

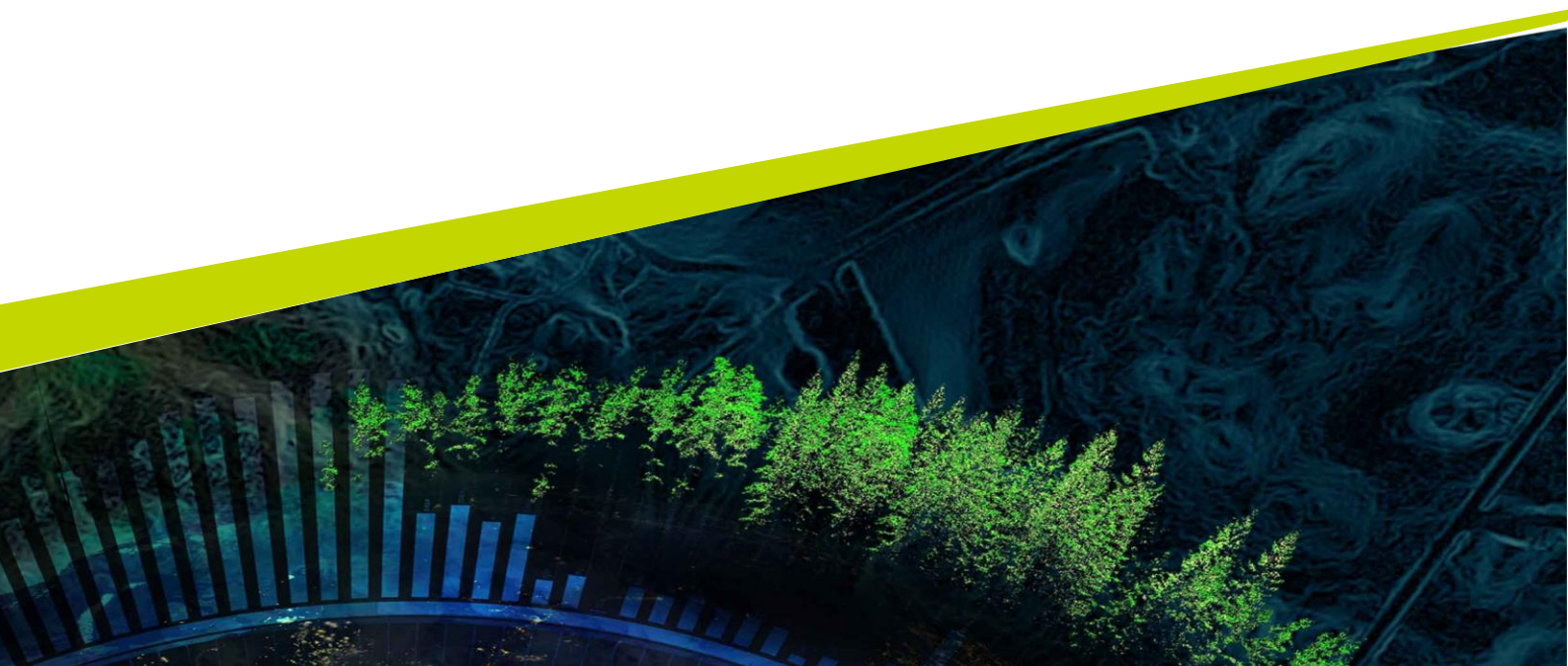


# Effects of climate, soil, and forest structure on specific leaf area of understorey foundation plants

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Master's thesis • 30 credits  
Swedish University of Agricultural Sciences, SLU  
Southern Swedish Forest Research Centre  
Sustainable Forest and Nature Management (SUFONAMA)  
Alnarp 2023



# Effects of climate, soil, and forest structure on specific leaf area of understorey foundation plants

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## Abstract

Forest overstorey's interaction with understorey vegetation is a crucial aspect that impacts the biodiversity and resilience of forest ecosystems. Particularly, the influence of the overstorey on the specific leaf area (SLA) in understorey plants remains poorly understood. This is due to limited research within particular climatic conditions and a narrow focus on limited biogeographical areas, which leaves significant knowledge gaps, especially in boreal regions. This study aims to address these gaps by exploring how the SLA of understorey plants responds to variations in forest structure, soil characteristics, and climate across diverse Swedish forests. To achieve this aim, this study embodied three distinct study designs, namely a large-scale study, a mixed forest study, and a transplant experiment. Cowberry and bilberry were chosen for the large-scale and mixed forest studies, while wild strawberry and goldenrod were selected for the transplant experiment. Leaf samples of these species were used for this study. Cowberry being evergreen, the leaf samples were collected from old shoots and new shoots, which are termed as “*cowberry old growth*” and “*cowberry new growth*”, respectively. The large-scale study consisted of three sites covering latitudes of 57° N to 64° N, each with 15-16 stands dominated by Scots pine or Norway spruce. The mixed forest study comprised a stand mainly with Norway spruce and birch where 40 plots were strategically placed across gradients of varying forest density and overstorey species composition. For the transplant experiment, understorey plants were planted in pairs with different climatic origins, at three sites in Sweden. Plants were planted in ten plots per site, established at diverse tree species composition and forest density values. Forest density had a significant positive effect on the SLA of understorey plants. The percentage of pine had a significant negative effect on SLA in the large-scale study. The percentage of broadleaves had a significant negative effect on SLA in mixed forest study and transplant experiment. Soil C-N ratio did not have significant effect on the SLA. Soil moisture availability had no significant impact on the SLA of the understorey plants except for the cowberry new growth in large-scale study and bilberry in mixed forest study. The interaction between forest density and the percentage of pine only significantly affected the cowberry new growth in the large-scale study. Furthermore, the SLA of wild strawberry and goldenrod was not affected by climatic origin, and the interaction between forest density and origin was also not significant. These findings help to predict how the SLA of understorey plants changes related to forest structure, as well as to changes induced by climate warming, while at the same time enriching our insight into plant-environment interactions.

*Keywords:* Specific leaf area, understorey vegetation, foundation species, forest structure, climate change

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## Abbreviations

|               |   |
|---------------|---|
| AIC           | Akaike Information Criterion                |
| BA            | Total Basal Area                            |
| C-N           | Carbon Nitrogen                             |
| DBH           | Diameter at Breast Height                   |
| GLMMs         | Generalized Linear Mixed Models             |
| SLA           | Specific Leaf Area                          |
| SLU           | Swedish University of Agricultural Sciences |
| SM            | Soil Moisture                               |
| % pine        | Percentage of pine                          |
| % broadleaves | Percentage of broadleaves                   |



# 1. Introduction

Forests are complex ecosystems that comprise different biotic and abiotic components, which interact among themselves and contribute to ecosystem functioning. While trees are the dominant structures in a forest ecosystem, it also hosts understorey vegetation which includes seedlings, herbs, shrubs, mosses, and lichens (Deng et al. 2023). Several studies have reported the role of the understorey in the functioning of forest ecosystems such as nutrient cycling, water balance, and carbon sequestration (Balandier et al. 2022a; b; Deng et al. 2023; Duan et al. 2023). In addition, understorey plants support biodiversity by providing food and habitat to animals, insects, and soil arthropods (Balandier et al. 2022b; Xiao et al. 2022; Zhang et al. 2022; Deng et al. 2023). Understorey plants are also found to increase bird diversity in the Mediterranean region (Dagan & Izhaki 2019).

The overstorey in northern forests can be composed of deciduous trees or evergreen trees, often in mixtures. Likewise, the overstorey trees also may vary in age and height. Such factors combinedly shape the overstorey forest structure. The heterogeneity in overstorey structure controls the amount of light entering the forest and thus microclimate buffering (Balandier et al. 2022b; Christiansen et al. 2022; Deng et al. 2023). Natural disturbance is considered an important factor that maintains the structural heterogeneity of the overstorey (Kuuluvainen et al. 2021). Naturally, forest disturbance is caused by biotic agents like insects or by events of windthrow and fire, and thus helps in maintaining biodiversity in the forest through species reassembly (Kuuluvainen et al. 2021). However, climate change has increased the frequency and severity of these natural disturbances (Seidl et al. 2014, 2017; Romeiro et al. 2022) and have resulted in adverse effects on the forest ecosystem. For instance, the tree canopy mortality rate has increased on average by 0.79% per year in Europe from 1984 to 2016 (Senf et al. 2018), which is attributed to climate change induced forest disturbances. This canopy mortality was found to increase by 0.41% for a 1°C rise in mean annual temperature (Senf et al. 2018). Moreover, the damage to timber volume from disturbances such as wind, bark beetle, and fire is predicted to increase by ca 230%, 760%, and 310% respectively in 2011-2030 as compared to 1971–1980 (Seidl et al. 2014). Similarly, a significant positive trend in the impacts of natural disturbance in Europe was documented in a study by Patacca et al. (2023). Such evidence

indicates that the severity of forest disturbances will increase leading to increased tree mortality, which will likely promote canopy openness and decrease tree density in the forest (Kumar et al. 2021). A study by Thom et al. (2020) shows that the amount of light reaching the understorey can increase by 227% for distributed disturbances to 387% for aggregated disturbances relative to the undisturbed area. Also, a 10% increase in light in the understorey was found to increase microclimatic temperature variation by 0.11°C (Thom et al. 2020). Another factor that affects overstorey structure is anthropogenic disturbances such as logging, overgrazing, and deforestation (Mcdowell et al. 2020). Silvicultural activities such as thinning, pruning, felling, and weeding also change forest structure which further effects light and water interception, evapotranspiration, and ultimately altering microclimate inside the forest which affects understorey plants (Balandier et al. 2022b; Christiansen et al. 2022; Deng et al. 2023).

Understorey plants respond to such changes in light and microclimate by altering their functional traits (Funk et al. 2017; Blondeel et al. 2020; Kemppinen & Niittynen 2022). Plant functional traits - characteristics of plant species that influence their ecological function and interactions with the environment, other species, and different trophic levels, are increasingly being used as a reliable and effective approach to investigate a direct link between individual plants and ecosystem-level functions (Pérez-Harguindeguy et al. 2016). Furthermore, functional traits can help explain the response of plants to past and future climates (Heilmeier 2019).

