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Relationship between topographic variables and live aboveground tree biomass on a large temperate forest plot

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ABSTRACT

Understanding local variation in forest biomass allows for a better evaluation of broad-scale patterns and interpretation of forest ecosystems' role in carbon dynamics. This study focuses on patterns of aboveground tree biomass within a fully censused 20 ha forest plot in a temperate forest of northern Alabama, USA. We evaluated the relationship between biomass and topography using ridge and valley landforms along with digitally derived moisture and solar radiation indices. Every live woody stem over 1 cm diameter at breast height within this plot was mapped, measured, and identified to species in 2019–2022, and diameter data were used along with species-specific wood density to map the aboveground biomass at the scale of 20 m × 20 m quadrats. The aboveground tree biomass was 211 $\mathrm{Mg\cdot ha^{-1}}$. Other than small stream areas that experienced recent natural disturbances, the total stand biomass was not associated with landform or topographic indices. Dominant species, in contrast, had strong associations with topography. American beech (*Fagus grandifolia*) and yellow-poplar (*Liriodendron tulipfera*) dominated the valley landform, with 37% and 54% greater biomass in the valley than their plot average, respectively. Three other dominant species, white oak (*Quercus alba*), southern shagbark hickory (*Carya carolinae-septentrionalis*), and white ash (*Fraxinus americana*), were more abundant on slopes and benches, thus partitioning the site. Of the six dominant species, only sugar maple (*Acer saccharum*) was not associated with landform. Moreover, both topographic wetness and potential radiation indices were significant predictors of dominant species biomass within each of the landforms. The study highlights the need to consider species when examining forest productivity in a range of site conditions.

1. Introduction

Eastern North America was once an expansive forest of tall, mature trees with large biomass, but most were cleared for agriculture and timber. Many areas regenerated, and the forest began to recover early in the 20th century, leading to the current patchwork of secondary stands among a few mature stands (McGrath et al., 2004; Pan et al., 2011; Williams et al., 2012; McGarvey et al., 2015; White et al., 2018). Extensive stands of small trees, however, are low in biomass and store relatively little carbon (Rhemtulla et al., 2009). Forest biomass is thus an indicator of the current status of a forest because it is related to its value for wildlife habitat and other raw materials and its potential for increasing carbon storage. Monitoring biomass can also reveal future effects of shifting climate, fire, or pest outbreaks.

To use biomass as an indicator of forest status requires knowledge of the distribution of forest biomass across North America and how it varies locally in undisturbed areas (McGarvey et al., 2015; Barton and Keeton, 2018). At broad scales, the distribution of biomass has been described as a function of environmental gradients using the U.S. Department of Agriculture Forest Service's nationwide Forest Inventory and Analysis (FIA) program (Ajaz Ahmed et al., 2017; Wiener et al., 2021). However, the small plots making up the FIA program are not appropriate for examining biomass variation at a fine scale. This poses the question about the unpredictable nature of forest structure locally, where fire,

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windstorms, and disease cause stochastic variation. Moreover, studies of biomass and its recovery usually ignore species composition, but the complementarity of competing species may be crucial to understanding regrowth of forest structure under an altered climate.

Our goal is to map a single forest at a fine enough scale so that local variation in structure, as revealed by tree biomass, can be evaluated relative to environmental gradients. To do so, we chose a site without recent human intervention and fully mapped 20 ha of forest. At this scale, we avoid bias in site selection that can arise if plots are the size of natural treefall gaps (Condit, 1998; Chave et al., 2003; Hanberry et al., 2012). By revealing detailed variations in forest biomass in response to local gradients of both the entire stand and the dominant species, the large plot can also reveal how much of the forest structure is not predictable due to stochastic events.

Our examination of the aboveground tree biomass investigated the distribution of the six most dominant species (in terms of their biomass): American beech (*Fagus grandifolia*), yellow-poplar (*Liriodendron tulipfera*), white oak (*Quercus alba*), southern shagbark hickory (*Carya carolinae-septentrionalis*), white ash (*Fraxinus americana*), and sugar maple (*Acer saccharum*). Sugar maple and American beech are the two most shade-tolerant deciduous species of the eastern United States and, as a result, are the most common midstory and understory species in these forests (Niinemets and Valladares, 2006; Burns and Honkala, 1990). Our site is at the southern edge of the range of sugar maple (Godman et al., 1990), while beech extends further south for an additional 5° latitude (Tubbs and Houston, 1990). Sugar maple grows in a variety of soil conditions (on sands, loamy sands, sandy loams, loams, and silt loams), but its highest growth rates are on well-drained loams (Godman, 1965). Sugar maple does not do well on acidic soils, and this is primarily due to its need for a high amount of calcium (its leaves contain 1.8% calcium of dry weight). Calcium is an immobile nutrient and is lost when the leaf falls. Thus, it is most competitive on soils where limestone provides the necessary calcium. Beech is rarely found on limestone-rich soils, with the greatest growth and largest trees usually found on alluvial soils (Tubbs and Houston, 1990). Beech is generally considered sensitive to low soil moisture.

