at alpine meadow and alpine steppe sites, but had no effect on ANPP in a higher elevation, shrub-dominated site with higher soil moisture (Klein et al. 2007, Ganjurjav et al. 2016). Similarly, in a synthesis of warming experiments across the Tibetan Plateau, soil moisture responses to warming and site soil moisture status both mediated ANPP responses (Yang et al. 2018). Across Arctic, alpine, and Antarctic sites, warming increased tundra plant growth at wetter sites or at sites with permafrost (Elmendorf et al. 2012b). While there is mounting evidence regarding the importance of soil moisture for tundra ANPP responses to warming, there have been few studies of belowground productivity responses to warming that advance snowmelt timing, elevate temperature, and address soil moisture constraints (Xue et al. 2015).

The responses of alpine ecosystems to climate changes may be mediated by plant functional traits (Díaz et al. 2007, Suding et al. 2008, Schumacher and Roscher 2009, Roscher et al. 2012). Plant functional traits are the “morphological, anatomical, biochemical, physiological or phenological features of individuals or their component organs or tissues” that affect ecosystem function, such as NPP (Kattge et al. 2011). Understanding how plant functional traits respond to warming can help predict the structural and functional implications of warming (Soudzilovskaia et al.
2013, Debouk et al. 2015) and provide a means to scale from the plant to the community level for ecosystem modeling. Plant functional trait responses to warming can inform process responses such as carbon storage and nutrient cycling (Bjorkman et al. 2018). For example, leaf mass per area (LMA) is a trait that distinguishes slow-growing from fast-growing species (Wright et al. 2004). Leaf dry matter content (LDMC, the ratio of leaf dry mass to fresh mass) is increasingly used as an indicator of a plant species’ resource use strategy and correlates negatively with potential relative growth rate and productivity (Pérez-Harguindeguy et al. 2013). Carbon isotope discrimination (δ13C) is commonly used as a measure of long-term water use efficiency (WUE) because of a strong theoretical basis for the correlation between δ13C and WUE (Ehleringer et al. 1990). Specific root length (SRL) is defined as the ratio of root length to root dry mass; plants with a high SRL generally have acquisitive strategies, with relatively high rates of nutrient and water uptake per unit mass, short root life span, and high relative growth rate (Tjoelker et al. 2005, Roumet et al. 2016). Large diameter and high root tissue density (RTD, root dry mass per root volume) are trait values generally indicative of a conservative strategy due to the greater longevity of these roots (McCormack et al. 2012).

In a synthesis of warming experiments that included 117 locations across the tundra biome, Bjorkman et al. (2018) found strong temperature–plant trait relationships, the strength and direction of which were contingent on soil moisture. This space-for-time synthesis approach yielded important findings, but the authors cautioned that such an approach could potentially not represent near-term ecosystem change and that additional experimental studies are needed for more accurate predictions of future intraspecific trait change.

To address these knowledge gaps regarding single and interactive temperature and precipitation effects on plant trait-mediated above- and belowground primary productivity, we conducted a climate manipulation experiment in alpine tundra at Niwot Ridge, Colorado, USA. We employed active infrared heaters to advance snowmelt and increase growing season temperatures crossed with manual watering to offset the drying effect of warming. We measured above- and belowground primary productivity, leaf and root functional traits, and community structure. We addressed the following questions: (1) Do previously reported increases in aboveground productivity with combined heating and watering also occur belowground? (2) How do above- and belowground plant functional traits respond to warming and water addition? (3) Is variation in plant above- and belowground production driven more by soil microclimate or community composition?

**Materials and Methods**

**Study site**

This study was conducted on a 15° south–southeast-facing slope above local treeline at Niwot Ridge, in the Front Range of the Colorado Rocky Mountains, USA (40°03’ N, 105°35’ W, 3540 m a.s.l.). Continuous climate data collected from 1981 to 2008 at the nearby LTER Saddle weather station site indicate a mean annual air temperature of ~2.15°C and mean annual precipitation of 966 mm, with approximately 80% of the precipitation falling as snow (Blanken et al. 2009). From 2010 to 2013, mean annual temperature observed at our site was 2.9°C and cumulative precipitation, as reported from a nearby Natural Resource Conservation Service weather station (http://www.wcc.nrcs.usda.gov), was 818 mm (Winkler et al. 2016). Vegetation composition in the study site shares similarities with moist and dry meadow community types (May and Webber 1982). The site is dominated by forbs, with graminoids, succulents, and cushion plants all contributing significant biomass. Abundant species include Geum rossii, Selaginella densa, Lewisia pygmaea, Chionophila jamesii, Minuartia obtusiloba, Phlox condensata, Carex rupestris, Luzula spicata, Trisetum spicatum, Artemisia scopulorum, and Bistorta bistortoides (see Winkler et al. 2018 for a full species list).