Among such traits, specific leaf area (SLA) is a commonly used trait for ecological studies. SLA is defined as “*the one-sided area of a leaf divided by its oven-dry mass, expressed in m<sup>2</sup>/kg or in mm<sup>2</sup>/mg*” (Cornelissen et al. 2003). SLA is a valuable indicator of plant performance and ecological strategies, as it reflects the balance between growth and resource acquisition rate levels (Pérez-Harguindeguy et al. 2016). SLA is also crucial in influencing the productivity of plants, as variations in SLA indicate changes in leaf structure and therefore their nutritional composition. SLA was, for example, found to be the best predictor of tree species response to climate change in mixed sub-tropical forests (Schlickmann et al. 2020). Species growing in areas with abundant resources tend to have higher SLA compared to species growing in resource-deficit areas (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). Therefore, we can consider SLA to be a proxy for the costliness of leaf production. Leaves with higher SLA (lower thickness and/or density) are more efficient in utilizing low amounts of diffuse radiation, and they have greater relative growth rates under favourable conditions. On the other hand, leaves with lower SLA (greater thickness and/or density) are more efficient in utilizing high levels of radiation and are more tolerant to water and nutrient deficiencies (Burns 2004). Such plasticity of SLA can increase the resilience of plants to disturbance and changing

environmental conditions (Römermann et al. 2011). Additionally, SLA influences the expansion and growth of plant canopies by affecting the overall leaf area per plant, thereby impacting light interception and utilization efficiency (Poorter et al. 2019).

Plant species characterized by high SLA demonstrate increased nutrient absorption and photosynthetic capacity, contributing significantly to the primary productivity of the community (Wright et al. 2001; Chelli et al. 2019; Anderson et al. 2020), and thus reflecting their importance within the community. This also implies greater availability of food for herbivorous organisms. A higher SLA is also linked to increased susceptibility to herbivory due to the higher palatability of the tissue (Funk et al. 2017). Furthermore, variations in SLA influence the changes in vegetation dynamics in an ecosystem ultimately affecting ecosystem processes, including energy flow and nutrient cycling. A review by Shome et al. (2023) provides evidence for a positive association of SLA with several ecosystem services including water regulation, biomass production, litter decomposition, nutrient cycling, and aesthetic appeal. The same review shows a strong negative association of SLA with phytoremediation, a process by which plants naturally absorb, store, and transform harmful chemicals from soil, water, and air (Shome et al. 2023). Additionally, previous studies have documented a strong positive correlation of SLA with aboveground net primary productivity (Garnier et al. 2004), and aboveground biomass (Ali et al. 2017). Moreover, SLA plays a role in determining the amount of new leaf area produced per unit of biomass (Niklas et al. 2007), and it directly affects the decomposition process by influencing the relative exposure of leaf litter surfaces to abiotic factors such as UV light, soil moisture, and soil microbes (Liu et al. 2018). High SLA values are also associated with higher litter decomposition rates (Garnier et al. 2004; Mokany et al. 2008), implying that species with thinner leaves experience a faster breakdown of organic matter. SLA has been found to have a negative relationship with aboveground carbon stocks of trees, and this association increases with increasing spatial scale (Bu et al. 2019). Additionally, SLA is negatively related to soil C-N (carbon to nitrogen) on a global scale (Garnier et al. 2004; Ordoñez et al. 2009), and it is also negatively correlated with total soil carbon and total soil nitrogen while being positively correlated with the rate of litter mass loss (Garnier et al. 2004). Such correlation of SLA to diverse factors which in turn shapes ecosystem functioning highlights the significance of the use of SLA in ecological studies.

The factors that impact SLA may vary based on the plant species and environmental conditions but typically include factors such as light, nutrients, water, temperature, and disturbances (Poorter et al. 2009; Gong & Gao 2019; Blondeel et al. 2020; De Pauw et al. 2022). Previous studies on the effect of such factors on SLA have been limited to homogenous climatic conditions (Wasof et

al. 2013) or based on limited biogeographic regions (Chelli et al. 2019). Yet, such studies in boreal regions are scarce. A comprehensive understanding of such factors can help to predict how individual plant species and ecosystems may respond to environmental changes and provide valuable insights into plant-environment interactions. Moreover, the relationship between the SLA of understorey plants and forest structure, along with the combined effect of climate is yet to be explored. Quantification of such relationship is crucial for forest management decisions and to study the effects of climate change.

This study endeavours to bridge the knowledge gap on how the SLA of understorey plants responds to varying forest structures, soil, and climate. The outcomes of this study can be insightful for policymakers in framing plans for reducing the effects of climate change and land-use impacts and adapting to them in preserving biodiversity and improving ecosystem services. Also, it will assist as a reference for national and international organizations involved in conserving biodiversity and lowering the effect of climate change on understorey vegetation in similar systems.

## 1.1 Objectives

The general objective of this study was to identify key drivers of SLA of understorey plants.

The specific objectives of this study are as follows:

Objective 1: To quantify the influence of forest structure on the SLA of understorey plants.

Research question: How does variation in forest structure influence the SLA of understorey plants?

Objective 2: To investigate the relationship between soil variables and the SLA of understorey plants.

Research question: How do soil nutrient and soil moisture availability affect the SLA of understorey plants?

Objective 3: To investigate the effect of climate change on understorey plants.

Research question: How does warming affect the SLA of understorey plants?

## 2. Methodology

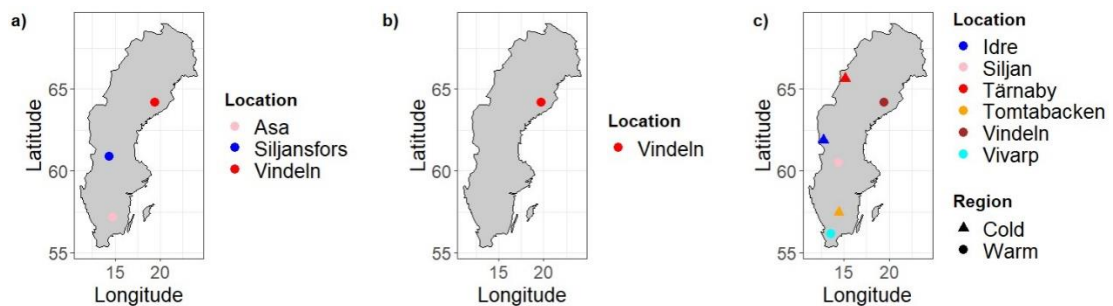


Figure 1. Map of Sweden showing study locations. a) the large-scale study, b) the mixed forest study, c) the transplant experiment (Triangle shapes represent cold regions whereas the solid circles represent the warm regions. Transplant was done from Tärnaby, Idre, and Tomtabacken to Vindeln, Siljan, and Vivarp, respectively.)

This study was based on available datasets from three different studies, here called the large-scale study, the mixed forest study, and the transplant experiment. All the sites used in the study were located in Sweden (Figure 1). The understorey plants used for the large-scale study and mixed forest study were cowberry (*Vaccinium vitis-idaea* L.), and bilberry (*Vaccinium myrtillus* L.). Wild strawberry (*Fragaria vesca* L.), and goldenrod (*Solidago virgaurea* L.) were selected for the transplant experiment.

Cowberry, bilberry, wild strawberry, and goldenrod are common understorey species occurring all over Sweden (Sjörs 1999; Nilsson & Wardle 2005). Cowberry and bilberry are woody dwarf shrubs, whereas wild strawberry and goldenrod are herbaceous. Regarding the dwarf shrubs, cowberry is evergreen whereas bilberry sheds its leaves yearly in autumn (Ritchie 1955, 1956). Moreover, cowberry and bilberry often dominate the ground vegetation, provide fruits, have significant positive impacts on soil microbial activities and litter decomposition, influence the regeneration of tree seedlings, and play a significant role in the functioning of the forest ecosystem (Nilsson & Wardle 2005). Such characteristics qualify cowberry and bilberry as foundation species, which can be defined as “a species (or group of functionally similar taxa) that dominates an assemblage numerically and in overall size (usually mass), determines the diversity of associated taxa through non-trophic interactions, and modulates

fluxes of nutrients and energy at multiple control points in the ecosystem it defines” (Ellison 2019).

## 2.1 Study area and Study design

### 2.1.1 Large-scale study

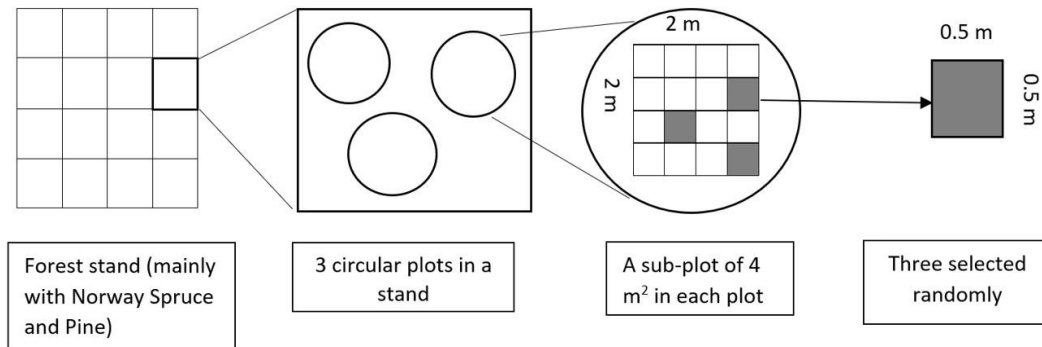


Figure 2. Sampling design for the large-scale study

The study design and data collection for the large-scale study were done in August and early September 2020. The conceptual figure for study design is shown in Figure 2. Three sites (Asa, Siljansfors, and Vindelns; Figure 1a), were selected, spanning a latitudinal gradient from 57° N to 64° N to include a wide environmental and climatic variation. Asa and Siljansfors had 16 forest stands each whereas Vindelns had 15 stands. The stands were selected based on species composition, age, and stand fertility. This data was already available at each SLU field station. The stands were divided into four categories based on age: early (6-15 years), young (16-48 years), middle (49-75 years), and old (>76 years old). The stands were either dominated by Scots pine (*Pinus sylvestris* L.; hereafter pine) or Norway spruce (*Picea abies* (L.) H. Karst.; hereafter Norway spruce). Three circular plots (which acted as replicates) of 5 m radius (in the young stand) or 8 m (for the other tree age categories) were placed in each stand to measure tree data and soil data. A 4 m<sup>2</sup> square sub-plot was located in the centre of each plot which further consisted of sixteen 0.25 m<sup>2</sup> squares. Three sub-plots were selected randomly in each plot, where all understorey plant measurements and sampling took place.

