Deciduous Tundra Shrubs Shift Toward More Acquisitive Light Absorption Strategy Under Climate Change Treatments

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Abstract The effects of climate change on plants are particularly pronounced in the Arctic region. Warming relaxes the temperature and nutrients boundaries that limit tundra plant growth. Increased resource availability under future climate conditions may induce a shift from a conservative economic strategy to an acquisitive one. Following the leaf economics spectrum that hypothesizes a strategy gradient between survival, plant size and costs for the photosynthetic leaf area, light absorption of tundra plants may increase. We investigated climate change effects on light absorptance and the relationship between light absorptance (fraction of absorbed photosynthetically active radiation, FAPAR) and structural and nutritional leaf traits, performing a soil warming and surface soil fertilization experiment on two deciduous tundra shrub species. Our results show that fertilization and warming combined increase light absorptance in Arctic shrubs and that FAPAR is correlated with leaf nutrients but not with structural leaf traits. This indicates an economic strategy shift of shrubs from conservative to acquisitive induced by warming and fertilization combined. We found species-specific differences: FAPAR was influenced by warming alone in *Betula nana* but not in *Salix pulchra*, and FAPAR was correlated with leaf phosphorus in *B. nana* but not in *S. pulchra*. We attribute this to water limitation of *B. nana* that generally grows in drier areas within the study site compared to *S. pulchra*. We conclude that FAPAR is a measure that opens up more possibilities to estimate nutritional leaf traits and nutrient cycles, plant economic strategies, and ecological feedbacks of the tundra ecosystem on broader scales.

Plain Language Summary The effects of climate change on plants are very strong in the Arctic. Tundra plants are usually limited by temperature and nutrients. Tundra plants usually have an energy saving strategy, with long lifespan and small leaves. A warmer environment with more nutrients may shift their strategy to faster growth, larger leaves, and more light absorption. We examined climate change effects on the light absorptance of two tundra shrubs. In order to do this, we made an experiment in which we warmed and fertilized the soil. We furthermore studied the relationship between light absorptance and plant traits. Our results show that fertilization and warming combined increase light absorptance in Arctic shrubs. Furthermore, we could show that light absorptance is strongly related to the concentration of nutrients in the leaves. We also found differences in light absorptance between the two shrub species. We believe that these differences are due to *Betula nana* growing in drier areas with less water compared to *Salix pulchra*. We think that light absorptance is a good measure for predicting changes in nutrient cycles and plant strategies in the tundra ecosystem.

1. Introduction

Climate change has a major effect on plant performance by altering environmental variables and ultimately the physiological functioning of plants (Becklin et al., 2016). Thus, plant functional traits can predict the reaction of plants to climate and the associated ecosystem changes (Green et al., 2022; Kühn et al., 2021; Soudzilovskaia et al., 2013). The effects of climate change on plants are particularly pronounced in the Arctic region, where temperature is rising faster than the global average (Chylek et al., 2022; Rantanen et al., 2022).

Warming affects tundra vegetation as it relaxes the growth boundaries of tundra plants, which are usually strongly limited by low temperature and nutrient availability (Chapin et al., 1995). Through increased soil temperatures,

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nitrogen and phosphorus availability is increased by enhanced decomposition and mineralization (Jonasson et al., 2004; Keuper et al., 2012). Nitrogen availability also increases through permafrost thaw, since permafrost generally stores higher amounts of nitrogen compared to active layer soils (Salmon et al., 2016; Schuur et al., 2007). The resulting increase in plant N levels and productivity increases the input of high-quality litter (Elmendorf et al., 2012).

Nutrient availability is an important factor that defines the ecological strategy of a plant within a gradient from conservative (slow-growing) to acquisitive (fast-growing) strategies (Grime et al., 1997). The leaf economics spectrum (LES) hypothesizes that this strategy gradient is reflected in leaf economics traits and thus describes correlations between leaf traits (Shipley et al., 2006, 2016; Wright et al., 2004). The LES is present across different plant life forms as well as habitats and can be related to underlying physiological and structural trade-offs between growth and survival (Pan et al., 2020; Reich et al., 1997; Wright et al., 2001).

The LES can easily be placed into an expanded picture of trait variation. The global plant trait spectrum shows main trends of variation not only for leaf traits, but also, for example, the sizes of plants and respectively, their seeds (Díaz et al., 2016). The main axes of this spectrum span between the size of plants and their organs and between the costs for building the photosynthetic leaf area, forming an individual space between growth survival and reproduction for each plant (Díaz et al., 2016).

In tundra habitats with low resources, plants adapt to a conservative strategy and usually demonstrate lower values for leaf area, specific leaf area (SLA), leaf nutrient content and photosynthetic rates, but higher values for leaf dry matter content (LDMC), leaf mass per unit area (LMA), and leaf thickness, as well as longer life span (Bruelheide et al., 2018; Edwards et al., 2014; Happonen et al., 2022; Onoda et al., 2017). Plants with a conservative strategy invest more nutrients in size-structure traits than in photosynthetic efficiency (Onoda et al., 2004, 2008). Plants with an acquisitive strategy show opposite traits (Onoda et al., 2017). An acquisitive strategy means greater light acquisition through increased leaf area and increased nutrient availability for photosynthesis (Farquhar et al., 2002; Osnas et al., 2013; Wilson et al., 2000).