Of the remaining species, the southern shagbark hickory is the only one that is considered intermediate in shade tolerance, with the rest (white oak, white ash, and yellow poplar) being shade intolerant (Burns and Honkala, 1990). As a result, they are rarely found in the understory, with the exception of the hickory. Yellow-poplar is the fastest growing of the six species and one of the fastest growing in the eastern US forests. It generally does well on many soil types but can rarely be competitive on very wet or very dry soils, achieving its best growth rates and size on rich, moist soils, particularly alluvial and soils on lower slopes (Beck, 1990). White oak is a valuable tree species, both ecologically and economically, and widespread throughout the eastern US, occupying sites with a wide variety of soils and exhibiting competitive growth rates, compared to associated species, on all but the dryest soils (Minckler, 1965) and on soils that are extremely wet (Rogers, 1990). White ash is similarly widespread and is the most common and most economically valuable of the native ash species (Schlesinger, 1990). It is never found as a dominant species, and unlike many of the other species discussed, it is more demanding in terms of soil moisture and nutrients, growing primarily on productive soils with a high amount of nitrogen and calcium. Soil moisture is an important determinant for its growth and distribution, with the best performance occurring on moderately well-drained soils with light texture where its roots can penetrate to a depth of at least 40 cm (Schlesinger, 1990). It has a higher tolerance for flooding than the other species on which we focus. The last of our focus species, the southern shagbark hickory, is often considered a variety of shagbark hickory (*Carya ovata*). Its ecological requirements are least well-studied but expected to be similar to those of the shagbark hickory, which is a common and valuable species with high-quality nuts and strong, dense wood (Graney, 1990). The shagbark hickory grows in a wide variety of soil conditions. In the northern parts of its range, it is found on warmer, often south-facing slopes, while in the south, it is found mostly on alluvial soils (Nelson, 1961, 1965), while in the Cumberland Mountains, it is found primarily in coves and the north and east facing slopes. Further south, it is even found in the bottomlands (Graney, 1990).

In this study, we examine the relationship between aboveground tree biomass and local topography on a fully censused 20 ha plot located in an extensive mature forest in the southern Appalachians, in one of North America's most diverse woody community plots (Ricketts et al., 1999; Kartesz, 2015). We map all trees on the plot to test whether biomass differs between broad slope and valley landforms and whether quantitative measures of environmental gradients of moisture and radiation predict biomass (Beven and Kirby, 1979; Jones et al., 2000; Kumar, 2009; Villwock et al., 2011; De Reu et al., 2013; Xu et al., 2015; McLaughlin et al., 2017; Salinas-Melgoza et al., 2018; Mezei et al., 2019; Mohamedou et al., 2019). We also examine biomass variation in the six dominant species of the forest to see how their carbon storage potential varies locally with environmental gradients. Lastly, we compare the variation in biomass on subplots that are approximately the size of a single plot of the US National Forest Inventory Network of Plots (FIA). The study may inform the potential change in carbon storage in forests of the southern USA.

2. Materials and methods

Site description. The 20 ha site is in Jackson County, northeastern Alabama, in the mountain district of the Cumberland Plateau physiographic region (Fig. 1; Fenneman and Johnson, 1946). The paint rock forest dynamics plot is in the 1,600 ha Sharp Bingham Mountain Preserve owned by the Nature Conservancy. The Preserve is now fully protected from anthropogenic disturbance but allows limited hunting; there are agricultural areas 2 km outside the Preserve. The site's climate is humid subtropical (Beck et al., 2018), with hot, humid summers and cool, wet winters. Average precipitation is 155 $\mathrm{cm \cdot y^{-1}}$, at least 9 cm each month (NOAA, 2023). The Preserve is on a deeply dissected karst landscape with a sandstone cap overlaying several layers of limestone. The variable geology and topography offer a broad range of water availability, from dry benches to moist bottomland sinks (Fig. 2). The 20 ha plot is a 500 m × 400 m rectangle with its long axis oriented at 313° (Fig. 1). The southwesterly corner is at 34.76952° N, 86.30608° W, and the elevation ranges from 226 to 323 m (Fig. 1). The majority of the plot (95%) contains limestone rockland rough soils (Soil Survey Staff, 2025). They are well-drained with a parent material of residuum weathered from limestone, have a very low available water supply, and are characterized by containing stony silty clay from 0 to 45 cm depth and unweathered bedrock beyond 45 cm. The remaining 5% of the plot is described as containing Huntington silt loam, which occurs in the flood plains and toe slopes and is mostly flat. Similar to the limestone rockland rough soils, they are well-drained but with a parent material of loamy alluvium derived from sedimentary rock. They have a high water availability and are characterized by containing silt loam in the top 1.6 m of the soil profile.