### 2.1.2 Mixed forest study

The mixed forest study was based on a single stand in Vindelns (Figure 1b). The stand consisted of a mixed forest with mainly Norway spruce and birch (*Betula pendula* Roth and *B. pubescens* Ehrh.; hereafter birch) and other broadleaves in

small amounts. Within this stand, 40 circular plots with a 10 m radius were selected. These plots were located across a double gradient of forest density and species composition so that they captured the maximum variability of forest density and tree species composition. In each plot, a sub-plot of 2 m<sup>2</sup> was established, from which understorey plant biomass was collected. Samples were collected in July 2020.

### 2.1.3 Transplant experiment

In the transplant experiment, wild strawberry and goldenrod were collected from six sites in Sweden, organized into three pairs (Figure 1c). Each pair consisted of one site with a colder climate where the mean annual temperature was on average 2°C lower (Tomtabacken, Idre, and Tärnaby), and one site with a warmer climate (Siljan, Vindeln, and Vivarp). In 2020, plants original to the cold provenances were translocated to their relatively warmer sites (hereafter called *cold origin*). There, local plants were also reotted to standardize soil and stress conditions (hereafter called *local origin*).

The collection of understorey plants was done at 2-4 places, which were placed at least 1 km apart from each other, within forest stands at each location (both cold and warm sites). For wild strawberry, a distance of at least 7 m between individuals was considered during collection to avoid collecting ramets from the same clone. For goldenrod, individuals with mature seed were collected without taking distance between individuals into consideration. The collection was done during summer of 2020. Wild strawberry was then planted in container trays and kept in a garden at each warm site until replanting in the bigger pots, and finally placed in the forest in spring 2021. The goldenrod seeds were stored over winter and germinated. They were planted in container trays in spring and summer 2021 and were placed in the forest in August 2021. In each warmer site, 10 circular plots of a 10 m radius were established within a single forest stand. Forest stands consisted mainly of Norway spruce and birch. Large variations in tree species composition and forest density were present within these plots, allowing for the capture of maximum variability in both factors. A 7.5 L pot was used, and four plant individuals were planted in each pot. The pots were inserted into the soil at the destination site and plot with a spade. A soil with medium pH- "Hasselfors P-jord" was used. All plots within a site had similar soil conditions and slight altitudinal variations. Additionally, the plots in Vivarp were fenced to protect them from big herbivores. Strawberries were sampled in August 2021 and 2022 whereas goldenrods were sampled in August 2022.

## 2.2 Data collection

### 2.2.1 Collection of samples from understorey plants

The rhizomatous nature of understorey plants (bilberry and cowberry) limited the sampling of individual plants. Therefore, three clonal units per species (hereafter called ramets) that were free from damage were selected randomly in each sub-plot in the large-scale study. In the mixed forest study, six ramets were collected for bilberry and cowberry. The total number of terminal shoots per ramet was recorded, and shoots growing from the ramets were detached and air-dried. For cowberry, the leaf samples were collected from old shoots and new shoots, which are hereafter called “cowberry old growth” and “cowberry new growth”, respectively. New shoots were separated from old shoots by comparing the colour of the stem and leaves to older biomass. Bilberry is deciduous and hence only newly grown leaves samples were collected. The leaves were selected randomly, ensuring that they represented the various leaf sizes present within each ramet and maintaining the proportional occurrence of these sizes. A total of 50 leaves were sampled from each bilberry ramet and 25 from each cowberry ramet and growth section (i.e., old, and new growth). In instances where only a smaller quantity of leaves was available, all of them were utilized.

In the case of the transplant experiment, one leaf from each pot of wild strawberry and goldenrod (of both cold and local origin) was collected in August 2021.

### 2.2.2 Collection of overstorey data

The species of all living trees taller than 1.3 m and their diameter at breast height (DBH) were recorded in each plot. The total basal area per plot (BA) and basal area contribution of each tree species were calculated. BA was used as a proxy for forest density in this study and was calculated in units of  $\text{m}^2/\text{ha}$ . Further, the percentage of basal area of broadleaves (% broadleaves; for the mixed and transplant experiments) or pine trees (% pine; for the large-scale experiment) per plot was calculated from the basal area contribution of each tree species. The age of measured trees at 1.3 m was determined using a core sample taken at breast height. The height of the tree with the largest DBH was measured in two plots per stand. If the largest tree had a damaged or crooked stem, the next biggest tree was selected.

### 2.2.3 Collection of soil data

Four soil samples within each circular plot and outside the 4  $\text{m}^2$  sub-plots for plant data collection were collected in the large-scale study and the mixed forest study. Litter was removed from the soil surface before sampling. Any rock and



other impediments were avoided during the collection of soil. A 10 cm deep soil sample including both humus and mineral soil was collected. Using a Theta Probe (Type ML1; Delta-T Devices, Cambridge, UK), soil moisture (SM) was measured and was expressed in percentage. In the mixed forest study, SM was measured taking three measurements per sub-plot, taken within 2 m from the sampled ramet. The three measurements were taken at different locations within the 4 m<sup>2</sup> sub-plot, trying to account for the sub-plot heterogeneity.

All soil samples from the same plot were pooled and dried at 60°C to remove most SM. The soil sample was then analyzed for total carbon and nitrogen content with an Avio 200 ICP spectrometer (PerkinElmer, Waltham, Massachusetts, USA), from which the C-N ratio was calculated.

## 2.3 Data preparation

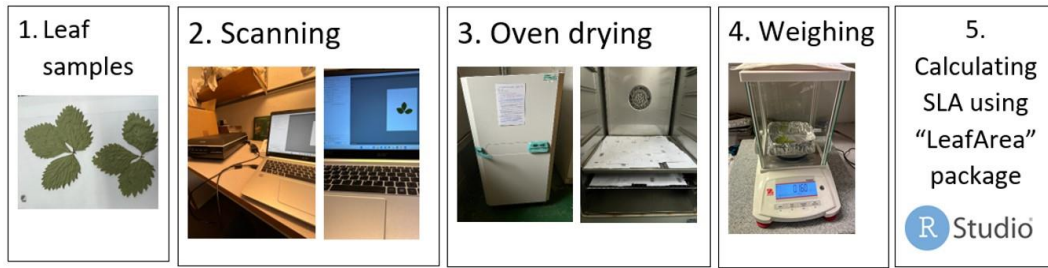


Figure 3. Procedures for SLA calculation

SLA (in mm<sup>2</sup>/mg) for each leaf sample was determined following standard procedures (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). The procedure involves leaf sample scanning, drying, and measuring the dry weight of leaves as shown in Figure 3. Leaf samples were scanned using a flatbed scanner. The leaf area of the scanned leaves was calculated by importing scanned images of leaf samples into R version 4.1.3 (R Core Team 2022) and utilizing the 'LeafArea' package, which enables leaf area calculation through batch-processing of several images in the ImageJ software (Katabuchi 2015). After scanning leaf samples, they were dried in an oven at 60°C for 48hrs. SLA was calculated for each leaf sample using Equation 1.

$$SLA = \frac{\text{One sided area of leaf}}{\text{Oven dry weight of the leaf}} \quad (1)$$

The available explanatory variables were checked for collinearity by making scatter plots in R and checking their correlation with Spearman's correlation coefficients. Variables with a Spearman's correlation coefficient above 0.7 were removed from further analysis to ensure the inclusion of independent variables with minimal multicollinearity. Finally, the selected explanatory variable for each study is presented in Table 1.

Table 1. Variables selected for model generation and their abbreviations used in the text.

| Study                 | Explanatory variables                     |                     |
|-----------------------|---|---------------------|
|                       | Continuous                                | Categorical         |
| Large-scale study     | Total Basal Area (BA)                     | Stand               |
|                       | Percentage of pine (% pine)               |                     |
|                       | C-N ratio                                 |                     |
|                       | Soil Moisture (SM)                        |                     |
| Mixed forest study    | Total Basal Area (BA)                     |                     |
|                       | Percentage of broadleaves (% broadleaves) |                     |
|                       | C-N ratio                                 |                     |
|                       | Soil Moisture (SM)                        |                     |
| Transplant experiment | Total Basal Area (BA)                     | Site                |
|                       | Percentage of broadleaves (% broadleaves) | Origin (Cold, Warm) |
|                       |   |                     |

## 2.4 Data analysis

All data analyses were performed in R version 4.1.3 (R Core Team 2022). All the continuous explanatory variables were standardized before further analysis by subtracting their respective mean and dividing by their standard deviation. This standardization of variables ensures that all explanatory variables are on the same scale and magnitudes of coefficients can be directly compared. The coefficient values of explanatory variables mirror the change in the dependent variable (i.e., SLA in this study) linked with a one standard deviation increase or decrease in the standardized explanatory variable. Larger coefficient values of the explanatory variable indicate a more robust association with SLA. Generalized linear mixed models (GLMMs) were fitted using the *glmmTMB* function of the 'glmmTMB' package (Brooks et al. 2017). The 'glmmTMB' package was chosen for its ability to handle a wide range of response distributions which enables the selection of the best distribution and link function depending on the characteristics of the response variable and its efficient optimization techniques (adaptive Gaussian quadrature or Laplace approximation) (Brooks et al. 2017). In addition, the package allowed for the inclusion of random effects to account for within-group correlation, which is necessary when the data is clustered or hierarchical. The data used in this study had a hierarchical structure (i.e., multiple plots were present within a site). Gaussian distribution was chosen for the fitted models. Stand (in the large-scale study) and Site (in the transplant experiment) were included as random intercept effects in the fitted models to account for grouping or nesting (i.e., observations in

the same stand or site are likely to be similar as compared to observations between different stands and site). So, by including these variables as random intercept effects, the difference in SLA between the stand or site is accounted for. The fitted models are presented in Table 2.