A measure closely related to photosynthesis is the fraction of absorbed photosynthetically active radiation (FAPAR), defined as the fraction of the available light energy absorbed by plants for photosynthesis in the wavelength range of 400–700 nm of the electromagnetic spectrum (Gower et al., 1999). FAPAR thus represents optical properties of a leaf, that are related to the visible spectral domain. The most important plant trait in this context are photosynthetic pigments of the leaf, which closely depend on nutrient availability (Jacquemoud & Ustin, 2019). In addition to that, also leaf anatomy was shown to be closely related to optical properties: leaf thickness is correlated to reflectance and transmittance—but only at the >850 nm wavelength range and not in the visible domain (Gausman, 1972; Gausman et al., 1971; Knapp & Carter, 1998).

FAPAR can be sensed by earth observation sensors and through ground-based field measurements and represents a critical tool to extrapolate plant functions and strategies from leaf to the landscape scale (Majasalmi et al., 2017; Putzenlechner et al., 2019). Therefore, FAPAR can be used to map responses of vegetation to climate change effects (Pilaš et al., 2014).

The link between FAPAR and LES is not well-established. However, FAPAR is linked to the primary productivity of photosynthesis (Yang et al., 2021). FAPAR is also often used to quantify carbon dioxide assimilation through vegetation and is an essential variable for monitoring plant growth and yield (Fensholt et al., 2004; Sellers et al., 1997).

Under future predicted climate conditions, Arctic plants can shift from a conservative strategy to an acquisitive strategy due to increased resource availability and increase their absorption and light use efficiency as predicted by the LES (Bosiö et al., 2014; Iturrate-Garcia et al., 2020; Khan et al., 2022). These adaptations may be necessary under future conditions as conservative slow-growing species could be easily outcompeted by faster-growing species (Iturrate-Garcia et al., 2020). There are high levels of evidence that shrubs are responding to warming, especially by showing enhanced growth (Forbes et al., 2010; Myers-Smith et al., 2015; M. D. Walker et al., 2006), which may be an indication of a change from a conservative to an acquisitive strategy (Iturrate-Garcia et al., 2020).

The mechanisms of shrub encroachment in tundra ecosystems have been thoroughly investigated in the last years (e.g., Myers-Smith et al., 2011) and nutrients were found to play a key role in this process (e.g., Martin

et al., 2022). However, the connection between nutrients, plant traits, and light absorptance has not yet been examined regarding shrub encroachment in tundra ecosystems. By linking fertilization and warming to structural and nutritional leaf traits, as well as absorptance, it may be possible to better predict the joint effects of climate change on tundra plant performance. Furthermore, it will be possible to estimate energy and carbon fluxes in tundra ecosystems, as leaf traits were shown to be closely related to primary production (Tagesson et al., 2012), and changes between ecosystem carbon pools (Lees et al., 2018). Therefore we aim in this study to understand climate change effects on FAPAR and if FAPAR can be used to draw conclusions on nutritional and structural leaf traits.

We shed light on the effects of Arctic warming on plant light absorptance and on possible strategy changes through an experimental study of two deciduous tundra shrub species. As part of this experiment, three previous studies have examined the effects of warming and nutrient addition on above- and below-ground responses of different plant functional types (grasses, sedges, deciduous shrubs and evergreen shrubs) (Wang et al., 2017), as well as the effects on traits of four shrub species: two deciduous shrubs (*Betula nana* and *Salix pulchra*) and two evergreen shrubs (*Ledum palustre* and *Vaccinium vitis-idaea*) (Iturrate-Garcia et al., 2017, 2020). It was found that warming increased above-ground biomass of sedges, but not other plant types. Fertilization increased above-ground biomass of shallow-rooted dwarf shrubs, and had a strong effect on grasses, both above and below ground. Grasses had the highest plasticity in vertical root distribution, shifting to deep or surface soil in response to deep soil heating or surface soil fertilization, respectively (Wang et al., 2017). Shrub growth was mainly limited by nutrients and bark thickness decreased under combined fertilization and warming (Iturrate-Garcia et al., 2017). Warming furthermore had no significant effect on most shrub traits, but all shrubs responded to fertilization with increased growth. Leaf area, SLA and leaf nutrient contents were generally found to increase with fertilization, while LDMC decreased. Thus, Arctic shrubs shifted to a more acquisitive resource economy upon fertilization, with lower investment in defense mechanisms and increased vulnerability to herbivory and climate extremes (Iturrate-Garcia et al., 2020).

We expected in our study that:

1. light absorptance (FAPAR) of deciduous tundra shrubs increases with soil warming and nutrient addition, and
2. light absorptance (FAPAR) reflects a coordinated leaf trait shift from conservative to acquisitive.

2. Materials and Methods

2.1. Study Area

The study area is located within the continuous permafrost area in the Kytalyk National Park in the Indigirka lowlands of northeastern Siberia (70°49′N, 147°28′E, 10 m.a.s.l.). According to the closest climate station (Chokurdakh, 1981–2021 World Meteorological Organization station code 21946, 27 km from the study site), the annual precipitation is 201 mm, of which half falls as rain during the growing season, while the remaining falls as snow and the mean annual air temperature is −12.8°C (ECAD, 2023; Kazakov, 2023). The active layer thickness on the study site has a mean of 24.9 on the lakebed site and of 34.6 on the ridge site (Iturrate-Garcia et al., 2016). The experimental site was located on a remnant Pleistocene Yedoma hill with tussock-sedge tundra vegetation and a high abundance of dwarf shrubs (Iturrate-Garcia et al., 2016).

2.2. Experimental Design

To test whether climate change influences light absorptance, we performed a soil warming and surface soil fertilization experiment from 2011 to 2014 (Wang et al., 2017). The experimental setup consisted of a fully factorial block design with five blocks each with six plots of 1.5 × 1.5 m, in randomly chosen locations. Each block had an area of approximately 10 × 10 m (Figure 1).

