Final Technical Report: Arctic Shrub Expansion, Plant Functional Trait Variation, and Effects on Belowground Carbon Cycling

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Executive Summary/Abstract

Terrestrial ecosystems are undergoing dramatic changes in response to climate warming, and these changes are expected to feedback to the atmosphere, potentially altering the trajectory of future climate change. Feedbacks from Arctic ecosystems are a major concern because the Arctic is projected to warm significantly in the 21st century and because >50% of global belowground organic carbon is stored in permafrost and overlying soils. Warming-driven release of this carbon could drastically increase atmospheric greenhouse gas concentrations and accelerate climate warming. Plant communities are also responding to warming, as evidenced by the widely documented increase in woody-shrub growth and "greening" across much of the Arctic tundra biome. This vegetation shift may offset or amplify warming by altering carbon cycling. The direction and magnitude of shrub effects remain highly uncertain, however, due to limited understanding of the consequences of shrub expansion for belowground carbon cycling and simplification of these relationships in models. The major shrubs expanding in the Arctic (*Betula, Salix,* and *Alnus)* vary widely with respect to aboveground and belowground traits (e.g., tissue production and chemistry, rooting depth, microbial symbionts), and may also exhibit substantial intraspecific variation in these traits in response to environmental conditions. Such variation is likely to have profound implications for soil carbon cycling.

The overarching goal of this project was to improve process-based understanding of the influence of shrub expansion on carbon cycling to enable improved representation of carbon dynamics in ecosystem and Earth system models. We investigated how plant functional traits vary among shrub genera, respond to environmental conditions, and affect belowground carbon and nutrient cycling by quantifying relationships among functional traits and biogeochemical cycling along edaphic gradients nested within a climate gradient in the Alaskan tundra.

We found consistent differences in leaf and root traits among shrub genera and between shrubs and a widespread sedge species, indicating diverse nutrient acquisition strategies and belowground impacts among different arctic shrubs. We also found striking differences in trait values among individuals within the same species or genera within sites. Soil parameters were more important than climate parameters for predicting size and leaf trait variation, and root trait responses were less dependent on climate overall. For all but one root trait, including parameters representing aboveground traits improved the predictive ability of models. These results demonstrate that tundra shrub traits vary considerably at local scales and soil factors drive this variation, especially belowground. Furthermore, leveraging information about aboveground traits and soil conditions can improve predictions of how belowground traits will respond to climate change.

Despite these differences, soil carbon and nitrogen pools in the active layer did not vary among plots dominated by different shrub or sedge genera. Instead, pool sizes generally decreased from warmer to colder sites, consistent with a productivity gradient. Patterns of isotopic N composition indicate that shrubs tighten nitrogen cycling via nitrogen resorption or immobilization of shrub litter. Overall, these results suggest that further identifying the specific shrub genera in the tundra landscape will ultimately provide better predictions of belowground dynamics across the changing arctic.

We also performed simulation experiments with the Terrestrial Ecosystem Model (TEM) incorporated in the Predictive Ecosystem Analyzer (PEcAn) framework, treats model parameters as probability distributions, estimates parameters based on a synthesis of available field data, and then quantifies both model sensitivity and uncertainty to a given parameter or suite of parameters. We performed simulations across different types of tundra, including shrub tundra. One key finding was that both model sensitivity and uncertainty to a given parameter could vary within the same type of tundra, but in a different geographical location, such as over the climate gradient of shrub tundra described above.

We organized a special session at the annual meeting of the Ecological Society of America in August 2019 to disseminate our results, refine recommendations for model improvement, and initiate collaborations to implement these recommendations in existing models of tundra carbon dynamics at ecosystem to Earth system scales.

Our results support DOE near-term priorities by providing mechanistic insights into the role of vegetation change in the terrestrial carbon cycle in a region that is inadequately represented in Earth system models. Current models reduce the complexity of Arctic vegetation to a small number of plant functional types (PFTs). This approach implicitly assumes that each PFT represents the average ecological function of its constituent species, thus ignoring the effects of trait variation on biogeochemical cycling and potentially leading to large uncertainty in the sign and magnitude of ecosystem feedbacks to climate. By quantifying variation of plant functional traits across broad gradients of climatic and edaphic conditions and elucidating the linkages of such variation with carbon and nutrient cycling, our results illustrate the need and create a foundation for further developing trait-based modeling approaches that allow the traits of PFTs to vary as a function of environmental conditions. These approaches should improve the capacity of simulation models to offer insights into ecosystem carbon dynamics associated with novel plant communities in a rapidly changing Arctic.

