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THE INFLUENCE OF BEDROCK TYPE ON FOREST GROWTH AND CARBON DYNAMICS IN THE CENTRAL PENNSYLVANIAN APPALACHIAN RIDGE AND VALLEY: FROM TREE RINGS TO FOREST INVENTORIES

A Dissertation in

Ecology

By

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ABSTRACT

Forests function as a major terrestrial carbon sink and provide countless other ecosystem services. Forests of the eastern United States are responsible for a large portion of the carbon storage and accumulation of North America's forest carbon sink. In the Ridge and Valley Province of the Appalachian mountains much of the upland forested terrain is underlain by shale and sandstone bedrock types. This dissertation investigates the role of shale and sandstone on forest structure and function in the Appalachian Ridge and Valley of Pennsylvania.

Chapter 1 of this dissertation provides a general overview of forests in the region, introduces the connection between forests and bedrock and then outlines the content presented here. In Chapter 2, forest carbon storage and accumulation are examined across forested public lands in Pennsylvania's Ridge and Valley and paired with Geographic Information Systems (GIS) derived landscape metrics to investigate the impact of shale and sandstone bedrock type. Using forest inventory plots, we found that forests on shale are storing and accumulating more carbon in live aboveground forest biomass than those on sandstone. By pairing forest biometric data with spatially specific landscape metrics, including various measures of climate, topography, and soil physical properties, we identified abiotic drivers of live aboveground forest carbon dynamics in relation to lithology. Furthermore, patterns of forest community composition and community dynamics were examined in forests of the most common age classes. Forests on both shale and sandstone are dominated by oaks; however, some common species store and accumulate more carbon on a specific bedrock type. Regionally, these results highlight the potential for underlying bedrock to exert differential influences on forest ecosystem structure and function.

Forests are examined at smaller spatial but longer temporal scales in Chapter 3. I use tree cores from chestnut oak and northern red oak to disentangle the impact of bedrock type, species and climate on the growth of dominant and codominant individuals at similar north facing midslope position on shale and sandstone bedrock. Results from this chapter suggest that northern red oak grows at a faster rate than chestnut oak regardless of the underlying substrate. Correlations between seasonal precipitation and oak growth for both species on sandstone bedrock type suggest that these oak species are at least partially limited by the amount of moisture availability on sandstone but not shale. In Chapter 4, forest carbon dynamics are reconstructed from forest plots on north facing midslopes on the two bedrock types. In this chapter I compare forest growth rates from 1975-2015 as well as metrics of resistance and resilience to three moderate–to–severe growing season droughts (1991, 1999 and 2001) that occurred over the period of 1975-2015. Average forest carbon accumulation rates were similar for forests growing on both bedrock types and were resistant and resilient to the droughts experienced over the time period. Results from decades of growth from tree-ring reconstructions are considered in context to more traditional forest inventories on varying slope positions to highlight the large amounts of variability across topographic positions on shale and sandstone bedrock in the region’s complex terrain. Chapter 5 offers reflection on the results presented in this dissertation, highlighting that bedrock type is most important to forest dynamics at the scale of the physiographic province.

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Chapter 1

General overview:

Physiographic patterns partly control ecosystem processes and the distribution of biota. Forest ecologists often study the structure, composition, and function of forests as “landscape ecosystems” or whole ecosystems rather than separating them by trees, communities, landforms or soils (Barnes et al 1998). This dissertation focuses on oak dominated forests of the Appalachian Mountains where much of the forest has regrown into mostly mature closed canopy forests following severe disturbances from human land use in the period from the late 1800s to early 1900s (Dey 2014). Forests such as these are mid-successional oak-dominated forests and are among the most abundant in eastern United States (Gough et al. 2016).

Recent scientific collaboration has sparked collective interest in understanding the processes that occur within the critical zone, or the area of earth that spans the top of forest canopy down to bedrock, with an interdisciplinary focus on physical, chemical and biological processes that are key to life (Brantley et al. 2017). Much of the research presented here is framed within this context. The role of underlying bedrock, soils, topography and the interrelationships among them have long been recognized as important in controlling the distribution of tree species communities in these forests (Braun 1935, Hack and Goodlett 1960). In addition to exerting a control on the spatial arrangement of forest communities, bedrock types and the associated lithologic properties are increasingly being recognized as important controls on forest productivity around the globe (Morford et al. 2011, Hahm et al. 2014, Eimil-Fraga et al. 2014, Hennigar et al. 2017, Ott 2020, Jiang et al. 2020, Krajnc et al. 2020).

In the Appalachian Ridge and Valley region of Pennsylvania, forest communities are associated with soil physical properties, topography and landscape position (Nowacki and Abrams 1992). The Ridge and Valley physiographic province consists of folded Paleozoic sedimentary rocks with characteristic linear mountain ridges that are often comprised of weathering-resistant sandstone rock and lower lying shale and limestone valleys. A large portion of the forested landscape is underlain by two common bedrock types, sandstones and shales, as many of the limestone valleys are occupied by other land uses.

The focal point of this work is forests and their relationship to shale and sandstone bedrocks. A major goal of this work is to expand upon the understanding of the degree that bedrock type influences the structure and function of forests in the region and to examine the spatial and temporal scale of its control. The forests of this region are an important part of a large carbon sink in the eastern deciduous forests that mitigates a portion of CO_2 that the United States emits (USGCRP, 2018) while also providing other important ecosystem services such as providing wood products and important habitat as part of a larger ecosystem (Luppold and Bumgardener 2006, McShea et al. 2007).

Chapter 2 of this dissertation investigates how forests store and accumulate carbon on shale and sandstone bedrock type on public lands across the entire Ridge and Valley of Pennsylvania on hundreds of thousands of hectares (Reed and Kaye 2020). Through this work, we found that typical forests across this physiographic province stores and accumulates more carbon growing above shale bedrock type than above sandstone. Elevation and soil texture are important abiotic factors that influence the forest carbon dynamics at this scale. These abiotic features are connected to bedrock type and potentially drive these patterns. The forest growing on these bedrock types are dominated by a variety of oak species, however just two species (chestnut oak [*Quercus prinus* L.] and northern red oak [*Quercus rubra* L.]) make up about half of the forest biomass. For a few species, distinct patterns in carbon storage emerged depending on the bedrock substrate. Chestnut oak, a species typically associated with harsh and xeric conditions, stores more carbon on sandstone while white oak (*Quercus alba* L.) and tulip poplar (*Liriodendron tulipifera* L.), associates of richer and mesic sites, store more carbon on shale. Differences in soil texture from weathered bedrock may drive these differences in forest productivity where soil moisture is more available in soils derived from shale compared to sandstone.

In the subsequent chapters 3 and 4 I report on field studies at a smaller spatial scale, from hectares to thousands of hectares, comparing tree and forest growth on shale and sandstone. Forest and tree growth were reconstructed over a period of 1975-2015 from tree cores. These chapters expand upon prior research at the Susquehanna Shale Hills Critical Zone Observatory and other local studies that aim to isolate impact of bedrock type on forest growth and biogeochemistry (Brantley et al. 2016, Hill 2016). Sites were selected on similar topographic positions on north to northwest facing midslopes to keep as many factors as possible other than bedrock similar in the Rothrock State Forest and the Stone Valley Forest in central Pennsylvania.

Chapter 3 focuses on the potential differences between bedrock, species and the climate-growth relationships for two forest dominants, chestnut oak and northern red oak, between 1975-2015. The relationship between species growth and climate can be complex, and northern red oak and chestnut oak have exhibited different potentials of their growth rate under different scenarios of competition and climate (Rollinson et al. 2016). On shale and sandstone, these two species could have different growth rates due to the differences in the substrate environment. Belowground site factors, such as soil texture, water table depth, bedrock porosity and bedrock hardness alter how trees grow (Phillips et al. 2016, Kannenberg et al. 2019, Nardini et al. 2020). In this study, differences between the two species were greater than differences attributed to the substrate environment over the period of 1975-2015. However, for both oaks, positive correlations between growth and seasonal precipitation were found only on sandstone. This suggests that the growth of oaks on sandstone bedrock is more sensitive to moisture in central Pennsylvania than on shale.

In chapter 4, patterns of forest growth are identified using tree cores to reconstruct forest carbon storage over a longer period (1975-2015) than in Chapter 2 from forest inventories (which spanned the years of 2009 – 2015). The main goals are to compare decades of forest growth and examine the impact of three moderate to severe droughts in forests on shale and sandstone bedrock type. Forest responses in relation to belowground properties such as soil texture, nutrient availability and water holding capacity are important to better understand the impacts of drought that are increasingly threatening forests globally (Allen et al. 2010, Phillips et al. 2016). Bedrock influences soil conditions that contribute to moisture availability, so I ask whether forests on sites with finer soils underlain by shale are more resistant and resilient to droughts than those on sites with coarser textured and rockier soils on sandstone over the study period. Oak forests on north facing midslopes on shale and sandstone bedrock in central Pennsylvania are resistant and resilient to droughts. To contextualize growth on north facing midslopes on shale and sandstone, forest inventories from the local area at different slope positions were compared to further understand how bedrock and topography interact to influence the variability of forest carbon dynamics. Few consistent patterns emerged across other topographic positions. However, the analysis of the forest inventories suggests that sites at higher elevation on sandstone are likely experiencing higher mortality rates that cannot be identified from the tree-ring record.

Together in these three chapters forest dynamics are contrasted on two common bedrock types of the Ridge and Valley and the results included here broaden the understanding of both the variability and general patterns of oak forest growth and carbon dynamics on differing substrates in the region. Patterns found on shale and sandstone across the Pennsylvania Ridge and Valley were different than those found on more local scales (i.e. on neighboring bedrock formations in Rothrock State Forest and

Stone and Stone Valley Experimental Forest). This interdisciplinary study aims to further the field of forest ecology through the fusion of critical zone science and provide a broader spatial and temporal understanding of the role of bedrock type on forest growth beyond those previously highlighted at the watershed scale.

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Chapter 2

Bedrock type drives forest carbon storage and uptake across the mid-Atlantic Appalachian Ridge and Valley

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Bedrock type drives forest carbon storage and uptake across the mid-Atlantic Appalachian Ridge and Valley, U.S.A.

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ABSTRACT

Lithology influences forest carbon storage and productivity yet is often overlooked for forests of the eastern United States, a large and important carbon sink. This research explores the influence of two common lithologies of the Ridge and Valley physiographic province in the Appalachian Mountains, shales and sandstones, on live aboveground carbon storage, carbon uptake, forest community composition and their interrelationships. We couple forest inventory data from 565 plots from Pennsylvania state agencies with a suite of GIS derived landscape metrics including measures of climate, topography and soil physical properties to identify biotic and abiotic drivers of live forest carbon dynamics in relation to lithology.

Forests growing on shale bedrock store more live aboveground carbon compared to forests on sandstone when controlling for stand age, which ranged from 20 to 200 years. Furthermore, forests in the dominant ages (81–120 years) store more live aboveground carbon (108.1 Mg/ha vs. 86.5 Mg/ha) and uptake live aboveground carbon at a faster rate (1.32 Mg/ha/yr vs 0.85 Mg/ha/yr) on shale compared to sandstone respectively. Overall forest communities on both lithologies are dominated by oaks (*Quercus* spp.), however northern red oak (*Q. rubra*) is more dominant at shale sites compared to chestnut oak (*Q. prinus*), which dominates on sandstone. Most species in the forest tend to be more productive on shale, which may account for differences in carbon pools and fluxes across the landscape. Tree species richness is higher in sites on shale bedrock, but biodiversity-productivity relationships within lithologic classifications fail to account for differences in forest productivity. Modeled live aboveground carbon storage points to topography (elevation and aspect) and soil physical properties (% clay and available water capacity) as important influences on forest productivity that related back to lithology. Incorporating lithology into forest management strategies that are focused on a variety of ecosystem services can aid future site selection, and we demonstrate that forests on shale bedrock grow faster, store more carbon and have higher species diversity. The results presented here highlight the potential for underlying bedrock to exert differential influences on forest ecosystem structure and function across a region.

1. Introduction

Differences in forest growth and carbon storage are linked to factors that span biotic to abiotic realms including but not limited to forest community composition (Jonsson and Wardle, 2010), age demographics (Pugh et al., 2019), climate gradients (Gough, 2008) and interannual weather and climate (Barford et al., 2001). In the United States, forests have the potential to offset 12–19% of the annual fossil fuel emissions (Ryan et al., 2010), much owed to forest biomass increases in the eastern U.S. (USGCRP, 2018). Most of this region is dominated by temperate forests, which globally are estimated to store ~10% of the Earth's terrestrial carbon (Bonan, 2008). Moreover, recent studies have highlighted that second growth forests of the eastern U.S. may continue to increase the amount of carbon sequestered for decades (McGarvey et al., 2015; Gough et al., 2016), further bolstering the importance of understanding the potential controls on forest growth across the region.

Past work has highlighted that 25% of global temperate forests productivity can be explained by the combination of mean annual temperature, mean annual precipitation and forest age (Reich and Bolstad, 2001) leaving 75% of variation to explain. One key abiotic factor that may be missing is the underlying bedrock composition (lithology), which has recently been demonstrated to influence forest carbon storage (Morford et al., 2011; Hahm et al., 2014). Incorporating lithology into forest productivity models in the far northeastern United States and Southeastern Canadian region was notably important to modeling forest growth (Hennigar et al., 2017) and site index models of Maritime pine (*Pinus pinaster*) yielded different responses of growth in relation to bedrock type (Eimil-Fraga et al., 2014). Additionally, lithology can influence forest community composition and linked soil properties (Nowacki and Abrams, 1992; Searcy et al., 2003). While there seems to be a growing recognition and quantification of the lithologic influences on forests, no study to our knowledge has documented its degree of influence on carbon storage and uptake in the temperate deciduous forest region of the eastern United States.

To fill this knowledge gap, we present an analysis of public lands

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across the Ridge and Valley physiographic province in the forested central Appalachian Mountains of Pennsylvania. We focus on two rock types characteristic of the region, shale and sandstones, which are commonly overlain by forests. Specifically, the objectives of this study are to 1) assess differences in storage and uptake of live aboveground forest carbon between shale and sandstone 2) explain how forest community composition, species growth rates and species diversity differ in relation to rock type 3) model live aboveground carbon storage using abiotic variables to understand the lithologic influence on forest growth and 4) categorize the abiotic features of forest sites underlain by shale and sandstone bedrock that we hypothesize would influence forest productivity. In this study we rely on forest inventory data that capture the spatial variability of differences in forest growth, structure and composition across the landscape. We pair forest sites with spatially explicit abiotic variables to illuminate patterns of forest productivity important at the local scale and explore drivers that may be important across more regional and global scales.

2. Methods

2.1. Study area

The Ridge and Valley physiographic province in Pennsylvania, USA is characterized by folded Paleozoic sedimentary rocks that result in a series of northeast trending linear sandstone ridges and intervening shale and carbonate valleys (Fig. 1). Soil properties and textures are linked to underlying bedrock and parent material (Ciolkosz et al., 1990). The mean annual temperature of the study area is 9.4 °C and mean annual precipitation is 1130 mm, relatively evenly distributed throughout the year. The elevation of study plots averages 449 m above sea level and ranges from 130 to 767 m.

The majority of forests in the region are typically second growth forests that have established following a period of tree harvesting from the late 1800 s into the early 1900 s and generally collocate with upland mountainous terrain, likely a relic of complex topography and poor soil fertility unsuited for agriculture. Sixty-five percent of the forest landscape is comprised of forests that are 81–120 years old, according to forest inventory data presented in this study. Forests are dominated by oaks, where 62.5% of the overall biomass is in a mix of oak species [chestnut oak (*Quercus prinus* L.), northern red oak (*Q. rubra* L), white oak (*Q.alba* L.), scartlet oak (*Q. coccinea* Muenchh), and black oak (*Q. velutina* Lam.) in order of oak dominance] and 89% of the total forest biomass across the landscape is comprised of 10 canopy tree species.

2.2. Forest inventory

Forest inventories conducted by the Pennsylvania Department of Conservation of Natural Resources Bureau of Forestry and the Pennsylvania Game Commission across state public lands within the Ridge and Valley physiographic province of Pennsylvania were combined in this study to quantify forest carbon storage. Plot locations were

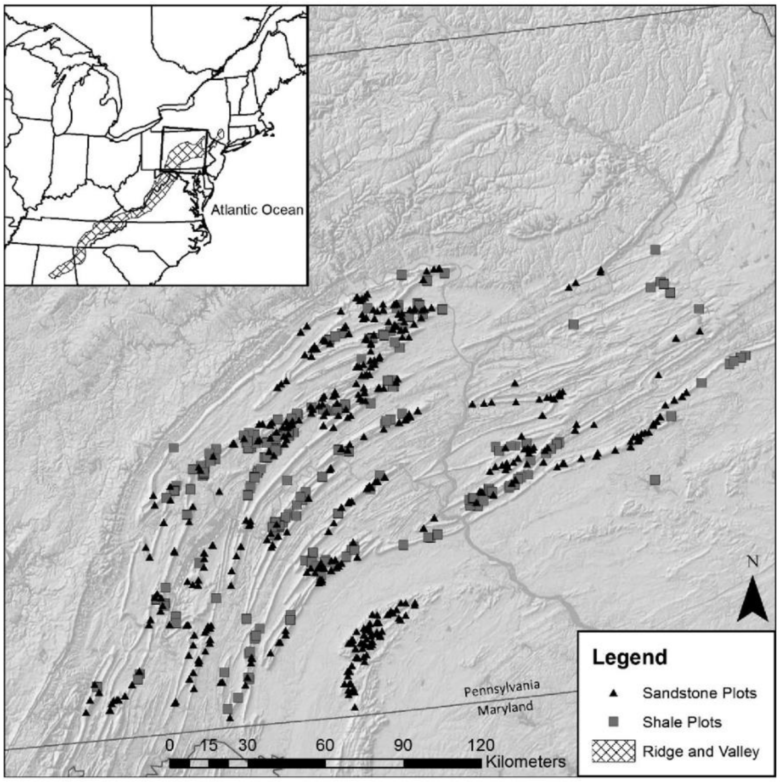

Fig 1. Forest inventory plots in the Ridge and Valley physiographic province in the eastern United States used in this study. Inventory plots are restricted to land owned and managed by the Pennsylvania Department of Conservation of Natural Resources Bureau of Forestry and the Pennsylvania Game Commission underlain by shale and sandstone bedrock.

selected by the state agencies to proportionally represent the major forest community types within the region and provide basic biological data on growth, mortality, structure, volume and change of public forest land. The sampling strategy of the inventories ensures that permanent plots are maintained and sampled multiple times, as well as continually adding newly established forest plots to inform short- and long-term forest management. Plots with repeated inventories were sampled after an average time period of 5.97 years, with a median of 6 and range from five to eight years prior.

Within the inventories, all trees with a diameter at breast height (DBH) $\geq$ 11.4 cm were measured and identified to species within 810.6 m^2 circular plots. Plots that experienced a documented disturbance ($<$ 1% of eligible plots) or silvicultural manipulation (7% of eligible plots) were removed from the dataset in this study to focus on the influence of bedrock lithology on forest carbon accumulation. We only included data from living trees to calculate the live aboveground component of forest ecosystem carbon. Forest stand age was categorized from tree core samples of three dominant or codominant individuals and binned into 20-year windows spanning 21–200 years of age. Thirteen plots were categorized as mixed age stands because trees within a plot were different ages and were removed to more parsimoniously consider the effect of forest growth as stands age.

2.3. *GIS and abiotic landscape metrics*

Coordinates of inventory plot centers were mapped onto a geologic map of Pennsylvania (Berg et al., 1980; Miles and Whitfield, 2001) to identify the primary bedrock lithology of each plot. Forest plots growing on shale, sandstone and quartzite were selected for further analysis. Plots with primary lithology of sandstone or quartzite were lumped together and categorized as sandstone. To better quantify the geophysical and abiotic features associated with underlying bedrock a suite of topographic, climatic and soil metrics were compiled across the central Pennsylvania Ridge and Valley (Table 1). Topographic metrics were derived in ArcMap 10.5.1 from a 10-meter resolution digital elevation model (DEM). Thirty-year annual climate normals (1981–2010) across the landscape at 800-meter spatial resolution were sampled from the PRISM database (PRISM, 2004). Soil metrics were derived in ArcMap using the Soil Data Development Toolbox from the Gridded Soil Survey Geographic Database (gSSURGO).

2.4. *Data analysis*

The analysis included 565 forest plots containing 23,119 trees from the most recent fully completed and available forest inventory data that were sampled between the years 2009 and 2015. Within the dataset 381 plots were on sandstone bedrock and 184 were on shale, a fairly similar ratio to the amount of Pennsylvania public land on each bedrock type in the Ridge and Valley (328,995 ha on sandstone vs 106,038 ha on shale). Estimates of aboveground individual whole tree biomass, or all of the tree material aboveground, were made from species group allometric equations (Jenkins et al., 2003) and then scaled to carbon by assuming a 48% carbon content of broadleaved trees in temperate forests (IPCC, 2006). Live aboveground forest carbon storage at the plot level was calculated as the sum of carbon content of all live trees divided by the plot area to produce values in Megagrams C per hectare (Mg/ha). Three hundred and sixteen plots ($n_{\mathrm{sandstone}} = 219$ and $n_{\mathrm{shale}} = 97$) with repeated inventory measurements were identified from the 81–120 year age class range, the most representative of the broader forest landscape (65% of plots), to understand the general patterns of forest carbon accumulation in the region on different bedrock types through time. Carbon accumulation at the plot level was calculated as

$$\Delta\,C = \ \mathrm{Carbon}_{t2} - \ \mathrm{Carbon}_{t1} / \ t2 - t1$$

where t2 is the year of the most recent inventory and t1 is the year of the prior inventory, and is represented in Megagrams per hectare per year (Mg/ha/yr). Herein, we use the terms “store” and “storage” to represent aboveground carbon stock and “accumulation” and “uptake” to represent net live aboveground carbon accumulation rate. Live aboveground forest carbon storage and live aboveground carbon accumulation were calculated for the top 10 dominant species in the region to better quantify differences in community composition and species growth. Despite removing plots with documented disturbances from the analyses, some plots had negative carbon accumulation values and are assumed to have experienced tree mortality not visually attributable during field sampling to a specific disturbance (e.g windthrow, harvesting).

2.5. *Statistical analysis*

To compare the amount of live carbon stored in forests growing on shale and sandstones we conducted an analysis of covariance that considers the effect of bedrock and stand age class using the Anova function with a type II test to address an unbalanced design (Langsrud, 2003) in the car package (Fox and Weisburg, 2011) in R (R Core Team, 2018) on all forest plots in the dataset. Initially the linear model included the interaction of the two factors, however there was no significant interaction between bedrock and stand age class ($p = 0.37$) so henceforth the interaction was not included. To understand differing rates of carbon accumulation on shale and sandstone bedrock, the subset of 316 forest plots from stands aged 81–120 years of age (the age of 65% of the forests in the study area) with carbon change data were compared using a Wilcoxon rank sum test after confirming the lack of normality using a Shapiro-Wilk normality test ($W = 0.78$, $p < 0.0001$). Results within this study are considered statistically significant at $\alpha = 0.05$, with correction for multiple comparisons when needed.

To test for differences in carbon storage and accumulation for species between the two lithologies, bootstrap confidence intervals were

Table 1
List of landscape metrics associated with forest inventory plot centers derived from GIS and source databases.

Variable	Category	Source
Primary rock type	Lithologic	Berg et al. (1980), Miles and Whitfield (2001)
Elevation	Topographic	Derived from PAMAP program
Compound Topographic Index	Topographic	Geomorphometry and Gradient Metrics ArcToolbox, Evans et al. (2014)
Slope	Topographic	3D Analyst Tools, ArcToolbox
Aspect	Topographic	3D Analyst Tools, ArcToolbox
Mean Annual Temperature	Climate	30-year climate normal, PRISM (2004)
Mean Annual Precipitation	Climate	30-year climate normal, PRISM (2004)
Available Water Content	Soil	Gridded Soil Survey Geographic Database
Percent Sand	Soil	Gridded Soil Survey Geographic Database
Percent Clay	Soil	Gridded Soil Survey Geographic Database
Bedrock Depth	Soil	Gridded Soil Survey Geographic Database
pH	Soil	Gridded Soil Survey Geographic Database

Table 2
Top ten dominant species by biomass in 81–120 year old forests, species codes and common names.

Species	Code	Common name
Quercus prinus	QUPR	Chestnut oak
Quercus rubra	QURU	Northern red oak
Acer rubrum	ACRU	Red maple
Betula lenta	BELE	Black birch
Quercus alba	QUAL	White oak
Nyssa sylvatica	NYSY	Black gum
Liriodendron tulipifera	LITU	Tulip poplar
Quercus coccinea	QUCO	Scarlet oak
Pinus strobus	PIST	Eastern white pine
Quercus velutina	QUVE	Black oak

calculated using the boot package in R (Canty and Ripley, 2017) with 5000 replicates on plot level estimates from 81 to 120 year old forests. We analyzed the data for the top 10 dominant species in this age class (Table 2). We account for multiple comparisons between lithologies across the 10 species by using a Bonferroni correction and calculated 99.5% bootstrap confidence intervals. When confidence intervals do not overlap, differences between species are considered statistically significant.

To further quantify indirect relationships between lithology and forest productivity we examined the relationship between biodiversity and productivity and tested for differences in the average number of species within a plot (species richness) by bedrock type and performed a correlation analysis between species richness and the rate of live aboveground carbon accumulation for all 316 forest plots included with multiple measurements. Because there may be differences in the biodiversity-productivity relationship between more and less productive forest ecosystems (Paquette and Messier, 2011), we separately compared species richness and the correlation with productivity for both rock types. To test for differences in species richness between shale and sandstone a Wilcoxon rank sum test was conducted after confirming the lack of the assumption of normality from a Shapiro-Wilk normality test ($W = 0.78$, $p < 0.0001$).