We installed six treatment combinations. The soil warming treatment had three levels: control plots without warming and no cables, control plots with unheated cables, plots with heated cables to simulate warming (no warming, control with cable, warming). The surface soil fertilization treatment had two levels (no fertilization, fertilization). Each combination was randomly assigned to one plot within a block.

For the soil warming treatment, heating cables were buried at a depth of 15 cm in all the plots except for the no-cable treatment plots and left buried until the end of the experiment. The cables were only heated at the
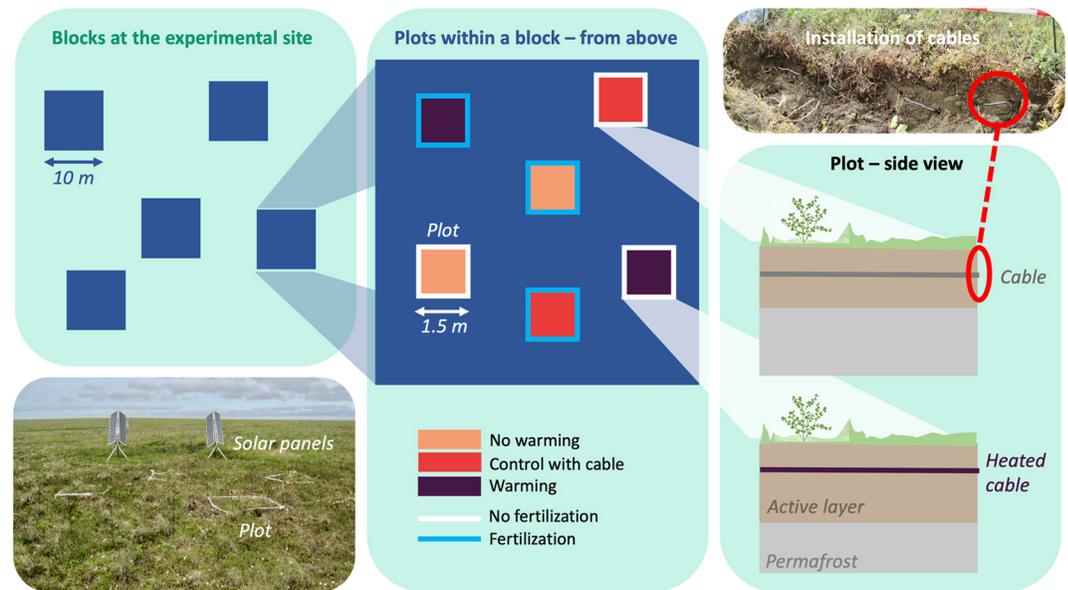
Figure 1. Experimental setup. Shown are the size of blocks and plots and how the installation of plots, solar panels and cables looks in the field. A side view of the plots provides insight into the installation of cables in 15 cm depth on control plots with cable and warming plots, where the cables were heated through solar energy.

warming treatment plots. For the control with cable, unheated cables were used to account for the soil disturbance effect of the cable insertion. As described in Wang et al. (2017), the heating cables were inserted into the soil from trenches at two sides of the plots to minimize root and microbial disturbance. The total length of the cable for a single plot was 15 m, with a total resistance of 15 Ω. One year after installation, the heating cables were connected to two parallel solar panels of 85 W each. The solar panels were removed before winter started. The solar energy directly enlarged the natural ground heat flux, allowing for diurnal and seasonal variation in solar intensity. The warming treatment enhanced the ambient ground heat flux, which is connected to the incoming solar energy that drives the seasonal thawing of permafrost. The two solar panels were angled at 60° to each other to capture sunlight for 20 hr per day.

The warming treatment warmed the 15 and 25 cm soil layers significantly from April to October, with the largest temperature difference occurring in July (measured from 2011 to 2014). The treatment furthermore increased thawing depth by an average of 7 cm, as measured in 2014 (Wang et al., 2017).

The surface soil fertilization treatment included the application of a slow-release NPK (nitrogen (N), phosphorus (P), potassium (K)) fertilizer tablet with micronutrients (Osmocote Exact Tablet, Scotts International, Heerlen, The Netherlands). The tablets were buried at approximately 5 cm depth in July 2011 and again in 2013, increasing the exchangeable nutrient content mainly in the upper soil layer (Wang et al., 2017). Fertilizer was added within a 1.75 × 1.75 m area for each plot, ensuring a complete fertilization treatment also for plants at the plot margin with roots exceeding the plot border. Within this area, 68 tablets of 5 g fertilizer were inserted into the soil with 25 cm spacing between the tablets. The added fertilizer consisted of 5.6 g N m^{-2} year^{-1}, 1.4 g P m^{-2} year^{-1}, and 3.7 g K m^{-2} year^{-1} (Wang et al., 2017). Wang et al. reported that (a) Fertilization reduced thawing depth in July 2014 by 4 cm. (b) Fertilization increased soil exchangeable nutrient concentrations in the top layer (upper 5 cm) four times for nitrogen and five times for phosphorus. In 25 cm depth fertilization only increased nitrogen significantly but not phosphorus. (c) Fertilization cooled all soil layers by 0.6–0.9°C.

Wang et al. (2017) furthermore reported that neither heating nor fertilization affected soil moisture at 0–10 cm depth significantly.

