Establishing a long-term forest and tree-growth monitoring network in threatened coastal spruce ecosystems

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Abstract:

Climate change is expected to increase stress to forests. The red spruce (*Picea rubens* Sarg.) forests of Maine's coast are particularly vulnerable to such stress. These forests exist in coastal climate refugia south of their typical range, and it is unclear if the coast will continue to be a refugium as ocean and atmospheric temperatures rise. Despite the ecological, economic, and cultural importance of this forest type, we lack long-term monitoring studies in these unique coastal ecosystems. The goal of this study was to establish a long-term monitoring network focused on sensitive coastal red spruce forests and link patterns of daily and annual radial growth with climate extremes. We conducted forest inventories (10 sites), monitored daily growth (using 100 automated point dendrometers that track small changes in tree diameter), and measured annual tree growth (using 300 xylem increment cores) across six coastal and four inland reference sites representing a broad range of climatic conditions. From these data we addressed three objectives: (*i*) determine the climate conditions that lead to tree water stress (stem shrinkage) and growth through measurements of daily stem diameter, (*ii*) determine if the factors that govern daily growth are the same as those that govern annual growth, and (*iii)* establish a long-term coastal spruce forest monitoring network. By combining climate-growth relations with long-term monitoring efforts we will improve our ability to predict how red spruce forests will respond to future climate stressors.

Introduction:

Historically, the ocean moderated the climate along the coast of Maine allowing red spruce (*Picea rubens* Sarg.) forests to exist south of their typical range (Davis, 1966). However, we have likely already exceeded the warming experienced during the mid-Holocene warming period when the coast served as a critical refugia for red spruce (Schauffler & Jacobson, 2002). The Gulf of Maine is warming faster than 99% of the world's oceans, calling into question the persistence of these coastal refugia (Pershing et al., 2015). With the rapid warming experienced in Maine and along the coast (Pershing et al., 2015), the majority of Maine is projected to be unsuitable for spruce as soon as 2060 (Iverson et al., 2008; Andrews et al., 2022). In contrast, some models suggest that warming may increase primary productivity of spruce due to earlier springs (Duveneck & Thomson, 2017). These conflicting forecasts highlight the need for long-term forest monitoring studies that link the biology of red spruce growth to climate change to guide continued stewardship.

In our previous research, with point dendrometers detecting small hourly changes in tree diameter, we see evidence that red spruce daily growth is sensitive to atmospheric moisture conditions (e.g., high humidity) and soil water availability (Barry, 2023; Etzold et al., 2022). These dendrometers can also detect daily and sustained stem shrinkage – a symptom of drought stress. A wide range of published data (Andrews et al., 2022; Day, 2000) including our own published (French et al., 2023; Wason et al., 2019) and ongoing research, suggest that red spruce is a climate-sensitive species that is negatively impacted by high temperatures and dry air regardless of other environmental conditions (e.g., adequate soil moisture). Furthermore, our previous work suggested that the factors that promote the daily growth of spruce (high humidity, fog) are not necessarily the factors that promote increases in annual growth of spruce (temperature, precipitation in previous year; Teets et al. 2018). Clearly, a stronger understanding of the linkage between the biology and phenology of spruce growth and environmental conditions is needed.

In this study, we addressed three objectives: (*i*) determine the climate conditions that lead to tree water stress (stem shrinkage) and growth through measurements of daily stem diameter, (*ii*) determine if the factors that govern daily growth are the same as those that govern annual growth, and (*iii)* establish a long-term coastal spruce forest monitoring network.

Materials and Methods:

Study sites:

This study took place at ten unique sites across the state of Maine. Six of the ten sites are located in coastal red spruce stands (≤2 km from the shore), with the remaining four located in inland red spruce stands (6-72 km from shore; **Fig 1)**. These sites represent a range of climatic conditions across the state of Maine varying by more than 4 °C in growing season average daily maximum temperature (**Table 1).** The sites for this study were selected to have >70% red spruce, presence of multiple age classes, advance regeneration, as well as an abundance of coarse woody debris, snags, and larger diameter spruce.

Tree selection criteria and dendrometer deployment:

In April- May of 2024 we randomly selected 10 trees at each site on which we would deploy automated point dendrometers (TOMST, Czech Republic) **(Fig 2)**. Each selected tree was fitted with one automated point dendrometer (Point Dendrometer, TOMST, Czech Republic) on the north side of the tree at breast height (1.37 m) and pre-programmed to record pin displacement to the nearest 1 µm every 15 minutes. For each tree, we recorded the starting diameter at breast height and canopy position. We returned to each site at the end of the growing season (September - October) to download all data.

Environmental variables:

In order to determine how daily environmental conditions impact radial growth, we monitored air temperature, relative humidity, and soil moisture at each site. At each plot center, we mounted a temperature and humidity sensor (HOBO MX2300 series, Onset Computer Co, Bourne, MA) 1 meter off the ground logging measurements at one hour intervals (**Fig 2)**. At each plot center we also deployed a soil moisture probe, logging soil moisture at 6 cm every 15 minutes (TMS-4, TOMST, Czech Republic). From these data at each site, we calculated daily maximum air temperature (T_{max}), daily maximum vapour pressure deficit (VPD_{min}), and daily minimum volumetric water content at 20cm (VWC_{min}) for the growing season (May 1st – September 30th, **Table 1)**. All calculations and analysis for this study were done in R (v4.5.0; R core team, 2025), and we calculated day length (DL) using the R package "geosphere" (Hijmans, 2024).