To better understand how forests differ between the two rock types, we summarized a set of forest structural characteristics for plots in the 81–120 year old category from 367 available plots of the most recent inventories. Tree stem density (stems/ha) and basal area (m^2/ha) were calculated at the plot level and averaged for each rock type. Additionally, we isolated the tallest and largest (DBH) individual trees from each plot and compared the average maximum tree height (m) and average maximum DBH (cm) by rock type. Statistical differences in stem density, basal area and maximum DBH were tested using Wilcoxon rank sum tests after testing the assumptions of normality with a Shaprio-Wilk normality test in which all sample groups had a p-value < 0.05 with the exception of tree stem density growing on sandstone. Maximum tree height data were normally distributed for forests growing on shale and sandstone bedrock (Shapiro-Wilk normality test, $p = 0.78$ and $p = 0.14$ respectively) and differences between rock types were tested using a Welch 2 sample *t*-test.

Linear models were constructed using backward stepwise regression to understand which abiotic variables contribute to live carbon accumulation and the direction of influence within and between bedrock types. We compared and confirmed variable selection with the results from a step function in R based on AIC (R Core Team, 2018). We built significant models using stand age and 11 GIS derived geophysical variables (Table 1). The importance of each variable was assessed by ranking significant predictors using the varImp function in the caret package in R (Kuhn et al., 2018) based on the absolute value of the t-statistic for each model parameter. Finally, to more fully understand which of the 11 geophysical variables are characteristic of each rock type, and potentially drivers of forest differences, we built classification and regression trees for all sites using the rpart package (Therneau et al., 2009) in R. The classification and regression tree was pruned to minimize the cross-validated error to avoid overfitting the data and for parsimony in interpretation.

2.6. *Allometric limitations*

Estimating forest biomass using generalized species group allometric equations, as with all allometric estimates, yields tradeoffs. Localized site- and species-specific equations are preferred when focusing on small study areas because they model local tree growth. However, parameters developed at one site may not apply to another due to variability in growing conditions and many of the published equations are often developed from relatively few trees (i.e. 10–20 individuals). The study area detailed here spans ~4,000,000 ha and is suited for the use of generalized equations that have been developed from many equations (i.e. 36–49) for each tree species group (Jenkins et al., 2003), which may represent more of the variability encompassed by ~23,000 trees than that of site and species specific equations. Additionally, a potential shortcoming of the equations used to predict biomass is the exclusive use of tree diameter and omission of tree height, which may alter the accuracy and precision of our forest carbon estimates by not capturing differences in tree architecture due to bedrock mediated site properties. However, other equations predicting tree biomass in temperate forests have found only very slight improvements by including height and recommend using DBH only equations, particularly for total biomass estimation (Wang, 2006). Furthermore, Smith et al. 2017 estimated a 10% uncertainty of biomass estimates from the sum of measurement, model prediction, and model selection uncertainty at a watershed scale in the Pennsylvania Ridge and Valley. They did not include sampling uncertainty due to their census of trees in the watershed, which means their 10% uncertainty can be considered a conservative estimate for results presented here that include sampling uncertainty. Lastly, this study focuses solely on the live aboveground carbon in trees and does not include belowground components of forest ecosystem carbon such as soil organic carbon, which has the potential to constitute more than half of total forest carbon stock in the United States (Domke et al., 2017).

3. Results

3.1. *Live aboveground carbon storage and growth by bedrock lithology*

Forests growing on shale bedrock store more live aboveground carbon when compared to forests growing on sandstone after considering the effect of stand age spanning 21–200 years ($F_{1,\ 562} = 74.4$, $p < 0.001$). Carbon storage is 25% higher in forests on shale that are 81–120 years of age (107.9 Mg/ha ± 2.5 Standard Error of the Mean, from here on SEM, $n = 113$), the demographic of the majority (65%) of forests in the region compared to those on sandstone (86.5 Mg/ha ± 1.7 SEM, $n = 249$) (Fig. 2). Additionally, forests growing on shale bedrock are accumulating carbon approximately 55% faster (1.32 Mg/ha/yr, ± 0.11 SEM, $n = 97$) than their sandstone counterparts (0.85 Mg/ha/yr ± 0.10 SEM, $n = 219$) ($W = 7932$, $p < 0.001$) (Fig. 3). Carbon accumulation was also examined across all age classes and because of the low number of plots on the tail ends of the age distribution we binned the data into wider age classes (0–80, 81–120, 121–200 years old) (Fig. 3, Supplementary Fig. 1). The trend of higher carbon uptake on shale increased from younger to older forests.

3.2. *Forest community and forest carbon accumulation rates by species*

Overall, forest species composition differed between shale and sandstone. For three of the ten tree species examined in this study, carbon storage was statistically different between the two bedrock types (Supplementary Table 2). Two species, chestnut oak and northern red oak, constitute 49% of all of the forest biomass in 81–120 year old

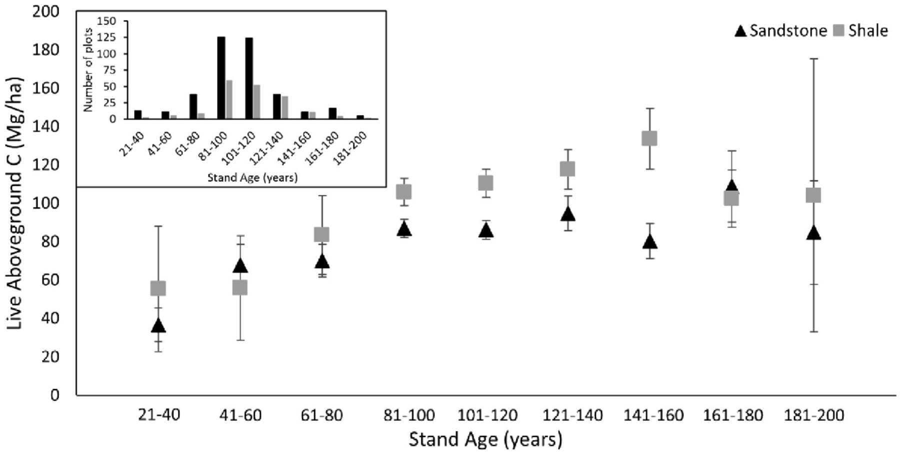

Fig. 2. Average live aboveground carbon (Mg/ha) across 21 – 200 year old forests by rock type, with inset of distribution of forest age classes. Gray squares represent forests growing on shale, black triangles represent forests growing on sandstone. Error bars represent 95% confidence intervals. Sandstone$_n$ = 381, Shale$_n$ = 184.

forests on shale and sandstone combined. However, the dominance of these two species on each bedrock type follows a contrasting pattern. Chestnut oak on shale has 18.8 Mg/ha (99.5% CI 13.0–24.0) of live aboveground carbon on average in contrast to 32.0 Mg/ha (99.5% CI 26.9–36.7) on sandstone, a difference of 52%. The inverse relationship exists for northern red oak. On shale northern red oak has 29.1 Mg/ha (99.5% CI 18.3–37.5) of live aboveground carbon on average compared to 17.2 Mg/ha (99.5% CI 13.1–20.8) on sandstone, however differences were not significant (Fig. 4, Supplementary Table 2). In addition to chestnut oak, two of the other ten dominant species store more carbon on a given bedrock type. White oak and tulip poplar (*Liriodendron tulipifera* L.) store more carbon on average in plots growing on shale bedrock, a difference of 102% and 183% respectively (Fig. 4, Supplementary Table 2).

Six of the ten species considered had an average carbon accumulation rate that was higher on shale bedrock compared to sandstone (Supplementary Table 3). However, only black gum (*Nyssa sylvatica* Marsh.) had significantly higher carbon accumulation rate on sandstone, owing to considerable variation in species growth rates across the study area (Fig. 5). Black gum accumulates carbon on sandstone at a rate of 0.13 Mg/ha/yr (99.5% CI 0.09–0.16) and is present in 64% of plots compared to 0.02 Mg/ha/yr (99.5% CI −0.02–0.08) and is present in 56% of plots on shale (Fig. 5). The two dominant species, northern red oak and chestnut oak, had the highest average rate of carbon accumulation on shale. Despite faster growth, rates were highly variable and not significantly different between bedrocks. For example, chestnut oak growing on sandstone has a confidence interval more than two times the species' average annual rate on that lithology (Supplementary Table 3).

3.3. Biodiversity productivity relationships and forest structural characteristics

Tree species richness is higher on shale compared to sandstone ($W = 1399$, $p < 0.0001$). The number of species per plot averaged 6.4 and ranged from 2 to 12 in plots on shale bedrock compared to an average of 5.4 (range 1 to 11) for sandstone bedrock. Within both shale and sandstone, there is no evidence of a positive relationship between species richness and forest productivity ($R = 0.03$, $p = 0.81$ and $R = 0.09$, $p = 0.17$ respectively) (Fig. 6).

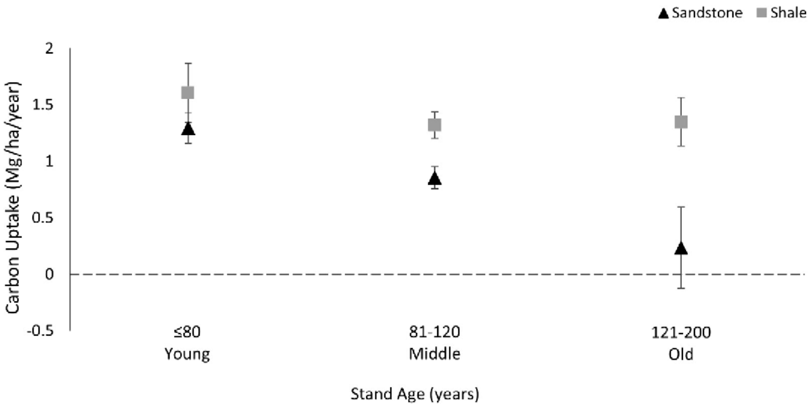

Fig. 3. Average rate of carbon uptake by rock type and stand age. Error bars represent the standard error of the mean (± SEM). Forests with ages 81–120 compared in analysis. Sandstone n_{young} = 82, sandstone n_{middle} = 219, sandstone n_{old} = 49, shale n_{young} = 28, shale n_{middle} = 97, shale n_{old} = 41.

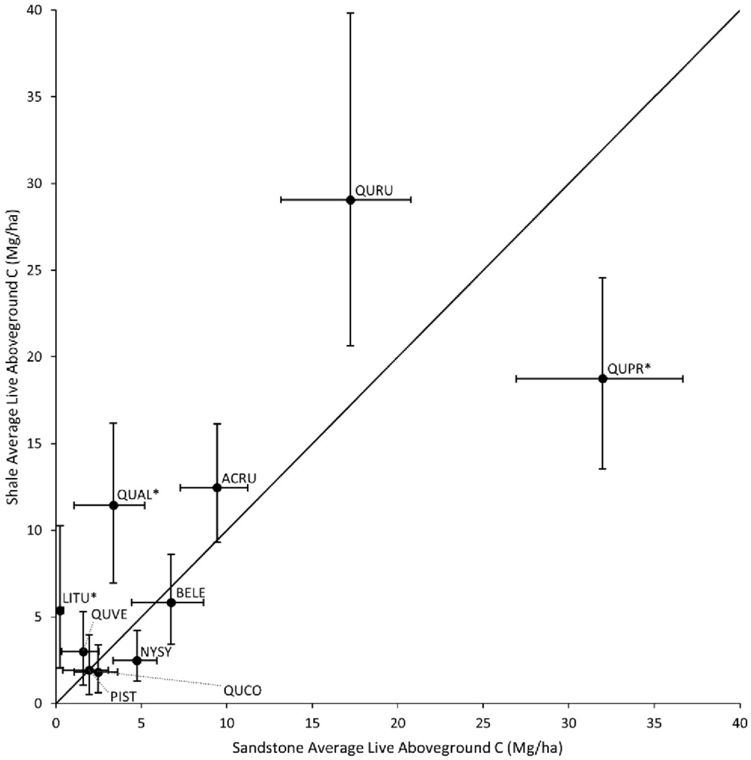

Fig. 4. Average live aboveground carbon by species and rock type, $n_{sandstone} = 97$, $n_{shale} = 219$. Error bars in both directions are 99.5% bootstrap confidence intervals and correspond to the bedrock type represented on the parallel axis. Species with asterisks represent statistically significant differences between shale and sandstone. The solid 1:1 line represents the theoretical relationship of equivalent biomass on shale and sandstone. Species codes correspond to nomenclature in Table 2.

Forest structure differed between the two rock types. Average stem density in forests growing on sandstone is higher than that on shale ($W = 19154$, $p < 0.0001$). In contrast, other forest metrics were higher on shale. Basal area ($W = 63.1$, $p < 0.0001$), average maximum tree height ($t = -12.79$, $df = 212.56$, $p < 0.0001$) and average maximum tree DBH ($W = 7371$, $p < 0.0001$) are higher on shale compared to sandstone (Table 3). On shale the average maximum tree height was six meters taller and the average maximum tree diameter was 20% larger.

3.4. *Multivariate analyses*

Twelve variables were regressed to model live aboveground carbon stored in forests on shale and sandstone separately. Significant models for shale ($F_{4,\ 179} = 10.47$, $p < 0.0001$) and sandstone ($F_{4,\ 376} = 22.53$, $p = < 0.0001$) were produced from just four variables. Stand age and elevation were significant in both models ($p < 0.001$) (Table 4). Age was the most important predictor of live aboveground carbon stored in forests on both shale and sandstone and was positively related to live carbon stored. Elevation, which has a significant negative influence for both rock types, was more important to modeled live aboveground carbon on sandstone compared to shale (Table 4). In the shale model, aspect and percentage of clay in the soil (% clay) were the other two significant predictors of live aboveground forest carbon ($p = < 0.01$ and 0.04, positive and negative relationships respectively). In the sandstone model, mean annual temperature (Tmean) and available water capacity (AWC) were also significant predictors of live aboveground forest carbon ($p = 0.03$, both variables, negatively and positively related respectively). The percent of variance explained for models on both lithologies was similar ($R^2 = 0.17$ and $R^2 = 0.18$, for shale and sandstone respectively).

A classification and regression tree was built using the 11 geophysical landscape variables for all sites in the forest inventory dataset to predict rock type. Trees were pruned by minimizing the cross-validated error. Only two variables, elevation and percent clay in the soil, were important to the classification of lithology (Supplementary Fig. 4). The classification and regression tree model preformed relatively well with a percentage of misclassified rock type based on these two variables of 18% for sandstone and 12% for shale plots.

4. Discussion

Forest carbon storage, carbon uptake and community composition differ in relation to underlying bedrock across the central Pennsylvanian Ridge and Valley. Specifically, forests that grow on shale store more live aboveground carbon in trees across forest age classes than those on sandstone. Forests within the most common age class (81–120 years old) are accumulating live aboveground carbon at a rate 55% higher on shale than those on sandstone. Despite greater forest growth on shale sites, none of the ten dominant tree species alone had significantly greater growth on shale. This finding combined with other statistical model results suggests that individual species are not driving

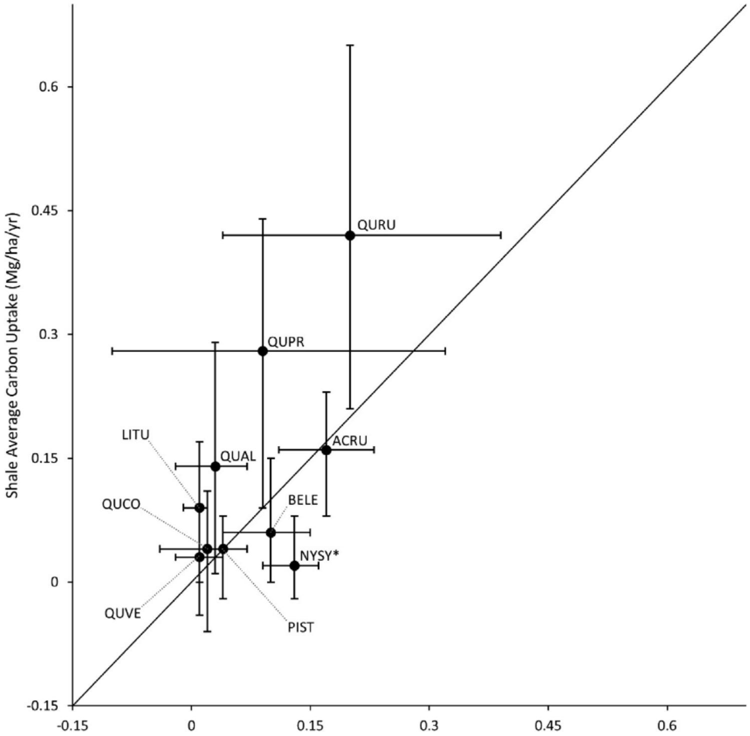

Fig 5. Average annual carbon uptake rate by species and rock type, $n_{sandstone}$ = 97, n_{shale} = 219. Error bars in both directions are 99.5% bootstrap confidence intervals and correspond to the bedrock type represented on the parallel axis. Species with asterisks represent statistically significant differences of carbon accumulation rates between shale and sandstone. The solid 1:1 line represents the theoretical relationship of equivalent carbon accumulation rates on shale and sandstone. Species codes correspond to nomenclature in Table 2.

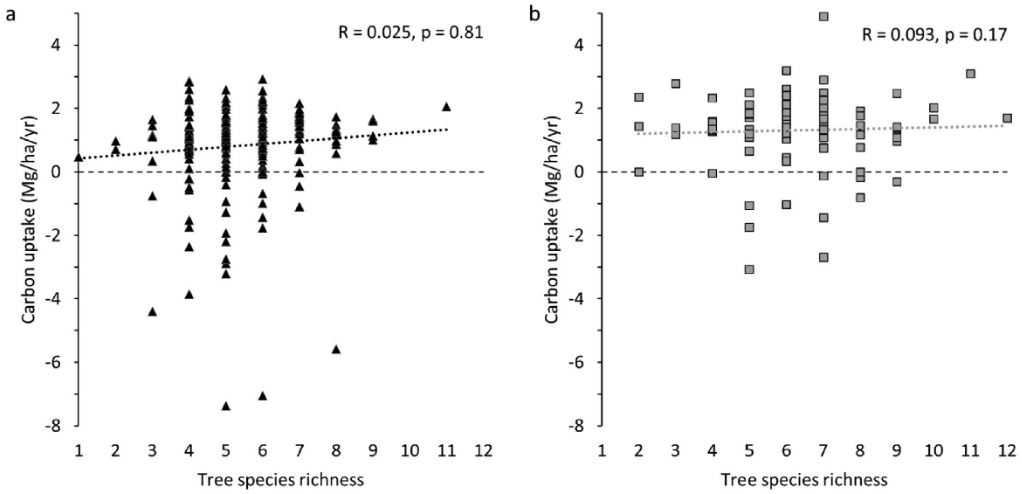

Fig. 6. Species richness and carbon uptake rates for forests on sandstone bedrock (a) and forests on shale bedrock (b). $n_{sandstone}$ = 219, n_{shale} = 97.

Table 3
Structure of 81–120 year old forests on sandstone ($n = 253$) and shale ($n = 114$) in the Ridge and Valley province of Pennsylvania. Mean, median, and standard error of the mean (S.E.M.) are included. P-values correspond to results from Wilcoxon rank sum tests and Welch two sample *t*-test in the case of average maximum tree height.

	Sandstone		Shale		
Structural metric	Mean (S.E.M.)	Median	Mean (S.E.M.)	Median	p-value
Stem density (trees/ha)	507.6 (9.4)	505.8	426.3 (11.7)	431.8	< 0.0001
Basal area (m^2/ha)	25.4 (0.40)	25.0	29.2 (0.56)	28.1	< 0.0001
Maximum tree height (m)	23.0 (0.26)	22.9	29.0 (0.39)	29.0	< 0.0001
Maximum tree DBH (cm)	48.0 (0.61)	47.2	57.6 (1.02)	56.1	< 0.0001

Table 4
Regression coefficients (b) standard error (SE) and p-values for multiple linear regression on live aboveground carbon stored based on final models containing only significant variables. Model fit is expressed in R^2. See Table 1 for variable sources. *Aspect is Beers' transformed aspect (Beers et al., 1966). Variable importance ranked from top to bottom for both rock types in the table.

Bedrock Lithology	N	Variable	b	SE	p-value	R^2
Shale	184	Intercept	87.11	14.57	< 0.001	0.17
		Stand age	3.71	0.74	< 0.001	
		Aspect*	7.95	2.91	< 0.01	
		% clay	−0.71	0.35	0.04	
		Elevation	−0.05	0.02	< 0.05	
Sandstone	381	Intercept	107.17	20.2	< 0.001	0.18
		Stand age	2.84	0.44	< 0.001	
		Elevation	−0.08	0.01	< 0.001	
		Tmean	−3.65	1.66	0.03	
		AWC	171.34	79.78	0.03	

the observed pattern of greater productivity on shale, and the differences can be indirectly accounted for through bedrock mediated soil and topographic properties such as soil texture (i.e. percent clay in the soil) and elevation that affect tree growth.

While other studies in the western United States have isolated more direct links between bedrock-derived essential nutrients and contrasting forest productivity through field measurements (e.g. Morford et al., 2011; Hahm et al., 2014), this study opportunistically capitalizes on a dataset comprised of hundreds of forest plots, many with repeated measurements linking forests with bedrock. Because we have not measured nutrient concentrations in bedrock and soils at these sites, we cannot account for the possibility that shale is higher in essential nutrients such as nitrogen or phosphorous that could limit carbon pools and fluxes in our study area. Somewhat counterintuitive, higher concentrations of phosphorous in sandstone-derived soils compared to those of shale have been reported in central Pennsylvania (Li et al., 2018) at sites where similar patterns of live aboveground carbon storage between shale and sandstone bedrock to this study have been documented (Brubaker et al., 2018). The bedrock type and phosphorous pattern found at critical zone field sites within this study region are different than what would be expected at larger scales for shale and sandstone rock types where larger grain sizes typically result in lower phosphorous concentrations (Porder and Ramachandran, 2013). Additionally, significantly lower soil moisture contents throughout the year are found in sandstone derived soils compared to those derived from shale (Li et al., 2018), which may limit forest growth and lead do the differences outlined here.

4.1. *Estimates of live aboveground storage and productivity in context*

Average live aboveground carbon storage estimates for forest on shale (108.1 Mg/ha for 80–120 year old forests) are more similar than sandstone (84.4 Mg/ha) to second growth forests in the northeastern United States that range from 100 to 116 Mg/ha (Barford et al., 2001; Siccame et al., 2007; Hoover et al., 2012) (Fig. 2). However, this general pattern is consistent with results from two forested watersheds in central Pennsylvania on shale (82 to 146.4 Mg/ha) and sandstone (58.1 to 91.9 Mg/ha) from ridgetop to valley bottom (Brubaker et al., 2018). Recent studies have highlighted variability in forest productivity across complex topography in the region at the watershed scale (Smith et al., 2017) and in other temperate forests of the mountain west (Swetnam et al., 2018). This study provides evidence that the spatial patterns of underlying bedrock contribute significantly to variability of forest carbon pools and fluxes within the Ridge and Valley physiographic province.

Forest carbon accumulation on shale was also more similar to other northeastern US forests than sandstone (this study: 1.32 and 0.85 Mg C/ha/year; other studies: 1.30 to 2.92 Mg C/ha/year, Barford et al., 2001; Curtis et al., 2002; Siccame et al., 2007). Furthermore, an inventory of forest productivity reported county-level estimates to range from 1.0 to 2.9 Mg/ha/year in the central Pennsylvanian region of our study (Brown and Schroeder, 1999). Similar to the pattern illuminated here for live aboveground carbon storage, carbon accumulation rates for forests growing on sandstone are low for what would be expected from other estimates. However, without taking into account rock type and forest age the overall average accumulation rate for 350 forest plots with repeated measurements that are 0–200 years old is 1.03 Mg/C/ha/year (± 0.8 S.E.M).

For forests on both rock types within this study, lower carbon storage and uptake estimates could be a relic of increased forest stress from exotic pests (i.e. gypsy moth and others) (Lovett et al., 2006). Forests containing chestnut oak on sandy dry ridges (particularly consistent with sandstone sites for forest in this study) are susceptible to gypsy moth, but tend to exhibit low levels of mortality (Houston and Valentine, 1977). To minimize the influence of disturbance and focus on forest productivity in relation to bedrock, we removed stands that were deemed to have experienced a 'natural disturbance' from the dataset, which made up just 0.5% of the initially considered plots. The vast majority of 81–120 year-old stands experienced positive carbon accumulations over the measurement periods, however, some stands exhibited decreases in standing live carbon (Fig. 6). Plots with negative accumulation rates that were not visually deemed disturbed in field inventories could result from the death of one to a few large trees, consistent with observations of low mortality rates in other published literature from temperate deciduous forests of the eastern United States (Gonzalez-Akre et al., 2016). Within stands that experienced negative live carbon accumulation rates chestnut oak and northern red oak, the two dominants, experienced the greatest amount of live carbon loss. The average change for chestnut oak and northern red oak on sites that lost live carbon on sandstone was −1.48 and −0.52 Mg/ha of live carbon compared to −0.11 and −0.41 on shale sites respectively. These findings fit with the understanding that mortality is generally the product of short- and longer-term stress, and that trees with slower growth rates are more likely to experience mortality regardless of disturbance (van Mantgem et al., 2003). The mortality in this study could be caused by exogeneous agents such as forest pests (e.g. gypsy moth) or by mid-successional forest dynamics transitioning to gap-dynamics, but likely reflect an indirect connection to underlying bedrock through species composition and physical stress.