Main Body

The goal of this project was to improve process-based understanding of the influence of shrub expansion on carbon (C) cycling so that we can better represent C dynamics in ecosystem and Earth system models. To achieve this goal, we accomplished the following objectives: (Obj. 1) Characterize aboveground and belowground plant functional trait variation for individual species and plant functional types in relation to air temperature and edaphic gradients, and determine how aboveground and belowground traits co-vary; (Obj. 2) Evaluate relationships between plant functional traits and C cycling by (Obj. 2a) conducting measurements of soil biogeochemical cycling and microbial activity in the areas where we collect plant functional trait data, and (Obj. 2b) determining the linkages of belowground soil processes to functional traits; and (Obj. 3) Develop a framework for incorporating information on tundra functional traits into ecosystem and Earth system models by (Obj. 3a) identifying key traits contributing to uncertainty in current models of tundra ecosystem dynamics, (Obj. 3b) evaluating tundra modeling approaches using dynamic plant functional types, and (Obj. 3c) assembling ecosystem modelers to disseminate our findings and discuss strategies for improving representations of belowground processes in ecosystem and Earth system models.

Objective 1: Characterize aboveground and belowground plant functional trait variation for individual species and plant functional types in relation to air temperature and edaphic gradients, and determine how aboveground and belowground traits co-vary.

This study is under review at the journal *New Phytologist.*

We aimed to improve understanding of shrub trait variation by investigating how the size, leaf, and root traits of three expanding shrub genera respond to environmental variation at different spatial scales along a latitudinal gradient in Northern Alaska. Our overarching hypothesis was that aboveground and belowground plant functional traits are determined primarily by air temperature, but edaphic conditions control trait response within a given air temperature range. We addressed the following research questions: (1) How do patterns of trait variation differ across sites with varying climates, among genera, and across plots with differing soil properties (but similar climate and genera)? (2) What are the primary environmental drivers of trait variation across spatial scales? (3) To what extent do aboveground traits predict belowground traits? Given evidence that tundra plants, particularly deciduous shrubs, possess a range of ecological strategies that are poorly represented by plant functional groups (Saccone et al. 2017, Thomas et al. 2019, Chen et al. 2020), we predicted that trait variation would be greatest among genera, followed by across sites, in alignment with the expected influence of climate. We further expected that climate would be the most important driver of shrub trait variation, but its effects would be mediated by local soil moisture. Finally, we expected that aboveground traits would explain a significant fraction of variation in belowground traits as a result of physiological and ecological tradeoffs (e.g., carbon and nutrient allocation).

Our study was conducted at five sites spanning a latitudinal gradient from the southern foothills of the Brooks Range to the Arctic Coastal Plain (latitude: 67.0 °N – 69.3 °N; longitude: 148.7 °W – 150.3 °W). At each site, we established nine plots locally dominated by species from each of three expanding deciduous shrub genera: *Alnus* (*A. viridis ssp. fruticosa*), *Betula* (*B. nana*), and *Salix* (*S. glauca, S. pulchra, S. arbuscoloides*, or *S. richardsonii*), respectively alder, birch, and willow (N = 27 shrub plots/site). Plots spanned an edaphic gradient from water tracks to upland areas, representing a wide range of soil conditions within each site (Fig. 1). All plots were 1-m-diameter circles surrounding the stem of the selected shrub individual; the target shrub was that which showed the largest cover among the three shrub genera. At each plot, we characterized local edaphic conditions (soil temperature, moisture, thaw depth, and organic layer depth) using standard methods. To characterize regional climate, we retrieved downscaled (1 km) monthly air temperature and precipitation data for each site from the Climatic Research Unit (CRU TS 4.0 datasets; Harris et al. 2020) and downscaled (60 m) water balance data from Morrison et al. (2019). In June and July of 2017, we measured leaf, size, and root traits of the target plant in each plot using standard techniques (Perez-Harguindeguy et al. 2013, Freschet et al. 2021). To address the first research question, we quantified trait variation within genera (i.e., congeneric trait variation, 'CTV') and across genera by calculating the coefficient of variation of each trait (trait standard deviation / trait mean x 100%). We also partitioned total trait variance across nested spatial scales and biological levels using linear mixed effects models and the lme4 package in R (Bates et al. 2015). To address the second question, we first fit a collection of hierarchical linear models for individual traits within a Bayesian framework using the brms package in R (Bürkner 2017). We next searched over the entire collection of models and identified the highest ranked model for each trait using leave-one-out cross-validation (LOO-CV; Vehtari et al. 2017). We then used pseudo Bayesian model averaging (pseudo-BMA; Yao et al. 2018) to evaluate the relative importance of each predictor across all competitive models, and calculate model averaged parameter estimates, SE, and 95% credible intervals. To address the third question, we modified the highest ranked model for each belowground trait by including aboveground traits as covariates and determined the highest ranked model, evaluated relative importance, and calculated model averaged parameter estimates as described above.