**Experimental design**

Twenty experimental plots were established in a fully crossed design in 2008–2009, with five plots assigned to each of four treatments: control (C), heated (H), watered (W), and heated and watered (HW). Heating began in early October 2009, and watering during the snow-free season...
began in 2010. The 3 m diameter plots were posi-
tioned 3–4 m apart and were assigned to treat-
ments, with assignments stratified by local
elevation, local aspect, and pre-existing vegeta-
tion cover. Six infrared (IR) heaters (Mor Electric
Heating, Comstock Park, Michigan, USA) were
suspended 1.2 m aboveground in hexagonal
arrays surrounding heated plots (Kimball et al.
2008), supplied with constant power between
March and November, and to avoid hydrological
artifacts, supplied at a lower constant level
December through February. The watering treat-
ment was designed to compensate for the effects
of soil drying that occur with heating, helping to
distinguish biological responses to warming
from responses to soil drying. Watering was initi-
ated once the average soil moisture in heated
plots dropped below that of control plots and
continued from ~2–3 weeks following snowmelt
until late September when site-level senescence
occurred. 2.5 mm of water was applied once per
week to watered and heated × watered plots
(see details in Winkler et al. 2016).

We divided each plot into four 1-m² quadrats
for plant observations and soil microclimate
monitoring. One quadrat within each plot was
randomly selected for installation of root in-
growth cores, characterization of species compo-
position, and leaf sampling for functional trait mea-
surements at the peak of the growing season in
2014. Both soil moisture and temperature at the
depth of 5–10 cm were recorded (ECTM or 5 TM,
Decagon, Pullman, Washington, USA) at 15-min
intervals in the center of each quadrat. Data were
used to quantify treatment effects on microcli-
mate, including date of snowmelt.

**Plant community survey and aboveground
productivity**

Vegetation surveys were conducted at peak
community biomass between late July and early
August in 2014 (Winkler et al. 2016). The percent-
age cover of all vascular plant species in each
quadrat was visually estimated to quantify per-
cent cover by species. To convert percent cover to
aboveground net primary productivity, thirty
50 × 50 cm quadrats were established off plot,
surveyed for species cover as above, and all
aboveground vascular plant biomass was har-
vested, sorted by species, dried at 60°C for 48 h,
and weighed. Linear regressions were used to
relate species-level cover to peak biomass mea-
surements, which is a widely used proxy of
aboveground productivity (see Winkler et al.
2016 for details). The mean R² of these species-
level relationships was 0.84 (range 0.35–1.00;
Winkler et al. 2016). The sum of all species-level
aboveground production was calculated to
obtain community-level aboveground primary
productivity in each quadrat. Species-level bio-
mass was also used to scale plant functional trait
measurements to community-weighted mean
traits, described below. We also use life-form (i.e.,
forb, cushion, graminoid, or succulent) cover
when examining community composition
responses because life-form cover includes all
species, while ANPP only includes species abun-
dant enough to create species-specific relations-
ships between cover and ANPP.