2.3. Model Species

We chose two model species, *B. nana* subsp. *exilis* (Sukaczev) Hultén and *S. pulchra* Cham., which are the most abundant shrub species in the study area and present in all experimental plots. Both species are shade-intolerant

deciduous erect shrub species with circumpolar Arctic distributions (Bliss & Matveyeva, 1992; Chapin & Shaver, 1985) and shown to be important contributors to the expansion of deciduous shrubs in the Arctic (Myers-Smith et al., 2011).

B. nana mainly grows in well-drained upland areas but also in moist areas with acidic soils, while *S. pulchra* is most prevalent in areas with shallow, perched water tables (eFloras, 2008).

B. nana has been shown to respond with growth and dominance to experimental warming and nutrient additions in the tussock tundra, while *S. pulchra* has so far not been found to show plasticity (Bret-Harte et al., 2002; Chapin et al., 1995).

S. pulchra grows erect up to a few meters high with relatively few branches, while *B. nana* has a height of up to 40 cm with many branches. In *B. nana* leafs on unfertilized plots were found to have following leaf trait measures: leaf area = 0.98 ± 0.02, SLA = 133.3 ± 2.1, LDMC = 0.55 ± 0.01, leaf nitrogen concentration (LNC) = 24.2 ± 0.5, leaf phosphorus concentration (LPC) = 2.05 ± 0.08, and *S. pulchra* leafs on unfertilized plots were found to have following measures: leaf area = 3.20 ± 0.14, SLA = 122.5 ± 2.5, LDMC = 0.50 ± 0.01, LNC = 16.6 ± 0.6, LPC = 1.57 ± 0.12 (Iturrate-Garcia et al., 2020). While the SLA values for *B. nana* were in the typical trait range compared to the global values of this species, LDMC values were in the upper part of the global range (Kemppinen & Niittynen, 2022).

2.4. Sampling

We carried out the sampling during the mid-growing season of 2014 (31 July to 12 August). We randomly selected healthy looking shrubs to measure FAPAR as well as 5 structural leaf traits (leaf area, SLA, LMA, LDMC, leaf thickness) and 4 nutritional leaf traits (LNC, LPC, C:N, N:P) on each plot (Iturrate-Garcia et al., 2020).

2.4.1. Structural and Nutritional Leaf Traits

To measure the structural and nutritional leaf traits, we randomly selected six healthy-looking *B. nana* individuals and one to four *S. pulchra* individuals per plot. To obtain fresh mass, the samples were weighed within 6 hr after being cut in the morning, wrapped in moist paper, and placed in sealed plastic bags (Pérez-Harguindeguy et al., 2013). To determine leaf area, we cut two leaves per individual and scanned them with a flatbed scanner (LiDE 70 Canon Inc., Japan, 300 DPI image resolution), using a reference for calibration (i.e., a black square of 1 cm² area). The scanned leaves were oven-dried at 60°C for 72 hr and weighed to determine the dry weight. Subsequently, SLA and LMA were calculated. We used the same leaves to determine LDMC following a variation of the partial rehydration method (Vaieretti et al., 2007; Vendramini et al., 2002). LDMC was calculated as the dry mass of a leaf divided by its fresh mass. The samples were kept in the dark at low temperatures. The whole procedure took place before scanning the leaves. We approximated leaf thickness by calculating $1/\text{SLA} \times \text{LDMC}$ (Vile et al., 2005).

To measure leaf nutrients, we milled oven dried-leaves (60°C for 72 hr) and determined LNC and leaf carbon concentration by dry combustion (TruSpec Micro-CHN analyzer, Leco Corporation, MI, USA) in samples of 2 mg. To measure the LPC, we combusted 0.05 g of milled samples in a muffle furnace (B180 Nabertherm, Germany) (1 hr heating ramp up to 600°C and 2.5 hr at 600°C). We added 2 ml of 0.1 M H_2SO_4 to the ashes, 5 ml of distilled water, and filtered the suspension (Macherey Nagel MN615) to determine phosphorus using a continuous flow analyzer (Skalar Analytical B.V., The Netherlands, calibrated with KH_2PO_4 standards). Concentrations were estimated by dividing the nitrogen, carbon or phosphorus amounts by the leaf dry mass. Further details are described in Iturrate-Garcia et al. (2020). Additionally, we calculated C:N and N:P ratios.

2.4.2. Light Absorptance

We collected the *B. nana* and *S. pulchra* leaves cutting one upper leaf and one lower leaf of each individual. We chose leaves that were healthy and fully-developed (based on visual inspection), prioritizing larger leaves to cover the 5-mm opening of the spectrometer.

We used a Jaz spectrometer Ocean Optics SpectroClip (OceanOptics Inc, 2012) probe to produce measurements of leaf optical properties (LOP), that is, the reflectance and transmittance of each leaf sample. The SpectroClip has two integrating spheres of about 20 mm in diameter. The two spheres are installed in a fixture that guaranteed that the sample ports of the two spheres remained aligned as the spheres move away from each other during the

leaf sample insertion. The sample was then fitted between the two spheres and the illuminated area was 5 mm in diameter. This method has several advantages over the conventional single-sphere substitution method. Importantly, the LOP can be measured without having to move the sample, removing not only the potential for substitution error but also increasing the speed of measurement (Mõttus et al., 2017).

After collecting, the cutting edge of individuals was wrapped with wet paper tissue following Pérez-Harguindeguy et al. (2013). For each leaf, we measured reflectance and transmittance on the adaxial and abaxial sides of the leaf, using an illumination beam and a device integration time of 412 ms.