Table 2. Table showing candidate models for the various studies. Note that Stand and Site were always used as random effects.

| <b>Study</b>                 | <b>Fitted models</b>   |
|------------------------------|--|
| <b>Large-scale study</b>     | <b>Model 1:</b> $SLA = BA \times \% \text{ pine} + C\text{-N ratio} + SM + \text{Stand}$ |
|                              | <b>Model 2:</b> $SLA = BA + \% \text{ pine} + C\text{-N ratio} + SM + \text{Stand}$      |
| <b>Mixed forest study</b>    | <b>Model 1:</b> $SLA = BA \times \% \text{ broadleaves} + C\text{-N ratio} + SM$         |
|                              | <b>Model 2:</b> $SLA = BA + \% \text{ broadleaves} + C\text{-N ratio} + SM$              |
| <b>Transplant experiment</b> | <b>Model 1:</b> $SLA = BA \times \% \text{ broadleaves} + \text{Site}$                   |
|                              | <b>Model 2:</b> $SLA = BA + \% \text{ broadleaves} + \text{Site}$                        |
|                              | <b>Model 3:</b> $SLA = BA \times \text{Origin} + \text{Site}$                            |
|                              | <b>Model 4:</b> $SLA = BA + \text{Origin} + \text{Site}$                                 |

Finally, SLA was predicted for low, mean, and high values of % pine for large-scale study and low, mean, and high values of % broadleaves for mixed forest and transplant experiments. Akaike Information Criterion (AIC) was used to select the best model, lower AIC indicating a better fit of the model. Geospatial package (Dunnington 2022) was used to create maps of the study area, and the *ggplot* function of the 'ggplot2' package (Wickham 2016) was used to create all the graphs.

## 3. Results

### 3.1 Large-scale study

The results demonstrate Model 2 (AIC = 820.6) shows slightly better fit when compared with Model 1 (AIC = 821.5) for bilberry. Both Model 1 (Z value = 3.56,  $p < 0.001$ ) and Model 2 (Z value = 4.13,  $p < 0.001$ ) show the effect of BA on SLA was significantly positive whereas both models showed that % pine had a significant negative effect on SLA (Z value = -2.12,  $p < 0.05$  in Model 1; Z value = -2.04,  $p < 0.05$  in Model 2) (Table 3). However, the C-N ratio ( $p = 0.311$  in Model 1;  $p = 0.223$  in Model 2) and SM ( $p = 0.791$  in Model 1;  $p = 0.633$  in Model 2) did not show significant effects on SLA in any of the models (Table 3). Furthermore, the interaction between BA and % pine was not significant (Z value = -1.04,  $p = 0.301$ ) (Table 3).

Table 3. Summary of model output for bilberry in the large-scale study.

| <b>Model 1 : <math>SLA = BA \times \% \text{ pine} + C\text{-N ratio} + SM + Stand</math> (as random intercept effect)</b> |                 |                       |                |                    |
|--|-----------------|-----------------------|----------------|--------------------|
| AIC = 821.5  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 7.36            | 0.47                  | 15.56          | <0.001             |
| BA   | 1.68            | 0.47                  | 3.56           | <0.001             |
| % pine   | -0.99           | 0.47                  | -2.12          | 0.034              |
| C-N ratio  | -0.62           | 0.62                  | -1.01          | 0.311              |
| SM   | -0.19           | 0.45                  | -0.27          | 0.791              |
| BA $\times$ % pine   | -0.51           | 0.49                  | -1.04          | 0.301              |
| <b>Model 2: <math>SLA = BA + \% \text{ pine} + C\text{-N ratio} + SM + Stand</math> (as random intercept effect)</b>       |                 |                       |                |                    |
| AIC = 820.6  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 7.442           | 0.49                  | 15.03          | <0.001             |
| BA   | 1.84            | 0.45                  | 4.13           | <0.001             |
| % pine   | -0.95           | 0.47                  | -2.04          | 0.041              |
| C-N ratio  | -0.74           | 0.61                  | -1.22          | 0.223              |
| SM   | -0.21           | 0.44                  | -0.49          | 0.633              |

For cowberry new growth, Model 1 (AIC = 432) had better fit than Model 2 (AIC = 442.5). Similar to the results of bilberry, both Model 1 (Z value = 7.83,  $p < 0.001$ ) and Model 2 (Z value = 8.80,  $p < 0.001$ ) showed that BA had a significant positive effect on the SLA of cowberry new growth whereas % pine had a significant negative effect on SLA for both Model 1 (Z value = -8.46,  $p < 0.001$ ) and Model 2 (Z value = -7.48,  $p < 0.001$ ) (Table 4). While the C-N ratio did not show a significant effect on SLA in any of the models, SM had a significant negative effect in Model 2 (Z value = -2.29,  $p < 0.05$ ) (Table 4). Furthermore, the interaction between BA and % pine was significant in Model 1 (Z value = -3.51,  $p < 0.001$ ), suggesting that the proportion of pine influences the effect of BA on SLA (Table 4).

Table 4. Summary of model output for cowberry new growth in the large-scale study.

| <i>Model 1: SLA = BA × % pine + C-N ratio + SM + Stand (as random intercept effect)</i> |          |                |         |          |
|---|----------|----------------|---------|----------|
| AIC = 432   |          |                |         |          |
| Variables   | Estimate | Standard Error | Z value | Pr(> z ) |
| Intercept   | 3.65     | 0.24           | 15.32   | <0.001   |
| BA  | 1.26     | 0.16           | 7.83    | <0.001   |
| % pine  | -1.42    | 0.17           | -8.46   | <0.001   |
| C-N ratio   | -0.11    | 0.20           | -0.52   | 0.604    |
| SM  | -0.20    | 0.15           | -1.36   | 0.174    |
| BA × % pine   | -0.63    | 0.18           | -3.51   | <0.001   |

| <i>Model 2: SLA = BA + % pine + C-N ratio + SM + Stand (as random intercept effect)</i> |          |                |         |          |
|---|----------|----------------|---------|----------|
| AIC = 442.5   |          |                |         |          |
| Variables   | Estimate | Standard Error | Z value | Pr(> z ) |
| Intercept   | 3.71     | 0.24           | 15.42   | <0.001   |
| BA  | 1.42     | 0.16           | 8.80    | <0.001   |
| % pine  | -1.28    | 0.17           | -7.48   | <0.001   |
| C-N ratio   | -0.22    | 0.21           | -1.04   | 0.3      |
| SM  | -0.35    | 0.15           | -2.29   | 0.021    |

For cowberry old growth, Model 2 (AIC = 434.1) had better fit than Model 1 (AIC = 435.3). Both Model 1 (Z value = 4.07,  $p < 0.001$ ) and Model 2 (Z value = 4.39,  $p < 0.001$ ) showed BA had significant positive effect on SLA whereas % pine had significant negative effect on SLA in both models (Z value = -5.04,  $p < 0.001$  in Model 1; Z value = -4.96,  $p < 0.001$  in Model 2) (Table 5). Both variables C-N ratio and SM did not show significant effects on SLA for any of the models. Furthermore, the interaction between BA and % pine was also not significant in Model 1 (Z value = -0.88,  $p = 0.379$ ) (Table 5).

Table 5. Summary of model output for cowberry old growth in the large-scale study.

| <b>Model 1: <math>SLA = BA \times \% \text{ pine} + C\text{-N ratio} + SM + Stand</math> (as random intercept effect)</b> |          |                |         |          |
|---|----------|----------------|---------|----------|
| AIC = 435.3   |          |                |         |          |
| Variables   | Estimate | Standard Error | Z value | Pr(> z ) |
| Intercept   | 3.19     | 0.17           | 18.46   | <0.001   |
| BA  | 0.65     | 0.16           | 4.07    | <0.001   |
| % pine  | -0.84    | 0.17           | -5.04   | <0.001   |
| C-N ratio   | -0.23    | 0.21           | -1.09   | 0.278    |
| SM  | -0.07    | 0.15           | -0.45   | 0.655    |
| BA $\times$ % pine  | -0.15    | 0.17           | -0.88   | 0.379    |
| <b>Model 2: <math>SLA = BA + \% \text{ pine} + C\text{-N ratio} + SM + Stand</math> (as random intercept effect)</b>      |          |                |         |          |
| AIC = 434.1   |          |                |         |          |
| Variables   | Estimate | Standard Error | Z value | Pr(> z ) |
| Intercept   | 3.2      | 0.18           | 18.12   | <0.001   |
| BA  | 0.69     | 0.16           | 4.39    | <0.001   |
| % pine  | -0.81    | 0.16           | -4.96   | <0.001   |
| C-N ratio   | -0.257   | 0.21           | -1.23   | 0.217    |
| SM  | -0.1     | 0.15           | -0.66   | 0.506    |

### 3.1.1 Model prediction for large-scale study

The model prediction is demonstrated in Figure 4 for low, mean, and high % pine along with respective regression equations and R-square values. For all species, the predicted SLA increases with an increase in BA for all categories of % pine, yet the lowest predicted SLA values occur in the presence of high % pine (Figure 4). Predicted SLA ranged from 4.7-16.3 mm<sup>2</sup>/mg (under low % pine), 3.5-15.1 mm<sup>2</sup>/mg (under mean % pine), and 2.5-14.1 mm<sup>2</sup>/mg (under high % pine) (Figure 4a). For every increase of 1 m<sup>2</sup>/ha in BA, the predicted SLA of bilberry increases by 0.137 mm<sup>2</sup>/mg in all three categories of % pine (Figure 4a). In the case of cowberry new growth, the effect of interaction between BA and % pine was significant (Table 4), and hence, variations can be seen in SLA among BA gradient between three categories of % pine, with the highest for mean % pine (SLA increases by 0.15 mm<sup>2</sup>/mg for every increase of 1 m<sup>2</sup>/ha in BA) (Figure 4b). Predicted SLA ranged from 1.4-12.7 mm<sup>2</sup>/mg (under low % pine), 0.8-8.03 mm<sup>2</sup>/mg (under mean % pine), and 0.4-4.9 mm<sup>2</sup>/mg (under high % pine) for cowberry new growth (Figure 4b). For cowberry old growth, predicted SLA ranged from 2.7-6.9 mm<sup>2</sup>/mg (under low % pine), 3.1-5.8 mm<sup>2</sup>/mg (under mean pine), and 0.8-5 mm<sup>2</sup>/mg (under high % pine) (Figure 4c). Also, the R-square value is high for each case indicating the strong association between predicted SLA values and BA.