Field protocols. We had a 20 m × 20 m grid professionally surveyed (Stanley Land Surveying) across the 20 ha. Then, we mapped and inventoried all living stems of woody plants (excluding vines) with a diameter of at least 1 cm at breast height (DBH, 1.37 m above ground). Each stem was marked with an aluminum tag stamped with six digits (style 161, 5/8″ × 1 3/4″ Oblong, 0.05 aluminum, National Band and Tag, USA). The diameter was measured at breast height unless there were irregularities, in which case the stem was measured a small distance above or below and noted (Condit, 1998). Trees with multiple stems were defined as those with aboveground forks off the main trunk, below breast height, at an angle <45° from the main stem, and having a diameter of at least one-third of the main stem. All multiple stems within one tree were tagged sequentially, starting with the largest stem. Clonal trunks that were clearly connected just below ground were also recorded as multiple-stemmed (Appendix 1). Trees were mapped using a laser

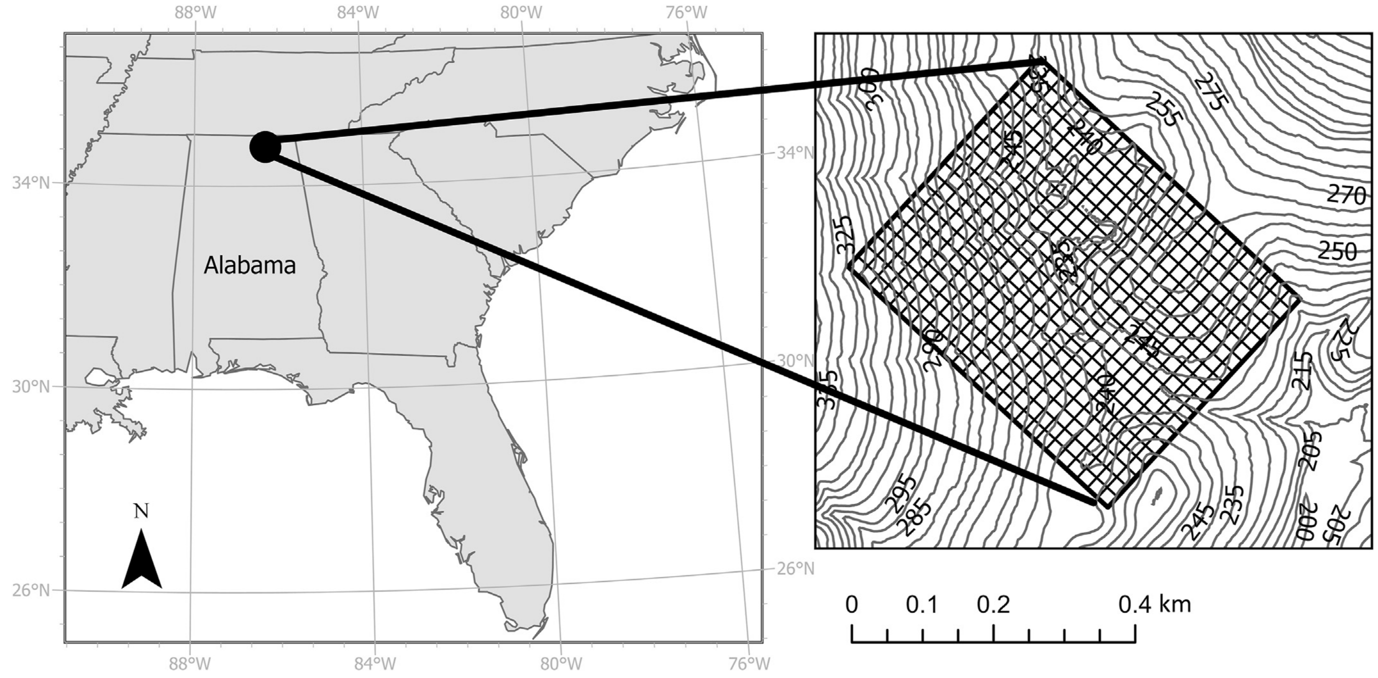

Fig. 1. Location map for the paint rock forest dynamics plot.