At the latest after every 40 measurements, but often earlier, we measured a dark and white standard and an empty measurement. Inbetween this interval we measured a dark standard after every 2–12 measurements. With help of these measurements, we can correct for dark current and backscattering of the light. The internal temperature of the spectrometer increased during use, leading to a change in the dark current, as the dark current is temperature dependent. This behavior was accounted for in the pre-processing of the LOP. Additionally, with the double-integrating sphere, one part of the light that enters the lower sphere is backscattered to the upper sphere, which also required further pre-processing so that the single-scattering properties of the leaves could be retrieved.

2.5. Pre-Processing of Leaf Optical Data

We used MATLAB R2018B (The MathWorks, Inc., MA, USA) for all pre-processing of the raw LOP data. Initially, we created two matrices: one for all the reflectance readings and one for all the transmittance readings. Then we corrected for dark current (caused when the light source was not shut down during the dark-readings) by sorting the dark-readings values in descending order and removing dark-readings with more than 20 very high values. We sorted the dark reading values in descending order to find the errant measurements. We then calculated the mean of all dark readings from the fifth value to avoid an overestimate of the mean. This mean was then multiplied by 1.25, a threshold set to allow for variability. We compared this value with the twentieth value in the dark readings, excluding all values where the mean was lower than the twentieth value. We then sorted our matrix by time and interpolated between two dark-readings, then subtracted the dark-reading from all our measurements. As a next step, we generated one white reference file by taking all the white readings and averaging them. We applied further corrections, according to Mõttus et al. (2017).

Because of these corrections, 0.001%–0.03% of the values in the spectral range of interest (visible spectrum: 400–700 nm) were missing. In these cases, we substituted the missing values with the value of the former wavelength (difference of 0.4 nm) as they did not occur consecutively, and the measurement interval was high. In addition, we replaced all transmittance values >1 with 1 and <0 with 0, to calculate the light absorptance for every wavelength between 400 and 700 nm. We used the corrected transmittance and reflectance values to calculate the light absorptance of each leaf. We integrated absorption between 400 and 700 nm to calculate the FAPAR per unit area. In this study, FAPAR refers to the unit area of the leaf, which was covered by the SpectroClip, namely 19.6 mm^2.

2.6. Statistical Methods

We carried out all statistics in R, Version 4.2.1. (R Core Team, 2022) and fitted all models in a Bayesian framework using the *brm()* function from the *brms* package (Bürkner, 2017, 2018).

To test expectation 1 (light absorptance by deciduous tundra shrubs increases with increasing soil warming and nutrient addition), we fitted a linear mixed model with FAPAR as a dependent variable. Species (factor with two levels: *B. nana*, *S. pulchra*), warming treatment (heating, control with cable, no heating) and surface soil fertilization (two levels: no fertilization, fertilization) and all interactions were included as fixed factors. Additionally, we included block (factor with five levels) as a random intercept to the model. Because of skewed FAPAR data, we used family = skew_normal. As we detected heterogeneity of variance with respect to species using a Levene test, we allowed different variances for each species in the model by adding the term sigma ~ species.

We defined the prior distributions for the parameters in our model setting the prior for class "b" (population-level effects) to normal (0,10), which means a normal prior with mean 0 and standard deviation 1 for all coefficients. As the intercept is not affected by general "b" priors, we also set the prior for the intercept to normal (0,10). To obtain the posterior distribution, we ran 10,000 iterations (warmup = 5,000) with four chains. The posterior distribution is a probability distribution and is the result of the prior distribution and the likelihood function
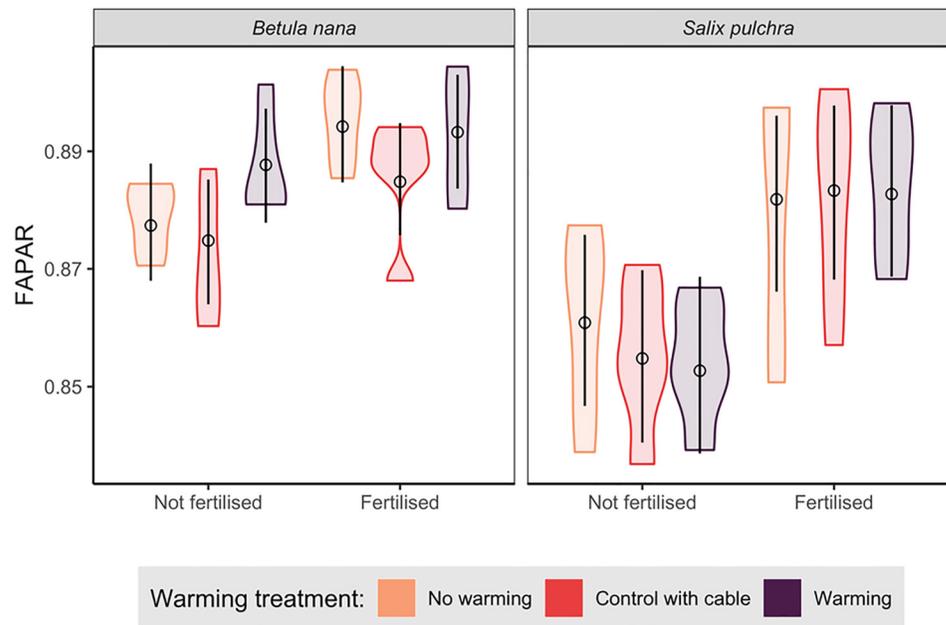
Figure 2. Effect of surface soil fertilization and soil warming on the fraction of absorbed photosynthetically active radiation (FAPAR). Violin plots show density of raw data. The black bordered dots are predicted mean values and the lines show 95% credible intervals (CrIs). Lesser overlap of CRIs suggests stronger differences.