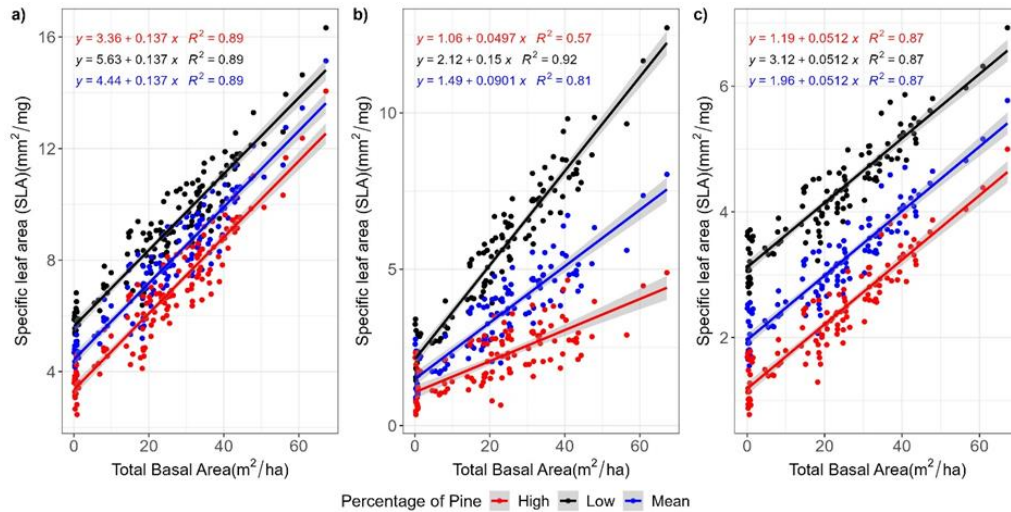


Figure 4. Predicted SLA for BA in the large-scale study using best model for a) Bilberry b) Cowberry new growth, c) Cowberry old growth. Model 1 (i.e., with the interaction between BA and % pine) resulted in the best fit for cowberry new growth. Model 2 (i.e., without interaction between BA and % pine) resulted in the best fit for bilberry and cowberry old growth. Grey regions represent a 95% confidence interval. Red, blue, and black colour indicates high, mean, and low values of % pine, respectively. Note the difference in y-axis values between the three figures.

### 3.2 Mixed forest study

For bilberry, Model 2 (AIC = 236.8) was slightly better than Model 1 (AIC = 238.2). Both models showed that BA has a significant positive effect on SLA (Z value = 4.68,  $p < 0.001$  in Model 1; Z value = 4.58,  $p < 0.001$  in Model 2) (Table 6). On the other hand, % broadleaves had a significant negative effect on SLA (Z value = -2.77,  $p < 0.001$  in Model 1; Z value = -2.78,  $p < 0.001$  in Model 2) (Table 6). Likewise, SM also had a significant negative effect on SLA in both models (Z value = -2.61,  $p < 0.001$  in Model 1; Z value = -2.54,  $p < 0.05$  in Model 2) (Table 6). However, the C-N ratio did not show significant effects on SLA for both models. Furthermore, the interaction between BA and % broadleaves was not significant (Z value = -0.81,  $p = 0.42$ ) in Model 1.

Table 6. Summary of model output for bilberry in mixed forest study.

| <b>Model 1: <math>SLA = BA \times \% \text{ broadleaves} + C\text{-}N \text{ ratio} + SM</math></b> |                 |                       |                |                    |
|---|-----------------|-----------------------|----------------|--------------------|
| AIC = 238.2   |                 |                       |                |                    |
| <b>Variables</b>  | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept   | 12.57           | 0.63                  | 19.87          | < 0.001            |
| BA  | 3.5             | 0.75                  | 4.68           | < 0.001            |
| % broadleaves   | -2.27           | 0.82                  | -2.77          | < 0.001            |
| C-N ratio   | -0.18           | 0.7                   | -0.25          | 0.801              |
| SM  | -1.9            | 0.73                  | -2.61          | < 0.001            |
| BA $\times$ % broadleaves   | -0.72           | 0.9                   | -0.81          | 0.42               |
| <b>Model 2: <math>SLA = BA + \% \text{ broadleaves} + C\text{-}N \text{ ratio} + SM</math></b>      |                 |                       |                |                    |
| AIC = 236.8   |                 |                       |                |                    |
| <b>Variables</b>  | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept   | 12.61           | 0.64                  | 19.82          | < 0.001            |
| BA  | 3.37            | 0.74                  | 4.58           | < 0.001            |
| % broadleaves   | -1.9            | 0.68                  | -2.78          | < 0.001            |
| C-N ratio   | -0.11           | 0.7                   | -0.16          | 0.874              |
| SM  | -1.86           | 0.73                  | -2.54          | 0.011              |

In cowberry new growth, Model 2 (AIC = 494.4) was better than Model 1 (AIC = 496.4). BA (Z value = 3.03,  $p < 0.001$  in Model 1; Z value = 3.05,  $p < 0.001$  in Model 2) had a significant positive effect on SLA whereas % broadleaves (Z value = -2.31,  $p < 0.05$  in Model 1; Z value = -2.65,  $p < 0.001$  in Model 2) had a significant negative effect on SLA (Table 7). The C-N ratio and SM did not show significant effects on SLA for any models. Furthermore, the interaction between BA and % broadleaves was not significant in Model 1 (Z value = -0.21,  $p = 0.835$ ) (Table 7).



Table 7. Summary of model output for cowberry new growth in mixed forest study.

| <b>Model 1: <math>SLA = BA \times \% \text{ broadleaves} + C\text{-}N \text{ ratio} + SM</math></b> |                 |                       |                |                    |
|---|-----------------|-----------------------|----------------|--------------------|
| AIC = 496.4   |                 |                       |                |                    |
| <b>Variables</b>  | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept   | 9.36            | 0.55                  | 16.91          | < 0.001            |
| BA  | 1.98            | 0.65                  | 3.03           | < 0.001            |
| % broadleaves   | -1.66           | 0.72                  | -2.31          | 0.021              |
| C-N ratio   | 0.04            | 0.61                  | 0.07           | 0.948              |
| SM  | -1.24           | 0.63                  | -1.95          | 0.051              |
| BA $\times$ % broadleaves   | -0.16           | 0.78                  | -0.21          | 0.835              |

| <b>Model 2: <math>SLA = BA + \% \text{ broadleaves} + C\text{-}N \text{ ratio} + SM</math></b> |                 |                       |                |                    |
|--|-----------------|-----------------------|----------------|--------------------|
| AIC = 494.4  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 9.36            | 0.55                  | 16.96          | < 0.001            |
| BA   | 1.95            | 0.64                  | 3.05           | < 0.001            |
| % broadleaves  | -1.57           | 0.59                  | -2.65          | < 0.001            |
| C-N ratio  | 0.05            | 0.61                  | 0.09           | 0.928              |
| SM   | -1.23           | 0.64                  | -1.94          | 0.052              |

Model 2 (AIC = 125) was slightly better than Model 1 (AIC = 126.9) for cowberry old growth. BA had a significant positive effect on SLA (Z value = 2.67,  $p < 0.001$  in Model 1; Z value = 2.79,  $p < 0.001$  in Model 2), indicating that an increase in BA was associated with higher SLA values (Table 8). On the other hand, % broadleaves did not have a significant effect on SLA in Model 1, whereas in Model 2 it had a significant negative effect (Z value = -2.06,  $p < 0.05$ ), suggesting that an increase in the proportion of broadleaves was associated with lower SLA values (Table 8). Yet, C-N ratio, SM, and interaction between BA and % broadleaves did not have significant effects on SLA in Model 1. Likewise, SLA was not affected by the C-N ratio or SM in Model 2.

Table 8. Summary of model output for cowberry old growth in mixed forest study.

| <b>Model 1: <math>SLA = BA \times \% \text{ broadleaves} + C\text{-}N \text{ ratio} + SM</math></b> |                 |                       |                |                    |
|---|-----------------|-----------------------|----------------|--------------------|
| AIC = 126.9   |                 |                       |                |                    |
| <b>Variables</b>  | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept   | 2.81            | 0.16                  | 17.86          | < 0.001            |
| BA  | 0.5             | 0.19                  | 2.67           | < 0.001            |
| % broadleaves   | -0.32           | 0.2                   | -1.57          | 0.116              |
| C-N ratio   | -0.15           | 0.17                  | -0.87          | 0.382              |
| SM  | -0.03           | 0.18                  | -0.21          | 0.832              |
| BA $\times$ % broadleaves   | 0.05            | 0.22                  | 0.24           | 0.809              |
| <b>Model 2: <math>SLA = BA + \% \text{ broadleaves} + C\text{-}N \text{ ratio} + SM</math></b>      |                 |                       |                |                    |
| AIC = 125   |                 |                       |                |                    |
| <b>Variables</b>  | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept   | 2.81            | 0.16                  | 17.88          | < 0.001            |
| BA  | 0.51            | 0.18                  | 2.79           | < 0.001            |
| % broadleaves   | -0.35           | 0.17                  | -2.06          | 0.039              |
| C-N ratio   | -0.16           | 0.17                  | -0.91          | 0.364              |
| SM  | -0.04           | 0.18                  | -0.23          | 0.819              |

### 3.2.1 Model prediction for mixed forest study

The predicted values of SLA for bilberry ranged from 7.9-23.5 mm<sup>2</sup>/mg (under low % broadleaves), 5.2-20.9 mm<sup>2</sup>/mg (under mean % broadleaves), and 1.5-17.15 mm<sup>2</sup>/mg (under high % broadleaves) (Figure 5a). Further, predicted values of SLA for cowberry new growth ranged from 6.9-16.5 mm<sup>2</sup>/mg (under low % broadleaves), 4.7-14.3 mm<sup>2</sup>/mg (under mean % broadleaves), and 1.7-11.3 mm<sup>2</sup>/mg (under high % broadleaves) (Figure 5b). Furthermore, SLA for cowberry old growth ranged from 2.1-4.2 mm<sup>2</sup>/mg (under low % broadleaves), 1.7-3.8 mm<sup>2</sup>/mg (under mean % broadleaves), and 0.9-3.1 mm<sup>2</sup>/mg (under high % broadleaves) (Figure 5c). For every 1 m<sup>2</sup>/ha increase in BA, the increase in the SLA of bilberry was by 0.5 m<sup>2</sup>/mg in all categories of % broadleaves (as shown by the regression equation in Figure 5a). For cowberry new growth the increase in SLA for every 1 m<sup>2</sup>/ha increase in BA was 0.3 mm<sup>2</sup>/mg (Figure 5b) whereas, for cowberry old growth, this value was only 0.07 m<sup>2</sup>/ha (Figure 5c).