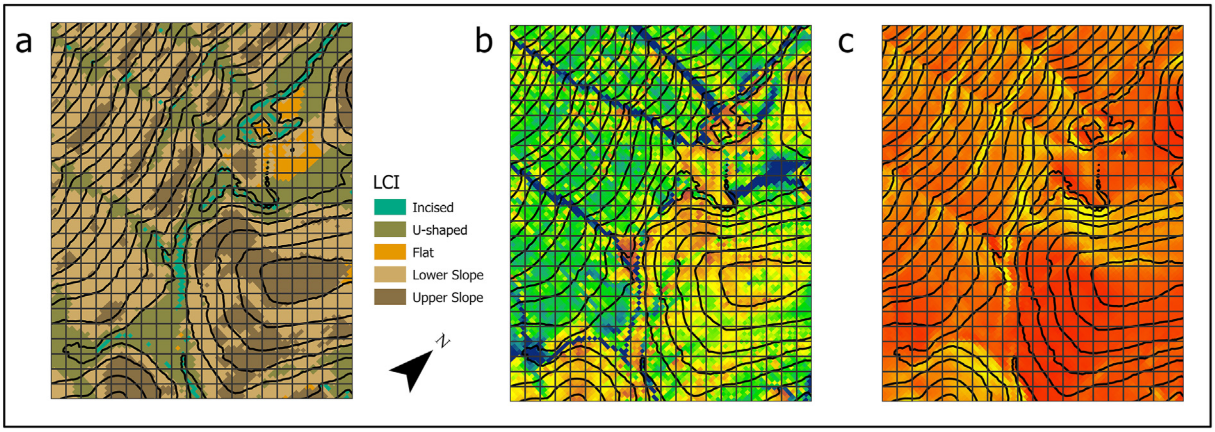

Fig. 2. Topographic variables on the paint rock forest dynamics plot based calculated from 5 m resolution data: **(a)** land position index with classification based on fine-scale radius of 10 m and a large-scale radius of 50 m; **(b)** topographic wetness index (TWI), with blue areas of higher wetness and red areas of lower wetness; **(c)** potential radiation (PotRad), with red areas of the highest potential radiation and yellow areas of lower potential radiation.

rangefinder and digital compass to measure the distance and azimuth from true north to the base of each tree from one corner of the 20 m × 20 m surveyed grid. These were converted to *x*–*y* coordinates.

Taxonomy. Our nomenclature follows that of the PLANTS online database (USDA NRCS, 2024), the Flora of the Southeastern United States (Weakley et al., 2023), and the Alabama Plant Atlas (Keener et al., 2024). In this analysis, we focus on the six most dominant species of the plot, those with the greatest biomass (each was over 6% of the total). This was an arbitrary choice, but our goal was to include species abundant enough to allow analysis of their distributions. Of the six, five are well-known, easy-to-recognize trees of North America, but one of the six is difficult to identify: the potentially polymorphic white ash, *Fraxinus americana.* We found three close relatives, *F. americana*, *F. biltmoreana*, and *F. smallii*, but these are sometimes treated as varieties of white ash, and they are difficult to differentiate without access to samaras, twigs, and leaves. We have not yet identified all individuals in the plot, so we designate the entire group as the white ash complex. Our preliminary estimate is that white ash in the narrow sense (*F. americana* sensu stricto) accounts for approximately 90% of the total biomass of this complex, while *F. biltmoreana* and *F. smallii* are uncommon. Among the entire species list, there are several more problematic or unidentified taxa, but our focus here is only on the dominant six, so we omit further discussion of taxonomy.

Aboveground biomass. Aboveground biomass was estimated from DBH using the updated generalized biomass equations for North American tree species (Chojnacky et al., 2014) along with estimates of wood specific gravity taken from Miles and Smith (2009) or, if unavailable from global datasets (Chave et al., 2009; CTFS wood density, http://ctfs.si.edu/Public/Datasets/CTFSWoodDensity). Biomass was calculated in Mg for all stems over 1 cm DBH. We also separately calculated biomass for stems >2.54 cm DBH, allowing comparison with other plot studies that include only stems > 1-inch DBH.

To assess spatial variation in biomass within the 20 ha plot and test its association with topography, we divided the plot into non-overlapping, square cells of either 20 m × 20 m or 10 m × 10 m. All analyses were repeated firstly using 20 m × 20 m quadrats, then separately using 10 m

× 10 m quadrats. These sizes were chosen to provide measures of topography that are relevant to large trees, where most biomass is held, and the 20-m scale is often used in analyzing local variation in forest biomass (Chave et al., 2003; Xu et al., 2015). In addition, we calculated the variance in stand biomass across quadrats of 25 m × 25 m, aimed to match the size of the forest inventory and assessment plots, which are 672 m^2 (four adjacent circles, each with a radius of 24 feet; Bechtold and Scott, 2005). While we focused on the relationship between biomass and topographic variables, we recognized and acknowledged that many factors influence it, including past management and disturbance. The current forest has regenerated from widespread repeated high-grading that occurred in the late 19th and early 20th centuries (McGrath et al., 2004). Bottomlands within the plot were farmed during the 19th and early 20th centuries. The Nature Conservancy started acquiring the property in 2004 (The Nature Conservancy, 2008).

Topographic indices. A digital elevation model based on 1 m LiDAR data (Dewberry, 2012) was used to calculate topographic variables in and around the plot (Stoker and Miller, 2022). We smoothed the 1 m resolution to a 5 m grid size using a running average (low-pass filtration in Gillin et al., 2015). From the 5 m elevation grid, we derived three ecologically relevant topographic variables: landform, topographic wetness, and potential solar radiation.