(Korner-Nievergelt et al., 2015). We calculated the posterior probabilities for our anticipations by using the proportion of simulated values of the posterior.

To test expectation 2 (light absorptance [FAPAR] reflects a coordinated leaf trait shift from conservative to acquisitive), we fitted a multivariate model (containing multiple dependent variables). Therefore, we calculated the means for all structural and nutritional traits (thickness, Leaf area, SLA, LMA, LDMC, LNC, LPC, CN-ratio, and NP-ratio) of each species per plot since we had only one value per species and plot for FAPAR.

We fitted the model by including scaled FAPAR and all scaled structural and nutritional leaf traits as dependent variables using mvbind to indicate within the *brms* package that all traits were separate dependent variables. In the first model, we included species (*B. nana*, *S. pulchra*) to control for species. Block was included as random intercept to the model using the term $(1 \mid p \mid \text{block})$ to account for varying intercepts with $\mid p \mid$ indicating that all varying effects of block are modeled as correlated. We used family = student(). We allowed different variances for each species in the model by adding the term sigma ~ species. We used default brms priors and ran 4,000 iterations (warmup = 2,000) with four chains. Finally, we extracted residual correlations and their 95% credible interval (CrI) for all correlations that included FAPAR to show the unmodeled dependency (not explained by species and treatments) between FAPAR and the structural and nutritional leaf traits and plotted them in a figure.

To show the correlations for each of the two shrub species, we constructed and ran models separately for each species using two data subsets, one for each species, in the same fashion as the model described in the paragraph above to test expectation 2. However, we did not include species as a fixed factor here, and additionally removed the sigma term. Finally, we extracted residual correlations and their 95% CrI for all correlations that included FAPAR and plotted them in a figure for each model.

3. Results

3.1. Surface Soil Fertilization and Soil Warming Effects on FAPAR

We show that soil fertilization and warming combined had positive effects on FAPAR in both species. If surface soil fertilization and soil warming were applied together, FAPAR increased strongly in *B. nana* ($P_{\text{no treatment} < \text{all treatments}} = 0.99$) and in *S. pulchra* ($P_{\text{no treatment} < \text{all treatments}} = 0.99$) (Figure 2, Figure S1 in Supporting Information S1).

In *B. nana*, warming showed a positive effect on FAPAR in unfertilized plots ($P_{\text{no warming} < \text{warming}} = 0.96$) but not in fertilized ones ($P_{\text{no warming} < \text{warming}} = 0.44$). In *B. nana*, we found also increases of FAPAR through fertilization for
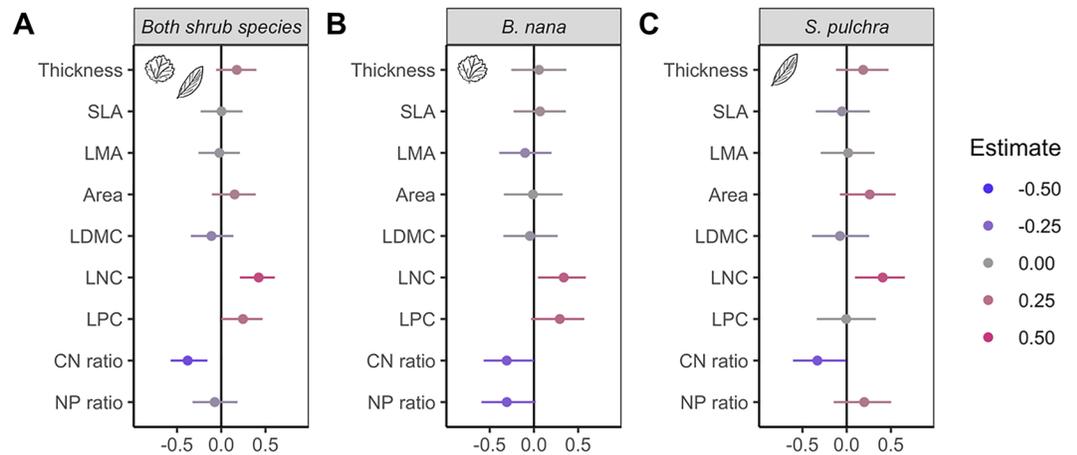
Figure 3. Correlation estimates and 95% credible interval for unmodeled dependencies between fraction of absorbed photosynthetically active radiation and structural and nutritional leaf traits, modeled for the whole data set with species included as fixed factor to control for species effects (a) and for a subset of each species (b), (c). Strong blue colors indicate a significant negative correlation and strong pink a significant positive correlation. SLA, specific leaf area; LMA, leaf mass per area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; CN ratio, carbon-to-nitrogen ratio; NP ratio, nitrogen to phosphorus ratio. The icons for the leaves are not shown at their true size. *S. pulchra* leaves are larger than *Betula nana* leaves in reality.

plots without warming ($P_{\text{unferilized<fertilized}} = 0.99$) and control plots with cable ($P_{\text{unferilized<fertilized}} = 0.95$), but not for warmed plots ($P_{\text{unferilized<fertilized}} = 0.85$). Warmed plots already showed increased FAPAR and hence no additional effect was shown when adding nutrients (Figure 2).

In *S. pulchra*, warming alone had no effect on FAPAR in unfertilized as well as in fertilized plots ($P_{\text{no warming<warming}} = 0.18$ & $P_{\text{no warming<warming}} = 0.51$). Fertilization effects alone led to a significant increase of FAPAR in *S. pulchra* (no warming, control with cable, warming: $P_{\text{unferilized<fertilized}} = 0.95$ & 1.00 & 1.00) (Figure 2).