4.2. Species growth and community

Only one species in this study, black gum, accumulated more carbon for a given rock type. Counterintuitively, black gum trees accumulate more carbon on sandstone, the rock type with lower overall forest productivity. Black gum is known for its almost ubiquitous presence across an extreme gradient of moisture availability, however, is almost always a small component of any forest type across its range (Abrams, 2007). Faster carbon accumulation rates on sandstone for black gum are likely a testament to the harshness of the growing conditions on some of the sites, where the species' reputation for extreme tolerance is expressed in the forest community compared to more productive sites on shale.

Environmental harshness has been hypothesized to limit species diversity in temperate forests across North America and co-vary with maximum tree height (Marks et al., 2016), which is sometimes used as a proxy for high levels of forest biomass and productivity (Fricker et al., 2019). Forests in this study region parallel this pattern, where maximum tree height (Table 4) and species richness are lower on sandstone. Despite a lack of relationship between species richness and forest productivity found here, the lower observed patterns of diversity, shorter maximum tree height, lower standing carbon, and lower productivity of forests on sandstone bedrock generally point to poorer growing conditions mediated through abiotic characteristics of bedrock (i.e. soil texture and topography) in relation to those on shale.

4.3. Bedrock linked topographic and soil properties

Sandstone bedrock in the Ridge and Valley is often found on ridges (Nowacki and Abrams, 1992; Li et al., 2018), and is generally at higher elevation due to increased resistance to erosion. In the southern Appalachians, average temperatures were found to be cooler at valley bottoms than at sideslopes and higher elevations (Boldstad et al., 1998) and while less extreme differences in elevation exist in the mid-Atlantic region, similar patterns likely exist here. Elevation is negatively related to the amount of live aboveground carbon across the forest of central Pennsylvania and was the first branch of the classification and regression tree predicting bedrock from geophysical characteristics of the forest plots in this study (greater elevations associated with sandstone bedrock). Patterns of lower productivity in these forests at higher elevation align with other observations of forest productivity and leaf area index in the Appalachian Mountains (Bolstad et al., 2001). While elevation may be confounded with the impact of rock type on forest growth, the inherent properties of bedrock are what sets the template for topography. In forests on shale and sandstone bedrock with overlapping elevation, patterns of live aboveground carbon storage and uptake parallel those from the entire dataset however are somewhat less pronounced for carbon uptake (Supplementary Fig. 5 and Supplementary Table 6). This supports our conclusion that the differing abiotic characteristics between shale and sandstone bedrock are driving differences of forests and the carbon cycle but still leaves open the possibility that within forests at higher elevations productivity may also negatively interact with bedrock and other exogenous stressors (e.g gypsy moth, acid deposition, and more variable and extreme microclimatic effects).

The amount of clay in soils derived from the two rock types can have contrasting impacts on forest growth by being at both extremes of plant available water (Brady and Weil, 2002). The percentage of clay in the soil was negatively associated with modeled live aboveground carbon for forests growing on shale and was the only other important branch of the classification and regression tree predicting bedrock type (Supplementary Fig. 4). On the other side of the spectrum, available water capacity (linked to soil texture) was positively related to regressed live aboveground carbon on sandstone bedrock. Both scenarios are inherently linked to the physical properties of underlying bedrock; sandstones produce coarser-grained soils with less clay than shales. These properties of bedrock likely exert an indirect influence on modern day forest growth through long term pedogenic processes. The relative control of tree growth (specifically tree height) by soil properties, parent material and geology across elevation gradients in the Sierra Nevada has been difficult to disentangle (Fricker et al., 2019) and similar challenges exist in this study.

5. Management implications

Forest provide a wide range of ecosystem services, with carbon storage and uptake manifesting as one of the many assets of forests in the central Appalachians. In addition to carbon storage and uptake, these oak-dominated forests produce economically important wood products (Luppold and Bumgardener, 2006), support wildlife populations (McShea et al., 2007), and provide recreation and tourism opportunities as well as other services (Krieger, 2001). As future forests grow and respond to warming, shifts in precipitation patterns, and invasive species across "complex hydrobiogeochemical templates" (Groffman et al., 2012), managers will benefit from incorporating lithological influences on forest composition and productivity. For example, identifying and conserving forests with higher species diversity will likely lead to greater resilience in the face of exogeneous perturbation (Peterson et al., 1998; DeClerck et al., 2006) and forests with more vigor due to site conditions have been shown to be more resilient to climatic stressors (Camarero et al., 2018). Additionally, geology can mediate soil organic carbon, another large and important carbon sink, and patterns of carbon storage and uptake likely exist belowground as well (Barré et al., 2017; Angst et al., 2018). Forests underlain by shale in this region may be seen as higher priority for management or conservation, particularly in light of the fact that they make up a smaller portion of the landscape, typically have a higher species richness, as well as store and uptake carbon at a faster rate, characteristics that will likely persist as forest respond to global change.

6. Conclusion

In the Ridge and Valley province of Pennsylvania forest carbon storage is 25% greater and annual uptake is 55% higher in forests growing on shale bedrock compared to sandstone. This difference is often overlooked despite the dominance of these rock types within a large and important carbon sink. The Ridge and Valley spans the Appalachian mountain chain from southern New York to northern Alabama where much of the forested upland topography is dictated by similar geologic patterns to the study area presented here. Although there are confounding factors associated with the geography of topographic and soil related features in relation to lithology, bedrock geology maps are readily available. As forest managers adapt to meet a variety of ecosystem services, including sequestering atmospheric CO_2, incorporating potential influences of lithology on forests into management plans can help target areas such as those underlain with shale that have higher diversity and faster growth, features that may add up to longer-term resilience.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117881.

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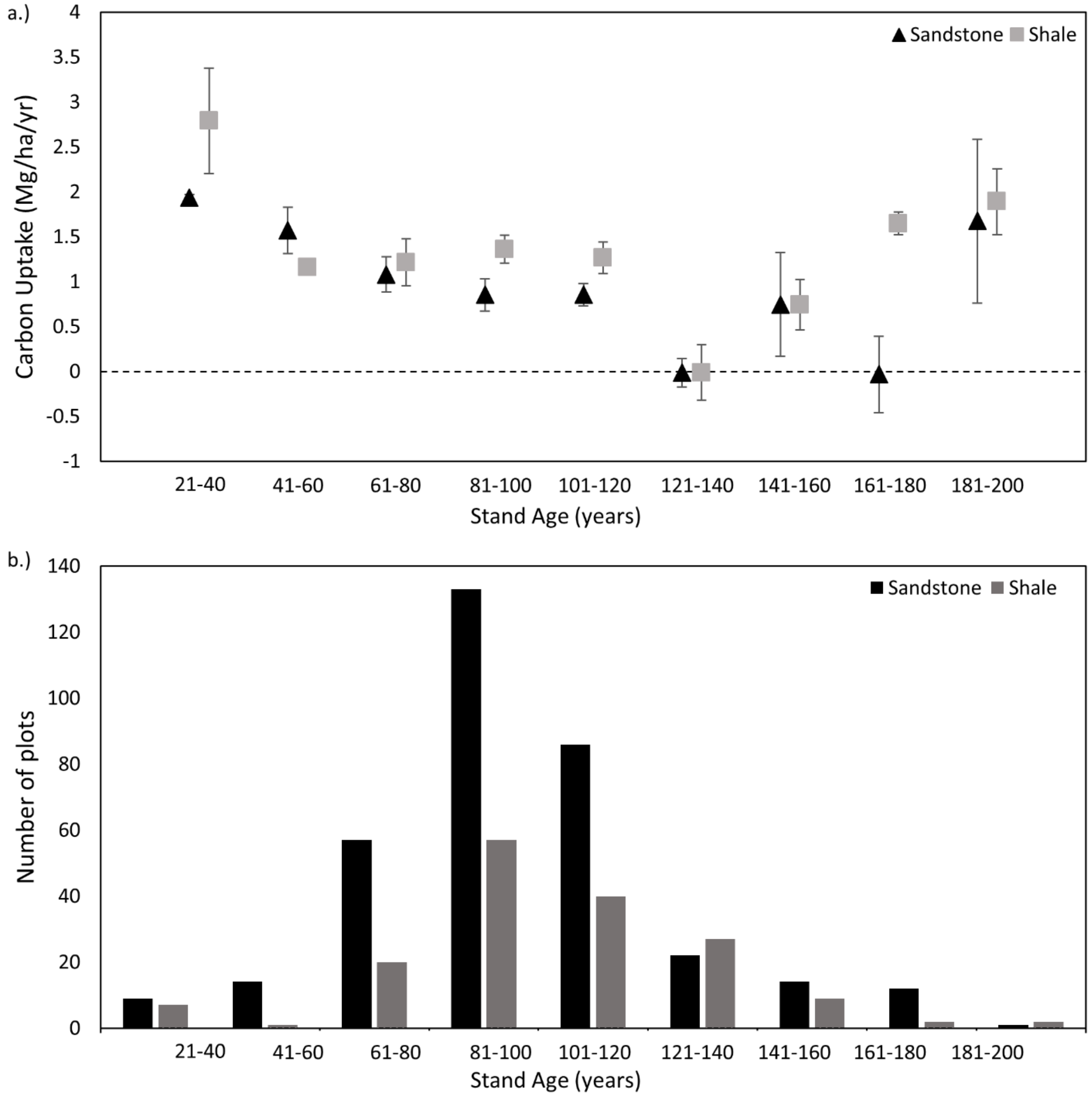


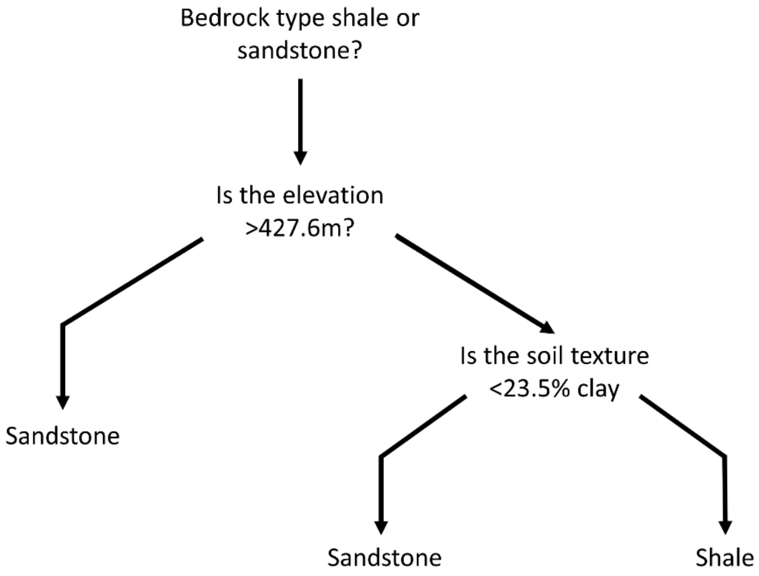
S1. a.) Average carbon uptake (Mg/ha/year) across forest 21 - 200 years old by rock type. Gray squares represent forests growing on shale, black triangles represent forests growing on sandstone. Error bars represent standard error of the mean, lack of error bars for 41-60 year old shale forests are due to sample size of one. b.) distribution of forests age classes for plots with repeated sampling used to calculate average carbon uptake values.

S2. Average live aboveground carbon storage of the top ten dominant tree species on sandstone and shale bedrock from forest plots 81-120 years old ($n_{sandstone}$ = 219, n_{shale} = 97).

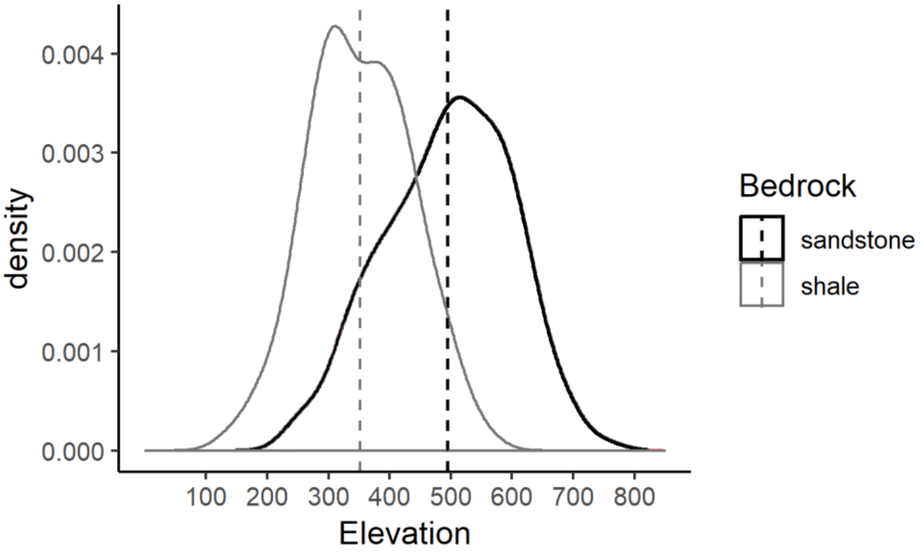
	Sandstone		**Shale**	
Species	**Live C (Mg/ha)**	**99.5% CI**	**Live C (Mg/ha)**	**99.5% CI**
Quercus prinus*	**32.0**	**(27.3, 37.1)**	18.8	(13.0, 24.0)
Quercus rubra	17.2	(13.1, 20.8)	29.1	(18.3, 37.5)
Acer rubrum	9.4	(7.2, 11.2)	12.5	(8.8, 15.7)
Betula lenta	6.7	(4.4, 8.5)	5.8	(3.0, 8.2)
Quercus alba*	3.4	(1.1, 5.2)	**11.4**	**(9.7, 15.9)**
Nyssa sylvatica	4.7	(3.3, 5.9)	2.5	(0.8, 3.7)
Liriodendron tulipifera*	0.2	(-0.5, 0.04)	**5.4**	**(0.5, 8.7)**
Quercus coccinea	2.5	(1.1, 3.6)	1.82	(0.2, 3.0)
Pinus strobus	2.0	(0.4, 3.1)	1.9	(-0.1, 3.3)
Quercus velutina	1.6	(0.3, 2.5)	3	(0.7, 4.9)

S3. Average carbon accumulation rates of the top ten dominant tree species on sandstone and shale bedrock from forest plots 81-120 years old ($n_{sandstone}$ = 219, n_{shale} = 97).

	Sandstone		**Shale**	
Species	**ΔC rate (Mg/ha/yr)**	**99.5% CI**	**ΔC rate (Mg/ha/yr)**	**99.5% CI**
Quercus prinus	0.09	(-0.10, 0.32)	0.28	(0.09, 0.44)
Quercus rubra	0.20	(0.04, 0.39)	0.42	(0.21, 0.65)
Acer rubrum	0.17	(0.11, 0.23)	0.16	(0.08, 0.23)
Betula lenta	0.10	(0.04, 0.15)	0.06	(0.00, 0.15)
Quercus alba	0.03	(-0.02, 0.07)	0.14	(0.01, 0.29)
Nyssa sylvatica*	**0.13**	**(0.09, 0.16)**	0.02	(-0.02, 0.08)
Liriodendron tulipifera	0.01	(-0.10, 0.02)	0.09	(0.00, 0.17)
Quercus coccinea	0.02	(-0.04, 0.07)	0.04	(-0.06, 0.11)
Pinus strobus	0.04	(0.01, 0.07)	0.04	(-0.02, 0.08)
Quercus velutina	0.01	(-0.02, 0.04)	0.03	(-0.04, 0.09)



S4. Schematic representation of a classification and regression tree predicting bedrock lithology from 11 GIS derived geophysical landscape variables corresponding to inventory plot centers. The cross validation error of the model stabilized using two splits, retaining only two predictor variables.



S5. Density plot showing the distribution of elevation for forest plots growing on shale and sandstone bedrock in the study area. Dashed lines represent the mean elevation for each rock type with corresponding shade.

S6. Mean live aboveground carbon stored (Mg/ha) and Carbon accumulation rate (Mg/ha/yr) for 81-120 year old forests on sandstone bedrock between 351 – 495 meters in elevation.

Live aboveground carbon Stored	**Mean (Mg/ha)**	**95 % CI**	**n**
Sandstone	88.8	(83.8, 93.8)	91
Shale	109.8	(101.6, 118.0)	47
Carbon accumulation rate	**Mean (Mg/ha/yr)**	**95% CI**	**n**
Sandstone	1.07	(0.79, 1.34)	81
Shale	1.29	(0.93, 1.65)	45

Chapter 3

Impact of bedrock and climate on the growth of two dominant oak species of the central Pennsylvanian Ridge and Valley

Abstract:

The growth of oak-dominated forests and their associated ecosystem services vary across diverse mountainous landscapes. In this study, I compare the contemporary growth of two dominant oaks in central Pennsylvania on shale and sandstone bedrock characterized by differences in soil texture and soil rock content. Annual basal area increment reconstructed from cores from 86 trees over the period of 1975-2015 is used to compare growth rates and the seasonal climate response of the two species on similar aspect and hillslope position. Northern red oak growth exceeded chestnut oak growth regardless of the bedrock type. The average growth rate for a northern red oak over the study period was 87% higher than chestnut oak sampled from all plots and both bedrock types, 17.2 cm^2/yr (± 1.8 Standard Error of the Mean) compared to 9.2 cm^2/year (± 0.9 Standard Error of the Mean), respectively. Average seasonal temperature and precipitation were analyzed to investigate relationships with annual tree growth. Northern red oak growth was positively correlated with summer precipitation and chestnut oak growth was positively correlated with winter precipitation when growing on sandstone bedrock. However, positive correlations with precipitation for both species on sandstone suggest that trees growing on sandstone sites are limited by seasonal moisture which may be useful in predicting future forest growth in a changing climate.

Introduction:

Physiographic variations across landscapes influence ecosystem structure and function in many ways (Swanson et al. 1988). Species distribution and forest community types in the eastern United States are associated with landforms that relate to the underlying bedrock type of the substrate in which they grow (Hack and Goodlett 1960, Brush et al. 1980, Searcy et al. 2003).

These forests play an important role in regulating the climate globally by sequestering atmospheric carbon (USGCRP, 2018). An interdisciplinary understanding of the interacting processes that drive ecosystem and climate services, such as tree growth, can help us understand the potential of forests to help curb global climate change (Bonan 2008). While forests have the potential to mitigate the effects of global climate change, their growth is also subject to complex direct and indirect effects of climate such as increasing temperature, altered precipitation patterns as well as changes in the frequency of disturbances and droughts (Rustad et al. 2012). The way that trees respond to climate events, like drought, can vary depending on a variety of circumstances (Clark et al. 2016).

Belowground site factors, such as soil texture, water table depth, critical zone thickness and bedrock porosity can all alter a tree's response to drought and may depend on the species present as well as their associated life history traits (Phillips et al. 2016, Kannenberg et al. 2019, Hahm et al. 2019, Nardini et al. 2020). Moisture stresses for trees and forests are not always delivered as discrete events, and even mild but chronic water stress has the potential to decrease the size of the carbon sink in the eastern deciduous forest (Brzostek et al. 2014). With warmer temperatures and more variable precipitation predicted in a changing climate, these conditions are likely to occur more often in forests of the eastern United States (Hayhoe et al. 2007). Despite a growing recognition of the influence of bedrock type on forest structure and function and its impact on site-specific belowground properties, the degree to which climate, bedrock type and forest species growth interact remains under explored in oak dominated forests.

In the Ridge and Valley physiographic province of the Appalachian Mountains, forest composition is related to past land use practices, topography, substrate and soil properties (Nowacki and Abrams, 1992), as well as belowground moisture regimes linked to the characteristics of bedrock (Hack and Goodlett 1960). The Ridge and Valley region is dominated by the oak-hickory forest type (Iverson and Prasad, 2001) where upland forest terrain is commonly underlain by shale or sandstone bedrock types. Across the region, chestnut oak (*Quercus prinus* L.) tends to dominate on the sandstone bedrock type while northern red oak (*Q. rubra* L.) dominates on shale, with the two species currently constituting about half of the forest biomass (Reed and Kaye, 2020).

Typically chestnut oak, also referred to as rock oak, is associated with xeric rocky sites and competes well on west and southwest aspects while northern red oak tends to occupy a wider range of soil-moisture conditions and expresses a wider range of fitness across aspects (Fekedulegn et al. 2003, Fekedulegn et al. 2004). These two species grow best on deep, well drained soils and both are intermediate in shade tolerance, but chestnut oak is considered to be more shade tolerant and slower growing than northern red oak (Burns and Honkala 1990). Regardless of the relative similarities or differences in their natural history the dominance of these two species sorts by bedrock type across the larger landscape (Reed and Kaye 2020). Soil moisture availability driven by soil texture is one of the many physiographic parameters known to influence tree growth that are modulated by bedrock type in the Appalachian Mountains (Dryness 1965, Ciolkosz et al. 1990) and a study examining its control on mature contemporary growth in these two oak dominant species is warranted.

Climate can control the growth dynamics of mixed species eastern deciduous forest (Pederson et al. 2015). Growth-climate relationships have revealed that early- to mid-growing-season moisture correlates with oak growth across common species in the eastern United States (Speer et al. 2009) and the consistent signal across sites has been posited to imply a cause-effect relationship (LeBlanc and Terrell 2011). However, the relationship between species growth and climate is complex; northern red oak and chestnut oak exhibit varying degrees of amplitude in their growth rate under different scenarios of competition and climate (Rollinson et al. 2016). Because these relationships are complex and can vary across terrain, bedrock type may filter the way that species and climate interact within these forests.

The goals of this study are to examine the impact of bedrock type, climate and the interaction between the two on the growth of two of the dominant tree species of the forested upland central Appalachian mountains. Specifically, the hypotheses tested were 1.) growth rates of northern red oak would be greater on shale bedrock type while chestnut oak growth rates would be highest on sandstone bedrock types 2.) the response of northern red oak and chestnut oak growth to temperature and precipitation would differ between trees growing on shale and sandstone bedrock types and chestnut oak would be less sensitive to precipitation given its dominance on sandstone. To parse out the impact of bedrock and climate on interspecies tree growth I used a combination of four decades of tree-ring derived northern red oak and chestnut oak growth paired with locally downscaled climate data from trees growing on similar aspects and hillslope positions on shale versus sandstone bedrock types. I used a combination of linear mixed effects models and correlation analyses to test these hypotheses from trees sampled from forests on similar aspects and slope positions in central Pennsylvania to isolate the impact of bedrock type.

Methods:

Study Area

This study took place in the forested Appalachian Mountains of central Pennsylvania within the Ridge and Valley Physiographic province. Plots were sampled in Rothrock State Forest managed by the Pennsylvania DCNR and Stone Valley Forest managed by the Pennsylvania State University. The climate at the Shale Hills Critical Zone Observatory, a centrally located and well-studied reference point for the study sites, is characterized as humid continental with an average annual temperature of 9.4° C and an average annual precipitation of 1016 mm over the study period (Wang et al. 2016). On average in central Pennsylvania there is a high degree of seasonality where winter temperatures have been below freezing on average and summers are warm with peak temperatures in June, July and August. Precipitation patterns are generally evenly distributed throughout the year and are less seasonal but monthly amounts over the years have been highly variable (Figure 7). All sampled plots are within 15 km of the observatory and experience similar climate conditions. Much of the upland forested mountains are underlain by Paleozoic sedimentary rock types such as shale and sandstone. The two formations are the Silurian-aged Rose Hill shale and the Tuscarora quartzite (a predominant sandstone in the region). The Rose Hill shale is an iron-rich and organic-poor formation (Dere et al. 2016) and the Tuscarora quartzite is an orthoquartzitic sandstone (Li et al. 2018). Two watersheds, the Shale Hills site and Garner Run are a part of extensively studied locations in the CZO network serve as example conditions of the forest ecosystems on shale and sandstone in central Pennsylvania (Brantley et al. 2018, Li et al. 2018).

Shale-derived soils at the study sites are more mesic and have higher clay content, have a lower percentage of rock and more organic matter compared to those derived from sandstone that are more likely to be classified as xeric. Soil profiles from north facing midslopes, the same topographic position where I sampled the trees, at the Shale Hills Critical Zone Observatory (CZO) are essentially free of rock in the upper 50 cm while soils from north facing midslopes at the sandstone-based Garner run CZO consist of large portions of boulders (Figure 8). Percent rock in the soil profile from sandstone sites depicted in figure 2 are likely as less rocky than typical, given that the data are from pits with few boulders that allowed for excavation. However, these soil profiles highlight physical differences in these soil and rooting environment. Soils at the shale sites are classified as Weikert series (silt loam) and soils at the sandstone sites are classified as Hazelton series (gravely/sandy loam). Shale-derived soils from the hillslopes detailed in this study are higher in magnesium, calcium, sulfur, and potassium compared to sandstone sites, however phosphorus concentrations are higher in sandstone derived soils (Hill, 2016). Additionally, Pleistocene dust input may play an important role in the bioavailable chemical composition of soils in this study and the region (Marcon et al. 2021). Forests at the study sites detailed here have similar basal area and number of species per plot on both bedrock types, but forests above sandstone have a higher density of trees (Table 5).