Forest inventories:

In order to characterize the forests at each site, we conducted forest inventories in the summer of 2024 (**Table 2)**. The six coastal plots in this study are a part of a larger research project and we therefore conducted more in-depth forest inventories at those sites. At each of the six coastal sites we established a 50 ✕ 50 meter plot. Within each plot, the location of all trees with a diameter at breast height (DBH) > 10cm was mapped (including all trees with dendrometers). For each tree we recorded DBH, species, and canopy class. For the four inland plots, we used circular fixed radius (11.3 m radius) inventory plots. We measured and tagged all trees with a DBH ≥10 cm, and recorded the azimuth and distance from each tree to plot center.

Each plot was monumented with metal rebar (at the plot center for inland plots and SW corner for coastal plots) for relocation and continued monitoring.

Increment core collection and analysis:

To test if the environmental factors governing daily growth were similar to those governing annual growth, we collected increment cores from red spruce trees at each site (**Fig 2)**. At each of the six coastal plots, we randomly selected at least 10 trees from each of three DBH size classes (10 – 19.9 cm, 20 – 29.9 cm, and ≥30 cm) including collecting a core from all trees with dendrometers. At least 30 trees were cored at each coastal site. Each selected tree was cored at breast height, with a second core taken only if the first core significantly missed the pith. For trees with dendrometers, we cored at least 45° away from the dendrometer. At each of the four inland plots we collected increment cores from each dendrometer tree in the fall of 2024. At the time of the inventories in the spring of 2024 we collected increment cores from 10 randomly selected red spruce (10 – 19.9 cm DBH). We cored 20 trees total per plot at the inland sites, representing smaller (10 – 19.9 cm DBH) and larger (≥20 cm DBH) size classes.

Increment cores were processed and cross dated following standard dendrochronological procedure (Fraver et al., 2011). We measured raw ring widths of cores using a sliding scale micrometer (Velmex, Inc., Bloomfield, NY; Wason et al., 2019; Teets et al., 2018). During the cross dating process, 1 out 100 of the cores from trees with dendrometers could not be cross dated and was eliminated. Out of the 257 tree cores from trees without dendrometers, 20 cores could not be cross dated and were eliminated (7.8% of total cores) (**Table 2**). Next we calculated site-level subsample signal strength (SSS) (Wigley et al., 1984) and used a threshold of SSS ≥ 0.85 to identify the earliest year in each site chronology that is statistically robust, and eliminate data prior to that year. Finally, we calculated the average basal area increment (BAI) for each site

(**Fig 4**). All analyses of increment cores were done using the R package “dplR”(v1.7.8; Bunn et al., 2025).

Dendrometer data processing:

Prior to processing and analyzing dendrometer data, we visually assessed the raw time series data for each individual dendrometer to check for anomalies. Through this process, we eliminated data for 6 dendrometers across 4 sites (6% of total sample) in 2024 (**Table 2)**. These dendrometers exhibited very low or zero growth for the majority of the growing season which we attributed to sampling error. In addition, there were three dendrometers from site 7 which were trimmed at earlier points in the growing season due to anomalous jumps and/or decreases in displacement, likely due to wildlife interference.

We calculated and used the daily maximum displacement for all further analysis, in accordance with the zero growth concept (Zweifel, 2016). To determine the starting displacement for each dendrometer, we averaged daily maximum displacement for a 15 day period prior to the onset of growth. To determine the average end-of-season displacement for each dendrometer, we averaged the daily maximum displacements in September.

We identified the growth period for each tree as the dates when daily maximum displacement was between the 5th and 95th percentile of total growth for that year (Etzold et al., 2021). Using the zero growth method we determined which days the current maximum displacement exceeded the previous running maximum, indicating that a tree exhibited irreversible radial growth (Zweifiel et al., 2016, Zweifiel et al., 2021). We also determined the daily magnitude of growth by subtracting the running maximum from the new daily maximum on days that the tree grew. On days where the tree did not grow, we calculated the magnitude of the tree water deficit by subtracting the daily maximum from the previous running maximum (Zweifiel et al., 2016).

We also built preliminary mixed effect models to evaluate how various factors (DL, VPD_{max}, VWC_{min}, and T_{max}) impact the probability (binomial model; link = 'logit') and magnitude (log-transformed) of growth and the magnitude of tree water deficit (log-transformed) using the "lme4" package in R (Bates, et al., 2015).

Preliminary Results:

Daily and seasonal growth and climate conditions:

We found that within sites there was variation in growth sensitivity to daily conditions (daily fluctuations) and total growth of trees (**Fig 3**). On average, we found that there were 48 growth days per tree per site and that the number of growth days was a strong predictor of the total growth of that tree (**Fig 4).**

In order to better understand how our sites were arranged by climate we performed a principal components analysis (**Fig 5).** We found that there was a wide distribution among our sites, illustrating differences in climate means. We found that sites clearly clustered by warm and dry air (T_{max} and VPD_{max}) compared to cool and moist air. Within the cooler sites (6 – 10), in particular, there was also some separation among sites related to VWC_{min}. Interestingly, we found no correlation between the position of sites in our ordination with average number of growth days per site or average total growth per site. This suggests that while climate variables played a key role in differentiating sites, the day length and timing of climate conditions may have played a larger role in growth than the overall site averages.