We found substantial intraspecific and congeneric variation in shrub traits within sites and less variation along the latitudinal gradient and between shrub genera. Consistent with these patterns, local edaphic factors were relatively more important than climate or taxonomic identity for structuring trait variation, especially for root traits. Interactions between soil variables and climatic water deficit were common however, indicating that local drivers can have non-uniform effects on trait distributions at the regional scale. For all belowground traits except root $\delta^{15}N$, including parameters representing aboveground traits (size or leaf) improved the predictive ability of models. Collectively, our results demonstrate that arctic shrub trait patterns are heterogeneous at the regional scale and strongly shaped by soil factors, with climate mediating these relationships. Our results also demonstrate potential opportunities to improve predictions of belowground trait distributions by leveraging information about aboveground traits, soil and climate conditions.

Objective 2: Evaluate relationships between plant functional traits and C cycling by conducting measurements of soil biogeochemical cycling and microbial activity in the areas where we collect plant functional trait data, and determining the linkages of belowground soil processes to functional traits.

This study is published in: Chen, W., K. D. Tape, E. S. Euskirchen, S. Liang, A. Matos, J. Greenberg, and J. M. Fraterrigo. 2020. Impacts of arctic shrubs on root traits and belowground nutrient cycles across a Northern Alaskan climate gradient. Front Plant Sci 11:588098. DOI: 10.3389/fpls.2020.588098

We examined multiple traits of absorptive roots relevant to the nutrient acquisition of common sedge and shrub genera in Northern Alaska. Root samples were collected along a latitudinal gradient to study the influence of climate on root traits. We also quantified the biomass of absorptive roots and mapped their vertical distributions in the active soil layer across the latitudinal gradient. Finally, we examined differences in the soil N pool and C: N among shrub-dominated and sedge-dominated plots. We hypothesized that (1) Absorptive root traits differ among arctic plants and vary along the climatic gradient; (2) Absorptive roots and ectomycorrhizal fungal colonization are functionally complementary among the arctic shrubs; (3) Both plant genera and local climate can influence the belowground absorptive root biomass and productivity, soil N pool size, and soil C to N ratio.

In June and July of 2017, we collected roots and soil from the sampling sites and plots described above. We harvested root samples from the target plant for trait measurements in the upper 20 cm of soil in each plot. In shrub-dominated plots, we excavated intact root branches linked to the target shrub individual. At least six intact root branches, which included the 1st to 6th or higher orders using a stream-based ordering system with the first order being the most distal roots (*sensu* Guo et al. 2008), were carefully cut and stored in coolers before returning to the lab. In sedge-dominated plots, the live intact roots (light color and dense tissue) that connected to the rhizome of *E. vaginatum* were also cut and stored. In addition, at least 10 sun-leaves of the target plant from which roots were harvested were collected. Traits were measured in the laboratory using standard techniques (Perez-Harguindeguy et al. 2013, Freschet et al. 2021). Within each plot, an intact soil core (moss + organic + mineral layer) was manually sampled using a 7.6-cm-diameter soil corer with a post driver until reaching the permafrost layer and used to determine the vertical distribution of live root biomass. Root ingrowth cores were used to estimate community-level root productivity in both shrub and sedge dominated plots.