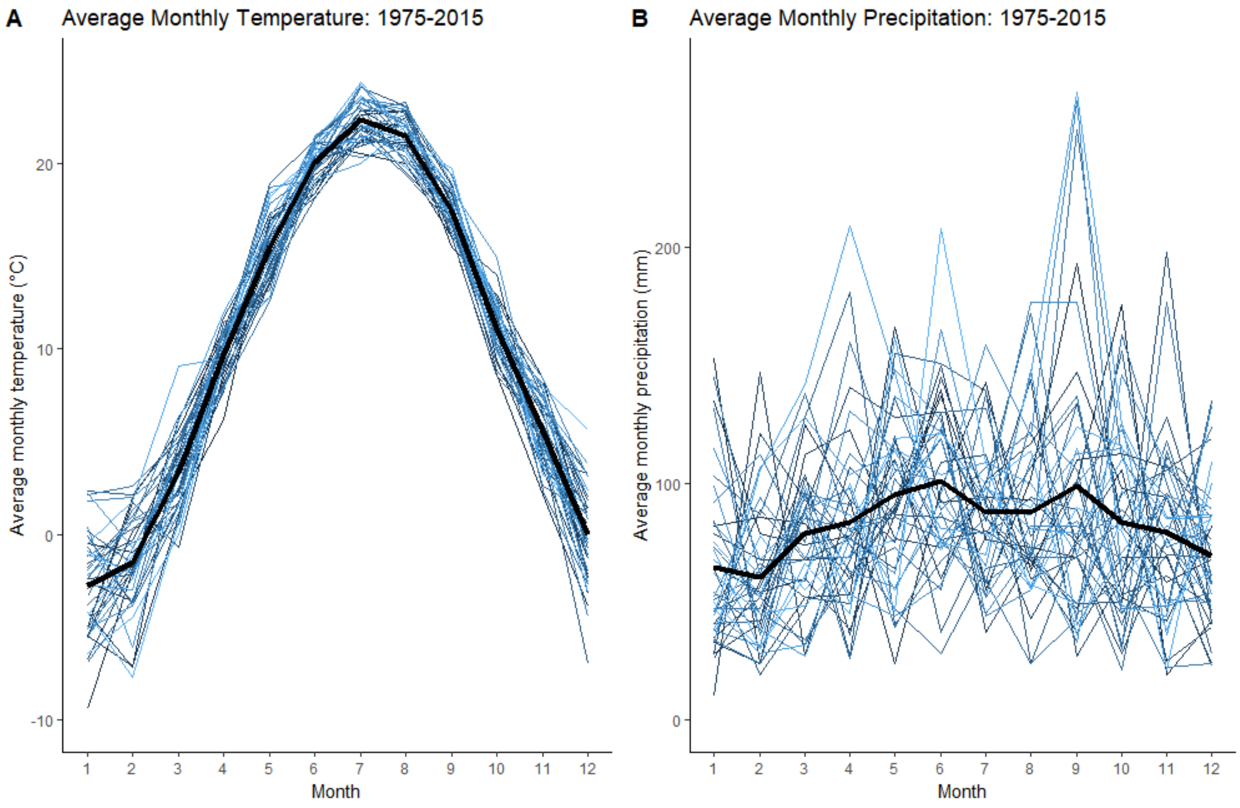


Figure 7. Monthly temperature and precipitation at the Shale Hills Critical Zone observatory (data from Wang et al. 2016). Thick black lines represent the average over the study period 1975-2015 and thin blue-grey lines represent individual years.

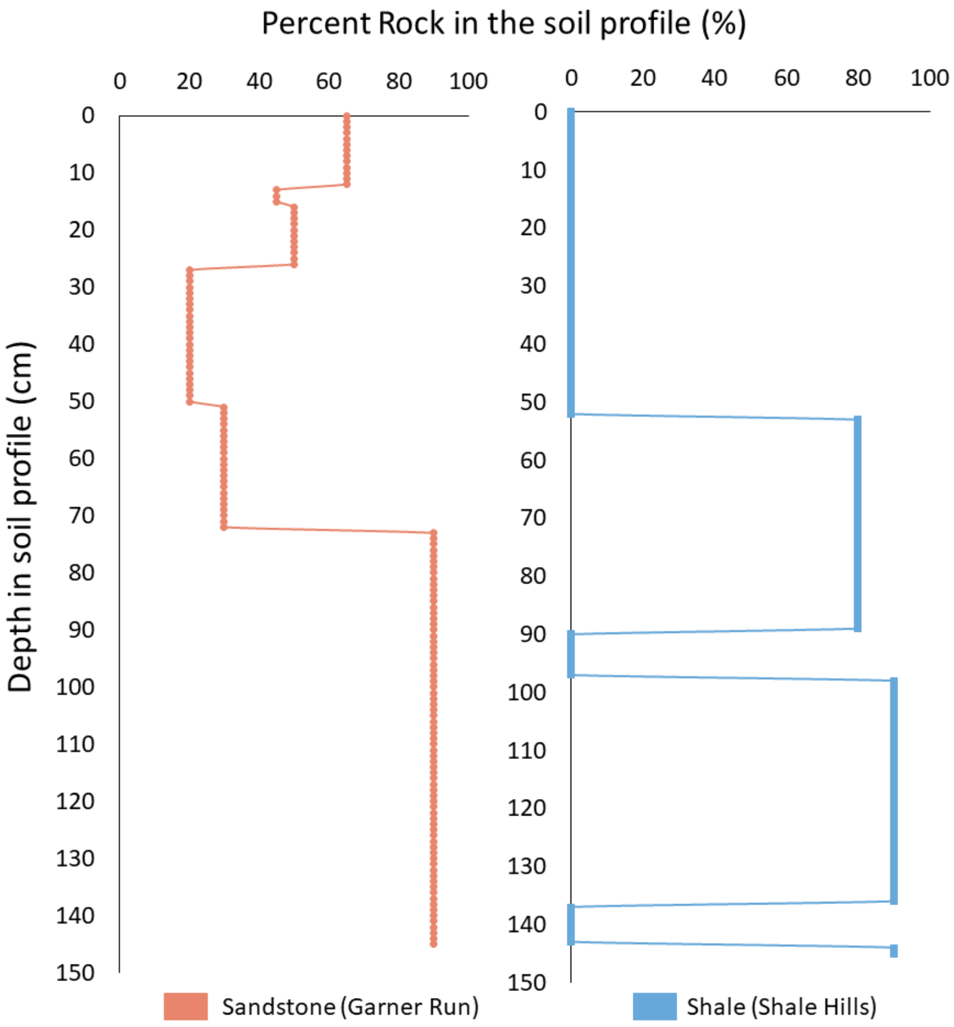


Figure 8. The percentage of rock in the soil profile at forested north-facing mid-slope positions from representative sandstone (Garner Run) Critical Zone Observatory and shale (Shale Hills) Critical Zone Observatory. Sandstone profile data from Brantley et al. 2016 and shale profile data from Lin, 2006 with data synthesize in table format in Hill 2016.

Table 5. Average forest characteristics and standard error of the mean from sites where trees were sampled on Shale and Sandstone. Shale$_n$ = 9, Sandstone$_n$ = 11.

	Shale	**Sandstone**

Basal Area (m^2/ha)	29.8 (2.4)	30.8 (2.5)
Species per plot	4.3 (0.5)	4.7 (0.2)
Stem density (stems/ha)	441.3 (18.7)	526.7 (53.3)

Sampling Approach and Site selection

Plots in this study were selected as a part of a larger field sampling design aimed to isolate the impact of bedrock type on forest growth and biogeochemistry. In an attempt to keep as many factors as possible the same between forest on the two bedrock types, sites were selected on north to northwest facing midslopes on the two formations of interest identified using the Geological Map of Pennsylvania in ArcMap 10.5.1 (Berg et al. 1980, Miles and Whitfield 2001, Hill 2016). On eight north-facing hillsides I generated randomized points using ArcMap on the midslope position of the hillslope to identify sample plot locations spaced at least 100 meters apart. Sampled plots were within the interior forest and lacked visual signs of human and natural disturbance (i.e. trails, logging, windstorms). I recorded topographic characteristics in the field (elevation, aspect and slope) at each of the plots. The aspect and slope angles were similar for both bedrock types. Similar to the trend across the landscape at larger scales (Reed and Kaye, 2020), plot elevation is on higher on average at sites on sandstone than on shale (Table 6).

Table 6. Average topographic characteristics and standard error of the mean of sampled plots on Shale and Sandstone. Shale: n = 9, Sandstone: n =11.

	Shale	**Sandstone**

Elevation (m)	300.5 (8.5)	557.3 (28.2)
Aspect (°)	343.3 (4.4)	333.6 (2.8)
Slope (%)	16.4 (1.7)	18.5 (3)

At the randomly selected plot locations I established 314.2 m^2 circular plots in which all trees with a diameter at breast height (DBH) were identified to species, measured and recorded to document forest structural conditions within each plot (Table 5). Each individual tree was assigned a tree crown class of dominant, codominant, intermediate or suppressed based on a visual assessment in relation to its neighbors. To focus on the impact of climate on northern red oak and chestnut oak, this study relies on tree-ring data from trees deemed dominant and codominant in relation to their neighbors to lessen the presence of competition from neighboring trees.

Tree coring and Processing

Two increment cores were extracted from each tree that had a DBH >10 cm between summer of 2016 and spring of 2019. Trees were cored on each side parallel to the hillslope contour to avoid reaction wood at ~1 – 1.37 meters high. In this study I focus only on cores from northern red oak and chestnut oak resulting in data from 86 dominant and codominant trees (northern red oak * shale: n = 25, northern red oak * sandstone: n= 22, chestnut oak *shale: n = 25, chestnut oak * sandstone: n = 14) from 20 different plots (shale: n = 9, sandstone: n = 11). After collecting the tree cores, they were air dried for at least 3 days and glued onto mounts. Cores were sanded using a belt sander with progressively finer sandpaper from 220 to 400 grit.

After sanding, cores were visually dated from the outermost fully developed ring inward and annual rings measured to the nearest 0.01 mm using a movable stage and Velmex measuring system. Cores were statistically crossdated using the program COFECHA (Holmes, 1983). Descriptive cross dating summary statistics were calculated using the dplR: Dendrochonology Program Library in R (Bunn et al. 2024) and are detailed in Summary Table 1 of this chapter. After crossdating, annual ring widths from the two core samples from an individual tree were averaged by tree resulting in 3,440 annual growth measurements from 86 trees considered in this study over the study period of 1975 - 2015. There were two instances where tree core sampling resulted in only one intact core (one northern red oak on shale and one northern red oak on sandstone) and both were kept in the analysis.

Data Analysis

Basal area increment (BAI) in cm^2/year was calculated to express tree growth in this study because of its ability to remove age/size related growth trends typically found in tree-ring data (Peters et al. 2015). BAI was reconstructed from initial diameter measurements taken in the field at the time of coring and is calculated as

$$BAI_t = \pi R^2_t - \pi R^2_{t-1}$$

where t is a given year, R_t is the stem radius at the end of an annual increment and R_{t-1} is the stem radius at the beginning of the increment (Biondi and Fares, 2008). I focused on the contemporary period from 1975 – 2015 to highlight modern trends in forest growth in the region and to attempt to limit the amount of non-climatic related growth due to forest dynamics (i.e. neighboring tree mortality resulting in release from competition). The truncated time period should exclude the majority of tree mortality (and releases) experienced in the “stem exclusion phase” (Oliver and Larson, 1996) as these forests typically are regenerating following widespread clearcutting of the late 1800s and 1900s.

To analyze and focus on the impact of seasonal climate on northern red oak and chestnut oak growth I relativized BAI measurements to account for surrounding competition that an individual stem is experiencing. Past research has highlighted that tree growth can be a product of both climate and competition in closed canopy forests in this region (Rollinson et al. 2016). To relativize BAI by the surrounding competition I divided it by the sum of basal area of all species within the forest plot at the time of sampling. Holding competition static over the period of 1975 -2015 may not represent the temporal dynamics of competition of mixed species forests, but serves as a proxy for the non-climatic influence on individual tree growth and is a metric for the initial stand level stocking. Trees experiencing a high level of competition at the time of sampling likely experienced high levels of competition in 1975. An average relative BAI for each year over the study period (1975-2015) was calculated for all northern red oak and chestnut oak trees from shale and sandstone bedrock type sites resulting in four different series that were correlated with climate.

To test for the correlation between seasonal climate variables and average relative BAI for each species and bedrock combination, average temperature and total precipitation data were compiled into 3-month seasonal windows from the Shale Hills Critical Zone Observatory location using the ClimateNA program (Wang et al. 2016). I included both current and previous year seasonal temperature and precipitation data, as previous years climate is known to impact current year growth in trees. Seasonal windows were split into four periods and are divided by months rather than the lunar calendar and are classified as winter (December, January, February), Spring (March, April, May), Summer (June, July, August, and Autumn (September, October, November).

Statistical Analysis

To compare the effect of species and bedrock type and the potential interaction between the two factors on tree growth I fit linear mixed effects models to reconstructed basal area increment data with species and bedrock type as fixed effects and individual tree as a random effect using the nlme package (Pinheiro et al. 2018) in R (R Core Team, 2018). Due to the non-normal structure of the reconstructed BAI data, a log transformation was performed on the response variable to meet model assumptions. To account for the impact of the prior growing season on the current year's growth and the time series nature of tree ring data I incorporated an autocorrelation structure with a 1-year lag. Model fit and assumptions were evaluated by plotting the fitted vs standardized residuals. The statistical notation of the model took the form of:

$$Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \beta_3 (X_{1ij} \text{ x } X_{2ij}) + u_j + \epsilon_{ij}$$

where $\epsilon_{ij} \sim AR(1)$

and

X_1 = species

X_2 = bedrock type

Following the previously mentioned analysis, with the goal of disentangling the effect of seasonal climate on the growth of the two oak species by bedrock type I correlated annual relative basal area increment and seasonal climate variables from the current and prior growing season for the years 1975-2015 for northern red oak and chestnut oak on shale and sandstone separately. Only summer and autumn were included from the previous growing season. All analyses were considered statistically significant at $\alpha = 0.05$.

Results:

Table 7. Average tree characteristics for northern red oak and chestnut oak by bedrock type included in this study. Standard deviation and the standard error of the mean are included in parenthesis. Northern red oak * shale: n = 25, northern red oak * sandstone: n = 22, chestnut oak * shale: n =25, chestnut oak * sandstone: n = 14

	Northern red oak	**Chestnut oak**
Shale	n = 25	n = 25
Average tree DBH (dm)	42.7 (st.dev = 14, SEM = 2.8)	30.1 (st.dev = 8,SEM = 1.6)
Average BAI (cm^2/year)	18.9 (st.dev = 2, SEM =0.4)	8.4 (st.dev = 0.5 ,SEM = 0.1)
Average plot level relative basal area (unitless)	0.16 (st.dev = 0.1, SEM = 0.02)	0.07 (st.dev = 0.05, SEM = 0.01)
Sandstone	n = 22	n = 14
Average tree DBH (dm)	37.0 (st.dev = 12.7, SEM = 2.7)	35.9 (st.dev = 14.6, SEM = 3.9)
Average BAI (cm^2/year)	15.1 (st.dev = 1.9, SEM = 0.4)	10.4 (st.dev = 1.5, SEM = 0.4)

Average oak species relative basal area (unitless)	0.13 (st.dev = 0.1, SEM = 0.02)	0.12 (st.dev = 0.1, SEM = 0.02)

I hypothesized that the two oak species would have different growth rates by bedrock type and that northern red oak growth would be the greatest on shale, while chestnut oak growth would be greatest on sandstone. The average growth rate for a northern red oak over the period of 1975 – 2015 was 87% higher than chestnut oak sampled from all plots and both bedrock types (Table 7, Figure 9). When I explored the differences of average growth rate by species, bedrock and the interaction between the two I found that species was the only significant driver of different growth rates examined in this study (p = 0.02). Counter to the first hypothesis, bedrock type and the interaction between bedrock and species were not significantly different (p=0.71 and p=0.65 respectively) (Figure 9 and Figure 10). There was a great degree of variability between the BAI of individual trees between species and bedrock types, with northern oak on shale expressing the most variability and chestnut oak expressing very little (Figure 11).

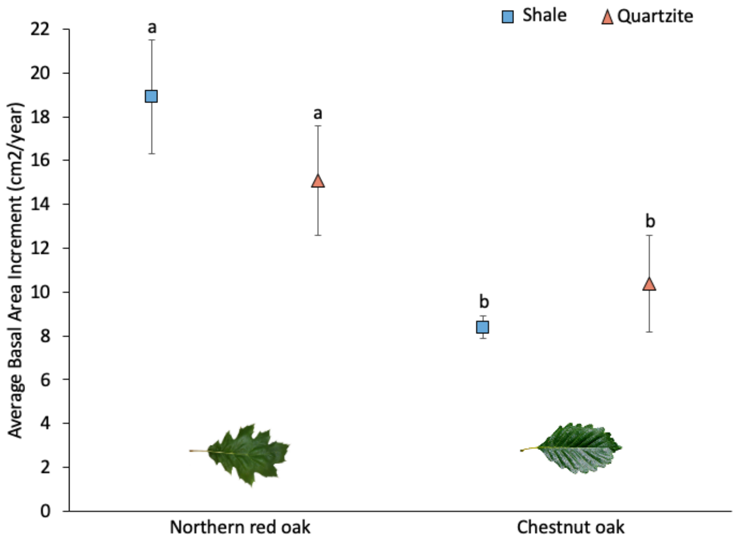


Figure 9. Overall average growth rates for northern red oak and chestnut oak growing on shale and sandstone bedrock types central Pennsylvania between 1975 and 2015. Error bars represent the standard error of the mean. Northern red oak * shale: n =25, northern red oak * sandstone: n = 22, chestnut oak *shale: n =25, chestnut oak * sandstone: n = 14

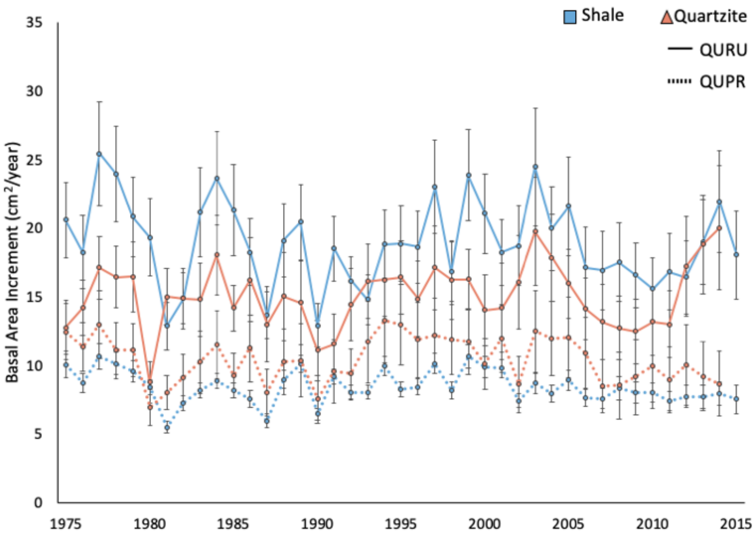


Figure 10. Average basal area increment of northern red oak and chestnut oak growing on shale and sandstone bedrock types across the study area between 1975 – 2015. Error bars represent standard error of the mean for a given year for the species and bedrock type presented. Northern red oak * shale: n =25, northern red oak * sandstone: n = 22, chestnut oak *shale: n =25, chestnut oak * sandstone: n = 14

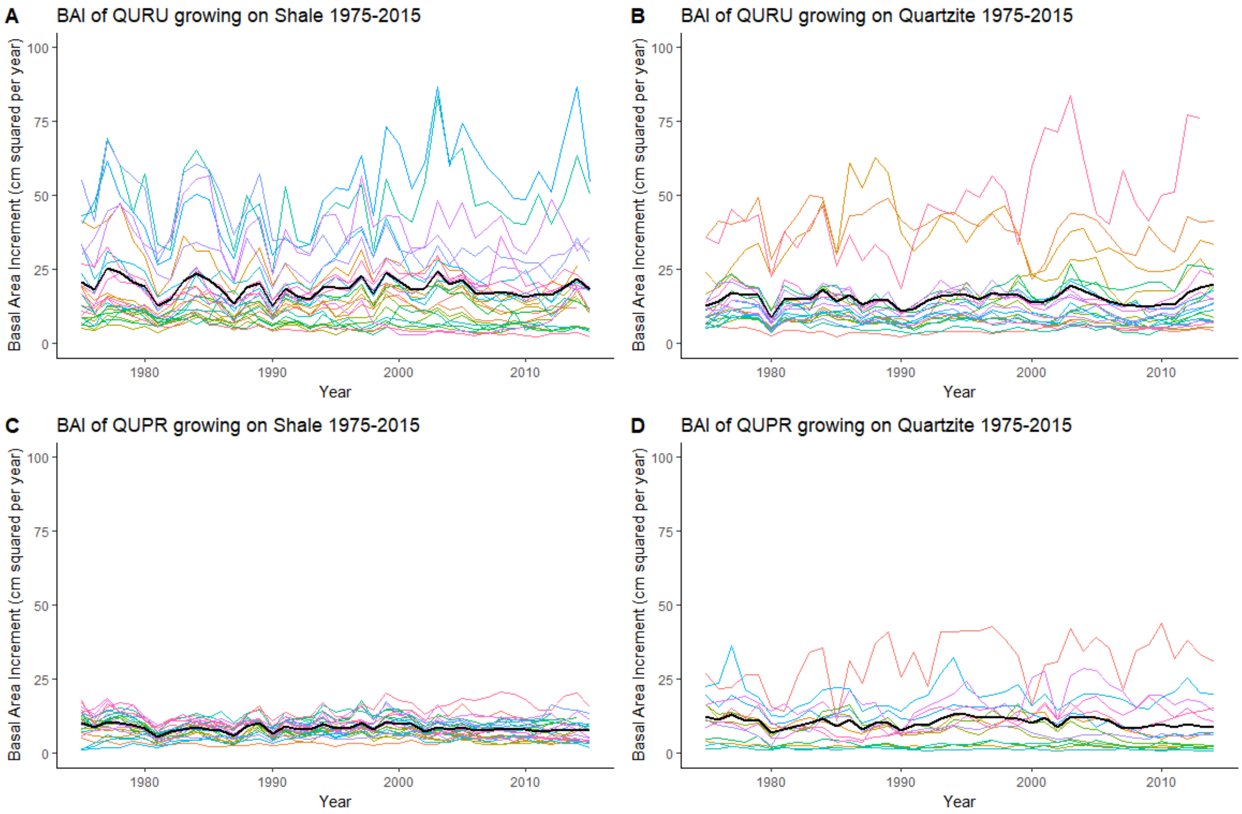


Figure 11. Basal area increment (BAI) from all trees used in this study for a.) Chestnut oak growing on shale b.) Northern red oak growing on sandstone c.) Chestnut oak growing on shale d.) Chestnut oak growing on sandstone. Colored lines represent individual trees and black line represents average for the species bedrock combination**.**

The second hypothesis was that these two species would respond differently to seasonal temperature and precipitation on shale and sandstone bedrock because of the coarse and rocky nature of the soils and that chestnut oak would be less sensitive to precipitation because of its general dominance on sandstone. Based on the correlation analysis performed in this study, I found evidence supporting this hypothesis for sandstone bedrock only and differences between species are nuanced. Both northern red oak and chestnut oak growing on sandstone had relative

BAI values that were significantly correlated with precipitation, however seasonal windows differed for the two species. Northern red oak growing on sandstone in this study was positively correlated with summer precipitation (r = 0.33, p=0.035) (Figure 12). In contrast, chestnut oak growing on sandstone was positively correlated with winter precipitation (r =0.35, p = 0.026) (Figure 13). For both northern red oak and chestnut oak growing on shale, no significant correlation existed between seasonal average temperature or precipitation with relative BAI (all p > 0.05) (Figure 12 and 13).

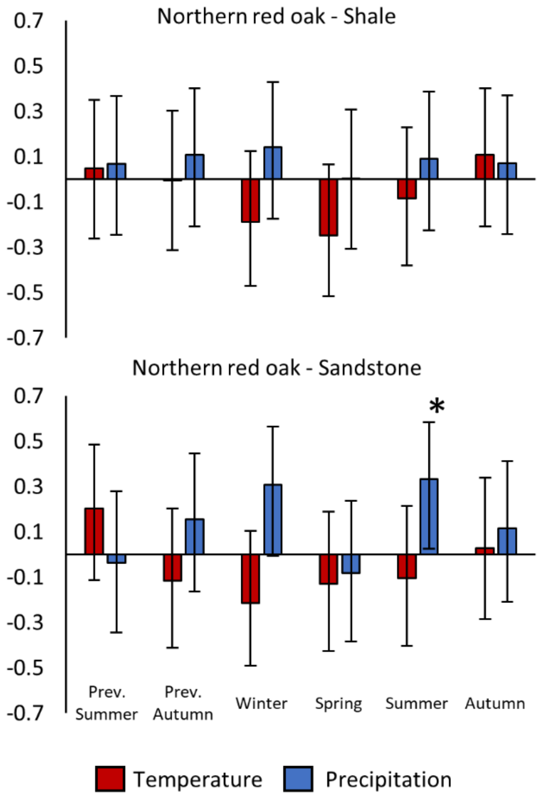


Figure 12. The correlation between relative basal area increment and seasonal climate for northern red oak growing on shale and sandstone bedrock types. The y-axis depicts the correlation coefficient. Asterisks represent a statistically significant correlation with a seasonal climate variable.