**Foliar functional trait measurements**

We measured three foliar traits, (1) water
use efficiency (WUE) estimated using ¹³C/¹²C
isotope ratio of leaf tissue, (2) leaf mass per
area (LMA, g/m²), and (3) leaf dry matter con-
tent (oven-dry mass divided by water-satu-
rated fresh mass, LDMC, g/g), on six abundant
species that occurred in each of the 20 quad-
rats (Appendix S1: Table S1). The six species
accounted for 80% of the cover in the experi-
mental quadrats in 2014. Mature, current-year
leaves from 5 to 10 random individuals per
species were sampled at peak biomass in all
quadrats, sealed in plastic bags to maintain
moisture content, and kept in a cooler and
then refrigerator until processing. Leaves from
each species were weighed and scanned within
24 h of sampling to measure leaf area, which
was quantified using ImageJ software (Schnei-
der et al. 2012). Leaves were then dried at
60°C and weighed dry to quantify LDMC and
LMA. Ground subsamples were analyzed for
carbon isotope ratios using a Picarro G2121-
iCO₂ analyzer coupled to a Costech 4010 Ele-
mental Analyzer and a Picarro Liaison to coor-
dinate gas sample delivery at the U.S.
Geological Survey, Forest and Rangeland
Ecosystem Science Center (Boise, Idaho, USA).
All leaf trait measurements followed protocols
described by Pérez-Harguindeguy et al. (2013).
Community-weighted traits followed Garnier
et al. (2004) and were calculated as
\[
\text{CWM}_{\text{trait}} = \sum_{i=1}^{n} P_i \times \text{trait}_i
\]

where \( P_i \) is the relative contribution (fraction) of species \( i \) biomass to the total biomass of the community, \( n \) is the number of sampled species, and \( \text{trait}_i \) is the mean trait value of species \( i \).

Community root productivity and root traits

Community belowground net primary productivity (BNPP) was assessed using two root in-growth cores per quadrat (40 cores total). While root productivity measured using in-growth cores underestimates BNPP, which also includes root exudates and mycorrhizae, this is a generally accepted proxy for BNPP (Lauenroth 2000). In-growth cores were constructed with 2-mm fiberglass mesh with dimensions of 5 cm diameter \( \times \) 15 cm deep as previous work demonstrated that in these plant communities, 80–90% of the root biomass is located in the top 10 cm of soil (Webber and Ebert-May 1977). In-growth cores were filled with root-free soil collected off-plot and adjacent to the experiment, where soil from 0 to 15 cm depth was collected and air-dried to pass through 0.1-mm sieve. Holes the same dimensions as the cores were excavated with an auger after snowmelt in 2014, and in-growth cores were installed vertically. At the end of the growing season (mid-September), in-growth cores were harvested and refrigerated at 4°C for one week, after which roots were manually separated from soil in the laboratory. A representative subsample of the roots from each in-growth core was scanned using a digital root-imaging program (Winrhizo, Regent Instruments, Nepean, Ontario, Canada), which calculated total root length, total root volume, and average root diameter by length for the subsample. Both the subsample and remainder of each root sample were oven-dried, weighed, and used to calculate specific root length (SRL), root tissue density (RTD), total root length and volume, and belowground net primary productivity (BNPP).

Statistical analysis

Two-way analysis of variance (ANOVA) was used to evaluate the effects of heating, watering, and the interaction between these two factors on soil temperature and moisture (5–10 cm depth) in 2014, with plot as a random effect.

We compared linear mixed-effects models to determine the best-fit models for predicting above-and belowground, and total net primary productivity (ANPP, BNPP, and NPP), life-form-level ANPP and cover, as well as leaf and root traits. Our models tested for the effects of heating, watering, and their interaction as fixed effects. We included plot as a random effect in all models and soil core in belowground productivity models to control for pseudoreplication. Full models were compared to simpler models using changes in Akaike information criterion corrected for small sample sizes (\( \Delta \text{AIC}_c \); Aho et al. 2014, Johnson and Omland 2004). We then calculated Akaike weights (\( wi \)) to compare the relative likelihood that a given model was the best fit. We determined significance and the direction of treatment effects of each best-fit model. We carried out the same model evaluation steps to test the predictive power of soil temperature and moisture on productivity (ANPP, BNPP, and NPP). For ANPP models, soil temperature and moisture were calculated as averages between the day of snowmelt and the day cover measurements were made (at peak productivity) for each plot. For BNPP and NPP models, we used soil temperature and moisture values calculated between the day of snowmelt and 15 September when soil cores were removed from each plot.