While we are still in the process of refining our models relating daily growth to daily environmental conditions, our preliminary model results suggest that VPD_{max} plays the largest role in determining the probability and magnitude of growth, as well as the magnitude of tree water deficit at all sites (**Table 3**)**.** We also observed several important interactions, particularly with daylength suggesting that the time of year impacts daily growth and shrinkage responses to environmental conditions.

Long vs. short term climate growth trends:

Our increment core analysis suggests wide variation in BAI among sites (**Fig 7)**. In addition we found some sites, such as site 1, 4 and 5, had relatively younger age stands with a strong signal strength going back to around 1940-1960 (**Fig 7**). In contrast sites such as 2 and 10 had older age stands with a strong signal strength going back to the 1880's (**Fig 7)**. Our preliminary climate-growth analysis has revealed that annual growth (quantified as a ring-width index) is highest following a cool and moist previous-year late-summer. Growth is also highest following a warm and relatively dry spring. Interestingly, although daily VPD was a dominant feature driving daily growth in our dendrometer models, these prior-year late-summer and spring metrics, before annual growth commenced, were the largest determinants of annual growth from increment cores suggesting that the factors that govern daily growth differ in key ways from those that govern annual growth.

Establishing a monitoring network:

A major goal of this project was to establish a long term monitoring network across our sites to track changes in forest structure and composition. In addition to monumenting our plots with rebar, we performed forest inventories to characterize the composition and structure of each plot as a baseline for which to compare future conditions (**Table 2).** At all 10 of our sites we will be leaving dendrometers out for at least another two years in order to continue to assess climate growth patterns. In addition, we plan to return to these sites periodically to repeat forest inventories and characterize any potential changes in forest structure or composition. All data will be available in the FEMC data archive.

Conclusions:

We found that the major factors determining daily tree growth related to atmospheric water availability (VPD). However, the factors governing annual growth were more related to climate conditions from the previous year late-summer or from the early spring before secondary growth commenced. These results highlight the importance of ongoing monitoring efforts to reconcile these climate-growth relationships and the importance of cool and moist conditions for the growth of red spruce. Our future work will focus on refining models of daily climate growth and further addressing this knowledge gap.

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Figures and tables:

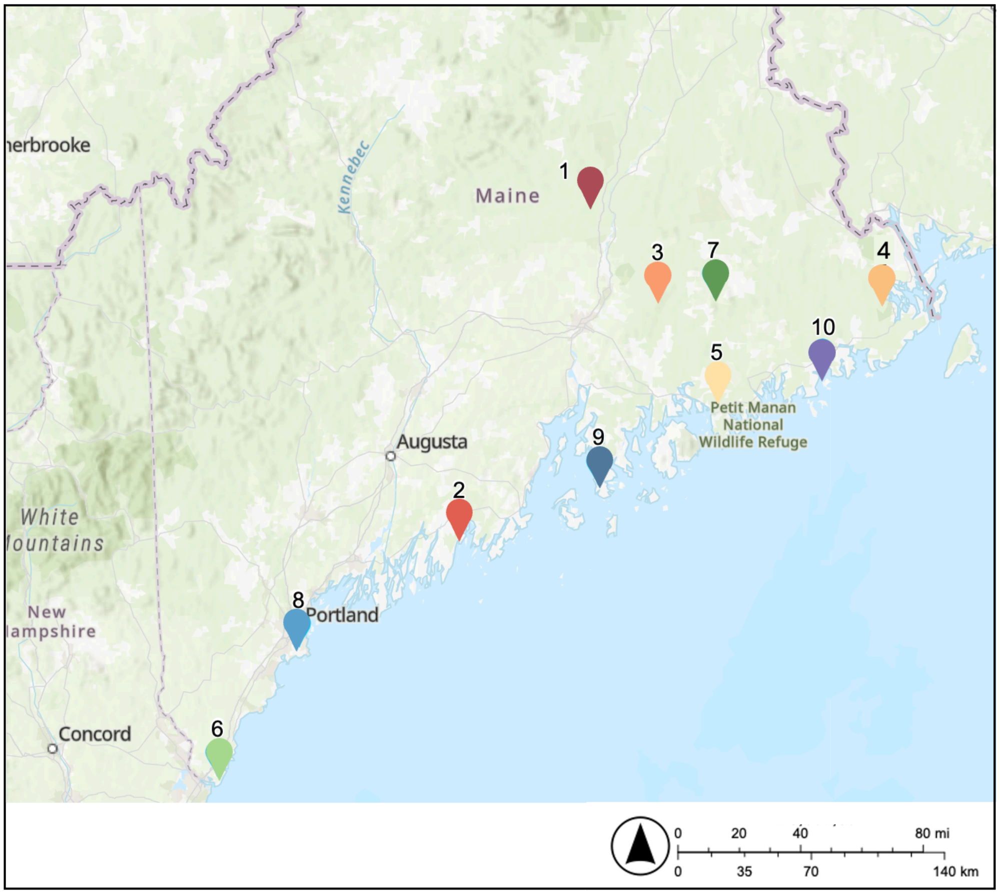


Figure 1: Map of the 10 study sites across the state of Maine. Sites are numbered based on the average temperature over the 2024 growing season (**Table 1**) and colors generally follow that pattern from warm colors (red – orange) through cooler colors (green – blue – purple).