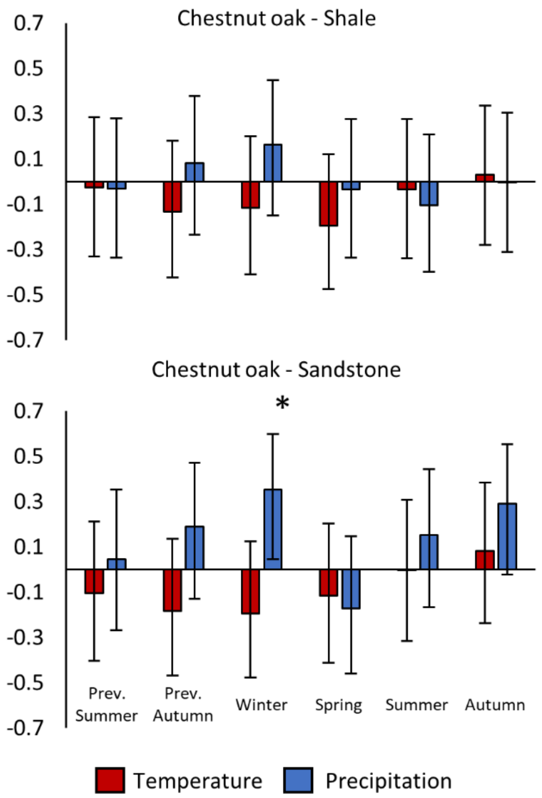


Figure 13. The correlation between relative basal area increment and seasonal climate for chestnut oak growing on shale and sandstone bedrock types. The y-axis depicts the correlation coefficient. Asterisks represent a statistically significant correlation with a seasonal climate variable.

Discussion

Differences in growth rates between northern red oak and chestnut oak outweigh differences that can be attributed to bedrock type on the Rose Hill shale and the Tuscarora sandstone. This is at least the case when considering relatively productive interior forests where slope, aspect and hillslope position have been taken into consideration, factors that are known to influence growth rates and can vary by species (Fekedulegn et al. 2003, Swetnam et al. 2017, Smith et al. 2017). Based on observed patterns that are expressed between shale and sandstone and these two oak species at larger scales, I expected that the differences between the bedrock substrate environment (rocky conditions, coarser texture soils, lower nutrient availability on sandstone) would impute different dominance mechanisms where northern red oak would express competitive dominance on the more favorable shale bedrock type and chestnut oak would express stress-tolerant dominance (and faster growth than northern red oak) on sandstone (Grime 1977). Chestnut oak growth is slower than northern red oak in general, and chestnut oak competes better on south facing xeric sites (Fekedulegn et al. 2003). Chestnut oak may take on stress-tolerant dominance on even drier and more sun exposed hillslopes than studied here where northern red oak's typical competitive advantage could be displaced. Alternatively, the chestnut oaks higher productivity detailed on south facing slopes in other research may have less to do with moisture and more to do with increased solar energy that compared to northern red oak is closer to the edge of it's northern range (Smith et al. 2017).

However, oak species do have different growth rates associated with soil-site moisture availability. A congener to the two species examined here, White oak (*Quercus* alba L.), has highest growth rates on sites classified as intermediate in moisture index compared to sites classified as xeric and mesic in Ohio (Anning et al. 2013). It seems plausible that resource availability on north to northwest facing midslope topographic positions underlain by either shale or sandstone bedrock types are sufficient to support mixed oak forests dominated by the faster growing northern red oak that does not lead to stress-tolerant dominance or more competitive growth rates in favor of chestnut oak on the more weather resistant, sandy and rockier substrate derived from the Tuscarora quartzite. This is somewhat surprising given that soil profiles on sandstone midslopes are so boulder-rich in typical rooting zones (Figure 8). Additionally, as a testament to northern red oaks affinity for north facing midslopes, there is a remarkable amount of variation in growth rates on both bedrock types (but see shale in particular) compared to chestnut oak (Figure 11). In contrast, chestnut oak growth on shale is likely muted by competition from surrounding trees which is contributing to the lack of variability seen here (Table 7, Figure 9, 10 and 11).

This study also sought to examine the impact of seasonal precipitation and temperature, species and bedrock type on annual tree growth. I hypothesized that these two oak species would respond differently to seasonal patterns of temperature and precipitation by substrate because bedrock mediated sandy and rocky soils would alter the way that these tree species can capitalize on necessary inputs for growth (i.e. heat and moisture). Oak species here grow more in years that receive more precipitation on sandstone bedrock type, but not shale (Figure 12 and Figure 13). This suggests that the range of water availability and temperature experienced from 1975-2015 are not limiting oak tree growth for these two species that grow in this region above the Rose Hill formation shale bedrock type. On the contrary, positive correlations between seasonal precipitation and the growth of oak trees on the sandstone bedrock type suggest that these species are in-part limited by available moisture.

This research provides evidence that the properties of these neighboring bedrocks impose different belowground moisture environments substantial enough to impact tree growth of two canopy dominant trees. This is in line with examinations of nutrient availability in Critical Zone research where bioavailable phosphorous were found to be negligible between the two bedrock types (Marcon et al. 2021). This response is likely linked to differences from bedrock through soil properties such as texture and rock volume from parent material that has been demonstrated to cause variable responses to climate in conspecific tree species (Orwig and Abrams 1997, Voelker et al 2008). However, more recently, experiments have demonstrated that trees can access water from bedrock and heterogeneity of bedrock types across the landscape leads to different responses of trees to moisture stress (Nardini et al. 2020).

Northern red oak and chestnut oak growth on sandstone are positively associated with precipitation in different seasons. Northern red oak growth was positively correlated with precipitation during June, July and August and chestnut oak growth was positively correlated with precipitation during the winter months of December, January and February. Northern red oak's climate-growth relationship on sandstone was similar to other studies in the southern Appalachian mountains where positive relationships with summer precipitation were identified, however a negative relationship with late growing season temperature was also reported (Speer et al. 2010). That result could in part reflect an interaction between growth and a generally warmer climate of the area much further south than the trees detailed here, be a relic of a methodology that identified significance at the less conservative $\alpha = 0.1$, or both. Research on northern red oak trees compiled more broadly across the eastern United States report correlations with early to mid-season (May-July) water availability and negative relationships to early growing season temperature (LeBlanc et al. 2011). Northern red oak growth in this study did not correlate with any temperature windows examined here. Compared to seasonal precipitation across the study period, temperature seems to have less seasonal variation between years which could play a role or it could be owed to the fact that central Pennsylvania is very close to the latitudinal center of the species' geographic range.

Somewhat surprisingly, the positive winter precipitation-growth relationship for chestnut oak does not match the reported results outlined in the southern Appalachians where growth was even more strongly correlated to summer precipitation (Speer et al. 2010). Mismatched seasonal precipitation-growth correlations between the two species here may reflect differences in early growing season phenology where chestnut oak could be accessing and capitalizing the moisture made available from snow or ice melt leftover from winter precipitation trapped in the characteristically rocky substrate of the Tuscarora quartzite formation sandstone. Climate models project a future with wetter winters as well as hotter and drier summers in the Northeastern United States (Hayhoe et al. 2007) and those condition could favor the growth of chestnut oak over northern red oak at the sites examined here. The way that forest life history traits influence species response to temperature and precipitation are complex in mixed deciduous forests (Xie et al. 2015) and that seems to be the case here as well.

Conclusion

The results presented here highlight two main findings. First, differences in growth rates between northern red oak and chestnut oak trees are greater than the hypothesized interactive effect of species and bedrock on shale and sandstone at the scale examined here. Despite challenges associated with maintaining oak dominance in eastern forests (Fei et al. 2011) continued silvicultural efforts on north-north west facing slopes in this region that is focused either on wood products or carbon storage would likely benefit from managing northern red oak compared to chestnut oak. Regardless of bedrock type, northern red oak basal area increment is nearly double that of co-dominant chestnut oak sites from north-west facing midslopes. However, it is possible that lower growth rates in chestnut oak may be driven by the effects of local competition with neighboring trees which could also be altered through silviculture. Second, climate-growth correlations for both species and seasonal precipitation patterns on sandstone bedrock types point to drier belowground conditions that likely contribute towards the aggregated biomass differences that are expressed between forests on shale and sandstone bedrock type across the region. Results presented here may be useful in earth system ecosystem models (ESMs) that incorporate processes from the atmosphere, land surface and biogeochemical cycles. This type of work could be particularly relevant as ESM models strive to increase in spatial resolution (Flato 2011). Additionally, results from this study suggest that dry belowground differences of bedrock have not negatively influenced the contemporary growth (1975-2015) of these under the climate conditions experienced thus far.

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S7. Cross dating descriptive statistics for tree-ring data derived from Northern red oak and Chestnut oak on shale and sandstone bedrock. Summaries and statistics were compiled using *dplR: Dendrochronology Program Library in R* (Bunn et al. 2024).

	Northern red oak	**Chestnut oak**
Shale		
Number of dated series	49	50
Number of measurements	4,965	4,843
Average series length (years)	101.33	96.86
Years included	1865 - 2018	1866 - 2017
Mean series intercorrelation (st.dev)	0.617 (0.116)	0.499 (0.149)
Mean sensitivity (raw data)	0.207	0.227
Sandstone		
Number of dated series	43	28
Number of measurements	4,139	3,116
Average series length (years)	96.26	111.29
Years included	1882 – 2016	1783 - 2016
Mean series intercorrelation (st.dev)	0.583 (0.101)	0.402 (0.165)
Mean sensitivity	0.192	0.201

S8. Species present within plots included in this study and the percentage of basal area by bedrock type.

	Shale		Quartzite	
Species	**Basal Area (m^2/ha)**	**Rel. BA (%)**	**Basal Area (m^2/ha)**	**Rel. BA (%)**
Acer pensylvanicum	<0.1	<1	0.1	<1
Acer rubrum	0.1	<1	1.4	4.6
Acer saccharum	2.1	6.7	0	0
Amelanchier spp.	0.2	<1	0.2	<1
Betula allegheniensis	0	0	0.3	<1
Betula lenta	0.2	<1	6.2	20.1
Carya glabra	0.1	<1	0	0
Carya ovata	<0.1	<1	0	0
Carya tomentosa	0.3	<1	0	0
Fagus grandifolia	<0.1	<1	0	0
Fraxinus spp.	0.1	<1	0	0
Nyssa sylvatica	<0.1	<1	1.5	5.0
Ostrya virginiana	0.3	<1	0	0
Pinus strobus	2.8	8.7	1.3	4.1
Pinus virginiana	0.3	<1	0	0
Quercus alba	2.9	9.0	1.3	4.4
Quercus prinus	7.4	22.8	7.6	24.6
Quercus rubra	14.2	43.7	8.6	28.1
Quercus velutina	.4	1.3	0	0

Chapter 4

Carbon dynamics of forests on north facing midslopes underlain by shale and sandstone bedrock type demonstrate resistance and resilience to drought while patterns at wider spatial scales exhibit great variability

Abstract:

Large variations in forest carbon storage and uptake are driven by many environmental factors that vary across space and time. Bedrock types influence the forest substrate that alters a forest's response to potential stressors such as droughts. This study compares the reconstructed accumulation of live aboveground forest carbon over the period of 1975-2015 on north facing midslope positions underlain by shale and sandstone bedrock types in the central Appalachian Ridge and Valley, a period that experienced three moderate to severe droughts. Forest carbon storage and accumulation on the two bedrock types across elevation, aspect and terrain positions are used to contrast the variability of forest carbon dynamics across space and time. Forest carbon accumulation was resistant and resilient to the three most severe drought years over the study period in 1991, 1999 and 2001. Average rates of carbon accumulation and the average interannual variability over the 40-year period were not different for oak forests growing on shale or sandstone bedrock types on north facing positions. Carbon accumulation in forests growing above sandstone slightly increased over the study period. Forest carbon accumulation over the wider spatial area was negatively correlated with increasing elevation, which tended to be on sandstone bedrock. Forest carbon accumulation over a 40 year period on the single terrain position of north facing mid-slopes on shale and sandstone was stable (average of 1.54 and 1.52 Mg/ha/year respectively) even under drought conditions compared to the variability that exists across space over shorter time periods of four to eight years.

Introduction:

Forests uptake an equivalent of more than 14% of the CO_2 produced by the United States on an annual basis and have the potential to uptake a greater share of these climate-changing emissions (Domke et al 2020). Forests in the eastern United States are responsible for a large portion of this carbon emission mitigation due to natural forest regrowth from past land clearing (USGCRP, 2018). Environmental factors such as weather and climate can influence interannual variations of ecosystem carbon dynamics in eastern deciduous oak forests, a common and important forest type in the region (Barford et al. 2001, Xie et al. 2014). Additionally, variations in geomorphic features are known to have differential effects on ecosystem structure and function at multiple spatial and temporal scales (Swanson et al. 1988). There is considerable interest from scientists, policy makers and forest managers to understand where and how the variability of forest carbon accumulation exists to maximize the terrestrial carbon sink (Cook-Patton et al. 2020).

Complex mountainous terrain can exert strong controls on forest function (Zald et al. 2016). Variations in bedrock properties can have large influences on forest and the terrestrial carbon that they store (Morford et al. 2011, Hahm et al. 2014, Reed and Kaye 2020). Lithologic properties of bedrock influence topography as well as nutrient and water availability, three factors that have the ability to control vegetation productivity (Ott 2020). Variations in bedrock types across mountainous landscapes influence the response of trees to extreme drought that lead to spatial and structural forest heterogeneity (Nardini et al. 2020). In the central Appalachian Mountains of the mid-Atlantic U.S.A., oak forests growing above shale bedrock are storing and accumulating more carbon than those on sandstone (Reed and Kaye 2020).

Many abiotic features such as topography vary across bedrock types and forested landscapes of the Ridge and Valley of the Appalachian Mountains. Forest structure can differ by terrain position along hillslopes, with carbon storage generally increasing from ridges to toeslopes or from higher to lower elevation (Boldstad et al. 2001, Swetnam et al. 2017, Brubaker et al. 2018). Other topographic features such as aspect can have significant effects on forest productivity and depending on the temperature and moisture limitations of a forest ecosystem the relationship between productivity and aspect varies (Smith et al. 2016, Swetnam et al. 2017, Kobler et al. 2019). Improving the understanding of how forests vary across different bedrock types in relation to topography could aid the management of forests and the resulting ecosystem services they provide including the storage and uptake of atmospheric carbon.

While there is potential for forests to mitigate the impacts of anthropogenic climate change through carbon uptake, climate induced impacts from extreme weather and disturbances pose considerable risks to the productivity and permanence of forests (Rustad et al. 2012, Anderegg et al. 2020). Forests are increasingly impacted by droughts globally (Allen et al. 2010). Even forests of the humid eastern deciduous region of the United States can be impacted and effects can be diverse, ranging from reductions in growth to drought induced tree mortality (Demchik and Sharpe 2000, Voelker et al. 2008, Brzostek et al. 2014, Au et al. 2020). Many questions remain about which parts of the landscape in the eastern United states may see the most reduction in growth as conditions are likely to shift towards drier and hotter growing seasons that can limit soil available water content (Hayhoe et al. 2007, Clark et al. 2016, Xie et al. 2014).

Belowground properties such as bedrock-mediated soil texture, nutrient availability and water holding capacity vary across complex landscapes and are underrepresented in our understanding of how forests respond to drought (Phillips et al. 2016). Trees of the eastern U.S. can exhibit differential growth rates and responses to droughts depending on the soil water availability of sites that they occupy and species responses are complex (Orwig and Abrams, 1997, Anning et al. 2013, Kannenberg et al. 2018). Parent material has the ability to create poor site conditions for red oaks of the Midwest that can lead to growth declines in response to drought (Volker et al. 2008). The resistance and resilience of tree growth to drought, or the degree to which tree growth is impacted compared to pre- and post-drought conditions, has been highlighted as an important metric to identify forests that are potentially vulnerable to drought (D’Amato et al. 2013, Merlin et al. 2015, Meyer et al. 2020). Regionally, differences in growth rates between forests are attributed to bedrock mediated site properties between shale and sandstone in oak dominated forests of the central Appalachians (Reed and Kaye 2020). Trees with more vigor tend to be more resilient to droughts (Camarero et al. 2018, Hereş et al. 2018) and therefore forests subjected to droughts on shale may be less impacted in regards to their carbon storage and accumulation than neighboring forests on sandstone in the Ridge and Valley of the Appalachians. Considering evidence that small scale (i.e. watershed) variations in forest carbon dynamics can be quite large (Smith et al. 2016) multiple sources of data at different scales may be best suited to quantify variations in forest growth across mountainous topography.

The fusion of forest inventory data and tree-ring measurements has been helpful in detecting patterns in forest growth and provides context from longer time scales compared to recent trends (Biondi 1999). Reconstructions of forest carbon uptake from tree rings produce similar estimates compared to forest census data and offer the benefit of illuminating the interannual variability in patterns of forest carbon accumulation while extending our view into the more distant past (Dye et al. 2016, Kleese et al. 2016). Longer-term records of forest growth at annual resolution from tree rings can be a tool to examine the impacts of annual climate variations (such as drought) on forest productivity, but the time and labor required for these measurements may limit their spatial extent (Teets et al. 2018, Xu et al. 2019). Pairing tree-ring derived estimates of productivity with more spatially extensive forest inventories offers an opportunity to ask questions about the influence of bedrock type, complex terrain and annual climate variability on temporal and spatial dynamics of forest carbon storage and accumulation.

The main goals of this research are to compare the effect of bedrock type and drought on decades of forest carbon accumulation rates in the central Pennsylvanian Appalachian Ridge and Valley. The use of tree-ring reconstructions of carbon accumulation permits me to analyze how forests growing on shale and sandstone bedrock have responded to three individual drought years over the contemporary growth period between 1975-2015 as well as compare trends in interannual variability of forests as carbon accumulators. Estimates of carbon accumulation from tree rings at the forest level are relatively novel because they utilize historical growth of all trees in a stand rather than a subset of individuals that tend to be more climate sensitive trees. The selection of climate sensitive trees to infer the impact of climate on tree growth compared to more spatially unbiased methods in dendroclimatological research can over inflate climate-growth relationships of forests (Kleese et al. 2018). Furthermore, research on the impacts of drought in the eastern United States has typically lacked information reflecting stand scale drought response, which more closely mimics the scale at which forest are managed (Clark et al. 2016).

In this study, longer term estimates of forest productivity from tree rings at specific topographic locations are considered in relation to the variability in forest growth derived from repeated inventories at coarser temporal resolution over a shorter time period and at wider spatial scales from inventory data sources to assess how they vary. Specifically, the research questions outlined here are 1.) Do forests growing above shale uptake carbon at a faster rate compared to forests on sandstone on similar aspects and slope positions considering growth from 1975-2015? 2.) Is forest growth above shale bedrock more resistant and resilient to drought compared to forest growing on sandstone? 3.) Do forest carbon storage and accumulation differ from ridgetop to toeslope position when bedrock type is considered? 4.) How do elevation and aspect interact with forest carbon storage and accumulation on shale and sandstone bedrock types in local region? and 5.) Does considering data at multiple temporal and spatial scales contribute novel understanding of patterns of forest growth and response to drought in this region? The results presented here contribute towards a broader understanding on the impact of bedrock type on forest growth and better fill spatial and temporal gaps in understanding about the potential impact of belowground properties in forest response to drought.

Methods:

Study Area:

This study takes place in Centre and Huntingdon County Pennsylvania, situated in the Ridge and Valley of the Appalachian Mountains of the mid-Atlantic. Forests were sampled in the Rothrock State Forest that is managed by the Pennsylvania Department of Conservation and Natural Resources and the Stone Valley Forest that is managed by the Pennsylvania State University. The climate at the Susquehanna Shale Hills Critical Zone Observatory (SSCZO), a centrally located and well-studied reference point for the all of the study sites detailed here, is characterized as humid continental with an average annual temperature of 9.4° C and an average annual precipitation of 1016 mm over the study period (Wang et al. 2016). Much of the upland forested mountains are underlain by Paleozoic sedimentary rock types classified as shale and sandstone. The two formations of focus in this study are the Silurian-aged Rose Hill shale and the Tuscarora quartzite. The Rose Hill is an iron-rich and organic-poor formation (Dere et al. 2016) and the Tuscarora quartzite is an orthoquartzitic sandstone (Li et al. 2018). These rock formations will be referred to as shale and sandstone in this chapter. For sites containing field data that I collected within this study, soils on shale are classified as Weikert series (silt loam) and soils on sandstone sites are classified as Hazelton series, (gravely/sandy loam). The shale-derived soils are higher in magnesium, calcium, sulfur, and potassium compared to sandstone sites; however, phosphorus concentrations are higher in sandstone derived soils (Hill, 2016). For forest inventory sites that were sampled by the Pennsylvania Bureau of Forestry in the wider area, soils likely reflect a similar composition to those outlined above as soil properties and texture in the area are linked to the underlying bedrock and parent material (Ciolkosz et al. 1990) and here I focus on just two specific bedrock formations.

***Field and Laboratory Methods*:**

Data sources and objectives

This study uses three data sources: tree rings, Critical Zone Observatory forest inventories, and the Pennsylvania Department of Conservation and Natural Resources Bureau of Forestry forest inventories to examine the spatial and temporal trends of forest carbon storage and accumulation of forests growing on the two bedrock types. Data derived from tree rings are used to reconstruct long term patterns of carbon uptake, impacts of drought, and the interannual variability of forest growth on shale and sandstone bedrock type north facing midslopes. Forest inventory data are analyzed here to broaden the scope of inference outside of specific hillslope and aspects on the two bedrock types. Forest inventory data from north slopes in two Critical Zone Observatory watersheds are used to examine the impact of hillslope position (ridgetop, midslope and toeslope) on forest carbon storage and uptake in relation to bedrock type. Additionally, forest inventory data at a wider spatial scale are examined for trends in forest carbon dynamics across elevation gradients and expand our understanding of the impact of north and south facing aspects (Figure 14).

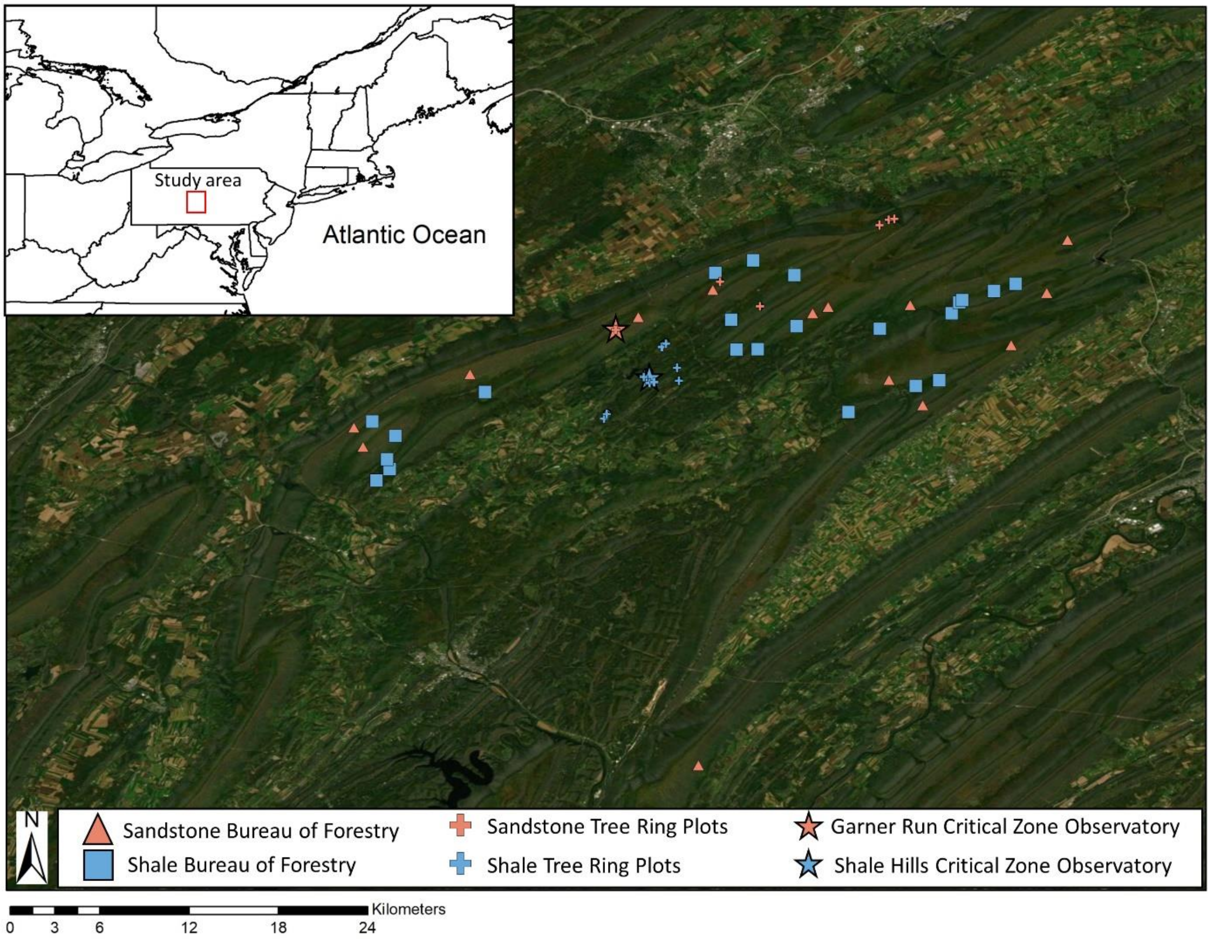

Figure 14. Map of study locations and data sources in the Rothrock State Forest and the Stone Valley Forests of the central Pennsylvanian Appalachian Ridge and Valley. Shale Hills Critical Zone Observatory is located at 40° 39’ 52.29” N, 77° 54’ 18.34” W.

Tree-ring reconstructions

Field sites for tree-ring based reconstructions of carbon accumulation in this study were selected as a part of a larger field sampling design aimed to isolate the impact of bedrock type on forest growth and biogeochemistry (Hill 2016, Marcon et al. 2021). To keep as many factors as possible the same between forests sampled on the two bedrock types, north to northwest facing midslopes on the two formations of interest were identified using the Geological Map of Pennsylvania in ArcMap 10.5.1 (Berg et al. 1980, Miles and Whitfield 2001, Hill 2016). All tree-ring reconstruction plots are within 15 km of the Shale Hills CZO. To select plot locations in an unbiased manner I generated randomized points using ArcMap on the identified midslope hillsides. Sampled plots were within the interior forest and lacked visual signs of human and natural disturbance (i.e. trails, recent logging, windstorms). I recorded topographic characteristics in the field (elevation, aspect and slope) at each of the plots. Aspect and slope angles were relatively similar for both bedrock types. Similar to the trend across the landscape at larger scales (Reed and Kaye 2020), plot elevation tended to be higher at sites on sandstone than on shale (Table 8).