We also used linear mixed-effect models to evaluate the extent to which community composition was a driver of ANPP and BNPP. We quantified community composition by performing a non-metric multidimensional scaling ordination (NMDS) on plot species cover. The ordination scores were collapsed by averaging the first and second NMDS scores and included in models as fixed effects. We checked variance inflation factors (VIF) of explanatory variables. If VIF < 3, we assumed no multi-collinearity among explanatory variables. We selected the best models using the same AIC method discussed above. All models were built using the lme4 package, and our NMDS and ANOVA were carried out using the vegan package in R (Bates et al. 2013, R Development Core Team 2017).
about the same time for all treatment groups (Fig. 1). From snowmelt until 15 September, when in-growth cores were collected, there was a marginal heating treatment effect \((P < 0.1)\) and no significant watering treatment effect on soil temperature at 5–10 cm (Table 1). Heating significantly increased only late summer soil temperature, but there was a significant interaction between heating and watering for all periods, early, late, and whole summer (Table 1). Watering appeared to amplify the heating effect—the heated and watered plots were, on average, warmer by 13% than only-heated plots (Fig. 1), perhaps due to a darker surface (lower albedo) in watered plots or chance heater outages that preferentially affected heated but not heated and watered plots. There was no significant heating, watering, or interactive effect on soil moisture at 5–10 cm depth during whole summer period (Table 1, Fig. 1). However, heating significantly decreased late summer soil moisture, while watering significantly increased early summer soil moisture (Table 1).

**Treatment effects on net primary production and variation by life-form**

For all measures of plant productivity, models with the highest predictive power included heating, watering, and their interaction as fixed effects (Table 2; Appendix S1: Tables: S2–S3). Both ANPP and total NPP showed no significant response to heating or watering, but heating increased BNPP by 80% (Table 2, Fig. 2). ANPP of graminoid, cushion, and succulent plant life-form groups showed no responses to the treatments. Heating marginally increased forb ANPP when combined with watering, but not alone \((P = 0.06; \text{Table 2})\). Forb ANPP in heated plus watered plots increased by 1.5% compared with controls, by 45% compared with heated alone, significantly increased only late summer soil temperature, but there was a significant interaction between heating and watering for all periods, early, late, and whole summer (Table 1). Watering appeared to amplify the heating effect—the heated and watered plots were, on average, warmer by 13% than only-heated plots (Fig. 1), perhaps due to a darker surface (lower albedo) in watered plots or chance heater outages that preferentially affected heated but not heated and watered plots. There was no significant heating, watering, or interactive effect on soil moisture at 5–10 cm depth during whole summer period (Table 1, Fig. 1). However, heating significantly decreased late summer soil moisture, while watering significantly increased early summer soil moisture (Table 1).

![Fig. 1. Soil temperature (A) and soil water content (B) in 2014 averaged for sensors at 5–10 cm depth from snowmelt until in-growth cores were removed from the soil. The horizontal lines represent the first and last days of snow disappearance in each treatment group.](image)

Table 1. Statistical analysis (ANOVA) of treatment effects on soil microclimate in alpine tundra 2014, with heated, watered, and the interaction between heated and watered as fixed effects and plot as a random effect.

| Microclimate variable | Date       | Heated Coefficient | Heated P  | Watered Coefficient | Watered P  | Heated × watered Coefficient | Heated × watered P  |
|-----------------------|------------|--------------------|-----------|---------------------|------------|-------------------------------|---------------------|
| Soil temperature      | Whole summer | -0.219             | 0.0659    | -0.425              | 0.195      | 1.735                         | 0.018               |
|                       | Early summer| -1.929             | 0.798     | -1.945              | 0.781      | 3.495                         | 0.024               |
|                       | Late summer | 0.997              | <0.001    | -0.393              | 0.214      | 1.790                         | 0.035               |
| Soil moisture†        | Whole summer| -0.032             | 0.347     | 0.005               | 0.202      | 0.038                         | 0.279               |
|                       | Early summer| 0.001              | 0.742     | 0.037               | 0.046      | 0.020                         | 0.625               |
|                       | Late summer | -0.072             | 0.0065    | 0.003               | 0.181      | 0.043                         | 0.215               |

Notes: Whole summer is the period from plot-level snowmelt date to 15 September, when in-growth cores were harvested. Early summer is the period from plot-level snowmelt date to 7 July, which is the first snow-free day for the last melting plot. Late summer is the period from ANPP measurement at peak biomass to 15 September. For \(P < 0.05\), taken to indicate a significant treatment effect, the value is given in bold type.