3.2. Correlations of FAPAR With Structural and Nutritional Leaf Properties

We found that FAPAR was correlated with leaf nutritional traits, whereas correlations with leaf structural traits seemed to play a minor role. When correlating FAPAR with structural and nutritional leaf properties while accounting for species effects, we found that LNC and LPC were positively correlated with FAPAR ($P_{\text{cor>0}} = 1.00$ & $P_{\text{cor>0}} = 0.97$), and consequently found that the C:N-ratio was negatively correlated with FAPAR ($P_{\text{cor<0}} = 1.00$). All other variables showed no strong positive or negative correlations with FAPAR (Figure 3a, Figure S2 in Supporting Information S1).

For the subset of *B. nana* (Figure 3b), we found LNC and LPC to be positively correlated with FAPAR ($P_{\text{cor>0}} = 0.99$ & 0.97), and the C:N-ratio as well as the N:P-ratio to be negatively correlated with FAPAR ($P_{\text{cor<0}} = 0.98$ & 0.97).

In *S. pulchra* (Figure 3b), LNC was positively correlated with FAPAR ($P_{\text{cor>0}} = 0.99$), and the C:N-ratio was negatively correlated with FAPAR ($P_{\text{cor<0}} = 0.98$).

4. Discussion

We found considerable warming and fertilization effects on the light absorptance of two deciduous tundra shrubs and could show that light absorptance is strongly linked to nutritional leaf traits but not to structural leaf traits.

4.1. Surface Soil Fertilization and Soil Warming Effects on FAPAR

Surface soil fertilization and soil warming combined had strong positive effects on FAPAR in both of the studied tundra shrubs. This result agrees very well with expectation 1 (FAPAR increases with increasing soil warming and nutrient addition).

Sensitivity to nutrient addition was expected. Compared to other functional groups of tundra vegetation, deciduous shrubs are the most sensitive to nutrient addition: they show increased leaf nitrogen contents and a strong increase in photosynthesis if nutrient availability increases (Baddeley et al., 1994; Prager et al., 2020). This

advantage over other functional groups is only possible because deciduous shrubs generally have higher nutrient uptake and photosynthesis rates (Atkin, 1996; Johnson & Tieszen, 1976). Sensitivity to nutrient addition in general is unsurprising because leaf nitrogen is an essential part of the energy capture of a plant, being a key component of chlorophyll and a component of ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO), a protein which takes part in photosynthetic processes (Lambers et al., 2008). This explains why fertilization alone had overall positive effects on FAPAR in *S. pulchra* across all warming treatments, and on unwarmed plots on FAPAR in *B. nana* (Lv et al., 2021). Additionally, this can be explained by the positive warming effect on *B. nana*, which already increased FAPAR values and dampened the fertilization effects (Heskel et al., 2013).

These findings are also generally consistent with the results of a previous study of this experiment that showed positive warming effects on multiple shrub traits and especially on SLA and nutrient concentration (Iturrate-Garcia et al., 2020), which was also linked to the expectation that nutrient addition released shrubs from their growth limitation through ecosystem conditions. Thus, shrubs under fertilization generally followed a more acquisitive growth strategy compared to permafrost thaw, which had higher soil temperatures and deeper thaw depth (Iturrate-Garcia et al., 2020). Those findings were also consistent with the other study performed in the same experiment that could show that shallow-rooted shrubs could monopolize nutrients in the surface soil and take advantage from nutrient addition (Wang et al., 2017).

In contrast to fertilization, warming alone did not have effects on FAPAR in *S. pulchra* and no significant effects on *B. nana* in fertilized plots. Also here, our findings are consistent with the results of previous studies of this experiment that found shrubs are not flexible enough to profit from an increased thaw depth with their shallow roots that did not expand (Wang et al., 2017).

In our study, warming had a positive effect on *B. nana* in unfertilized plots. It may be possible that *B. nana* profitted via facilitation through mycorrhizas under warming while *S. pulchra* did not. It has been shown for *B. nana* that carbon was efficiently transported through below-ground mycorrhizal networks under warmer conditions (Deslippe & Simard, 2011).

4.2. Correlations Between FAPAR and Structural Leaf Traits

We found no structural leaf trait associations with FAPAR. Because several studies show that warming and fertilization cause changes in structural plant traits (e.g., Hudson et al., 2011; Iturrate-Garcia et al., 2020), we assume that those structural changes are not important for the absorption of visible light, and thus not reflected in FAPAR. We know that leaf thickness is linked to reflected and transmitted light in wavelength higher than the visible spectrum (Gausman et al., 1971; Jacquemoud & Ustin, 2019; Knapp & Carter, 1998). However for optical traits in the visible wavelength domain, photosynthetic pigments are more important than leaf structure (Jacquemoud & Ustin, 2019).

4.3. Correlations Between FAPAR and Nutritional Leaf Traits

FAPAR showed a positive correlation with leaf nutritional traits, which was the expected outcome regarding our expectation 2 (light absorptance (FAPAR) reflects a coordinated leaf trait shift from conservative to acquisitive). On a landscape scale, correlations between light use and nutrient concentrations in plants have been shown previously in temperate and boreal ecosystems (Kergoat et al., 2008; Ollinger et al., 2008). This correlation pattern is also congruent with previous studies in tundra ecosystems, in which fertilization was shown to increase photosynthetic activity (Chapin & Shaver, 1996; Oberbauer et al., 1989). LNC is strongly correlated with photosynthesis, because a large part of leaf nitrogen is invested in RuBisCO enzymes that determine through their amount and activity the photosynthetic rate (Kattge et al., 2009).