At the randomly selected locations I established 314.2 m^2 circular plots in which all trees with a diameter at breast height (DBH) were identified to species, DBH was measured and recorded to document forest structural conditions within each plot. Each individual tree was assigned a tree crown class of dominant, codominant, intermediate or suppressed based on a visual assessment in relation to its neighbors. Two increment cores were extracted from each tree in the plot that had a DBH >10 cm between summer of 2016 and spring of 2019. Trees were cored on each side parallel to the hillslope contour to avoid reaction wood at ~1 – 1.37 meters high.

Cores were then air dried for at least 3 days and glued onto mounts. Cores were sanded using a belt sander with progressively finer sandpaper from 220 – 400 grit. After sanding, cores were visually dated from the outermost fully developed ring inward and annual rings measured to the nearest 0.01 mm using a movable stage and Velmex measuring system. Cores were statistically crossdated using the program COFECHA (Holmes, 1983). Not all trees from every plot visually or statistically crossdated well with plot level tree-ring series due to poor ring visibility and suppressed growth rings. This was particularly common in ring porous species such as red maple (*Acer rubrum* L.) black birch (*Betula lenta* L.) and black gum (*Nyssa sylvatica* Marsh.) often found in suppressed canopy positions in these forests. When a majority (50% or more, but often more) of the cores sampled from a plot were unable to statistically (low or negative site level correlations between trees) and visually cross date (unclear ring boundaries), plots were deemed undatable and not included in this analysis. Of the 27 plots that were sampled, nine plots on shale and six plots on sandstone had greater than 50% of the cores crossdating and were used in this analysis. A limitation to this crossdating threshold is that plots with more suppressed growth are not included in this analysis, which may bias the results with faster than average growing stands. Following crossdating, annual ring widths from the two core samples from an individual tree were averaged and the reconstructed radius was used to calculate tree diameters through time. I focused on the contemporary period from 1975 – 2015 to highlight modern trends in forest growth as well for the fact that all of the trees measured at the time of

Table 8. Forest and topographic metrics of tree-ring sample plots growing on the Rose Hill shale (n = 9) and the Tuscarora quartzite sandstone (n = 6). Species ordered in rank of dominance by site. Live carbon stored (Mg/ha) is at the time of plot sampling (2016 – 2019). Inter-series correlation represents the strength of crossdating among tree-ring series within a plot for the entire tree-ring record.

Plot	**Bedrock type**	**Relative species composition by biomass (trees ≥ 10cm)**	**Live carbon stored (Mg/ha)**	**Elevation (m)**	**Slope (%)**	**Aspect (°)**	**Number of trees**	**Inter-series correlation**
CW1	Shale	QUAL (46%), QUPR (22%), QUVE (14%), QURU (12%), ACSA (6%),	94.9	311	14	346	17	.407
CW2	Shale	QURU (50%), QUPR (40%), QUAL (10%),	80.5	305	12	323	17	.509
MAS2	Shale	QURU (44%), QUAL (19%), PIST (14%), PIVI (13%), QUPR (7%), QUVE (2%), CAGL (1%)	75.7	266	12	344	14	.488
MAS3	Shale	QUAL (61%), CAOV (14%), CAGL (12%), CATO (11%), JUVI (1%), QUPR (1%)	70.6	251	17	339	15	.517
SAS1	Shale	PIST (53%), QUPR (38%), QURU (5%), BELE (4%)	119.9	333	16	320	13	.395
SH1	Shale	QUPR (75%), QUAL (12%), QURU (9%) ACSA (2%), Am. spp (>1%), PIST (1%)	99.2	294	23	345	11	.472
SH2	Shale	QURU (89%), ACSA (11%)	173.5	281	19	350	16	.213
SH3	Shale	QURU (92%), ACSA (8%), CAOV (>1%)	181.1	269	16	359	9	.359
SP1	Shale	QURU (64%), QUPR (20%), QUAL (9%), CATO (6%), Am. spp (1%)	94.8	336	9	353	12	.403
GM3	Sandstone	QURU (56%), QUPR (20%), BELE (15%), ACRU (9%)	165.2	408	7	330	9	.225
GR2	Sandstone	PIST (51%), QUPR (32%), BELE (14%), NYSY (2%), ACRU (1%)	91.7	572	20	331	12	.139
LIT1	Sandstone	QURU (44%), BELE (30%), QUPR (26%), ACRU (1%)	79.9	645	28	330	18	.314
LIT5	Sandstone	QUPR (73%), BELE (11%), TSCA (9%), ACRU (5%), ACPE (1%)	150.0	623	35	340	21	.222
LIT6	Sandstone	QURU (84%), QUPR (8%), BELE (7%), ACRU (1%)	111.1	607	26	337	14	.422
RR1	Sandstone	QURU (49%), QUAL (23%), QUPR (20%), NYSY (7%), ACRU (1%)	123.1	509	6	333	8	.184

sampling typically had solid cores and lacked heart rot through that time period. Carbon accumulation estimates reconstructed from tree-rings over 1975-2015 were derived from 207 trees of 17 different species containing 7,846 annual radial growth measurements (Table 8).

Shale Hills and Garner Run Critical Zone Observatory

Forest data presented here from the Shale Hills and Garner Run subcatchments of the Shaver's Creek Watershed were collected as a part of the Critical Zone Observatory designed to understand interactions among bedrock, water, energy, gas, solute and sediments as well as to facilitate cross-site comparisons between lithology (Brantley et al. 2018, Li et al. 2018). At Shale Hills (shale bedrock type), all trees with a DBH greater than 20 cm were tagged with a number for relocation, identified to species, and DBH was recorded in 2008 within the 8.53 ha catchment (Smith et al. 2016). All tagged stems were mapped in a GIS. In the fall of 2016 trees were revisited and DBH was measured and recorded. To compare the effect of hillslope position on forests across bedrock types in this study, I used ArcMap to generate transects across the watershed in a similar fashion to Brubaker et al. 2018 at the ridgetop, midslope and toeslope. Because only part of the Garner run watershed had all hillslope locations sampled across the watershed I focused only on the north facing aspect here. Five transects were drawn 50 meters in length parallel to the contour from west to east, and buffered by 5 meters on each side to mimic that of the forest sampling design in Garner Run. Transects at Shale Hills covered an area of 500 meters squared covering an area of 0.75 ha of the 8.5 ha watershed. 229 trees within the transects were used in the data analysis.

The forest inventory at the Garner Run watershed was collected in a different manner compared to Shale Hills due to the much greater size of the size of the watershed (134 ha). The initial forest inventory was collected in the summer of 2014. To consistently capture variations across the watershed, three transects were utilized in this analysis from the toe-slope, mid-slope, and ridge-top of the northern aspect of the watershed. As above, only transects on the north aspect are considered due to a lack of available data on ridgetop and toeslope positions on the south aspect of Garner Run. Multiple connected transects 10 meters wide by 100 meters long were run parallel to the contour encompassing a sample area of 3.1 ha in total. All trees with a DBH greater than 10 cm were identified to species, measured and recorded (Brubaker et al. 2018). The second forest inventory took place in the early to mid-spring of 2019, before trees were leafed out. Additionally, to keep the diameter measurements the same as at Shale Hills, only trees greater than 20 cm were used in carbon calculations. Eight hundred and forty trees within the transects were used in the data analysis.

Pennsylvania DCNR Forestry Inventory

The Pennsylvania Department of Conservation and Natural Resources Bureau of Forestry maintains a continual forest inventory of forests growing within Pennsylvania State Forest land that is established to proportionally represent the major forest community types within the region and provide basic biological data on growth, mortality, structure, volume and change of public forest land. The sampling strategy of the inventories ensures that permanent plots are maintained and sampled multiple times, as well as continually adding newly established forest plots to inform short- and long-term forest management (PA DCNR, 2010). Within the inventories, all trees with a DBH greater than 11.4 cm are measured and identified to species within 810.6 m^2 circular plots. As a part of the continual forest inventory design, the DCNR also records site description metrics at each plot. Terrain position is recorded in the field in reference to hillslope position based on seven categorical options and I classified them as closely as possible into three groups (ridgetop, midslope and toeslope) in an attempt to compare forests from this dataset with the Critical Zone sites.

The location of the plot centers is recorded in the field using a GPS. Coordinates of the inventory plot centers were mapped on to the geological map of Pennsylvania (Berg et al. 1980; Miles and

Whitfield, 2001). Plots included in this study were selected based on multiple criteria to ensure that the abiotic characteristics of the forest would be similar to the other sampling strategies outlined in this study. First, forests that were located on top of either shale or sandstone (the same bedrock types as the CZO sites and tree ring plot network) were selected. Second, to ensure that the climate and other local features were similar, I selected forests within a 30 km radius around the Shale Hills CZO research site (Figure 14). Plots were included in the dataset if they were not deemed disturbed in the inventory (i.e. field crews did not consider plots disturbed even when some trees within them died). This selection process yields a total of 36 different forest plots with at least 2 inventory measurements from the most recently available measurement cycles and were 81-138 years old (sandstone n = 14, shale n = 22). I compared growth data for the most recent measurements cycles that took place in 2006 and 2012 because only 4 plots also had earlier measurements. Elevation and aspect of each plot were derived from digital elevation models in ArcGIS. Aspect was very broadly defined as north (271-90°) and south (91-270°) facing for each plot.

***Data Analysis*:**

Carbon accounting:

To account for the amount of carbon that is stored and accumulated from these forest measurements several steps are required. For all trees at each sampling period, I estimated the amount of individual whole tree biomass (all of the tree material aboveground) using species group allometric equations (Jenkins et al. 2003) and then scaled them to carbon assuming a 48% carbon content of broadleaved trees in temperate forests (IPCC, 2006). Live aboveground storage was calculated as the sum of the carbon content in all live trees divided by the area sampled to produce values in Megagrams of carbon per hectare (Mg/ha). Carbon accumulation at the plot, or stand level (in the case of the two CZO sites) was calculated as

$$\text{Carbon accumulation} = \Delta \text{ carbon storage} / \Delta \text{ time}$$

which produces values in Megagrams of carbon per hectare per year (Mg/ha/year). To capitalize on the temporal resolution of tree-ring derived estimates, carbon uptake is calculated on an annual basis. At the Shale Hills site, carbon uptake is calculated over eight years while Garner Run is calculated over a period of 4.5 because initial forest measurements were recorded mid growing season. All Bureau of Forestry uptake data are calculated at a six-year interval. For clarity, I use the terms “store” and “storage” to represent aboveground carbon stock and “accumulation” and “uptake” to represent net live aboveground carbon accumulation rate.

Drought:

To investigate the impact of drought on the carbon uptake of forests growing on shale and sandstone bedrock type I identified known drought years using the Palmer Drought Severity Index (PDSI) that couples temperature and precipitation on a monthly basis (Palmer, 1965). PDSI was aggregated for the months of May – September to isolate the growing season. On the PDSI scale, negative values represent dry periods, where values -1.00 to -1.99 represent a mild drought, -2.00 to -2.99 represent a moderate drought, -3.00 to -3.99 represent a severe drought and ≤ -4.00 represent an extreme drought (Palmer 1965). In the study period of 1975-2015 three droughts that ranged from moderate to severe occurred in the years 1991, 1999 and 2001 (Figure 15).

To quantify and compare the impact of drought on the rate of forest carbon accumulation, I calculated modified metrics of drought resistance and resilience as an index following D’Amato et al. 2013 where:

Resistance is defined as the ability to experience a drought without a change in growth increment and is calculated here as:

$$\text{Drought}_{\text{reisistance}} = \Delta C_{\text{(in the year of drought)}} / \Delta C_{\text{(average } \Delta \text{ C in the 5 years prior to drought)}}$$

and

Resilience is defined as the ability to return to pre-drought growth and is calculated as:

$$\text{Drought}_{\text{resilience}} = \Delta\, C_{(\text{average 5 years post drought})} / \Delta\, C_{(\text{average } \Delta \text{ C in the 5 years prior to drought})}$$

Calculated index values for both measures of drought impact that are greater than or equal to one are interpreted as resistant or resilient while values below demonstrate a degree of vulnerability. Index values in this case are calculated at the plot level. Definitions and metrics of drought resistance and resilience were chosen following similar methods for basal area increment in D’Amato et al. 2013.

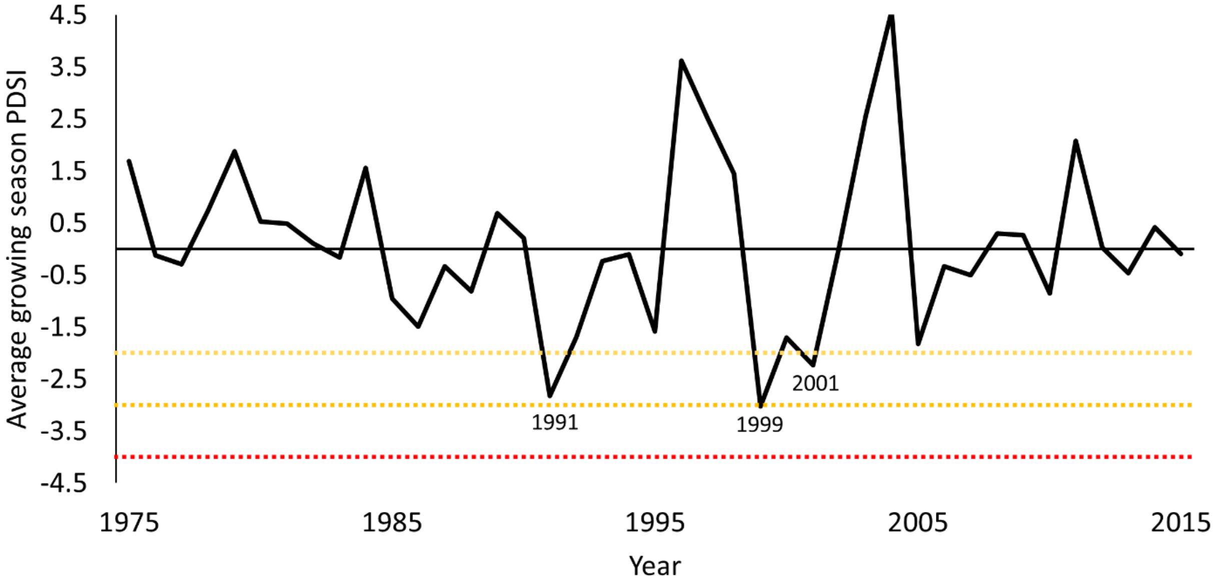

Figure 15. Average growing season (April – September) Palmer Drought Severity Index from 1975-2015 for Pennsylvania’s Region 8 that encompasses the forests detailed in this study. Drought years are labeled within the study period and are identified as having an average PDSI value below the threshold of -2.

Droughts are classified as moderate (below -2, yellow), severe, (below -3, orange) and extreme (below -4, red).

***Statistical Analysis*:**

Longer temporal patterns of forest carbon uptake:

To compare the effect of bedrock type on carbon accumulation between forests growing on shale and sandstone I fit linear mixed effects models on reconstructed carbon uptake with sample plot as a random effect using the nlme package (Pinheiro et al. 2018) in R (R Core Team, 2018). To account for the impact of the prior growing season on the current year's growth and the time series nature of tree ring data I incorporated an autocorrelation structure with a 1-year lag. To test for appropriateness of incorporating the autocorrelation structure into the model, I compared AIC values of the models fit with and without the AR-1 structure. AIC values were lower when the autocorrelation structure was incorporated (242.4 vs 368.4). Model fit and assumptions were finally confirmed after plotting the fitted vs standardized residuals. Statistical significance is considered when $\alpha = 0.05$. To quantify the interannual variability of forest carbon uptake I calculated the coefficient of variation over the study period for each plot and compared them by bedrock type using two-sided t-test using the tree-ring data. To illuminate potential increasing or decreasing trends through time in forests I conducted a simple linear regression on the average reconstructed annual carbon uptake from tree rings with year over the sampling period for forests on each bedrock type.

To investigate the impact of the three growing season droughts in terms of the resistance and resilience of forests I utilized one sided t-tests. I assumed a mean of one on the resistance and resilience index values for forests both forests growing on shale (n = 9) and sandstone (n = 6) bedrock types for the drought years of 1991, 1999 and 2001. α values in drought analyses were corrected for multiple comparisons using a Bonferroni correction because I conducted the repeated tests on the same datasets over three droughts and two bedrock types. To contextualize the climate in terms of growing season PDSI in the study period (1975-2015) to the remainder of the existing record (1895-1974) I performed a two-sided t-test on PDSI data from the two sample periods.

Spatial patterns of forest carbon storage and uptake

To explore the variability across hillslope position, bedrock type and their interaction for forest carbon storage and uptake I conducted an analysis of variance using the glm function in R using forests from the Shale Hills and Garner Run Critical Zone Observatory. Each transect across the hillslopes was considered a replicate ranging from 5 to 14 belt transects per bedrock terrain position combination from the two CZO sties. For significant differences of carbon storage and uptake, a post-hoc Tukey Honest Significant Difference test to determine which bedrock and slope positions are different from each other. Additionally, to contrast the impact of aspect and bedrock type on forest carbon storage and uptake I conducted an analysis of variance on forest carbon storage and uptake from forests growing on the Rose Hill formation shale and the Tuscarora quartzite formation sandstone using the 36 forest inventory plots from the 30 km buffer region of the CZO.

Study Limitations

The forest biometrics presented within this study, like all measurements, have limitations for representing the complex biological world. The tree ring plot networks include an inherent bias towards sites dominated by oaks (Table 8) rather than diffuse porous species because of the difficulty identifying ring boundaries. Fifty-six percent of the 27 cored plots were reliably crossdated and included in carbon reconstructions. Shale plots tended to crossdate better, and 75% of the 12 plots are included compared to 40% of the 15 on sandstone. For this study, I measured all trees within a fixed area plots in mixed species eastern deciduous forests and still include data from 17 different species. Oaks (*Quercus rubra* L., *Quercus prinus* L., *Quercus alba* L.) dominate the forest biomass on shale and sandstone bedrock types across the region (Reed and Kaye 2020), and despite this oak heavy sampling bias this research still offers a deeper look into how forests carbon dynamics function as a single unit on the two bedrock types of interest.

This study focuses only on the live aboveground biomass portion of the carbon in a forest ecosystem. It is important to acknowledge that the belowground components of forest ecosystem carbon such as soil organic carbon as well as fine- and coarse-roots are omitted from these quantifications and can proportionally contain more than half of the total forest carbon stock (Domke et al. 2017). Additionally, because this study focuses on bedrock type it is also important to note that geology can play a role in mediating soil organic carbon stocks (Barré et al. 2017, Angst et al. 2018) and those could differ across landscapes dominated by shale and sandstone bedrock as well.

To estimate forest carbon, I rely on the use of species group allometric equations to predict biomass from DBH alone that were not derived from local sites (Jenkins et al, 2003). While this methodology is widely used in carbon accounting for many scientific and applied forestry projects it may exclude allometric details associated with site- and species-specific local tree growth studied here. In a study estimating forest carbon at the local Shale Hills CZO, Smith et al. 2017 attributes a 10% uncertainty of biomass estimates from the product of measurement, model prediction, and model selection and can be relied on as a conservative estimate for the results presented here.

Results:

Tree-ring reconstructions

Forest growing on north-facing midslope positions on the Rose Hill formation shale and the Tuscarora quartzite sandstone did not differ in the amount of carbon they stored (t = -0.32662, df =

12.649, p = 0.75) in the years that forest were sampled from 2016-2019. Forests growing on shale store 113.7 Mg/ha (± 14.4 SEM, n = 9) while forests growing on sandstone store 120.2 Mg/ha (± 13.5 SEM, n = 6). Over the period of 1975-2015 forests on the two bedrock types also accumulated carbon at the same rate (f = 0.01051, df = 13, p = 0.92) (Figure 16). The average carbon accumulation rate for forests on shale was 1.52 Mg/ha/yr (± 0.03 SEM) while the average carbon accumulation rate for sandstone was 1.54 Mg/ha/yr (± 0.03 SEM). The two bedrock types experienced their highest and lowest carbon accumulation rates in different years. Forests on shale accumulated the most carbon in 1999 (1.97 Mg/ha/yr ± 0.27 SEM) and the least in 1981 (0.98 Mg/ha/yr ± 0.13 SEM). Forests growing above sandstone experienced the most productive year in 2014 (1.93 Mg/ha/yr ± 0.29 SEM) and the least in 1980 (1.00 Mg/ha/yr ± 0.15). At the plot level, forests on both bedrock types saw a wide range of carbon accumulation rates through the study period. In fact, average annual estimates between the lowest and highest accumulating plots within each bedrock type on average differed by 219% and 169% for shale and sandstone respectively (S9). The interannual variability of carbon accumulation between bedrock types described by the average plot level coefficient of variation over 1975-2015 was not different between forests growing on shale (18.1% ± 1.82 SEM) and sandstone (20.4% ± 2.2 SEM) bedrock types (t = -0.82424, df = 10.98, p = 0.43). Over time, there was no increasing or decreasing trend of forests carbon uptake on shale (p = 0.36, $R^2 = 0.00$). However, forests growing on sandstone had a slight increasing trend in forest carbon uptake over the study period (p = 0.0001, $R^2 = 0.31$).

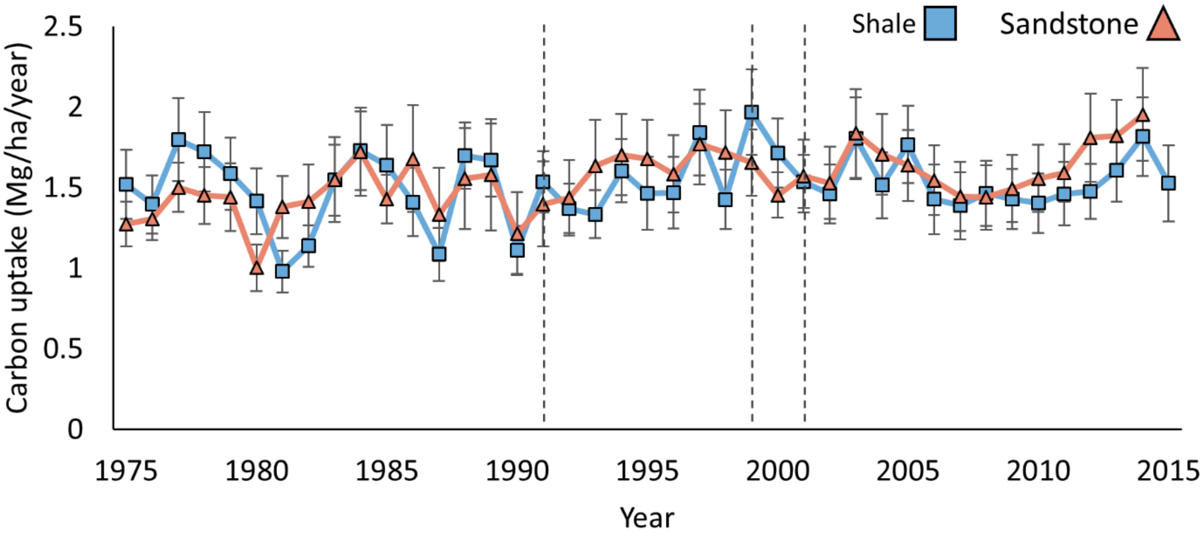

Figure 16. Average carbon accumulation rates of forests growing on shale (n = 9) and sandstone (n = 6) bedrock types in Rothrock State Forest and Stone Valley Forest. Error bars of annual uptake values represent standard error of the mean. Dashed vertical lines represent the mild-moderate drought years of 1991, 1999 and 2001.

Carbon accumulation rates during the moderate to severe drought growing seasons were similar or higher than overall average accumulation rates over the study period examined for forests on both bedrock types. Forests on shale accumulated 1.53 (± 0.19 SEM), 1.97 (± 0.27 SEM), 1.54 (± 0.17 SEM) Mg/ha of carbon while forest on sandstone accumulated 1.40 (± 0.26 SEM), 1.67 (± 0.27 SEM), 1.57 (± 0.23 SEM) Mg/ha of carbon in the years of 1991, 1999 and 2001, respectively (Figure 16). During the drought years, forests on both bedrock types were resistant and resilient to droughts (Table 9 and Table 10). During the drought of 2001 forest on shale had the lowest resistance and resilience metrics and sandstone had equally low metrics in 1991 and 2001, however, even for the most severe drought metrics differences of the index values were not statistically different from 1. Further analyzing the data, three consecutive years 1999, 2000 and 2001 all had PDSI values growing seasons with mild to severe droughts (PDSI: -3.03, -1.70, -2.29 chronologically) and still the average carbon accumulation over that period was equal to or higher than the study period average for both shale and sandstone (1.74 ± 0.13 and 1.56 ± 0.06 respectively). Considering the correlation between growing season PDSI and annual carbon accumulation, there is no relationship for either shale and sandstone bedrock type ($r = -0.0.2$, $p = 0.89$ and $r = 0.14$, $p = 0.39$ respectively) (S10). Finally, average growing season PDSI during the study period (1975-2015) was not different compared to the longer term record (1895-1974) ($t = -.95917$, $df = 82.848$, $p = 0.34$) in the same region.

Table 9. Resistance index values for forests growing on shale and sandstone bedrock type in in Rothrock State Forest and Stone Valley Forest during the 1991, 1999 and 2001 droughts. Values ≥ 1 are considered resistant. Statistical significance is set at $\alpha < 0.008$ to adjust for multiple corrections.