† Plot #54 soil moisture data were missing, so only four replicates were available for the heated × watered treatment group.
Table 2. Effect sizes (estimates ± SEM) from the best-fit linear mixed-effects model predicting community productivity, life-form productivity, life-form cover, community-weighted leaf functional traits, and root traits.

| Response variable | H (df = 14) | W (df = 14) | H × W (df = 14) |
|-------------------|-------------|-------------|-----------------|
|                   | Est ± SEM   | t           | P               | Est ± SEM   | t           | P               | Est ± SEM   | t           | P               |
| Productivity      |             |             |                 |             |             |                 |             |             |                 |
| ANPP              | –21.87 ± 26.22 | –0.83 | 0.42 | 1.79 ± 26.22 | 0.07 | 0.95 | 25.98 ± 37.08 | 0.70 | 0.49 |
| BNPP              | 24.88 ± 11.84 | 2.10 | 0.04 | 14.77 ± 11.94 | 1.24 | 0.22 | 10.35 ± 16.74 | –0.62 | 0.54 |
| NPP               | 28.05 ± 35.38 | 0.79 | 0.44 | 14.41 ± 35.38 | 0.41 | 0.69 | 2.78 ± 50.04 | 0.06 | 0.96 |
| Life-form ANPP    |             |             |                 |             |             |                 |             |             |                 |
| Forbs             | –2.98 ± 3.82 | –0.78 | 0.45 | –6.50 ± 3.89 | –1.67 | 0.11 | 11.30 ± 5.53 | 2.04 | 0.06 |
| Cushions          | 9.75 ± 13.60 | 0.72 | 0.48 | 12.10 ± 12.72 | 0.95 | 0.36 | –18.44 ± 18.82 | –0.99 | 0.34 |
| Graminoids        | 0.78 ± 1.35 | 0.58 | 0.57 | 0.68 ± 1.41 | 0.48 | 0.64 | –1.94 ± 1.90 | –1.02 | 0.32 |
| Succulents        | –3.27 ± 2.27 | –1.43 | 0.17 | –1.89 ± 2.35 | –0.80 | 0.43 | 2.14 ± 3.12 | 0.70 | 0.50 |
| Life-form cover   |             |             |                 |             |             |                 |             |             |                 |
| Forbs             | –13.77 ± 9.81 | –1.40 | 0.18 | –18.79 ± 9.81 | –1.91 | 0.08 | 32.03 ± 13.87 | 2.31 | 0.04 |
| Cushions          | 2.28 ± 8.04 | 0.28 | 0.78 | 11.48 ± 8.04 | 1.46 | 0.18 | –12.32 ± 11.38 | –1.08 | 0.30 |
| Graminoids        | 5.10 ± 4.01 | 1.27 | 0.23 | –0.69 ± 4.01 | –0.18 | 0.87 | –5.68 ± 5.67 | –1.00 | 0.33 |
| Succulents        | –2.71 ± 2.66 | –1.02 | 0.33 | 0.25 ± 2.66 | 0.09 | 0.93 | 1.13 ± 3.76 | 0.30 | 0.77 |
| Community-weighted leaf functional traits |             |             |                 |             |             |                 |             |             |                 |
| LMA               | –7.43 ± 5.45 | –1.36 | 0.19 | –10.33 ± 5.45 | –1.90 | 0.08 | 4.61 ± 7.71 | 0.60 | 0.56 |
| LDMC              | –0.16 ± 0.05 | –3.27 | <0.01 | – | – | – | – | – | – |
| δ13C              | –0.44 ± 0.18 | –2.46 | 0.02 | – | – | – | – | – | – |
| Root traits       |             |             |                 |             |             |                 |             |             |                 |
| T-Length          | 0.57 ± 0.17 | 3.31 | <0.01 | – | – | – | – | – | – |
| SRL               | 8.06 ± 19.12 | 0.42 | 0.68 | –22.97 ± 19.12 | –1.20 | 0.25 | 2.05 ± 27.04 | 0.08 | 0.94 |
| RTD               | – | – | – | – | – | – | – | – | – |

Notes: Heating (H), watering (W), and their interaction (H × W) are included as fixed effects, and plot is included as a random effect and, for BNPP, soil core is included as a random effect. Dashes indicate that the best-fit model did not include the factor.

and by 43% compared with watered alone. Our ANPP estimates exclude 10% of total vascular plant cover from rare species; therefore, we separately tested treatment effects on cover for each life-form group, with largely consistent results. Cover of graminoid, cushion, and succulent plant life-form groups did not show any response to treatments. Forb cover significantly increased with heating only when watered (Table 2). Forb cover in heated plus watered plots increased by 28% compared with heated only and by 43% compared with watered only, respectively.