While N has a role in photosynthesis as an enzyme component, P acts as part of the energy transfer in Adenosine triphosphate (Jiang et al., 2019). This explains the correlation between FAPAR and LPC, we found, which was also proposed by the literature for LPC and photosynthesis in a similar way (Ellsworth et al., 2015; A. P. Walker et al., 2014). However, only the inorganic form of leaf phosphorus can be used for photosynthesis, and the organic form requires prior hydrolyzation, and thus this relationship is often describe as weak and non-linear (Crous et al., 2015; Jiang et al., 2019; Thomas et al., 2006). The correlation between LPC and FAPAR is also an indicator of the phosphorus limitation of the tundra ecosystem. A similar relationship was described as well for phosphorus-limited tropical forests (Luo et al., 2021).

4.4. Differences in the Correlations Between the Two Shrub Species

When focusing only on the species *B. nana*, we found a similar pattern as described above: nutritional leaf traits were again strongly correlated with FAPAR while structural leaf traits showed no correlation with FAPAR. The correlation between FAPAR and LNC as well as LPC might point toward a possible nutrient co-limitation as a constraint of light absorption in *B. nana* shrubs that can be alleviated by fertilization (Klupar et al., 2021). If nutrients are sufficiently available, *B. nana* can adjust photosynthesis accordingly and absorb more of the available light. These relationships are particularly relevant, also for future models and predictions, since *B. nana* is the tundra shrub species that appears to benefit most from climate-related changes (Heim et al., 2021; Myers-Smith et al., 2011).

Surprisingly, we found different relationships between leaf traits and FAPAR in *S. pulchra*. In *S. pulchra*, FAPAR was correlated to LNC, like in *B. nana*, but not to LPC. Regarding the previous discussion of this study, it can be assumed that *S. pulchra* is not limited by phosphorus. *S. pulchra* grows in moisture areas within the study site and probably also within moisture microsites within plots. This is an advantage, as phosphate anions are generally not very mobile in soils (Hinsinger, 2001). The uptake of phosphorus is strongly dependent on the diffusion of phosphorus and therefore decreases with decreasing soil moisture (Bhadoria et al., 1991; Gahoonia et al., 1994).

A different strategy of *B. nana* and *S. pulchra* was also identified in a previous study of this experiment that explained differences in traits between both species by a whole-plant strategy (coordination of stem and leaf traits in the same direction) of *B. nana* (Iturrate-Garcia et al., 2020). The lack of coordination between stem and leaf traits in *S. pulchra* was explained by possible trade offs that lead to an independent coordination of stem and leaf traits (Fortunel et al., 2012; Iturrate-Garcia et al., 2020).

The correlation between FAPAR and nutritional leaf traits indicates that plant traits are a valuable tool to predict climate change effects on the strategy of deciduous tundra shrubs (Myers-Smith et al., 2019). This strategy shift from conservative to acquisitive often follows a clear linear relationship when regarding light acquisition and nutritional traits.

5. Conclusions

Our study reveals that light absorptance plays a major role in the strategy shift of tundra shrubs from conservative to acquisitive under increased nutrient availability and warming. This finding similarly promises us a better understanding of these trait-based relationships and also better possibilities for predicting future developments in the tundra ecosystem (Myers-Smith et al., 2019). This observed strategy change of tundra shrubs may even induce a positive reinforcing feedback loop, increasing shrub encroachment in tundra ecosystems (Myers-Smith et al., 2011): warming and fertilization effects lead to increased light absorptance, thus, to enhanced growth which is followed by increased high quality litter input.

The role of FAPAR for the strategy shift of tundra shrubs fits well with findings from previous studies of the experiment, which showed that tundra shrubs can profit from increased nutrient availability and turn to a more acquisitive strategy, evident through increased biomass and adapted leaf traits (Iturrate-Garcia et al., 2020; Wang et al., 2017).

The relationship between FAPAR and nutritional plant traits under fertilization and warming not only indicates the strategy change of these shrub species, but also shows that remote sensing methods may be able to use FAPAR for the estimation of nutritional plant traits and related nutrient cycles. The relationship between FAPAR and nutritional plant traits allows us to get information on nutrient cycling on a broader landscape scale via remotely sensed leaf traits (Ustin, 2013). As FAPAR is commonly used to describe the exchange of energy and mass between the land surface and atmosphere (Liu & Treitz, 2018; Myneni & Williams, 1994), remote sensing driven biogeochemical models that use FAPAR to estimate productivity may be able provide information on nutrient cycling in ecosystems. Of course, leaf area and number of leaves have to be accounted for along with scaling LOP to canopy level.

In this study, we demonstrate that there are differences between deciduous shrub species in terms of light absorption under the influence of fertilization and warming. We attribute these differences to mycorrhizal facilitation. Future studies and predictions must not only differentiate between functional groups, but also between species for a precise estimation of vegetation responses to fertilization and warming. Furthermore, habitat preferences of the

species should not be neglected when evaluating nutrient contents and related cycles, as well as light absorption. Nonetheless, we demonstrate that the use of FAPAR as a measure may provide new opportunities to better understand how Arctic plants, both in their form and function, are responding to global changes, in a rapidly thawing and warming Arctic.

Data Availability Statement

The data and R scripts used for this study are available at Zenodo via https://doi.org/10.5281/zenodo.7615321 and https://doi.org/10.5281/zenodo.7615735.

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