Figure 2: A: Photo of an automated point dendrometer deployed on a red spruce tree. B: Photo of a HOBO climate sensor mounted to a wooden stake. C: Photo of increment core being extracted from a red spruce tree.

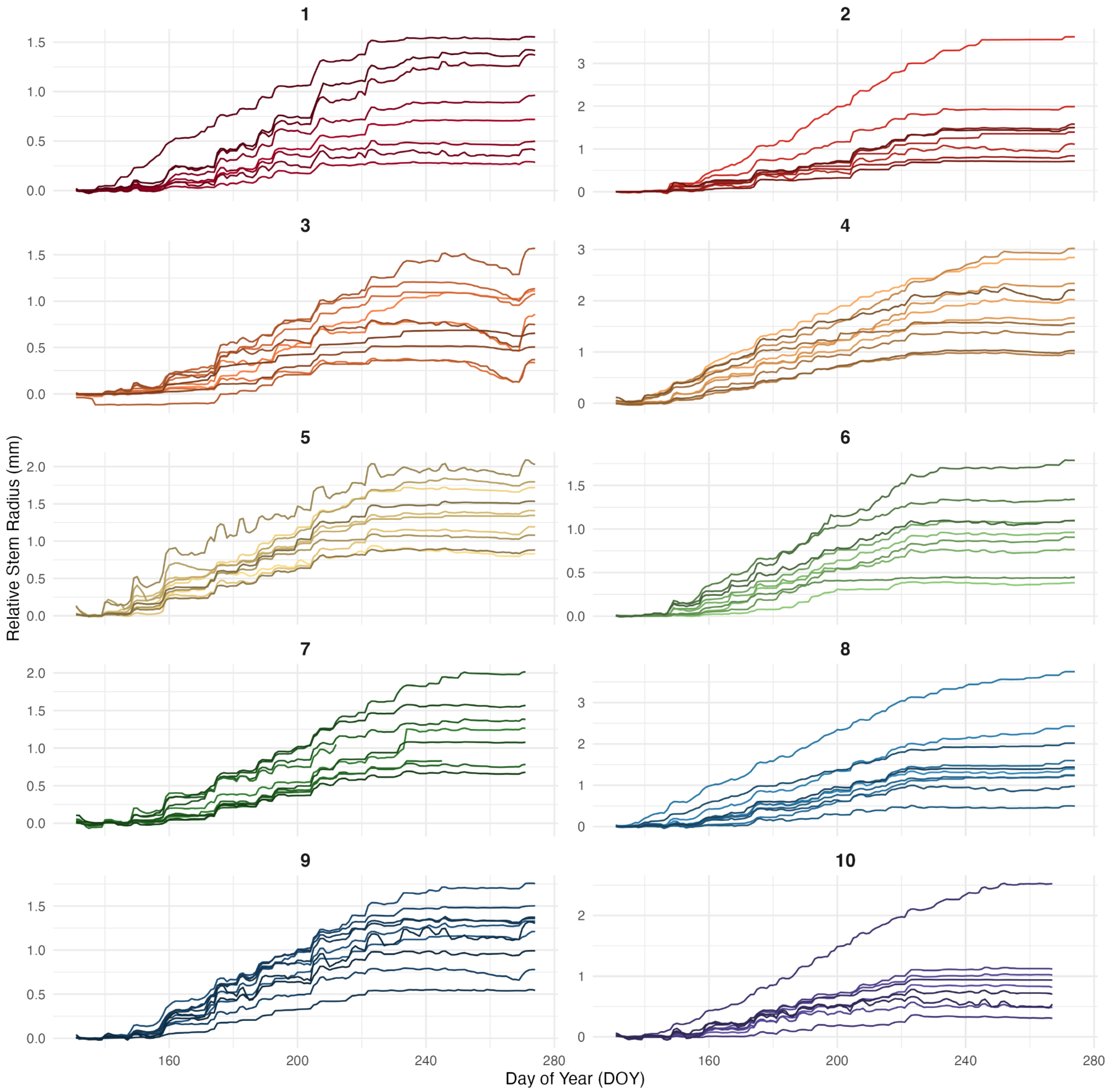


Figure 3: Raw dendrometer data across the 2024 growing season for each site and dendrometer . Each line represents a different dendrometer deployed within each site.