Landform is a categorical variable that is based on a topographic position index that compares the elevation of each pixel to its neighbors, identifying flat, convex, and concave sites. The pixel size can be varied to capture different scales of convexity, and we chose pixels of 10 and 50 m, following Weiss (2001). Combining the two scales, we distinguished ten of the Weiss (2001) landform classes across the entire reserve, from deeply incised streams to mountain tops. Within our 20 ha study area, we identified five of these classes: incised stream, U-shaped valley, flat terrain, mid-slope bench, and slope (Fig. 2). Landform was initially assigned to each 5 m × 5 m grid cell in the plot. Subsequently, the landform of 10 m × 10 m and 20 m × 20 m cells was assigned based on the majority of 5 m × 5 m cells within. Most of the plot was in U-shaped valleys, upper slopes, and mid-slope benches, which we designate valley, slope, and bench. Regression analyses were done only in those three landforms because of the limited sample size in incised and flat terrain.

The second topographic variable we used was a wetness index, a widely used surrogate for soil moisture (Beven and Kirkby, 1979). At a single location, the index is defined as the natural logarithm of the upstream catchment area multiplied by the tangent of the slope. Sites with greater up-slope catchment receive more moisture, and the moisture remains longer where the terrain is flatter. As for landforms, calculating entire catchments required topography outside the 20 ha plot. The wetness index was first estimated for every 5 m × 5 m pixel in the plot, and those were averaged within each 10 m × 10 m and 20 m × 20 m quadrat.

The third topographic index was potential radiation, defined as solar input energy at any location. This depends on topography, latitude, and average insolation (i.e., cloud cover). We could not measure radiation, but the area solar radiation tool (ESRI, 2023) allows it to be calculated on any day, at any location, based on local topography and average cloudiness. We calculated the index each summer day (Apr. 1 to Oct. 31) of our study period at a 1 m × 1 m scale, then averaged those within 10 m × 10 m and 20 m × 20 m quadrats.

Correlations of biomass with topography. We calculated aboveground biomass for the entire plot and then for each landform based on the 5 m × 5 m resolution map. For further statistics, all analyses were based on either the 500 quadrats of 20 m × 20 m within the plot or, separately, the 2,000 quadrats of 10 m × 10 m. Each quadrat had an estimated biomass plus the categorical landform, numerical wetness, and radiation indices. We used the mean and standard deviation of biomass across quadrats (both 10 m × 10 m and 20 m × 20 m) in order to determine statistical differences between landforms (*t*-test). We then ran multivariate regressions predicting biomass as a function of the wetness and radiation indices. Since the two predictors were only weakly correlated (at the 20 m × 20 m scale: $R = 0.09$, $p = 0.04$; at the 10 m × 10 m scale: $R = 0.13$, $p < 0.001$), they were used jointly in a single regression; each was standardized by subtracting the plot-wide mean then dividing by the standard deviation. Regressions were done separately within each of the three main landforms, so there was no concern about associations between landforms and the two continuous predictors. There were six separate regressions for three landforms at two quadrat sizes. We tested models using cube-root transformed biomass as well as untransformed biomass and found little difference in the results. We presented only the models based on untransformed data.

3. Results

Total biomass. The average biomass in trees across all 20 ha was 210.9 Mg·ha^{-1}, with 29,282 stems ≥1 cm DBH (Table 1). Those stems represented 27,418 individual trees of 73 species (Appendix 1 lists all species with their stem and tree counts). If only stems ≥1 inch (2.54 cm) DBH were included, biomass was barely different at 210.7 Mg·ha^{-1}. Biomass had a 25-fold variation among the 20 m × 20 m quadrats, from 28.3 to 705 Mg·ha^{-1} (Fig. 3). The 20 m × 20 m quadrats with the greatest biomass, number 0603, had only 24 stems, but one of those was the largest tree on the plot (*Quercus alba*, 147.5 cm DBH), and four other stems were ≥25 cm. Quadrats with low biomass generally had high stem counts and no large trees, such as quadrat number 1720 (28.3 Mg·ha^{-1}), which had 182 stems <10 cm DBH and four other stems <25 cm. The standard deviation of biomass at the scale of 20 m × 20 m was 80.2 Mg·ha^{-1}. Across 10 m × 10 m quadrats, it was 166.5 Mg·ha^{-1}, and for 25 m × 25 m quadrats, 61.3 Mg·ha^{-1}.