		Shale		**Sandstone**	
Year	**PDSI**	**Resistance Index**	**p-value**	**Resistance Index**	**p-value**
1991	-2.82	1.11 (± 0.05)	0.97	0.96 (± 0.06)	0.26
1999	-3.02	1.28 (± 0.05)	0.99	1.02 (± 0.09)	0.59
2001	-2.24	0.94 (± 0.03)	0.06	0.96 (± 0.08)	0.32

Table 10. Resilience index values for forests growing on shale and sandstone bedrock type in in Rothrock State Forest and Stone Valley Forest during the 1991, 1999 and 2001 droughts. Values ≥ 1 are considered resilient. Statistical significance is set at $\alpha < 0.008$ to adjust for multiple corrections.

		Shale		Sandstone	
Year	**PDSI**	**Resilience Index**	**p-value**	**Resilience Index**	**p-value**

1991	-2.82	1.03 (± 0.04)	0.80	0.96 (± 0.06)	0.90
1999	-3.02	1.05 (± 0.03)	0.90	1.02 (± 0.09)	0.33
2001	-2.24	0.95 (± 0.02)	0.04	0.96 (± 0.08)	0.49

CZO Sites and Bureau of Forestry Inventories

At the CZO sites, there was an interactive effect of hillslope position and bedrock type across the hill slope from ridgetop to valley bottom for both forest carbon storage and uptake (p > 0.001 and p = 0.015 respectively, Table 11). For both shale and sandstone, patterns of forest carbon storage and uptake did not increase uniformly from ridgetop to toeslope (Figure 17 and Figure 18). Overall, midslope positions in the Shale Hills CZO stored and accumulated the most carbon compared to other bedrock and hillslope positions (140.2 [± 14.6 SEM] Mg/ha and 2.38 [± 0.20 SEM] Mg/ha/year, respectively).

Table 11. ANOVA table summaries for forest carbon storage and uptake at the Shale Hills and Critical Zone Observatory sites across ridgetop, midslope and toeslope positions on shale and sandstone bedrock type.

ANOVA				
Carbon storage				
	Df	**Sum of Sq.**	**F-value**	**p-value**
Bedrock	1	16358	44.489	5.42e-08 ***
Slope position	2	2042	5.554	0.007438 **
Bedrock * Slope position	2	3135	8.526	0.000824 ***
Residuals	40	368		
Carbon uptake				
	Df	**Sum of Sq.**	**F-value**	**p-value**
Bedrock	1	3.37	2.127	0.153
Slope position	2	3.29	1.038	0.364
Bedrock * Slope position	2	14.80	4.671	0.015*
Residuals	40	63.38		

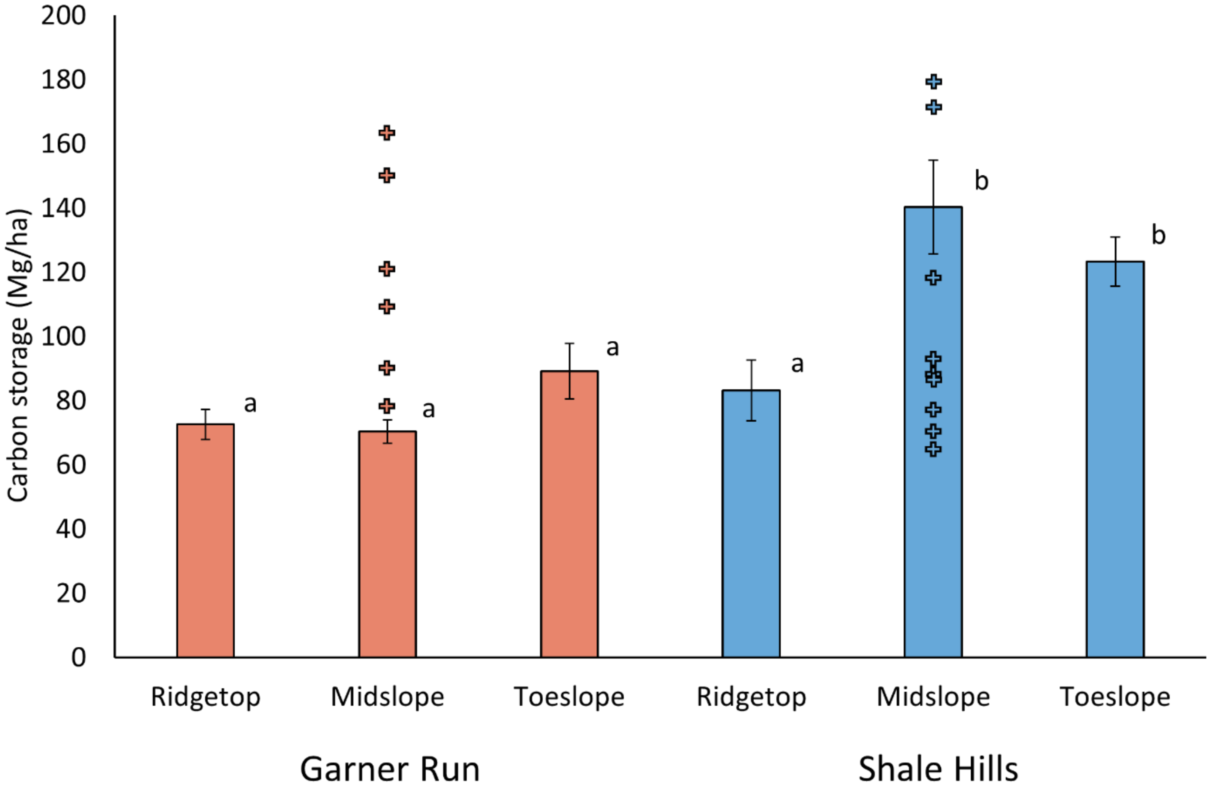

Figure 17. Average live aboveground carbon storage (Mg/ha) for forests at the Garner Run and Shale Hills CZO sites as well as forests sampled for tree ring-reconstructions. Bar graphs represent CZO sites and cross marks represent tree-ring plots. Error bars represent standard error of the mean (± S.E.M.). Different letters represent statistically significant differences from a Tukey HSD test at CZO sites.

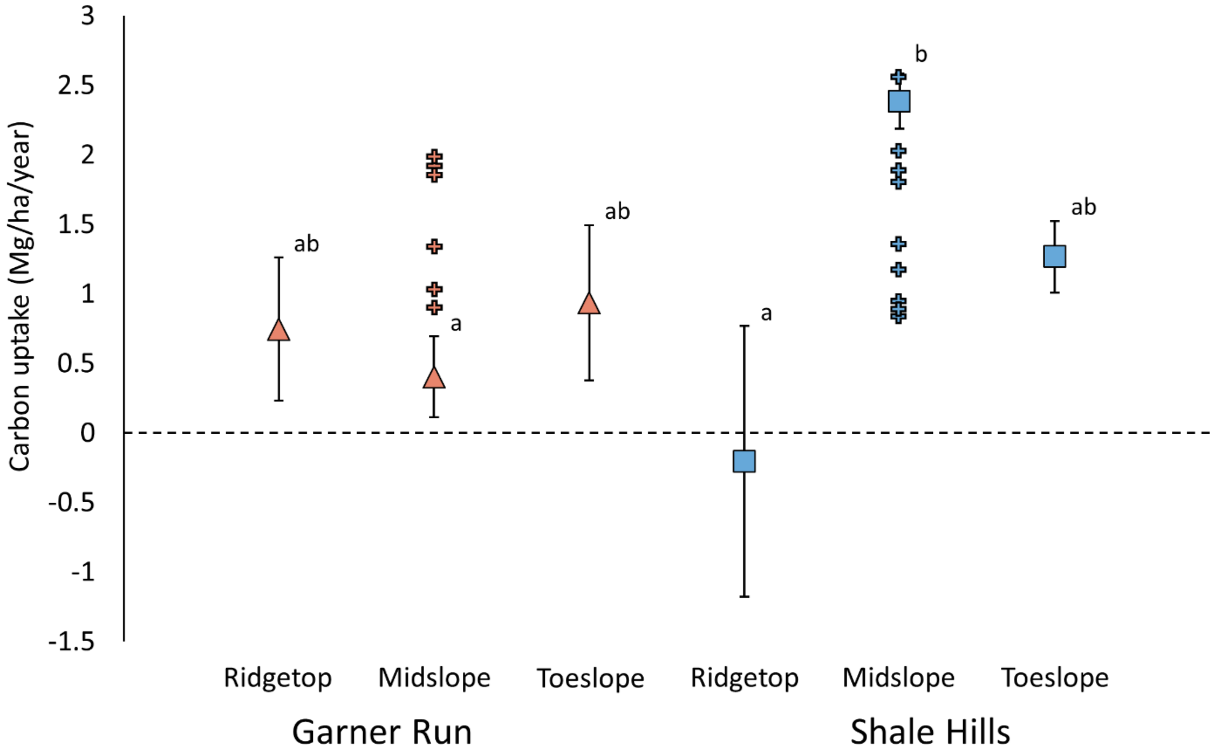

Figure 18. Average live aboveground carbon uptake (Mg/ha/year) for forests at the Garner Run and Shale Hills CZO sites as well as forests sampled for tree ring-reconstructions. Squares and triangles represent data from the CZO sites and cross marks represent tree-ring plots. Error bars represent standard error of the mean (± S.E.M.). Different letters represent statistically significant differences from a Tukey HSD test at CZO sites.

In the spatially wider network of plots Bureau of Forestry inventory that is included to capture a more broad range of elevation of the local landscape, forests carbon uptake was negatively correlated with higher elevation ($r = -0.33$, $p = 0.047$) while forest carbon storage was not ($r = 0.01$, $p = 0.95$) (Figure 19). Forests within a 30-kilometer radius of the Shale Hills CZO did not differ in the amount of carbon they stored by bedrock type, aspect or the interaction between the two (all $p > 0.05$, Table 12, Figure 20). Additionally, there was no statistical difference between aspects, or the interaction of aspect and bedrock type for forest carbon accumulation (p = 0.21 and 0.34 respectively). However, average carbon accumulation rate for these forests was different on the two bedrock types (p = 0.002, Table 12, Figure 21). Forest growing on shale bedrock accumulated an average of 1.37 (± 0.23 SEM) Mg/ha/yr of carbon live aboveground carbon in relation to sandstone which lost -0.03 Mg/ha/yr (± 0.50 SEM) on average. Interestingly, a higher number of plots on shale bedrock type were on more north facing aspects (n: shale: = 15, n: sandstone = 4) compared to a higher number of plots on sandstone bedrock on south facing aspects (n: shale = 7, n: sandstone = 10) (S11 and S12). Only 9% (2 out of 22) of forests on shale had negative carbon accumulation rates compared to 36% (5 out of 14) of the forest on sandstone. Forest inventory plots on shale included data from 791 trees while forests from sandstone inventories included 690 and equates to stem densities of 443.6 stems per ha and 654.8 stems per ha respectively.

In examining the terrain position of forests on shale and sandstone bedrock type in Rothrock State Forests, the majority of forest inventory plots were located on midslope positions (72% and 71%, respectively). Because the portion of the local landscape on each bedrock type is primarily in midslope locations, the continual forest inventory data do not allow for the comparison of forest carbon characteristics across the gradients of ridgetop to valley floor. Additionally, there were no plots on shale that captured a ridgetop position (S13).

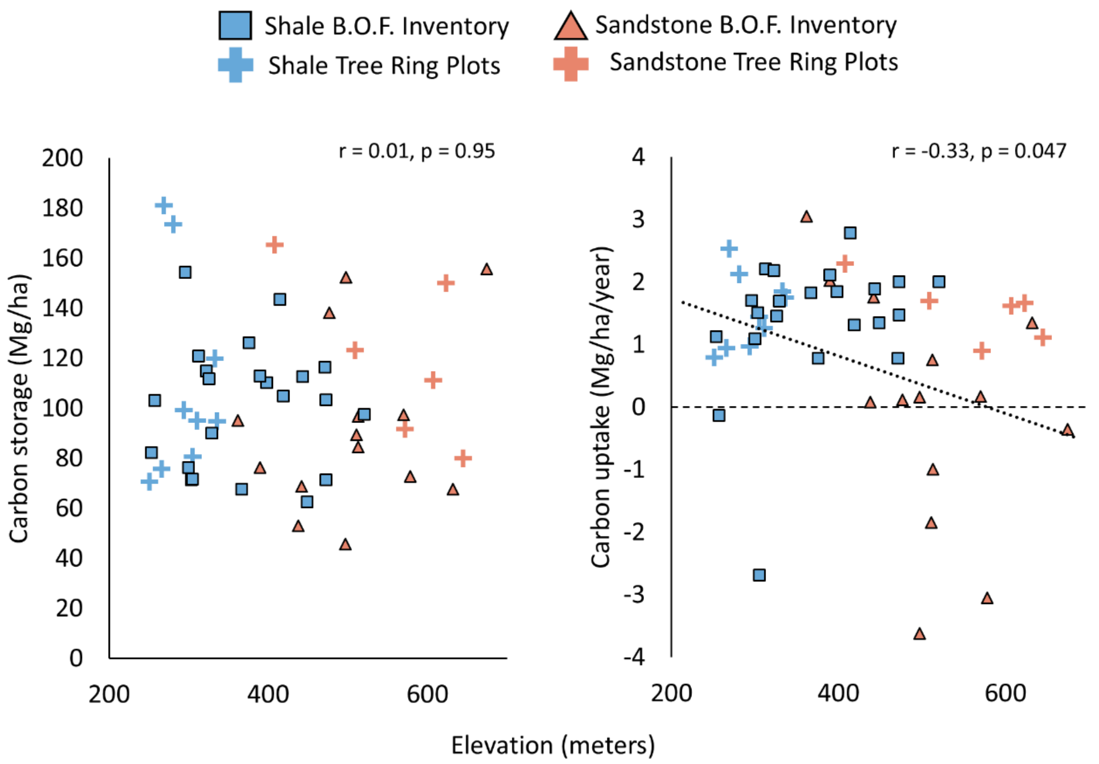

Figure 19. Forest carbon storage (Mg/ha) and uptake (Mg/ha/yr) across an elevation gradient for forests on shale and sandstone bedrock types in the Rothrock State Forest. Squares and triangles represent data from the Bureau of Forestry Continual Forest Inventory. Correlation statistics are included within the plots. The statistically significant negative trendline is included representing the relationship between forest carbon storage and elevation. Cross marks are added to visually represent live aboveground carbon storage and uptake to contrast the longer-term tree-ring record with spatially extensive inventory data. Colors represent corresponding bedrock type.

Table 12. ANOVA table summaries for carbon storage and uptake in forests growing on north and southward aspects on shale and sandstone bedrock types sampled in the Bureau of Forestry Continual Forest Inventory. Sandstone * North: n = 4, Sandstone * South: n = 10, Shale * North: n = 15, Shale * South: n = 7.

ANOVA				
Carbon storage				
	Df	**Sum of Sq.**	**F-value**	**p-value**
Bedrock	1	444.4	0.5983	0.446
Aspect	2	2878.6	3.8758	0.059
Bedrock * Aspect	2	640.9	0.8629	0.361
Residuals	28	20795.9		
Carbon uptake				
	Df	**Sum of Sq.**	**F-value**	**p-value**
Bedrock	1	20.011	11.3924	0.002*
Aspect	1	2.943	1.6754	0.206
Bedrock * Aspect	1	1.637	0.9318	0.343
Residuals	28	49.182	1.7565	

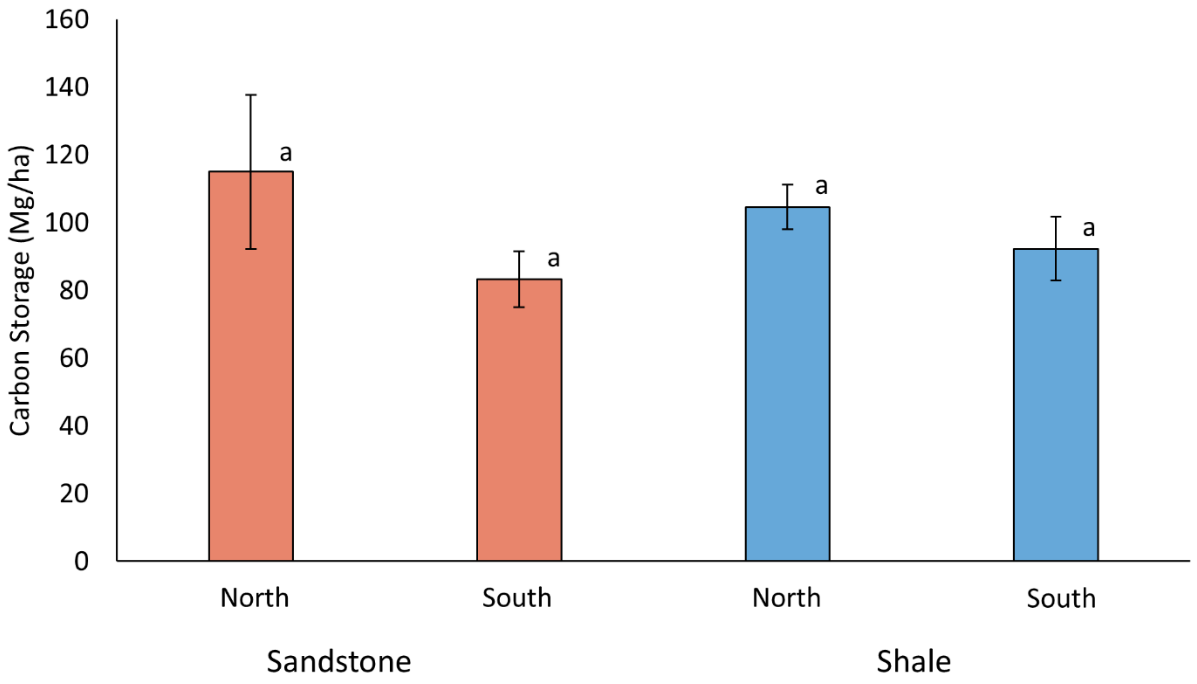

Figure 20. Forest carbon storage (Mg/ha) for forests growing on north and southward aspects on shale and sandstone bedrock types sampled in the Bureau of Forestry Continual Forest Inventory. Matching letters across the aspect and bedrock combinations represent lack of statistically significant differences. Error bars represent one standard error of the mean (± S.E.M.). Sandstone * North: n = 4, Sandstone * South: n = 10, Shale * North: n = 15, Shale * South: n = 7.

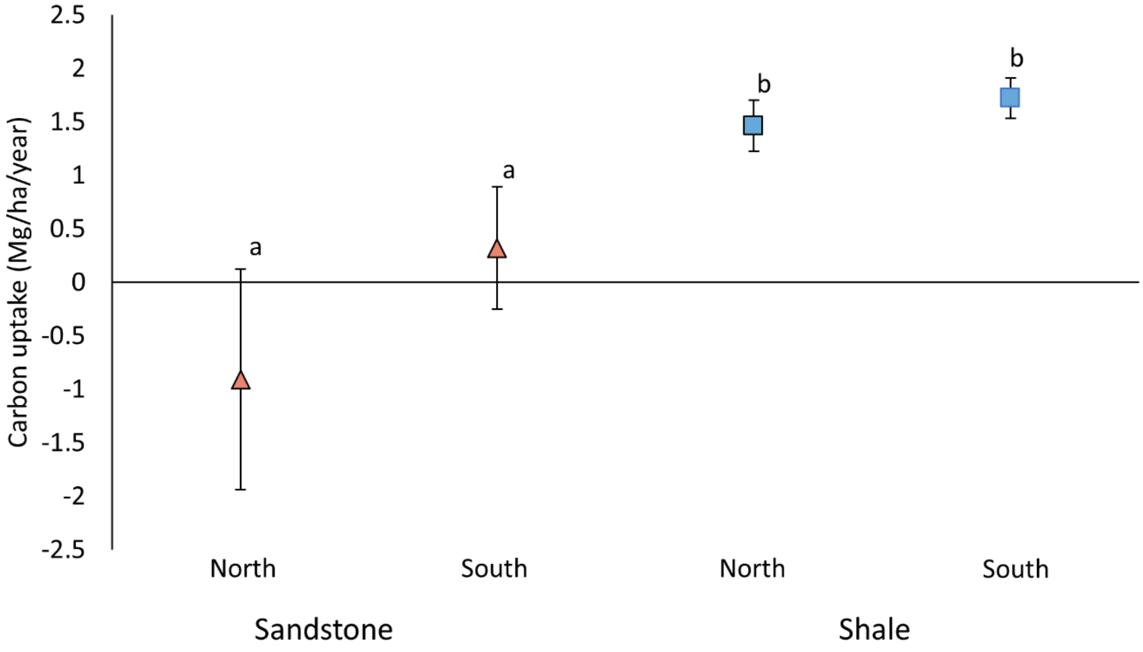

Figure 21. Forest carbon uptake (Mg/ha/year) for forests growing on north and southward aspects on shale and sandstone bedrock types sampled in the Bureau of Forestry Continual Forest Inventory. Different letters across the aspect and bedrock combinations represent statistically significant differences. Error bars represent one standard error of the mean (± S.E.M.). Sandstone * North: n = 4, Sandstone * South: n = 10, Shale * North: n = 15, Shale * South: n = 7.

Discussion:

Estimates of forest carbon accumulation over the longer-term from tree rings, where aspect and hillslope position were held constant, demonstrated that forests on shale and sandstone do not differ in the amount of carbon stored, accumulated, interannual variability or their resistance and resilience to drought (Figure 16, Table 9 and Table 10). These results are largely contrasted by the large amount of variability in the forest carbon dynamics at the plot level over the three data sources considered (45.5 – 180.6 Mg/ha for storage and -3.6 – 4.5 Mg/ha/yr for uptake) compared to the average for all tree ring data (114.1 Mg/ha ± 9.55 S.E.M. for storage and 1.53 Mg/ha/yr ± 0.02 S.E.M. for uptake). No one strong driver of forest carbon dynamics stands out across the multiple spatial and temporal scales that I examined. Within two watersheds on shale and sandstone bedrock types at CZO sites, mid- and toeslope positions on shale stored more carbon than the ridgetops on shale and all other terrain positions on sandstone, yet carbon uptake had no clear pattern over topographic positions or bedrock types (Figure 17 and Figure 18). Considering forests from the Bureau of Forestry inventory that were sampled across wider gradients, elevation is negatively correlated with forest carbon uptake and forests on sandstone tend to have more negative accumulation rates compared to shale regardless of north or south facing aspects (many of which are growing above 500 meters in elevation) (Figure 19 and Figure 20).

Evidence from the multiple data sources examined here suggests that tree mortality may be contributing to the high amount of variability in carbon dynamics across this landscape and that forests growing at higher elevations or topographic positions may be disproportionately impacted. The increasing growth trend in forests growing on sandstone observed in tree rings may reflect growth releases in surviving trees from competition as a result of the death of neighbors, however individual trees that have died are not recorded in this record as they are in the other forest inventories. There is also a lack of synchrony in the patterns of annual carbon uptake between forest on sandstone compared to shale supporting the idea that the death of individual trees is not the equal between plots and bedrock types (S9). In combination, these results paired with the negative correlation between elevation and carbon uptake (driven by greater mortality at higher elevations and sandstone sites, Figure 6 and Figure 8) provide evidence that tree death may be driving some of the variability of forest carbon dynamics. Mortality is an influential driver of carbon dynamics in eastern deciduous forests and both the species impacted and the agents of mortality are diverse (Gonzalez-Akre et al. 2016). Wind is an important source of mortality in oak forests and sites at higher elevations may be more exposed (Greenberg et al. 2011), potentially influencing the patterns described here. Susceptibility to wind damage, like carbon dynamics, is complex and is impacted by many factors including topographic position, exposure and soil properties (Everham and Brokaw, 1996). Despite the patterns highlighted above in carbon accumulation, differences in carbon storage are not apparent on higher elevation sites on sandstone bedrock type across the landscape (Figure 6 and Figure 7).

The use of tree-rings to improve upon the temporal resolution of multiannual forest inventories in forest carbon dynamics research has been encouraged by others, however, with some recommendations to apply cautious interpretation (Biondi 1999, Babst et al. 2014). In tandem with some of the apparent benefits to the use of tree-ring derived carbon dynamic estimates, notable biases have been pointed out. Potentially the most apparent in comparing these estimates to repeated inventories in the study presented here is the lack of the ability to account for the amount of live carbon loss through tree mortality. Reconstructions of carbon from tree-rings include details from the forest conditions at the time of sampling and does not include records of growth from trees that have died. This does not allow for a full representation of the transfer of carbon out of the live aboveground forest carbon pool that are clear in other sampling methods presented here and are important in comparing differences of forest on shale and sandstone bedrock type (i.e. Figure 18, Figure 19, Figure 21). This issue has been deemed the “fading record problem” and highlighted by others (Babst et al. 2014, Nehbass-Ahles et al. 2014, Dye et al. 2016). In this study I limited the study period to a 40 year temporal window to try to capitalize on as long of a reliable record as possible, but undoubtably this period excludes some of the forest carbon dynamics attributed to mortality. Dead trees generally contribute to a relatively small but important part of the carbon in second growth forests of the eastern United States thus far (Gough et al. 2007) and are not quantified here.

Despite some of the limitations encapsulated by the tree-ring estimates there is still a lot to be learned from this record. Long-term estimates of forest carbon uptake between 1975 and 2015, where topographic features are held relatively constant, displayed very similar patterns of average forest carbon accumulation rates between these two neighboring bedrock types (Figure 16). Furthermore, when examining carbon dynamics for the tree-ring plots, consistently there were no statistical differences between the forests on the two bedrock types in initial carbon storage, accumulation, interannual variation, and resistance or resilience to moderate to severe drought. The similarity between the average carbon dynamics for forests growing on the two bedrock types is somewhat notable considering how much variation there is across sites from the CZO and Bureau of Forestry Inventory across the larger area.