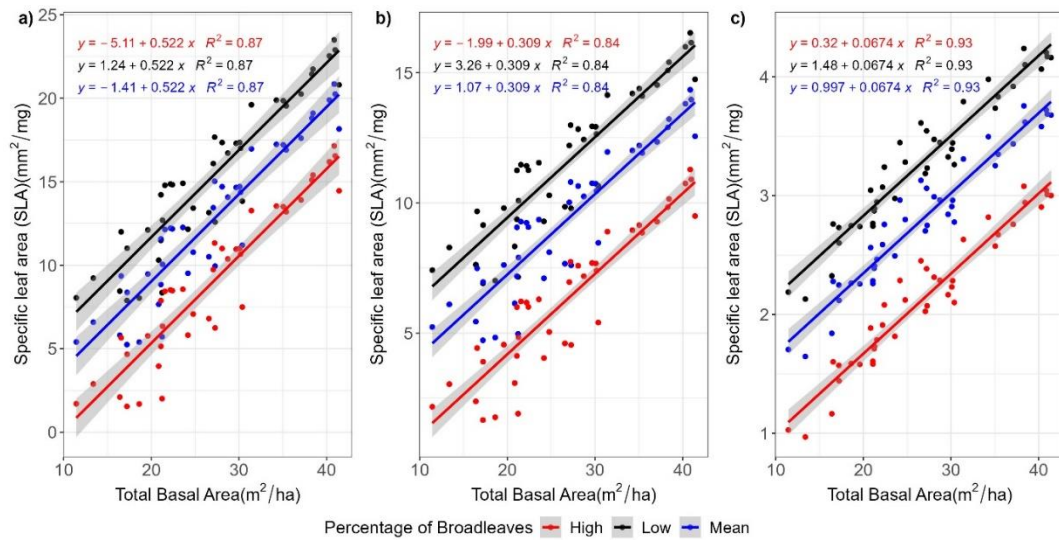


Figure 5. Predicted SLA for BA in the mixed forest study using best model for a) Bilberry b) Cowberry new growth, c) Cowberry old growth. Model 2 (i.e., without interaction between BA and % broadleaves) resulted in the best fit for all three. Grey regions represent a 95% confidence interval. Red, blue, and black colour indicates high, mean, and low values of % broadleaves, respectively. Note the difference in y-axis values between the three figures.

### 3.3 Transplant experiment

The best model for wild strawberry was Model 2 (Table 9). BA was highly significant in all models with positive estimates indicating a strong positive relation between BA and SLA (Table 9). The percentages of broadleaves were significant in Model 1 (Z value = -3.65,  $p < 0.001$ ) and Model 2 (Z value = -3.56,  $p < 0.001$ ) indicating the negative association between % broadleaves and SLA (Table 9). Besides, SLA did not vary significantly across different climatic origins (Model 3 and Model 4 in Table 9). Also, the effect of the interaction between BA and % broadleaves was insignificant, which indicates the relationship between SLA and BA is not modified by % broadleaves (Model 1 in Table 9). Likewise, the effect of interaction between BA and origin was also insignificant (Model 3 in Table 9), which indicates the relationship between SLA and BA is the same regardless of cold or local origin.

Table 9. Summary of model output for wild strawberry.

| <b>Model 1: <math>SLA = BA \times \% \text{ broadleaves} + \text{Site}</math> (as a random intercept effect)</b> |                 |                       |                |                    |
|--|-----------------|-----------------------|----------------|--------------------|
| AIC = 694.3  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 24.27           | 0.90                  | 26.83          | < 0.001            |
| BA   | 2.56            | 0.43                  | 5.88           | < 0.001            |
| % broadleaves  | -1.49           | 0.41                  | -3.65          | < 0.001            |
| BA $\times$ % broadleaves  | -0.35           | 0.47                  | -0.75          | 0.453              |
| <b>Model 2: <math>SLA = BA + \% \text{ broadleaves} + \text{Site}</math> (as a random intercept effect)</b>      |                 |                       |                |                    |
| AIC = 692.8  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 24.32           | 0.87                  | 27.96          | < 0.001            |
| BA   | 2.66            | 0.41                  | 6.44           | < 0.001            |
| % broadleaves  | -1.43           | 0.40                  | -3.56          | < 0.001            |
| <b>Model 3: <math>SLA = BA \times \text{Origin} + \text{Site}</math> (as a random intercept effect)</b>          |                 |                       |                |                    |
| AIC = 706.4  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 24.51           | 1.05                  | 23.26          | < 0.001            |
| BA   | 2.65            | 0.6                   | 4.45           | < 0.001            |
| Origin (warmer location)   | -0.39           | 0.83                  | -0.47          | 0.639              |
| BA $\times$ Origin (warmer location)   | 0.46            | 0.83                  | 0.56           | 0.576              |
| <b>Model 4: <math>SLA = BA + \text{Origin} + \text{Site}</math> (as a random intercept effect)</b>               |                 |                       |                |                    |
| AIC = 704.7  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 24.51           | 1.05                  | 23.25          | < 0.001            |
| BA   | 2.88            | 0.43                  | 6.73           | < 0.001            |
| Origin (warmer location)   | -0.39           | 0.83                  | -0.47          | 0.641              |

For goldenrod, the AIC value was 327.6, 326.2, 335.6, and 333.8 for Model 1, Model 2, Model 3, and Model 4 respectively, indicating Model 2 was much better than Model 3 and Model 4, and slightly better than Model 1. BA was highly significant in all models (Z value = 5.14,  $p < 0.001$  in Model 1; Z value = 5.17,  $p < 0.001$  in Model 2; Z value = 4.05,  $p < 0.001$  in Model 3; Z value = 5.37,  $p < 0.001$  in Model 4), and with positive estimates, indicating strong positive relation between BA and SLA (Table 10). On the other hand, % broadleaves had a significant negative effect in Model 1 (Z value = -2.57,  $p = 0.01$ ) and Model 2 (Z

value = -2.84,  $p = 0.005$ ) (Table 10). The effect of origin on SLA was not significant. Further, the effect of the interaction between BA and origin was not significant, which reflects that the effect of BA on SLA is not affected by warm or local origin (Model 3 in Table 10). Likewise, the effect of BA on SLA is not affected by % broadleaves (Model 1 in Table 10).

Table 10. Summary of model output for goldenrod.

| <i>Model 1: <math>SLA = BA \times \% \text{ broadleaves} + \text{Site}</math> (as a random intercept effect)</i> |                 |                       |                |                    |
|--|-----------------|-----------------------|----------------|--------------------|
| AIC = 327.6  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 21.55           | 0.82                  | 26.28          | < 0.001            |
| BA   | 2.56            | 0.5                   | 5.14           | < 0.001            |
| % broadleaves  | -1.22           | 0.47                  | -2.57          | 0.010              |
| BA $\times$ % broadleaves  | 0.42            | 0.53                  | 0.79           | 0.428              |
| <i>Model 2: <math>SLA = BA + \% \text{ broadleaves} + \text{Site}</math> (as a random intercept effect)</i>      |                 |                       |                |                    |
| AIC = 326.2  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 21.48           | 0.85                  | 25.29          | < 0.001            |
| BA   | 2.42            | 0.47                  | 5.17           | < 0.001            |
| % broadleaves  | -1.31           | 0.46                  | -2.84          | 0.005              |
| <i>Model 3: <math>SLA = BA \times \text{Origin} + \text{Site}</math> (as a random intercept effect)</i>          |                 |                       |                |                    |
| AIC = 335.6  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 21.54           | 1.06                  | 20.29          | < 0.001            |
| BA   | 2.93            | 0.72                  | 4.05           | < 0.001            |
| Origin (warmer location)   | -0.06           | 0.94                  | -0.07          | 0.947              |
| BA $\times$ Origin (warmer location)   | -0.5            | 0.95                  | -0.53          | 0.597              |
| <i>Model 4: <math>SLA = BA + \text{Origin} + \text{Site}</math> (as a random intercept effect)</i>               |                 |                       |                |                    |
| AIC = 333.8  |                 |                       |                |                    |
| <b>Variables</b>   | <b>Estimate</b> | <b>Standard Error</b> | <b>Z value</b> | <b>Pr(&gt; z )</b> |
| Intercept  | 21.53           | 1.06                  | 20.33          | < 0.001            |
| BA   | 2.65            | 0.49                  | 5.37           | < 0.001            |
| Origin (Warmer location)   | -0.06           | 0.95                  | -0.06          | 0.953              |

### 3.3.1 Model prediction for transplant experiment

Predicted values of SLA for wild strawberry ranged from 20.7-32.6 mm<sup>2</sup>/mg (under low % broadleaves), 18.8-30.8 mm<sup>2</sup>/mg (under mean % broadleaves), and 16.9-28.8 mm<sup>2</sup>/mg (under high % broadleaves) (Figure 6a). For goldenrod, predicted SLA values ranged from 18.2-29.1 mm<sup>2</sup>/mg (under low % broadleaves), 16.5-27.4 mm<sup>2</sup>/mg (under mean % broadleaves), and 14.7-25.6 mm<sup>2</sup>/mg (under high % broadleaves) (Figure 6b). The results show that every 1 m<sup>2</sup> increase in BA led to an increase of 0.358 mm<sup>2</sup>/mg in predicted SLA for wild strawberry (Figure 6a), and an increase of 0.325 mm<sup>2</sup>/mg in predicted SLA for goldenrod (Figure 6b).