We calculated summary statistics of root traits and tested the significant effects of genera (alder, birch, willow, or sedge; vegetation effect) and sampling site location (climate effect) with two-way ANOVA. We also performed a principal component analysis (PCA) to evaluate root trait co-variation. Plot-level root productivity, accumulative root biomass, and the soil C and N pool above the permafrost among plots with different dominant genera and sampling site locations were compared with two-way ANOVA. Soil C was regressed against soil N among shrub-dominated and sedge-dominated plots, and the regression slopes were compared to evaluate impacts of dominant genus on the amount of C stored per unit N. Data were log-transformed to meet the normality requirement. We also compared the [N] in the soil POM component in the organic layer among plots with different dominant genera and sampling site locations. Finally, we calculated the difference between plant and organic layer soil δ^{15}N values among dominant genus to evaluate the shrub impacts on the input and output of soil N.

We found consistent differences in root traits among shrub genera and between shrubs and a widespread sedge species. *Alnus* and *Betula* had relatively thicker and less branched, but more frequently ectomycorrhizal-colonized absorptive roots than *Salix*, suggesting complementarity between root efficiency and ectomycorrhizal dependence among the co-existing shrubs. Shrub-dominated plots tended to have more productive absorptive roots than sedge-dominated plots. At the northern sites, deep absorptive roots (>20cm depth) were more frequent in *Betula*-dominated plots. We also found shrub roots extensively proliferated into the adjacent sedge-dominated plots. Nonetheless, soil carbon (C) and nitrogen (N) pools in the active layer did not vary among plots dominated by different shrub or sedge genera. Instead, pool sizes generally decreased from south to north. To evaluate shrub impacts on the input and output of soil N, we calculated the difference between plant and organic layer soil $\delta^{15}N$ values among the dominant genus. In shrub-dominated plots, values of plant $\delta^{15}N$ (both leaf and root) were lower than the organic layer soil and POM $\delta^{15}N$, whereas in sedge-dominated plots values of plant $\delta^{15}N$ were higher than soil and POM $\delta^{15}N$. The effects of dominant genus on the difference in $\delta^{15}N$ between soil and plant were consistent across all sample sites. Our results reveal diverse nutrient acquisition strategies and belowground impacts among different arctic shrubs, suggesting that further identifying the specific shrub genera in the tundra landscape will ultimately provide better predictions of belowground dynamics across the changing arctic.

To further address the linkage between shrub functional traits and C cycling, we also installed four forced diffusion (FD) sensors (Eosense) in each of two sites in 2018: the northernmost and southernmost sites along our latitudinal gradient. The FDs, along with soil temperature and moisture sensors, were installed in patches dominated by one of the focal shrub genera and in patch dominated by *Eriophorum vaginatum*, a widespread tussock-formed sedge, to continuously measure soil CO_2 efflux. The malfunctioned shortly after field deployment. Troubleshooting was performed in 2019 and revealed that firmware corruption caused the malfunction. We attempted to update the firmware and re-deploy all FDs at both sites in July 2019; however, only a subset could be successfully updated. The remainder were updated in September 2020. We continue to maintain the FDs and will analyze the flux data from 2019-2022 in the coming year.

Objective 3: Develop a framework for incorporating information on tundra functional traits into ecosystem and Earth system models by (Obj. 3a) identifying key traits contributing to uncertainty in current models of tundra ecosystem dynamics, (Obj. 3b) evaluating tundra modeling approaches using dynamic plant functional types, and (Obj. 3c) assembling ecosystem modelers to disseminate our findings and discuss strategies for improving representations of belowground processes in ecosystem and Earth system models.

This study is published in: Euskirchen, E. S., S. P. Serbin, T. B. Carman, J. M. Fraterrigo, H. Genet, C. M. Iversen, V. Salmon, and A. D. McGuire. 2022. Assessing dynamic vegetation model parameter uncertainty across Alaskan arctic tundra plant communities. Ecol Appl 32:e2499. DOI: 10.1002/eap.2499

One fundamental uncertainty in ecosystem and Earth system models relates to model parameters (including plant traits), or configuration variables internal to the model whose value can be estimated from data. We incorporated a version of the Terrestrial Ecosystem Model (TEM) developed for arctic ecosystems into the Predictive Ecosystem Analyzer (PEcAn) framework.