The plot level forest carbon accumulation reconstructions that were included in this analysis were a summation of the growth of mixed species forests where 87% of the forest plots detailed here were dominated by oak species (northern red oak, chestnut oak and white oak) and the remaining 13% were dominated by eastern white pine (*Pinus strobus* L.), which make up four of the top ten dominant species by carbon mass across the Ridge and Valley region (Reed and Kaye 2020). In a recent comparison of 17 tree species from mesic forests of the eastern United States, the oaks and pines featured here exhibited limited legacy effects on growth in response to drought compared to species such black birch or tulip poplar *(Lirodendron tulipifera* L.) with diffuse porous wood anatomy (Kannenberg et al. 2018). The species composition of forests in the eastern US does influence the sensitivity and impact of drought on forest growth. Forests composed of more mesophytic species such as tulip poplar (*Liriodendron tulipifera* L.) and sassafras (*Sassafras albidum* Nutt.) and sugar maple (*Acer saccharum* Marsh.) are more sensitive to water stress and compositional shifts from oaks to these mesophytes may lead to large reductions in carbon accumulation, especially in scenarios of more frequent drought (Brzostek et al. 2014). When comparing white oak and sugar maple responses to drought, dry periods caused an 19% greater reduction in growth for sugar maple comparatively (Au et al. 2020). The species composition of the forest plots presented here are seemingly drought tolerant to the severity of growing season drought examined here regardless of bedrock type. If future forests shift in forest composition away from oak as a result of ongoing mesophication, regardless of the cause (Nowacki and Abrams 2008, McEwan et al. 2011, Fei et al. 2011, Kreye et al. 2013), there may be negative impacts on these forests as carbon sinks especially in a future with a warmer climate with more frequent drought across bedrock types.

In this study I have highlighted two growth metrics based on carbon, resistance and resilience, that compare the impact of three droughts. Carbon accumulation responses over the 1991, 1999 and 2001 droughts demonstrate that forests growing on both shale and sandstone bedrock type from fairly productive forests on north facing midslopes are both resistant and resilient to the drought intensity experienced over the contemporary period (Table 9 and 10). Resistance and resilience have been the focus of a number of studies on the impacts of drought on forests (D'Amato et al. 2013, Gazol et al. 2017, Camarero et al. 2018 and DeSoto et al. 2020). These metrics predict the probability of survival to subsequent drought events (DeSoto et al. 2020). This is a useful metric given the great amount of uncertainty in how forests will respond to more frequent and intense drought in a changing climate (Allen et al. 2010, Clark et al. 2016). In the northeastern US, where this study takes place, temperatures are predicted to rise and growing season droughts are likely to become more frequent (Hayhoe et al. 2007). Results presented here suggest that the outlook for the stability and strength of the forest carbon sink to future drought may be positive on both shale and sandstone bedrock, at least on north facing midslope positions if species compositions were to remain stable. One aspect to support this notion is that currently the oak hickory forest type is at the northern end of its range limit in the study area and is projected to move northward as the climate warms (Iverson and Prasad 2001). Drought may not be the factor limiting this community's productivity. However, recent work has highlighted that increased temperatures and reductions in growing season precipitation are likely to be detrimental even for northern red oak (a dominant tree within the forests presented here) in the much more northern forests of Vermont (Stern et al. 2020).

While other studies have highlighted that droughts have the ability to cause significant growth decline in eastern oaks (Pedersen 1998, Demchik and Sharpe 2000, Voelker et al. 2008) it seems that this is not the case for forests on north to northwest facing midslopes in the central Pennsylvania Ridge and Valley. Demchik and Sharpe 2000 compared northern red oak on sites in southwestern Pennsylvania with soil and foliar nutritional potassium and calcium deficiencies. They found that trees from sites where potassium and calcium were lower, drought induced mortality was higher and recovering growth of surviving northern red oak was lower following droughts of the 1960s. The nutritional status of soils on shale and sandstone bedrock display contrasting patterns of potassium and calcium in this study, where they are more available on shale (Hill 2016). Despite the differences in nutritional status, these oak forests on both shale and sandstone bedrock type are resistant and resilient to drought. In regards to the detection of evidence of the detrimental impacts of drought on these forests, it does remain possible that trees within these plots died and went undetected due to methodology. However, that may be unlikely given the relative consistency of carbon accumulation of the living trees outlined here.

Unlike much of the existing research where tree rings are used to investigate the impact of drought on tree growth, I examined the impact of drought at the plot level rather than the individual tree. The mixed species composition of the forest may contribute towards the resistance and resilience in carbon accumulation to drought. Mixed species stands have demonstrated the ability to resist the impact of drought compared to monospecific pure stands because more drought tolerant species preform better under reduced competition, balancing the out the growth that would otherwise be lost (Pretzch et al. 2013). Furthermore, in forests of the southeastern US tree species richness seems to buffer the impact of severe droughts (Klos et al. 2009). It is possible that forests on both bedrock types here are operating in a similar manner. In this study I used fixed radius plots to sample trees of all species >10 cm which includes multiple species of different canopy positions. Trees at lower canopy positions have been shown to recover more strongly and grow faster following a drought depending on site classifications (Orwig and Abrams 1997) which could also play a role here in of these forests' resilience to drought. Lastly, the inclusion of systematically sampled trees in dendroecological research from forest inventories on sites that are not considered to be the most climatically sensitive has been shown to temper the conclusions about the impact of climate on forest growth (Kleese et al. 2018). Other research that has described more negative impacts of drought on the growth of eastern oak forests may rely on older trees from more climate sensitive sites than from second growth north facing midslopes highlighted here. Considering the stable trends in forest carbon accumulation from the period of 1975-2015, mid-to-late successional second growth oak forests detailed here may continue to grow well under future climate scenarios.

The systematic sampling of the forest inventory data used here aims to sample a representative portion of forest community types of the larger landscape. Of the plots included in the Bureau of Forestry inventory network, 56% were recorded as being located on a midslope position, proportions that were similar on both bedrock types (57% of plots on sandstone and 55% of plots on shale). For forests dominated by oaks, which comprises 62.5% of the typical 81-120 year old forest in the Ridge and Valley (Reed and Kaye 2020), the longer-term estimates outlined here of stable aboveground live carbon accumulation and drought resilience may be considered fairly representative of much of the landscape of the region (minus patterns in tree mortality). Efforts to increase our understanding of forest-climate growth relationships across multiple landscape positions could benefit from expanding the tree ring plot network to include different extremes in the elevation gradient and south facing aspects. To maximize the efficiency of sampling tree cores for tree ring derived estimates of carbon dynamics a modified sampling plan is recommended with a proportional sampling focusing on large trees (Xu et al. 2019) that would increase the spatial extent compared to what is outlined here. However, it is possible that the trees in lower canopy positions may contribute to the resistance and resilience of forest carbon to drought that might not be captured under a modified sampling plan.

Considering the dynamics of forests from tree-ring plots to Bureau of Forestry plots sampled within a larger area of forest inventory and the CZO sites on shale and sandstone bedrock in the region highlights that drivers of forest growth and carbon dynamics are complex and interrelated between many aspects of ecosystem structure and function. Future patterns of forest mortality from multiple agents such as stress from invasive species, weather extremes and wind events are likely to play an important role in the forests of the central Appalachian Ridge and Valley. Evidence from the three data sources outlined here suggest that patterns of forest carbon dynamics are difficult to scale up in a linear fashion from plot to landscapes. Forest ecosystems and the carbon that they store function differently across complex environments and long-term observations will be important in helping shape the way we understand and manage landscapes (Groffman et al. 2012). The continued monitoring of the Critical Zone Observatory sites and large networks of forest inventory data will be valuable as we strive to understand our changing world.

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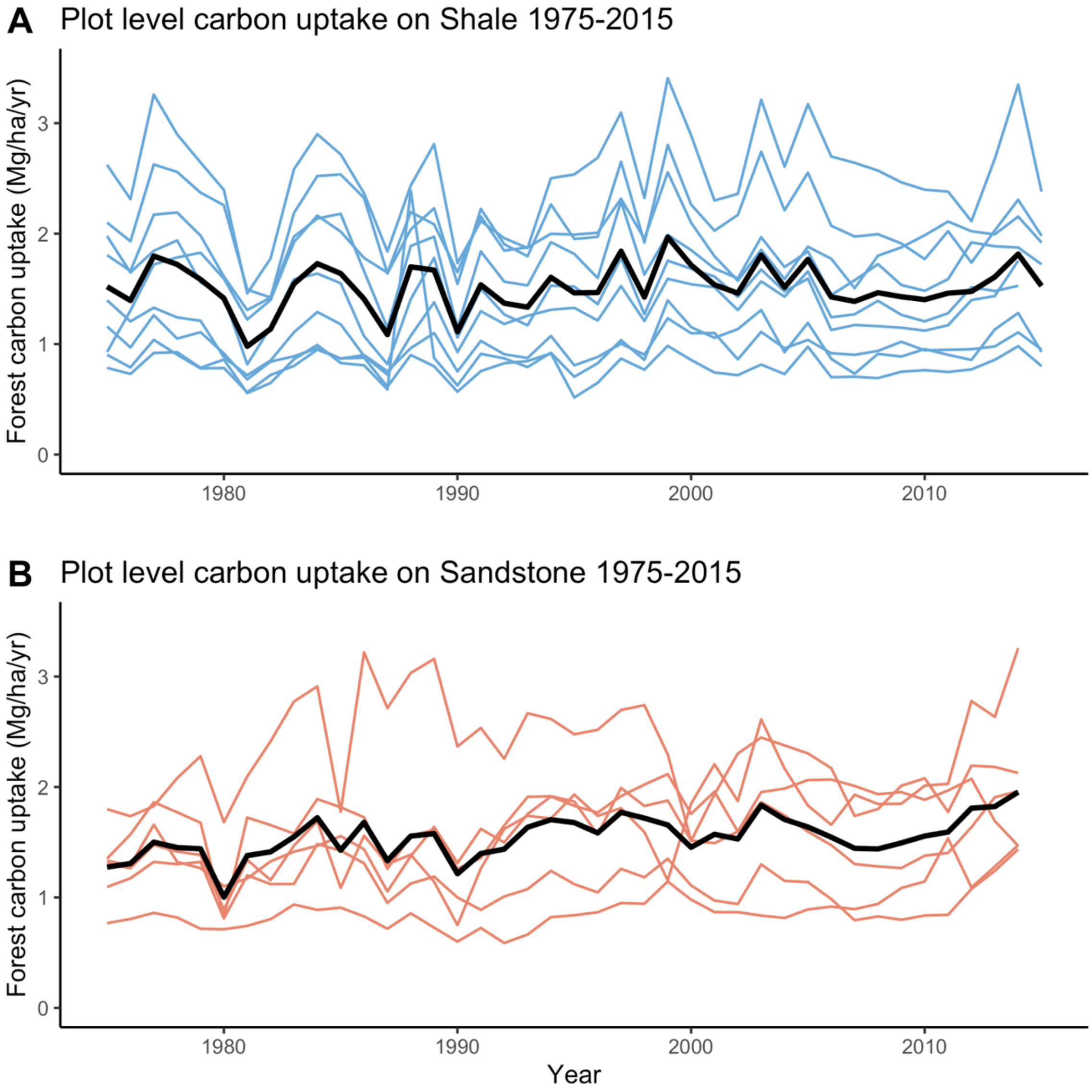
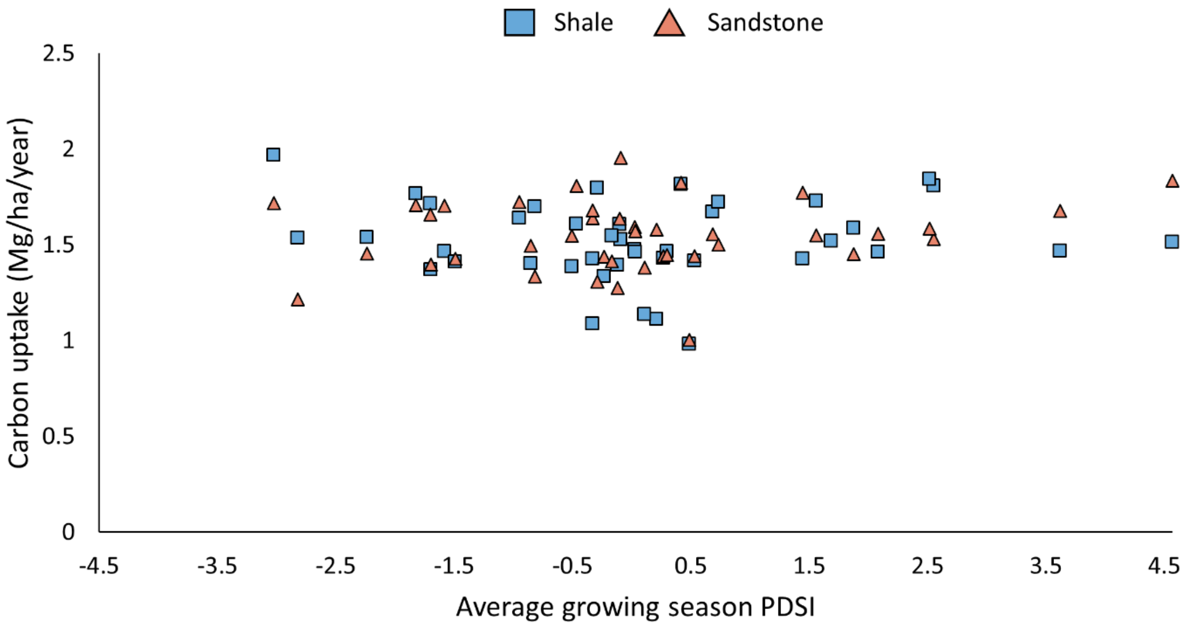
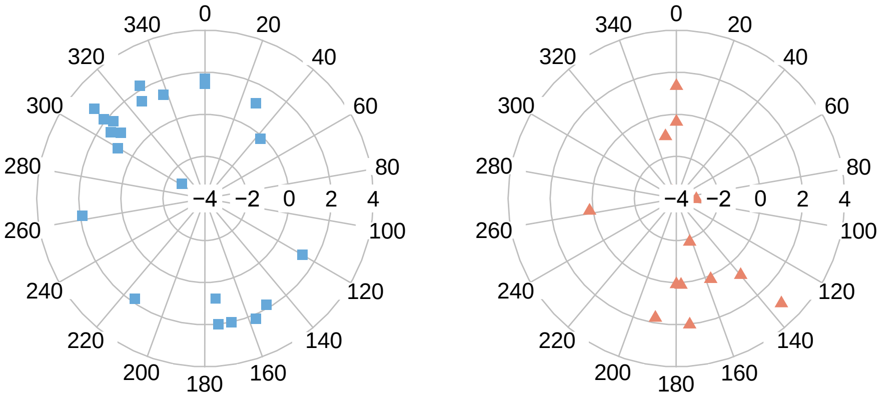


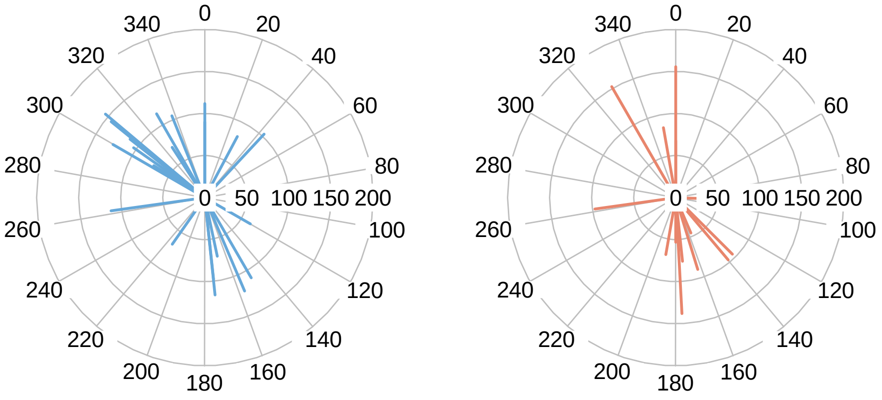
S9. Average forest carbon uptake (black lines) of forests growing on shale (n = 9) and sandstone (n = 6) bedrock type in Rothrock State Forest and Stone Valley Forest. Blue and salmon colored lines are plot level reconstructions.



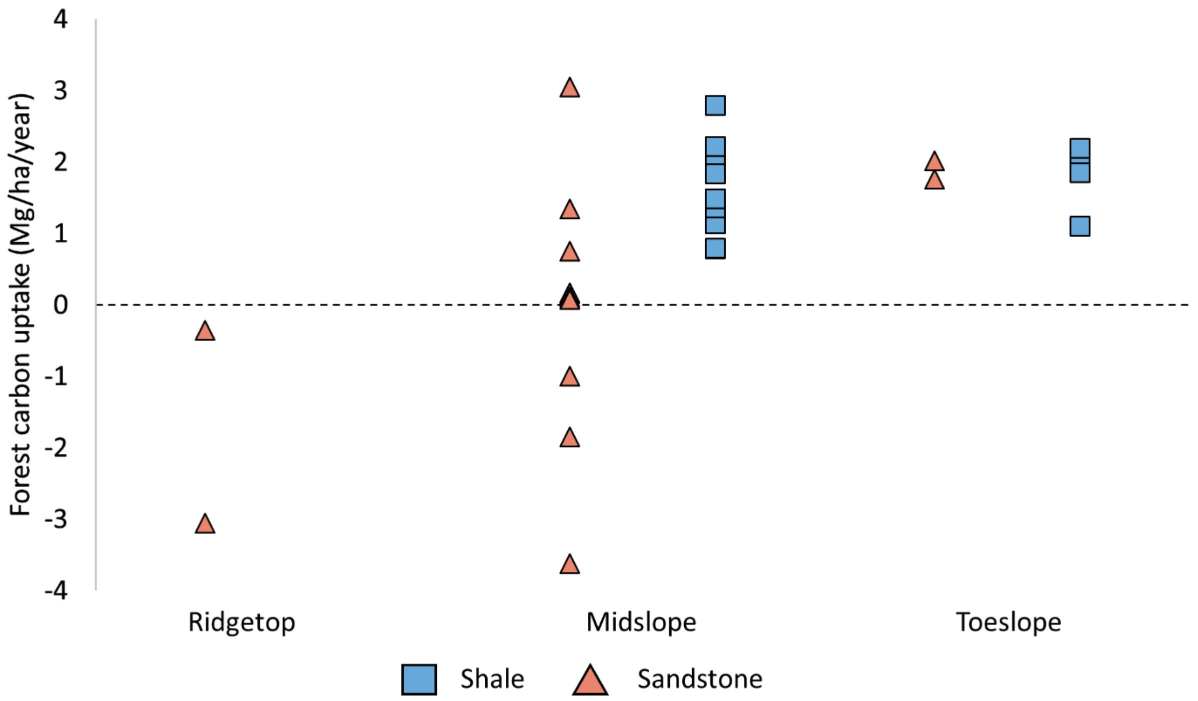
S10. Scatter plots of average annual forest carbon uptake (Mg/ha/year) of forests growing on shale and sandstone (n = 9) and sandstone (n = 6) bedrock type in Rothrock State Forest and Stone Valley Forest and average growing season Palmer Drought Severity Index. Each point represents the average uptake of all plots on shale or sandstone bedrock.



S11. Polar plots displaying forest carbon accumulation (Mg/ha/year) and the aspect of plots on Rothrock State Forest for shale (blue squares) and sandstone (salmon triangles). Outer circle numbers represent the aspect of the plot. The position within the circle represents the rate of uptake, Axis run from -4 to 4 Mg/ha/year.



S12. Polar plots displaying forest carbon storage (Mg/ha) and the aspect of plots on Rothrock State Forest for shale (blue squares) and sandstone (salmon triangles). Outer circle numbers represent the aspect of the plot. The position within the circle represents the rate of uptake, Axis run from 0 to 200 Mg/ha.



S13. Forest carbon uptake for forest in the Rothrock State Forests within 30 km radius of the Shale Hills CZO sites on different hillslope positions. No forests growing on shale were located on ridgetop positions in the continual forest inventory data and the vast majority for both bedrock types are located on midslopes.

Chapter 5

Conclusions

The main objective of this dissertation was to evaluate the degree to which differences in the lithologic properties of shale and sandstone bedrock type control forest growth and ecosystem function in the central Appalachian Ridge and Valley region. Results from the three chapters featured here highlight varying levels of importance of bedrock type depending on the scale that is examined in eastern deciduous oak forests of that region. The initial intent of this work was born out of observational differences in forests that are being studied at the Shale Hills and Garner Run Critical Zone Observatory research sites from an interdisciplinary perspective. Two main questions early on this research journey were: How representative are these forest sites to the broader landscape? and Do these forests respond differently to similar climate conditions on shale and sandstone? This dissertation significantly expands on the spatial and temporal understanding of how contemporary forests communities function on two of the most common upland bedrock types in the region.

At the widest spatial scale examined here across the entire Ridge and Valley of Pennsylvania covering hundreds of thousands of hectares, forests are storing 25% more and accumulating carbon at a rate 55% faster in the form of live aboveground biomass on shale bedrock types than forests on sandstone. This work expands on the ecological understanding of eastern oak forests by highlighting an important control on landscape ecosystem carbon dynamics through bedrock type. Bedrock type has been studied as a potential control on the spatial patterns of forest carbon and growth rates (Morford et al. 2011, Hahm et al. 2014, Eimil-

Fraga et al. 2014, Hennigar et al. 2017), however, at the time that this dissertation research was being conducted it was yet to be extensively studied in the central Appalachian Ridge and Valley. This physiographic province spans a large latitudinal gradient from north to south where upland terrain underlain by these bedrock types are commonly forested. Future research may expand upon the spatial extent of this work using Forest Inventory and Analysis data to see if these patterns are operating from the entire Ridge and Valley.

From a forest carbon management perspective, the patterns outlined in Chapter 2 could be important to the development of future forest carbon offset projects in the region as smaller land holdings begin to be enrolled in both in voluntary and potentially the regulatory markets. Forest carbon offset projects may serve as alternative forest product revenue generators for family forest landowners, and sites with higher initial stocking can lead to the greatest return on investment (Kerchner and Keeton 2015). In mid-to-late successional forests of central Pennsylvania, those underlain by shale bedrock could be targeted by forest project developers for forest carbon management.

Two species, northern red oak and chestnut oak, comprise about half of the biomass in this region within the typical forest featured in this dissertation (Reed and Kaye 2020). The dominance of these two species paired with their hard mast production and relatively high valued wood makes them ecologically and economically important species of the region. On both bedrock types, northern red oak basal area increment exceeded chestnut oak growth by an average of 87%. Differences in growth rates for these two species exceeded differences attributed to bedrock type on these fairly productive north-facing midslopes. Additionally, the impact of competition on chestnut oak may be quite substantial and future research further incorporating biotic interactions may better illuminate forest dynamics in this region. These findings suggest that silvicultural management favoring northern red oak over chestnut oak could lead to higher rates of biomass accumulation, factors that are beneficial in the form of traditional wood products and carbon management in this region.

Climate (particularly water availability) can be an important driver of tree growth across temperate forests of eastern North America (Martin-Benito and Pederson 2015). In Chapters 3 and 4, multidecadal patterns of tree and forest growth were reconstructed from tree rings on both shale and sandstone bedrock and analyzed in concert with seasonal climate variables. For the two species considered, growth was positively correlated with seasonal precipitation for both northern red oak and chestnut oak growing on sandstone but not shale. These provided evidence for a possible explanation of differences in forest growth rates across the wider landscape where faster growth and higher biomass storage happens on shale compared to sandstone bedrock type. Drier substrate environments for forests at sites on sandstone due to coarser textured soils and a higher concentration of solid weather resistant rock in the soil environment likely drives this process. Despite the apparent moisture limitations to oak growth on sandstone, Chapter 4 of this dissertation finds that the growth (depicted as carbon accumulation) of oak dominated forests is both resistant and resilient to contemporary moderate to severe droughts on north facing midslopes of both bedrocks examined here. Contrasting the results in Chapter 3 with Chapter 4, the resistance and resilience of these multispecies forest communities as a whole suggests the importance of species diversity even in forests dominated by oaks to their function. Unfortunately, this analysis is limited to sites that are predominantly comprised of oaks due to challenges associated with accurately dating and measuring annual growth of species with less clearly defined ring boundaries (i.e. trees from the genera *Acer*¸ *Betula*, and *Nyssa*). In a positive light, these results provide encouraging evidence that drought is likely not a threat to the persistence of oak dominated forests or their strength as a carbon sink in the region if species composition remains similar. However, that scenario may not be certain without significant management intervention (Hutchinson et al. 2008, Nowacki and Abrams 2008, Dey 2014).

The ecology of closed canopy mixed species eastern deciduous forests encapsulates many different dynamic abiotic and biotic factors. This dissertation focuses on bedrock type as a potential driver to the productivity and climate response of oak dominated forests in the Appalachain Ridge and Valley region. Differences of bedrock types between shale and sandstone contribute towards topographic and edaphic complexity in the landscape at the regional scale. Patterns of forest productivity at the smaller scale seem to be less pronounced when aspects and hillslope positions are held constant and at lower stress locations (north-facing and midslope). My hope is that this research will inform ongoing questions within critical zone science aiming to improve understanding of important carbon fluxes on a variety of substrates and land uses. This research may also be of interest to larger efforts to model terrestrial carbon fluxes at the regional to global scale, as differences in bedrock type are shown to be important within thousands of square kilometers. Additionally, I hope this work will serve as a reference and contribute towards the planning and management to sustain these treasured forests of the region.

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