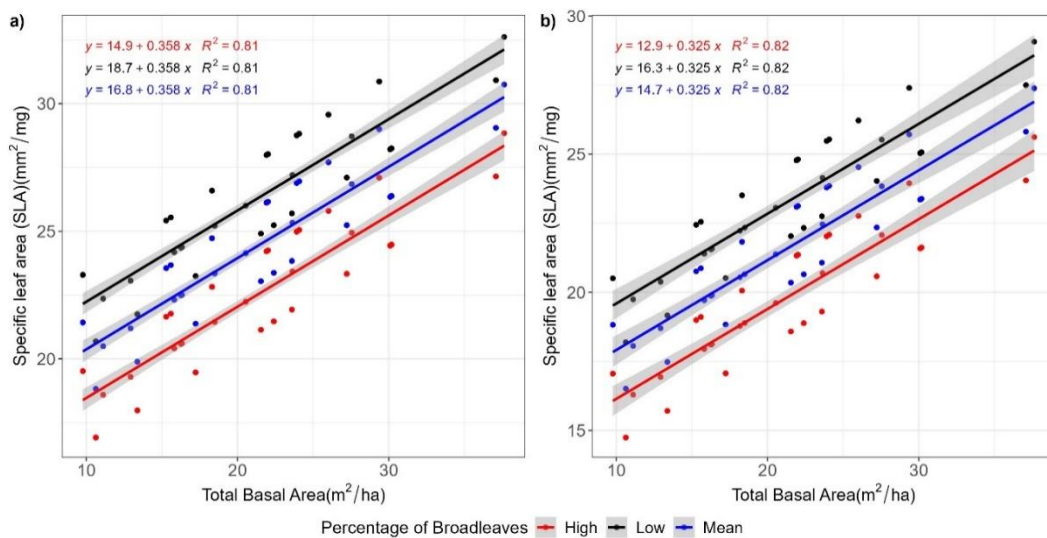


Figure 6. Predicted SLA for BA in the transplant experiment using the best model for a) Wild strawberry and b) Goldenrod. Model 2 (i.e., without interaction between BA and % broadleaves) resulted in the best fit for both species. Grey regions represent a 95% confidence interval. Red, blue, and black colour indicates high, mean, and low values of % broadleaves, respectively. Note the difference in y-axis values between the two figures.

## 4. Discussion

The results from this study show that the predicted SLA values were within the range of previous studies as documented in an open database showing traits of the Northwest European flora (LEDA- trait database) (Kleyer et al. 2008). This alignment between the predicted SLA values and SLA values from the LEDA database justifies that the prediction of the models in this study is reliable. SLA is often used as an indicator of how costly is it for plants to produce leaves (Villar & Merino 2001; Villar et al. 2021). For instance, a study by Villar and Merino (2001) in fourteen contrasting environmental conditions (from desert to rainforest), and with different life forms, shows that species with higher SLA tend to allocate less resources to leaf construction, resulting in lower leaf production costs. The models developed hence can thus be used in intraspecific SLA prediction and to analyse the production cost of leaves for the studied species, as previous studies for intraspecific SLA prediction models are rare. Nevertheless, it is essential to consider that intraspecific SLA variation (variation in SLA among individuals of the same species) can be influenced by habitat heterogeneity resulting from abiotic factors such as light, temperature, SM, and nutrient availability (Poorter et al. 2009; Kemppinen & Niittynen 2022). This study shows that the mixed forest study's SLA range for bilberry and cowberry new growth is noticeably higher than in the large-scale study (see model predictions in the results). The difference in the SLA value range can be attributed to variations in the time of leaf sample collection as the leaf samples from the mixed forest study were collected early in the summer season. Early summer is a time of active growth of leaves and as a result, plants devote more resources to enhancing photosynthesis which is brought by an increase in SLA (Chelli et al. 2019; Anderson et al. 2020). Concurrently, trees also develop their canopy during this time and increase shade. The synergistic effect created by the active growth phase and shade due to overstorey may result in high SLA in the mixed forest study. Contrarily, the mixed forest study's SLA range for cowberry old growth is lower compared to the large-scale study. This could be because plants do not allocate enough resources to old leaves for photosynthesis and leaf growth, and the response of SLA maybe only due to the shade of overstorey which was higher in large-scale study. Additionally, the SLA values of the cowberry new growth were noticeably higher than those of the cowberry old growth (see

results). This difference can be linked to the tendency of newly formed leaves to allocate more resources to photosynthesis and growth. For example, Karlsson (1985) found that the photosynthetic capacity of cowberry leaves in the second year was two-thirds of the value observed in the first year. This may be due to the beginning of leaf senescence in older leaves. Further older leaves may have started producing more carbon-rich compounds which results in thicker leaf tissues and hence low SLA as noted by some researchers in tree species (Reich et al. 1991; Milla et al. 2008). Moreover, biotic interactions, such as competition, facilitation, or amensalism, may affect species differently along the climatic gradient (Balandier et al. 2022b), which can contribute to trait variations.

## 4.1 Effect of overstorey structure and composition

Overstorey vegetation structure can either compete against or facilitate the understorey vegetation growth, influencing its SLA by controlling light transmittance and soil organic matter availability through leaf litterfall. The findings of this study demonstrate that forest density (as represented by BA) and overstorey composition (as represented by % pine or % broadleaves) are important predictors of SLA in understorey plant species. These findings are consistent with previous research (Chelli et al. 2019; Vanneste et al. 2019) and confirm the role of overstorey structure and composition in influencing the SLA of understorey plant species. Specifically, a denser overstorey limits the amount of light entering the forest understorey (Greiser et al. 2018; Govaert et al. 2020; De Pauw et al. 2022), and thereby influencing the forest microclimate (Thom et al. 2020; Deng et al. 2023). Under such conditions of low light availability, understorey plants respond by increasing their SLA (Pérez-Harguindeguy et al. 2016). The function of light transmittance can also vary based on overstorey species composition. With an increase in the percentage of pine, the SLA of the understorey decreases (see large-scale study results) and with an increase in the percentage of broadleaves, the SLA of the understorey decreases (see results from the mixed forest study and the transplant experiment). This observed decrease in SLA with an increasing percentage of pine (large-scale study results) or broadleaves (results from the mixed forest study and the transplant experiment) can be attributed to the fact that pine/ broadleaves transmit more light in the understorey as compared to Norway spruce (Petersson et al. 2019). Further broadleaves shed their leaves during winter allowing more entry of light and a wider time window in early spring for understorey plants to accumulate resources before leaf-out and canopy closure.

Likewise, a higher density of overstorey trees can lead to increased nutrient availability in the soil through increased litterfall and nutrient cycling. In fact, activities that reduce forest density are found to reduce soil organic contents



(Barbier et al. 2008; Yang et al. 2022) whereas a positive correlation between litter biomass and forest density has been observed (Pérez-alavez et al. 2023). Moreover, the composition of the overstorey can influence litter biomass. Broadleaves, being deciduous and shedding leaves in winter, contribute more litterfall and facilitate the accumulation of soil organic compounds compared to pine (Barbier et al. 2008; Sheffer et al. 2015; Pérez-alavez et al. 2023). Consequently, it increases soil fertility in broadleaved forests and enhances the conditions for understorey growth, resulting in higher SLA values compared to coniferous forests. Yet, below ground competition for soil resources between overstorey and understorey has been documented in past studies (Barbier et al. 2008; Balandier et al. 2022b) which will ultimately decrease SLA. Interestingly, even in the transplant experiment where the soil was not influenced by litterfall, the SLA of understorey plants increased with forest density, indicating that light has a stronger effect than soil organic matter, as supported by previous studies (Poorter et al. 2009, 2019; De Pauw et al. 2022).

In addition, the results indicate that there is no interaction between the variable BA and the % pine (in the large-scale study), and between the variable BA and the % broadleaves (in the mixed forest study and the transplant experiment). This indicates that the effect of forest density on SLA generally remains consistent regardless of overstorey species composition. However, a notable exception is observed in the case of cowberry new growth in the large-scale study, indicating that the impact of forest density on the SLA of cowberry's new growth is influenced by the presence of pine. Cowberry, particularly its new leaves during the early growth phase, may require increased light exposure due to their light demanding nature (Ritchie 1955) and active growth phase, and hence might have responded differently. Consequently, different combinations of forest density and pine presence can cause variations in light transmittance in the forest understorey, leading to significant variations in the SLA of cowberry new growth. For instance, in dense forests where the proportion of pine is high, the light conditions can still be better than in similar dense forests with Norway spruce (Pettersson et al. 2019), leading to lower SLA values of cowberry new growth than under Norway spruce forest. Nevertheless, stand structure has been often found to strongly influence light transmittance more than tree composition (Kovács et al. 2017). Therefore, forest structure is a major variable affecting SLA on understorey plants.

## 4.2 Effect of soil moisture and carbon-nitrogen ratio

A significant effect of SM and C-N ratio on the SLA of understorey plants was not observed except for two cases: in the large-scale study, where the SLA of cowberry new growth was negatively affected by SM (Model 2) and in the mixed

forest study, where the SLA of bilberry was negatively affected by SM (Model 1 and Model 2). However, a study in western Canadian forest understorey plant communities suggested that SM, and soil C-N ratio were key factors influencing interspecific SLA variation (Shovon et al. 2019). The study revealed that higher levels of SM and lower C-N ratio were associated with a shift towards more acquisitive resource-use strategies, which was reflected in an increase in SLA. Yet, this study was focused on intraspecific SLA variation which might have resulted in contrasting results. Nevertheless, SM was found to be an important predictor of SLA in an arctic region with a positive relationship for bilberry and goldenrod, while no relationship was found for cowberry (Kemppinen & Niittynen 2022). However, the difference in the direction of intraspecific trait response along climatic gradients has been documented in previous research (Roybal & Butterfield 2019). Moreover, a piece of research conducted by compiling datasets on SLA from various systems and growth forms demonstrated a negative relationship between SLA and soil C-N ratio, reflecting that decreasing soil C-N ratio corresponded to increased nutrient availability and higher SLA (Ordoñez et al. 2009) yet the results from this study did not find any significant relationship with soil C-N ratio. The same study suggested that up to 32-34% of the variation in SLA among sites could be explained solely by the soil C-N ratio. Differences in plant species and environmental conditions examined could be another reason accounting for the disparities between the result from this study and previous studies (Gong & Gao 2019). Further, a study with alder and spruce trees in boreal forests shows that SM has a negative linear relationship with SLA and that higher soil C-N values are correlated with lower SLA values (Anderson et al. 2020). The same research indicated that the relationship between SM and SLA can be non-linear showing the possibility that there is an optimum SM level where SLA is highest and then decreases with further increases in SM (Anderson et al. 2020), which could explain the contrasting conclusions across different studies. Besides, variations in measurement methods or analytical techniques could have influenced the results.

The complex interactions between environmental factors and plant traits make it difficult to draw conclusive findings on this relationship. Further research is needed to better understand the relationship between SM, C-N ratio, and understorey SLA at a global scale, as this has important implications for predicting understorey responses to how understorey responds to the changing environment. In addition, climatic variables (temperature and precipitation) can affect SM by affecting the evaporation and evapotranspiration processes, as well as driving the C-N ratio by affecting microbial biomass (Woo & Seo 2022). Hence, understanding how these variables in combination with forest overstorey affect the SLA of different understorey species under different environmental

conditions is essential considering the changes that will be brought about by climate change.