PEcAn treats model parameters as probability distributions, estimates parameters based on a synthesis of available field data, and then quantifies both model sensitivity and uncertainty to a given parameter or suite of parameters. We examined how variation in 21 parameters in the equation for gross primary production influenced model sensitivity and uncertainty in terms of two carbon fluxes (net primary productivity and heterotrophic respiration) and two carbon (C) pools (vegetation C and soil C). We set up different parameterizations of TEM across a range of tundra types (tussock tundra, heath tundra, wet sedge tundra, and shrub tundra) in northern Alaska, along a latitudinal transect extending from the coastal plain near Utqiaġvik to the southern foothills of the Brooks Range, to the Seward Peninsula. TEM was most sensitive to parameters related to the temperature regulation of photosynthesis. Model uncertainty was mostly due to parameters related to leaf area, temperature regulation of photosynthesis, and the stomatal responses to ambient light conditions. Our analysis also showed that sensitivity and uncertainty to a given parameter varied spatially, even within the same type of tundra, such as a shrub tundra gradient. At some sites, model sensitivity and uncertainty tended to be connected to a wider range of parameters, underlining the importance of assessing tundra community processes across environmental gradients or geographic locations. Generally, across sites, the flux of net primary productivity (NPP) and pool of vegetation C had about equal uncertainty, while heterotrophic respiration had higher uncertainty than the pool of soil C. Our study illustrates the complexity inherent in evaluating parameter uncertainty across highly heterogeneous arctic tundra plant communities. It also provides a framework for iteratively testing how newly collected field data related to key parameters may result in more effective forecasting of Arctic change.

To work towards disseminating findings and interacting with other ecosystem modelers on these issues, we convened an organized session at the Ecological Society of America Annual Meeting in August 2019. Or session, entitled ‘Advancing Arctic Vegetation Models Through Incorporating Newly Available Plant Trait Data’, included eight speakers with talks on belowground representation of plant traits in models as well as newly available belowground field data from studies in arctic tundra.

Products and Accomplishments

Publications

- Chen, W., K. D. Tape, E. S. Euskirchen, S. Liang, A. Matos, J. Greenberg, and J. M. Fraterrigo. 2020. Impacts of Arctic Shrubs on Root Traits and Belowground Nutrient Cycles Across a Northern Alaskan Climate Gradient. Front Plant Sci 11:588098. DOI: 10.3389/fpls.2020.588098

- Euskirchen, E. S., S. P. Serbin, T. B. Carman, J. M. Fraterrigo, H. Genet, C. M. Iversen, V. Salmon, and A. D. McGuire. 2022. Assessing dynamic vegetation model parameter uncertainty across Alaskan arctic tundra plant communities. Ecol Appl 32:e2499. DOI: 10.1002/eap.2499

Manuscripts in review

- Fraterrigo, J. M., W. Chen, J. Loyal, and E. Euskirchen. Above- and belowground arctic shrub traits respond more strongly to soil factors than climate. In review.

Conference presentations

- Euskirchen, E. S., J. Fraterrigo. 2019. Organized Oral Session: Advancing Arctic vegetation models through incorporating newly available plant trait data. ESA Annual Meeting, Louisville, KY.

- Chen, W. K. Tape, E. Eukirchen, S. Liang, J. Fraterrigo. 2019. Functional traits of absorptive roots in northern Alaska. ESA Annual Meeting, Louisville, KY.

- Euskirchen, E. S., S. Serbin, T. Carman, J. Fraterrigo, H. Genet, C. Iversen, V. Salmon, A.D. McGuire. 2019. Assessing dynamic vegetation model uncertainty across Alaskan arctic tundra plant communities. AGU Annual Meeting, San Francisco, CA.

Model code availability

- The version of TEM used in this study (DVM-DOS-TEM v0.3.0) is available online: http://github.com/ua-snap/dvm-dos-tem

- The DVM-DOS-TEM code and associated scripts for the PEcAn interfacing are available on Zenodo: https://doi.org/10.5281/zenodo.4281498

Published data sets

- Fraterrigo, J., and W. Chen. 2020. Arctic shrub root traits, northern Alaska, summer 2017. Arctic Shrub Expansion, Plant Functional Trait Variation, and Effects on Belowground Carbon Cycling. ESS-DIVE repository. DOI: 10.15485/1631262

- Fraterrigo, J., and W. Chen. 2022. Arctic shrub size and leaf traits, northern Alaska, summer 2017. Arctic Shrub Expansion, Plant Functional Trait Variation, and Effects on Belowground Carbon Cycling. ESS-DIVE repository. DOI: 10.15485/1889749

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