The 20 ha plot has a small stream valley flowing from north to south, with hills on either side. The slope landform was assigned to steeper parts of the hills, and the bench landform included flatter sections within the slopes. The U-shaped valley landform was assigned along the central valley and in gullies descending the hills. Two other landforms, flat regions and incised streams, occupied very small areas near the stream (Fig. 2). The wetness index was the highest in the valley and gullies and the lowest on slopes and hilltops. Radiation was the highest on hills and south-facing slopes (Fig. 2). The three main landforms were similar in total biomass, averaging 210 Mg·ha^{-1} in the valley to 223 Mg·ha^{-1} on the benches (Table 1). The two minor landforms had much lower biomass. None of the differences among landforms were statistically significant. Neither the wetness nor radiation index was a significant predictor of biomass within any landform. Radiation had a negative impact on biomass in all three, but effect sizes were small (Table 1).

Dominant species biomass. White oak had the highest biomass in the plot at 25.8 Mg·ha^{-1}, or 12% of the forest total. The other five dominant species each accounted for >12.5 Mg·ha^{-1} (Table 2). Oak, however, had low stem density, as did yellow-poplar and shagbark hickory. American beech and sugar maple, on the other hand, were the two most abundant species in terms of stem density and being dominant in biomass (Table 2).

Four of the dominant species—oak, maple, ash, and hickory—had low biomass in the valley landform relative to slopes and benches (Table 2). This was especially pronounced in hickory, which had only 5.1 Mg·ha^{-1} in the valley but 19.4 Mg·ha^{-1} on the slopes. The difference was statistically significant in three of the species but not in sugar maple, whose biomass in the valley was 75% of that on slopes and benches. The remaining two species, beech and yellow-poplar, were opposite and had their highest biomass in the valley. Both species had statistically significant variation with landform, especially yellow-poplar (Table 2). Maps of the biomass distribution of each species show these patterns conspicuously in the four species with the greatest variation: oak, hickory, ash, and yellow-poplar (Fig. 4). Spatial patterns in sugar maple and beech were less pronounced. For example, beech was abundant in the southern part of the valley but not in the northern.

Impacts of topographic wetness group out in similar ways to the landform associations. In the four species whose biomass was the highest

Table 1
Relationship between aboveground biomass and topography in the paint rock forest dynamics plot. Multiple regression between biomass and two topographic indices was done separately in the three dominant landforms. Area and biomass were calculated on landform polygons, and standard deviation (SD) was calculated based on 20 m × 20 m grids assigned the land from the majority.

Landform	Area (ha)	Biomass (Mg·ha^{-1})	# quads	SD	Wetness[a]	Radiation[a]	Adjusted R^2
Stream	0.5	106	1	–	–	–	–
Valley	5.4	210	137	±92	2.6	−13.8	0.003
Flat	0.4	158	7	–	–	–	–
Slope	9.4	213	259	±74	−11.6	−5.7	0.012
Bench	4.3	223	96	±65	0.6	−10.3	0.012

Note.
[a] Wetness is the topographic wetness index, and radiation is the index of potential radiation.

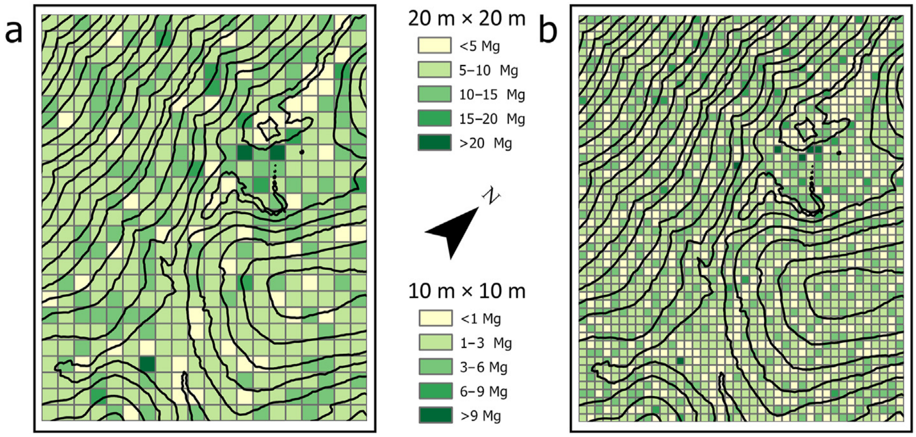

Fig. 3. (a) Plot map of aboveground biomass at 20 m × 20 m scale. **(b)** Plot map of aboveground biomass at 10 m × 10 m scale.

Table 2
Aboveground biomass and stem density of dominant tree species in paint rock forest dynamics plot, for the entire plot and within three dominant landforms.