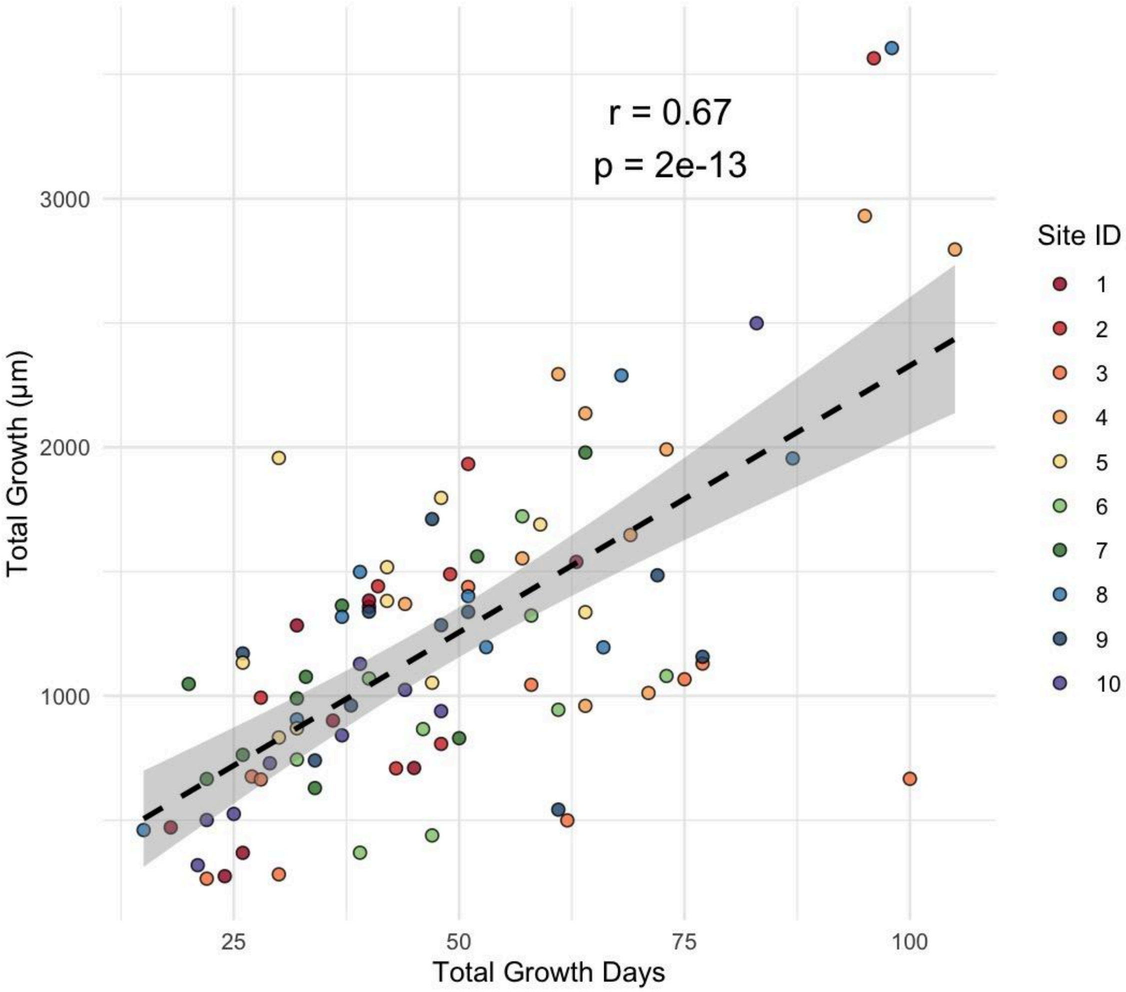


Figure 4: Relationship between the number of growing days and total growth for each tree, color coded by site. All data were derived from the automated point dendrometers deployed during the 2024 growing season. The Pearson correlation coefficient and associated p-value are reported on the figure.