Treatment effects on plant traits
Best-fit models for leaf and root traits often included only a single factor (Appendix S1: Tables S2, S4). Community-weighted LDMC and WUE decreased in response to the heating treatment, while LMA was unaffected by any treatment (Table 2, Fig. 3). Consistent with effects on BNPP, the heating treatment increased total root length by 93% in unwatered plots and by 67% in watered plots, but had no observable effect on specific root length or root tissue density (Table 2, Fig. 4).

Relationships between productivity, climate, and community composition
Soil temperature, soil moisture, and community composition (from NMDS scores) were robust predictors of productivity. We included community-level foliar and root traits in full models predicting productivity, but they did not emerge in the best models. ANPP increased with soil temperature, while BNPP decreased with increasing soil moisture (Table 3). Only NMDS scores significantly explained total NPP (Table 3). Higher NMDS scores were strongly positively correlated with both BNPP and species richness (Table 3; Appendix S1: Figs. S1–S2), suggesting a tight relationship between community-level BNPP, composition, and diversity.
DISCUSSION

**Community productivity response to climate change**

We were surprised to find a stronger increase in BNPP than ANPP with heating. The late summer increase in soil temperature with heating (Table 1) may have stimulated root growth directly, although temperatures in all treatments averaged near or above 10°C during the core of the growing season in July (Fig. 1A). Further, because ANPP was not significantly stimulated by heating, we expect that other factors may have been at play. While it did not alter soil moisture over the whole summer (Table 1), heating tended to advance the date of peak soil moisture and dry the soils in the late summer (Table 1, Table 1).
which could help explain the greater investment in belowground biomass. BNPP would be expected to increase with decreased mid-late season soil moisture as plants preferentially allocate resources to root system development when water is low, and not to aboveground plant growth, effectively increasing the water-absorbing root biomass relative to water-losing leaf biomass (Fig. 5). Further BNPP was negatively related to soil moisture (Table 3), suggesting that plants in drier plots invest more belowground.

Thus, an increased belowground biomass investment with heating may have enabled the community to maintain its aboveground productivity rather than resulting in a decrease in aboveground productivity with heating and soil drying, as was observed in other studies (Klein et al. 2007, Hopping et al. 2018). In this same experiment, from 2010 to 2013, Winkler et al. (2016) found a negative effect of heating on ANPP in the absence of watering and a positive effect with watering, but did not report changes in allocation belowground that could have mediated the aboveground response.

While the heating effect on soil temperature was only significant and positive in late summer, heated plots had higher annual net nitrogen (N) mineralization than unheated plots in 2014 (Winkler et al. 2019), suggesting that plants may also be responding to greater soil N availability. This supports the functional balance theory in which plants can flexibly change biomass allocation to different organs to maximize resource utilization for acquiring other limiting resources (Cannell and Dewar 1994, Lambers et al. 2008). This flexible strategy may be especially valuable in alpine environments, where more than 80% of biomass typically resides belowground. This finding has

Fig. 4. Community-scale root traits including (A) total root length, (B) specific root length, and (C) root tissue density in each root in-growth core (5 cm diameter × 15 cm deep). Means and standard errors (SE) are shown for each treatment group (n = 5).

Table 3. Effect sizes (estimates ± SEM) from the best-fit linear mixed-effects model predicting productivity.

| Response variable | Tsoil (df = 13) | Msoil (df = 13) | NMDS (df = 13) |
|-------------------|----------------|----------------|----------------|
|                   | Est ± SEM | t | P     | Est ± SEM | t | P     | Est ± SEM | t | P   |
| ANPP              | 43.30 ± 16.03 | 2.70 | 0.02 | 23.18 ± 180.94 | 0.13 | 0.90 | 20.59 ± 44.80 | 0.46 | 0.65 |
| BNPP              | 9.86 ± 6.59 | 1.50 | 0.16 | −373.06 ± 147.13 | −2.54 | 0.03 | 100.55 ± 34.52 | 2.91 | 0.01 |
| NPP               | 3.85 ± 14.01 | 0.25 | 0.79 | −75.31 ± 312.61 | −0.24 | 0.81 | 165.68 ± 73.35 | 2.26 | 0.04 |