### 4.3 Effect of warming

The results from the transplant experiment show that the SLA of understorey wild strawberry and goldenrod did not differ significantly based on their origin (i.e., cold and local origin). This result can be rationalized by two possible reasons. Firstly, there is no evidence of divergent SLA among understorey plants, as no pre-transplant material from the cold origin was available for comparison. While specific research for the same species is lacking, previous studies have demonstrated a general increase in SLA with an increase in latitudinal gradient (De Frenne et al. 2013; Sun et al. 2023), weakening the argument that SLA of wild strawberry and goldenrod originating from different regions were same. Secondly, the SLA of wild strawberry and goldenrod of cold origin may have shown rapid adaptation and reached a comparable level of SLA with the understorey plants of local origin assuming the SLA of plants of two origins varies significantly before transplantation. Such a rapid response of understorey plants may have been facilitated by the plastic nature of SLA (Liu et al. 2016). Consequently, this suggests that the SLA of the understorey plants will adapt to climate change induced temperature rise. The change in SLA as a response to adaptation to climate induced temperature rise can be supported based on previous research which shows SLA of some understorey species increases (De Kort et al. 2020) or decreases (Blondeel et al. 2020; Maes et al. 2020) with warming treatments. Contrarily, other research shows SLA did not change with experimental warming and it is light which is more important than temperature for the SLA of the understorey (De Pauw et al. 2022). Yet the transplant experiment design was made such that both warm and cold regions had similar overstorey density and species composition so that the plots receive similar light amount, indicating that understorey wild strawberry and goldenrod of cold origin changed their SLA in response to temperature warming. Furthermore, the interaction between BA (which represents forest density) and origin in the transplant experiment was not significant which implies that there is not a difference in adaptation of understorey to light between cold and local origin. Hence, even if climate change will shift the overstorey density, SLA of wild strawberry and goldenrod would not be affected significantly.

Different species may exhibit different response patterns for SLA (Liu et al. 2023) and conducting the same experiment with different species could yield contrasting results. A study in 76 natural ecosystems of China found that SLA (of various life forms: herbs, shrubs, trees) was positively correlated with mean annual temperature, yet this relationship changed when the temperature was either

below or above a certain threshold (20°C in this case) (Liu et al. 2023). The study also found that SLA has a limited range of variation. To adapt to changes brought by climate, SLA would need to potentially change by 12% (Liu et al. 2023). Moreover, the same study found that SLA is not easily passed down genetically from one generation to the next (Liu et al. 2023). Another factor to consider is that species tend to react at a slower velocity than the observed velocity of climate change (a phenomenon called climatic debt) (Zellweger et al. 2020; Richard et al. 2021). Even in the transplant experiment, wild strawberry and goldenrod were moved from their cold region to a warmer region in a way that the temperature difference that they experienced was much quicker than what would be expected under natural warming conditions. However, to account for this factor in the transplant experiment, understorey plants were left for a few seasons for acclimatization to new environmental conditions.

Furthermore, it should also be noted that uniform soil conditions and protection from herbivores in the transplant experiment might have inadvertently reduced the variability in the plants' environmental conditions, which might not be the case under normal conditions in forests (Nooten & Hughes 2017). Moreover, a possible caveat is that the transplant experiment study only tested for differences in SLA between two specific climate regimes (warm and cold) and did not investigate how plants might respond to more extreme or unpredictable climate conditions.

#### 4.4 Implications for forest management

Forest management is critical in the context of global climate and land-use change and its potential effects on understorey vegetation. Controlling the density of a forest stand, we can control light, provide temperature buffering, and mitigate the ongoing effects of climate change on the understorey (Balandier et al. 2022b; Christiansen et al. 2022; Deng et al. 2023). Especially, the density of Norway spruce plantations is prominent in Sweden (Felton et al. 2022). As observed in this study the increased density of the forest will also increase the SLA of bilberry, cowberry, wild strawberry, and goldenrod. High SLA values correspond to higher litter decomposition rates (Garnier et al. 2004; Mokany et al. 2008), directly influencing nutrient cycling, a pivotal ecosystem process. An increase in the SLA of the understorey is also linked to enhanced ecosystem services of water regulation, biomass production, and aesthetic appeal (Shome et al. 2023). On the other hand, berry production and growth of other understorey organs can decrease with an increase of SLA as plants allocate more resources for the expansion of leaf area. The rise in SLA can also lead to increased plant palatability (Funk et al. 2017), yet plants may decrease their SLA as a response to herbivores due to the plastic nature of SLA. It is worth considering that bilberry and cowberry are

foundation species that have a significant effect on shaping local and global biodiversity, non-trophic facilitation, and regulating ecosystem dynamics (Ellison & Degrassi 2017; Borst et al. 2018; Ellison et al. 2019; Forzieri et al. 2020; O'Brien et al. 2020; Lortie et al. 2022). Therefore, modification in the SLA of these foundation plants also means a change in the services provided by them.

Global phenomena such as climate change further make the interaction between overstorey and understorey complicated as the severity of forest disturbances may increase in the future due to climate change (Seidl et al. 2014; Patacca et al. 2023). These more extreme conditions may result in significant overstorey driven changes in SLA for these species, beyond those considered in this study. Climate change induced forest disturbances may lead to tree mortality, which will likely promote canopy openness and decrease tree density in the forest (Kumar et al. 2021). Consequently, the natural functions of light control and temperature buffering provided by the forest will be compromised (Balandier et al. 2022b; Christiansen et al. 2022; Deng et al. 2023). Under conditions of a severe decrease in forest density of overstorey, the understorey would decrease its SLA. On the contrary, replanting trees in higher densities after clearcutting will result in an understorey with high SLA.

Lately, there is also advocacy towards overstorey species mixtures due to their potential for providing multiple ecosystem services (Felton et al. 2016; Huuskonen et al. 2021; Ara et al. 2022). The findings from this study also support the promotion of overstorey mixing with pine and broadleaves to moderate SLA. Notably, mixing the overstorey species that permit greater light penetration can potentially moderate SLA and its related effects, and optimize understorey growth and berry production. The light transmittance, temperature, and resource availability in forest understorey can be optimized by mixing overstorey species with different structures and traits (Zhang et al. 2022).

## 5. Conclusion and Recommendations

Overall, this study developed reliable SLA prediction models for bilberry, cowberry, wild strawberry, and goldenrod which can improve our ability to predict the responses of understorey plant communities to changing environmental conditions and make better forest management decisions. The results from this study highlight that forest density positively influences the SLA of bilberry, cowberry, wild strawberry, and goldenrod. The influence of forest density is mainly through the control of light transmittance, which is an important resource affecting SLA. At the same time, the proportion of overstorey species with greater light transmittance capacity decreases the SLA of bilberry, cowberry, wild strawberry, and goldenrod. The general trend from most of the models demonstrated SM and C-N ratio did not affect SLA significantly. The interaction between forest density and the percentage of broadleaves was not significant whereas the interaction between forest density and the percentage of pine had a significant effect on cowberry new growth in large-scale study. Moreover, in the transplant experiment, SLA of wild strawberry and goldenrod did not change significantly with climatic origins. The temperature variations specific to different climatic origins did not have a significant impact on how forest density affects SLA of wild strawberry and goldenrod.

The findings from this research also open a door for future research which may involve quantifying to what extent functional traits of plants can adapt to a changing environment and even climate, and how long does it take to observe noticeable changes in SLA of understorey plants. It has also been suggested to combine large-scale studies that look at long-term adaptations of the understorey with small-scale experiments that focus on short-term acclimation (Liu et al. 2023). As intraspecific trait variations can comprise a range of values within an ecosystem, further studies should be conducted to understand the variation in trait values within species and how they are influenced by biotic interactions and environmental gradients. The mixed forest study was limited to a site that can limit the generality of the findings. Hence, a similar study in a wide latitudinal area is suggested. Conducting similar research works for other understorey species would also contribute to the addition of scientific knowledge. Additionally, studying the variation of SLA of the understorey during the whole growth season is encouraged to broaden the understanding of seasonal changes in

SLA for various understorey species. It is also important that future research focuses on the interactions between SLA and soil, specifically looking at how understorey vegetation and overstorey trees affect one another.

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## Popular science summary

### **Unravelling a mystery: What really influences Specific Leaf Area in Sweden's Understorey Plants**

Have you ever wondered how plants decide to change their leaves' size? In the fascinating world of forest ecosystems, where overstorey trees stand tall and understorey plants thrive beneath the canopy, a captivating interaction takes place. Specific leaf area (SLA), the secret code to how plants grow and survive, is at the centre of this mystery. SLA is like a plant recipe that informs us how effectively a plant develops, adapts, and uses the resources around it. The change in SLA value offers signals on how plants could respond to changes in the environment, different light, and several nutrient conditions. Yet, this fascinating relationship between the trees and the understorey's leaves has remained hidden until now.

In this study, I explored the factors influencing the SLA of understorey plants across various forests in Sweden, including overstorey structure, soil characteristics, and the impact of climate induced temperature rise by developing a mathematical relationship between these variables and the SLA of understorey plants. To conduct this study, I used plant samples of two species, bilberry and cowberry, collected from forest stands which represent a forest that expands from South to North of Sweden, as well as from a mixed forest. Additionally, I used plant samples of wild strawberries and goldenrod from a unique experiment. This experiment involved selecting naturally growing plants from a cold region and replanting them into pots. Subsequently, these plants were relocated to a warmer region together with the same plant species of local origin. The experiment aimed to find if SLA of understorey plants would change by climate change induced temperature rise.

I found that in denser forests where trees were closer to each other, the SLA of understorey plants was higher. But having a lot of pine trees or broadleaf trees instead of Norway spruce around made the SLA of understorey plants decrease. Among the understorey plants, the newly grown leaves of cowberry had its unique way of growing when grown in dense forest of pine trees. Surprisingly, the characteristics of the soil did not matter to understorey plants. Furthermore, the SLA of wild strawberry and goldenrod did not vary across cold and local origins indicating these understorey plants of local origins changed their SLA in response to temperature increase. Additionally, SLA of wild strawberry and goldenrod

decreased under denser trees even under the condition of climate induced temperature rise.

Such findings help us predict how changes in the forest due to climate change and forest management activities might affect the understorey plants. It can also help us protect biodiversity and manage the effects of climate change on forests similar to those studied here.

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