Species	Biomass (Mg·ha^{-1})				Stems (ha^{-1})
	Full plot	Valley	Slope	Benche	Full plot
Southern shagbark hickory	14.1 ± 29.2	5.1 ± 19.3^{S,B}	19.3 ± 33.3^{V}	13.4 ± 23.3^{V}	19.7
White oak	25.8 ± 54.0	17.5 ± 61.8^{S}	32.6 ± 54.9^{V,B}	21.3 ± 36.1^{S}	22.3
White ash complex	17.7 ± 30.0	11.8 ± 23.4^{S,B}	19.3 ± 29.9^{V}	23 ± 36.3^{V}	19.7
Sugar maple	17.9 ± 19.2	15.4 ± 23.3	19.0 ± 16.6	19.8 ± 18.1	268.9
American beech	12.7 ± 25.3	16.6 ± 30.2^{B}	11.5 ± 22.6	9.8 ± 21.3C^{V}	196.5
Yellow-poplar	18.4 ± 41.5	28.1 ± 44.7^{S,B}	15.2 ± 36.9^{V,B}	7.6 ± 26.1^{V,S}	30.2

Note: Biomass is given as mean over entire plot and each landform's polygons, ± the standard deviation across 20 m × 20 m quadrats. Significance of pairwise *t*-tests comparing biomass across landforms is indicated by superscripts: V, slope or bench differs from valley; S, valley or bench differs from slope; B, valley or slope differs from bench. Uppercase letters mean $p < 0.01$; lowercase $p < 0.05$.

on slopes and benches, wetness was positively correlated with biomass, but in the other two species, it was negatively correlated (Table 3). Most slope and bench landform wetness regressions were significant, while only sugar maple had a significant wetness regression in the valley.

Radiation was correlated with biomass in four of the six species and again with two opposite effects. There were significant negative effects of radiation on biomass in ash and maple and significant positive effects in beech and yellow-poplar (Table 3). There were, however, smaller and less significant effects of radiation on biomass compared to wetness. For example, beech showed a significantly positive effect of radiation on biomass on slopes, but on the other two landforms, the effects were negative but not significant. Oak and hickory had no significant associations with radiation.

4. Discussion

Overall biomass. The paint rock forest dynamics plot had stand-wide aboveground biomass of 211 Mg·ha^{-1}. This is much higher than the average forest plot in Alabama, which has only 83 Mg·ha^{-1} (Ojha and Dimov, 2017), though this number includes many plots in younger secondary forests. On the other hand, 211 Mg·ha^{-1} is lower than old-growth stands in eastern North America, which can reach 300–400 Mg ha^{-1} (Druckenbrod et al., 2005; McGarvey et al., 2015). Paint Rock can be considered a mature forest. However, we expect it to be able to grow at least 50% more biomass.

The 20 ha plot at Paint Rock includes a valley near its center and hills on either side. Across that catena, from upper slopes to valley, we found no variation in total forest biomass, as it differed little among the three main landforms. Moreover, quantitative indices of moisture variation and radiation had no significant influence on total biomass within the landform. Lack of variation with topography may seem counter-intuitive, but this forest is not considered water-limited since the average annual rainfall is close to 150 cm and is spread throughout the year, and mixed hardwood stands in the southeast are rarely water-limited (Masek and Collatz, 2006). As a result, local variation in moisture or radiation does not have a particularly strong influence on growth. Other studies evaluating how topography influences biomass within a stand also used large plots, and some do indeed report that local topography predicts biomass.