Notes: Soil temperature (Tsoil), soil moisture (Msoil), and ordination scores from non-metric multidimensional scaling to partition plot-level community structure (NMDS) are included as main effects, and plot is included as a random effect and, for BNPP, soil core is included as a random effect.
important implications for how we study the NPP responses to global change and also underscores the potential for additional belowground carbon storage in the alpine as climate warms.

Our results also highlight that aboveground responses are not necessarily representative of belowground responses, as we did not observe community-level heating effects on ANPP in the alpine tundra, nor was there an interaction between heating and watering as had been observed over the 5-yr period reported in Winkler et al. (2016; Table 1). The lack of an ANPP response to heating alone may reflect greater allocation to belowground biomass (Xu et al. 2013), as discussed above, or could reflect a lack of statistical power. The lack of an ANPP response to watering, may be attributed to the environmental conditions during 2014, our measurement year. Snowpack was relatively high in spring 2014, resulting in a snow-free season of 134 d (2010–2013 range: 120–176 d) in unheated plots. Snow-free season average soil moisture in 2014 was 28 ± 3% in control plots, which was the same as in 2013, but slightly higher than in earlier years (2010–2012 range: 21–23%) of the experiment, while air (6.1° ± 0.4°C vs. 6.1°–6.9°C in prior years) and control-plot soil (8.0° ± 0.2°C vs. 8.1°–9.5°C in prior years) temperatures were relatively cool. ANPP in 2014 was greater than in 2010–2013 (Winkler et al. 2016), suggesting these were generally favorable growing conditions. Given the relatively cool, moist conditions averaged over the growing season, we would have expected a positive heating effect on ANPP. Indeed, ANPP was positively related to soil temperature across plots in 2014 (Table 3). This positive relationship of soil temperature and ANPP in a relatively moist year is consistent with a synthesis of twelve experimental warming sites across the Tibetan Plateau that found aboveground net primary production responded more negatively to warming under drier conditions, due to both annual drought conditions and warming-induced soil moisture loss (Yang et al. 2018). However, in this study, the warmest plots on average were both heated and watered, and moisture averaged above 20% volumetric water content across plots (Fig. 1); therefore, heating
may not have sufficiently dried soil to reduce ANPP, but instead stimulated BNPP allowing ANPP to be maintained. This reinforces the notion that aboveground productivity responses to warming are contingent on moisture, with less pronounced effects in wetter years.

In the present study, forb cover increased with warming, but only when watered; otherwise, there were no significant shifts in life-form groups with treatments. A global tundra warming network reported that warming increased forb abundance only in the presence of near-surface permafrost (Elmendorf et al. 2012b). Harte and Shaw (1995) found decreased forb aboveground biomass with warming alone; Klein et al. (2008) found no forb ANPP changes in response to warming alone due to compensatory individualistic responses. Global meta-analyses across tundra sites found that forb responses to warming were contingent on soil moisture (Elmendorf et al. 2012a) or warming duration (Walker et al. 2006). Our results follow earlier findings from the present experiment, namely that forb responses to heating are contingent on soil moisture availability (Winkler et al. 2016). Increased forb cover with heating and watering suggested that resource shifts with higher temperature could drive the response of forbs, but our observed marginal ANPP response to heating in forbs also indicated that other factors, such as nitrogen, are likely also important in modifying alpine species responses to warming. However, community composition, quantified by NMDS, was not a significant factor predicting ANPP, suggesting this single life-form group response did not have a community-scale effect through differences in community composition.

**Community-level leaf trait responses to climate change**

Functional plant traits have become a tool for scaling up from individual plants to ecosystem function, and as indicators of system sensitivity to environmental changes. Community-level traits, determined as the weighted mean values across species, and functional trait diversity may respond more rapidly to climate change than species diversity (Suding et al. 2008). Our results are consistent with this expectation, in that heating alone had significant effects on some community-level leaf traits. In the present study, while we found no statistically significant treatment effects on LMA, heating decreased community-weighted mean LDMC. This may be an indirect effect of greater soil resource availability induced by heating combined with watering shifting the overall community to be faster-growing (lower LMA and LDMC; Laliberté and Tyllianakis 2012). With changed community-level traits and unchanged life-form cover in response to heating alone, our results suggest that community-level traits are more sensitive than species diversity if species-level traits are plastic.