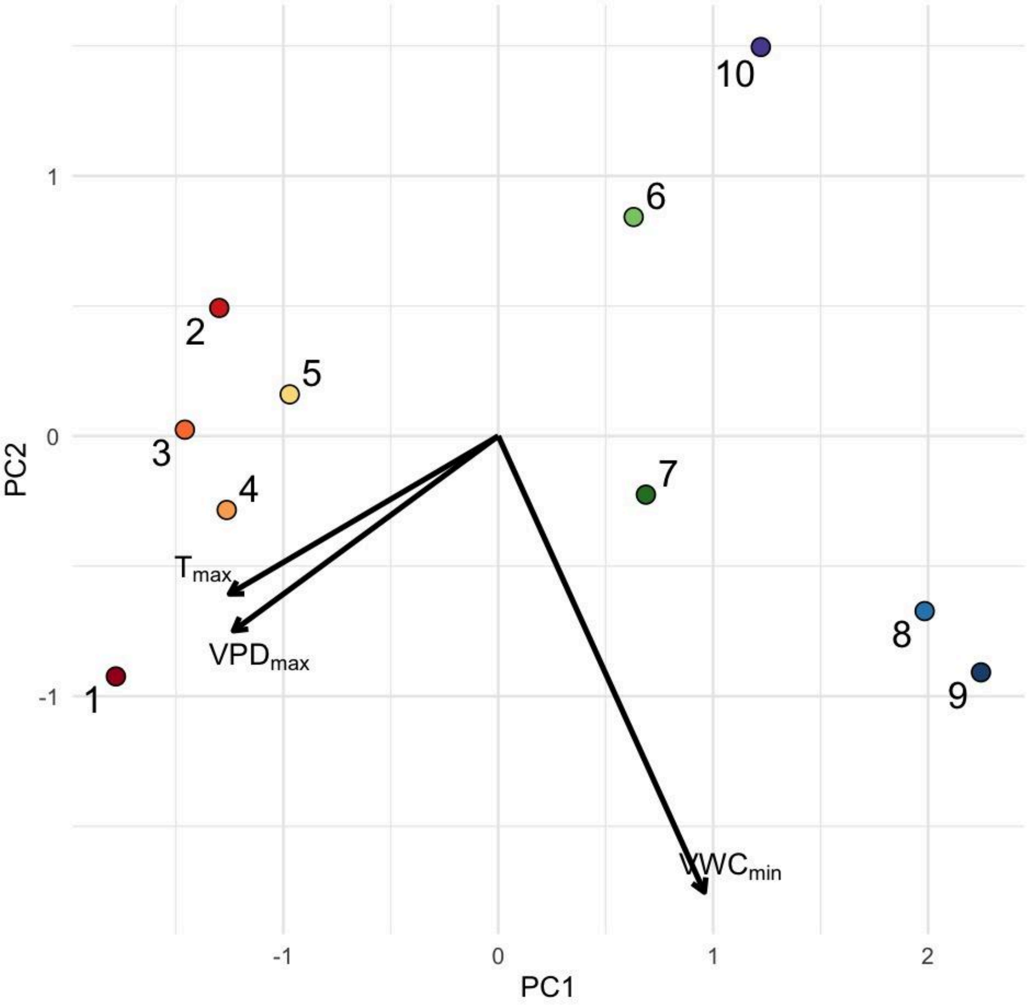


Figure 5: Principal components analysis for each site based on daily maximum temperature (T_{max}), daily maximum vapor pressure deficit (VPD_{max}), and daily minimum soil volumetric water content (VWC_{min}). Principal component 1 (PC1) explains 77.2% of variance and PC2 explains 20.3% of variance.

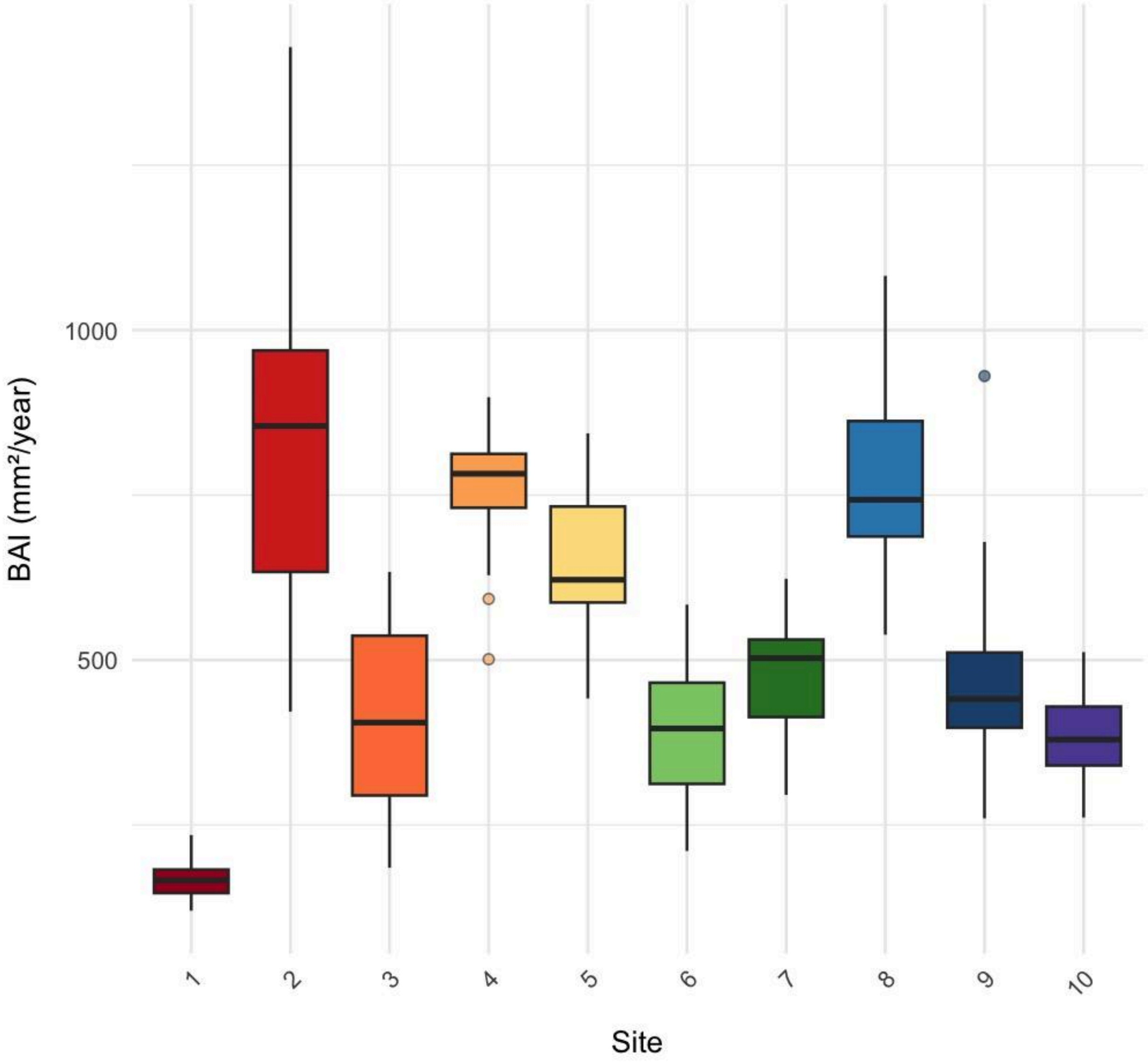


Figure 6: Box and whisker plot of basal area increment (BAI) for our ten sites over the most recent 20-year period of growth. Each box represents the interquartile range (IQR) of annual BAI values for individual trees at a given site, with the horizontal line showing the median. Whiskers extend to 1.5× the IQR, and points represent outliers.

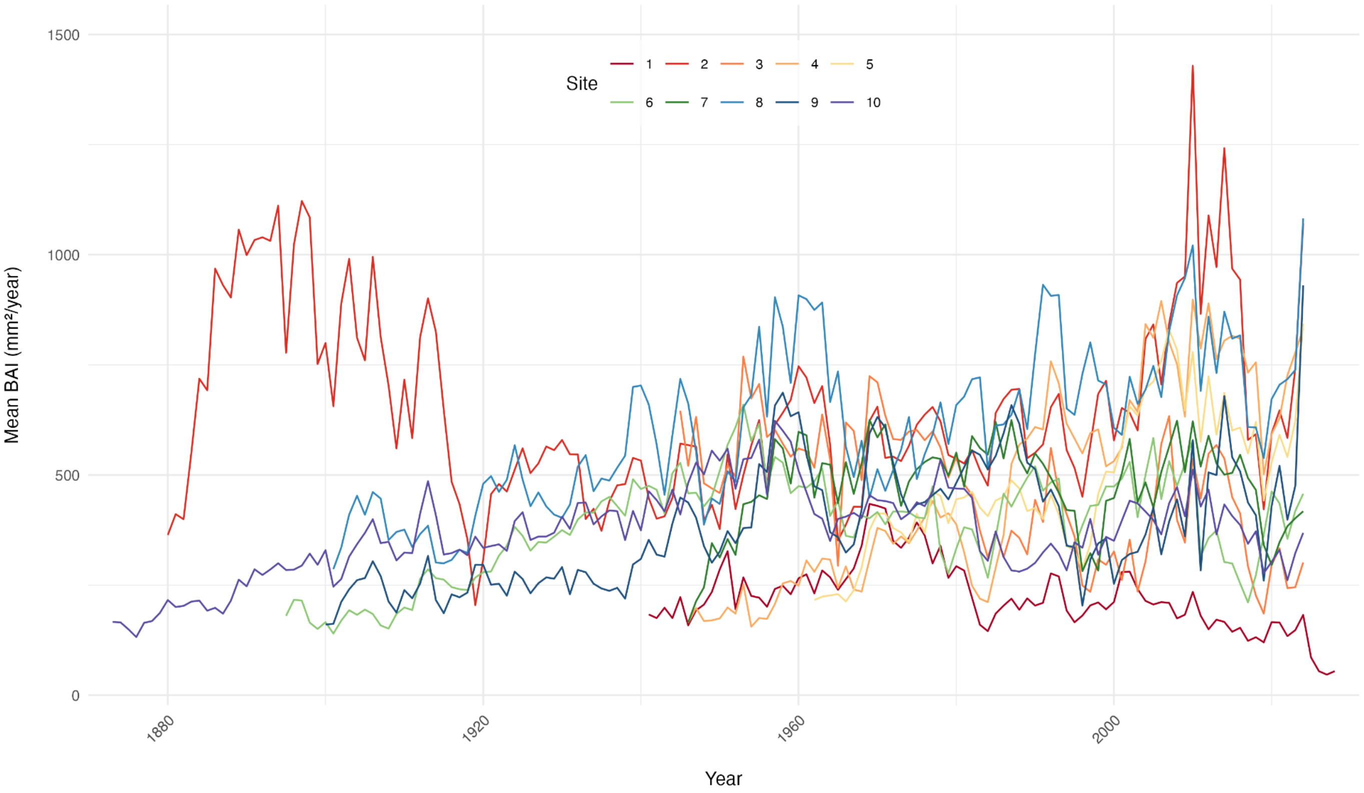
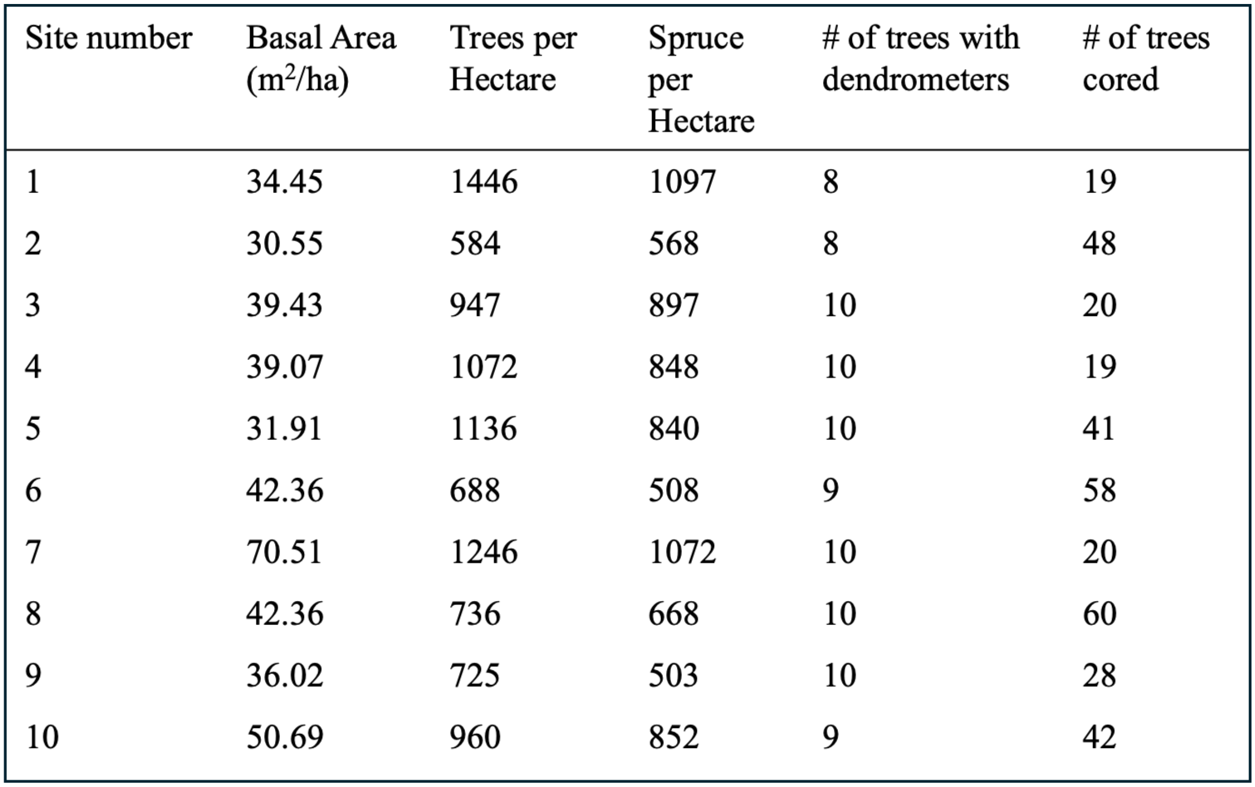