Community-level δ13C decreased (was more negative) with heating, indicating a decreased WUE in heated plots. At the community scale, this decrease in δ13C values could reflect a shift in the relative contributions from species that are more to less water use efficient. A decrease in WUE at the individual scale could be attributed to either increased stomatal conductance or to reduced demand for C in photosynthesis. Given that we observed no significant differences in NPP, it seems that greater stomatal conductance with warming is likely. Indeed, two species that were sampled across nearly all plots—*Geum rossii* and *Trifolium parryi*—had more negative δ13C (*P* < 0.05 for each) but had no difference in cover (*P* > 0.4) with heating. That the effect on δ13C tends to be slightly larger in heated and watered plots than in plots that were only-heated (Fig. 3C) is consistent with this individual-scale explanation. The greater allocation to roots in heated plots could have increased plant water supply, enabling increased stomatal conductance. Another possible factor contributing to the reduced δ13C is more days early in the growing season with adequate soil moisture due to earlier snowmelt with heating (Fig. 1B). Carbon assimilated during these early summer, high moisture conditions could be the primary substrate for leaf tissue construction then or later in the season if temporarily stored. Higher temperature has also decreased WUE in woody plants (Monclus et al. 2006, Xu et al. 2008). Experimental warming of subalpine tree seedlings establishing in our treeline and alpine sites drove decreases in δ13C as well (Lazarus et al. 2018), with δ13C more responsive to temperature than to watering or soil moisture. The higher soil temperatures in late summer with heating could have increased root
and plant conductance and contributed to decreased δ13C in alpine plants in this study.

**Root trait responses to climate change**

Plants can adjust their nutrient and water uptake relative to the resource cost of construction and maintenance of root tissue by altering resource allocation within the root system (Atkinson 2000). Fine root biomass and root length per unit soil volume have been employed as indicators of the ability of plants to explore soil for resources and effectively compete for nutrients (Björk et al. 2007). It also has been reported that higher specific root length (SRL)—root length per unit root mass—maximizes absorptive surfaces in soil, thereby enabling plants to more effectively compete with microbes for nutrients (Craine et al. 2005). While root order was not identified, our results match Björk et al. (2007), in which alpine species did not adjust SRL in response to warming. This could be due to the already high SRL observed in ambient plots, as well as low flexibility of species to adjust SRL (Hill et al. 2006). Alternately, similar SRL across treatments may reflect the similar species composition. Because we did not identify roots to species, we cannot evaluate these alternatives. In our study, heating increased total root length but had no effect on SRL or RTD, indicating that root growth may have been released from temperature limitations, enabling plants to acquire more water and nutrients (Winkler et al. 2019).

Overall, while there was no effect of watering on WUE, heating reduced plant water use efficiency, suggesting that our alpine community did not experience water stress during the period of carbon assimilation, which likely occurred earlier with advanced snowmelt in heated plots (Fig. 5). Further, decreased LDMC suggests that a community-level resource strategy shift occurred, from relatively conservative (slower growth) to relatively acquisitive (faster growth) in response to heating. Our BNPP results are corroborating in that enhanced growth was directed belowground, perhaps enabling acquisition of water and nutrients later in the growing season as the soils dried. Such a strategy shift could also have benefitted from enhanced soil nitrogen mineralization with warming in these plots (Winkler et al. 2019). However, aboveground alpine community productivity and aboveground forb productivity have been shown to be sensitive to water availability (Winkler et al. 2016; Table 2), raising the question of whether total productivity (BNPP + ANPP) and the overall community functional strategy will be more influenced by water or nutrient availability in a warmer world.

Future research on alpine tundra ecosystems would benefit from consideration of interactions among multiple climate and edaphic factors, as well as examination of both above- and belowground responses, to better understand the full consequences of future climate change in these important systems and the implications for alpine ecosystem functioning.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3270/full