Figure 7: Mean site level basal area increment (BAI) for all trees cored at each site, trimmed to the earliest year the subsample signal strength reached 85%.

Table 1: 2024 Seasonal average climate conditions across all sites for maximum temperature (T_{max}), maximum vapor pressure deficit (VPD_{max}), and minimum soil volumetric water content (VWC_{min}). Data were collected at each site using HOBO temperature and humidity sensors logging hourly conditions in the forest understory on wooden stakes 1-m above the ground (HOBO MX2300 series, Onset Computer Co, Bourne, MA), and TOMST soil moisture and temperature probes logging at 6cm every 15 minutes (TMS-4, TOMST, Czech Republic).

Site number	Distance to coast (km)	Mean T_{max} (°C)	Mean VPD_{max} (kPa)	Mean VWC_{min} (%)
1	72	23.91	1.22	30.50
2	<1	23.15	1.00	22.37
3	47	22.97	1.11	24.79
4	6	22.75	1.12	28.05
5	2	22.63	1.01	25.97
6	<1	21.48	0.69	27.03
7	43	20.88	0.86	35.65
8	<1	20.78	0.65	43.59
9	<1	20.20	0.67	44.72
10	<1	19.69	0.63	24.34

Table 2: Summary statistics of forest inventories at each of the 10 sites. The number of trees cored excludes cores eliminated that could not be cross dated.



Site number	Basal Area (m^2/ha)	Trees per Hectare	Spruce per Hectare	# of trees with dendrometers	# of trees cored
1	34.45	1446	1097	8	19
2	30.55	584	568	8	48
3	39.43	947	897	10	20
4	39.07	1072	848	10	19
5	31.91	1136	840	10	41
6	42.36	688	508	9	58
7	70.51	1246	1072	10	20
8	42.36	736	668	10	60
9	36.02	725	503	10	28
10	50.69	960	852	9	42

Table 3: Model summaries for our generalized liner mixed effects model (glmer) and linear mixed effect models (lmer) generated using the R package "lme4" (Bates et al., 2015). Marginal R^2 (including fixed effects only) and conditional R^2 (including fixed and random effects) were calculated using the "MuMIn" package in R (Bartoń, 2025). All models include random effects for day of year, site, and individual tree. DL = day length, VPD_{max} = daily maximum vapor pressure deficit (kPa) for the 2024 growing season, VWC_{min} = daily minimum volumetric water content of the soil (%) in the 2024 growing season, T_{max} = daily maximum air temperature (°C) for the 2024 growing season. NS indicated the fixed effect was not significant ($p > 0.05$).

Response Variable	Marginal R^2	Conditional R^2	Fixed Effects	- or + Effect
Probability of growth	0.13	0.73	DL	+
			VPD_{max}	-
			VWC_{min}	NS
			T_{max}	NS
			$VPD_{max} \times VWC_{min}$	-
			$DL \times VPD_{max}$	+
			$DL \times VWC_{min}$	+
			$DL \times T_{max}$	-
Magnitude of growth	0.13	0.52	DL	+
			VPD_{max}	-
			VWC_{min}	NS
			T_{max}	NS
			$VPD_{max} \times VWC_{min}$	-
Magnitude of TWD	0.14	0.72	DL	-
			VPD_{max}	+
			VWC_{min}	-
			T_{max}	-
			$VPD_{max} \times VWC_{min}$	+
			$DL \times VPD_{max}$	-
			$DL \times T_{max}$	+

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