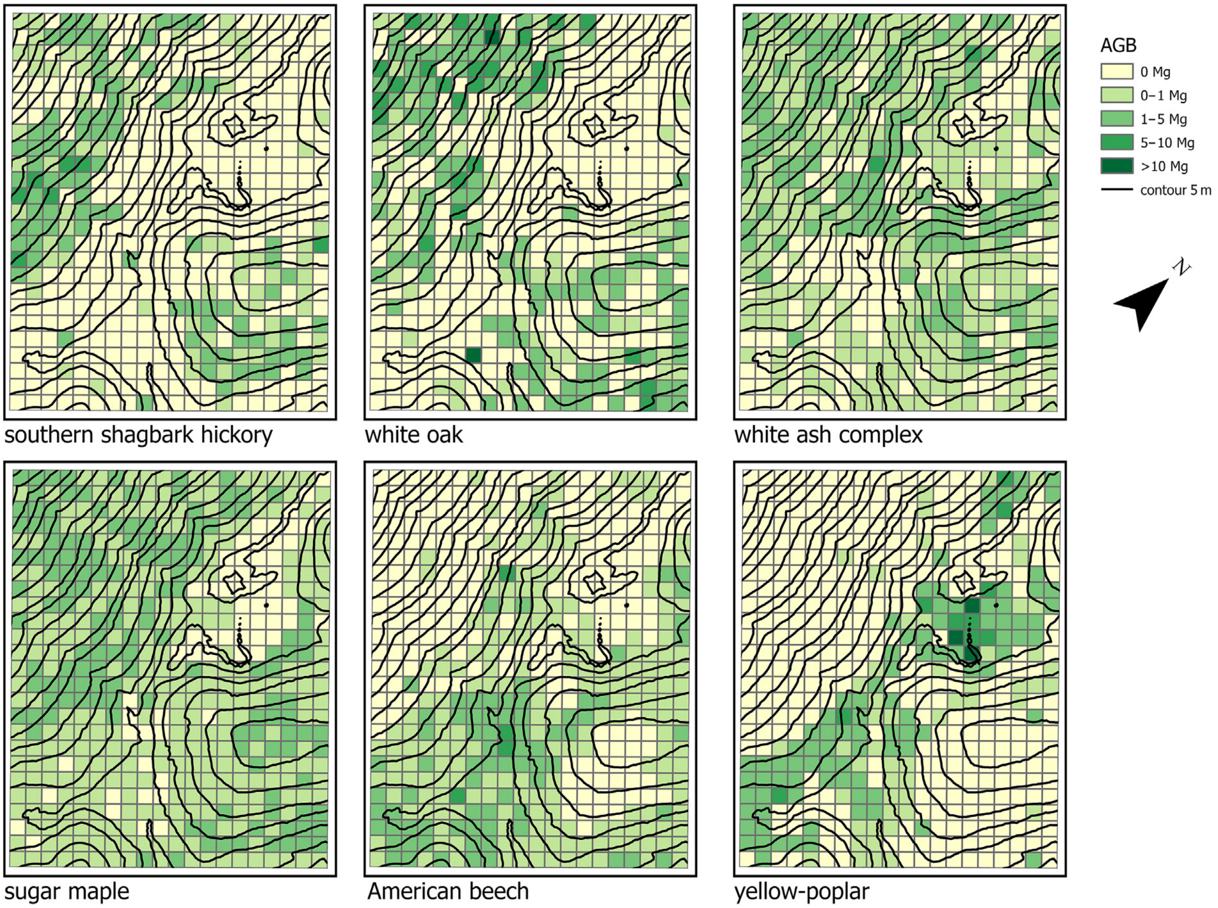

Fig. 4. Paint rock forest dynamics plot aboveground biomass for dominant species as measured in 20 m × 20 m grids.

Table 3
Aboveground biomass multiple linear regression based on continuous topographic variables, wetness and radiation, grouped by dominant landform.

	Landform	Wetness	Radiation	Adjusted R^2
Southern shagbark hickory	Valley	1.6	−0.3	−0.004
	Slope	9.1**	−1.5	0.03
	Bench	7.1*	3.7	0.07
White oak	Valley	3.9	−5.3	−0.01
	Slope	11.2*	−5.0	0.02
	Bench	4.3	−0.06	−0.01
White ash complex	Valley	−1.4	−5.0*	0.04
	Slope	6.5*	−7.6**	0.06
	Bench	11.8*	−4.1	0.06
Sugar maple	Valley	4.4**	−4.7*	0.06
	Slope	4.8**	−4.9**	0.10
	Bench	6.8**	−0.5	0.06
American beech	Valley	1.9	−2.2	−0.01
	Slope	−8.5**	5.3**	0.09
	Bench	−8.6**	−2.0	0.09
Yellow-poplar	Valley	3.0	9.2	0.02
	Slope	−12.2**	5.9*	0.06
	Bench	−2.2	−0.6	−0.01

Note: ** indicates $p < 0.01$ and * indicates $p < 0.05$.

The nature of the relationship, however, is not consistent. For example, ridge tops had lower biomass in forests in Panama and Pennsylvania (Chave et al., 2003; Fotis et al., 2018) but higher biomass in a forest in China (Xu et al., 2015; Wang et al., 2024). As we found in Alabama, solar radiation did not influence biomass in a forest in West Virginia (Ponczek, 2023). How local topography predicts biomass is clearly site-specific, undoubtedly depending on soil type and overall moisture balance.

Small sections of the 20 ha plot in the valley were classified into landforms defined as incised stream and flat. These areas include a small floodplain, which washes and sinks over karst limestone with shallow soil and or even exposed rock. We found low biomass on these landforms compared to the rest of the forest, and though a small area, we believe that these areas are disturbed often enough to restrict biomass growth.

Dominant species biomass. Though biomass of the entire stand was not correlated with topography, that of the individual species was, and often strongly. Of the six dominant species, only sugar maple had no significant landform association. Southern shagbark hickory, white oak, and white ash complex favored slopes and benches, with the hickory having four-fold higher biomass on slopes relative to the valley; beech and yellow-poplar favored the valley, and yellow-poplar also varied fourfold. Many tree species are associated with local topographic habitats (Harms et al., 2001; Kenfack et al., 2014), and an important feature of forest diversity is niche partitioning along catenas or elevation gradients (Whittaker, 1956; Bailey, 1988; McNab, 1993; Villwock et al., 2011). The complementarity of species relative to topography is what allows the forest stand as a whole to achieve high biomass everywhere. This highlights the value of diversity to forest productivity and the risks posed by pests or climate change in altering species composition.

There are no recent records of timber harvesting in and around the Paint Rock plot—other than occasional small stumps from eastern redcedar, which often persist for decades because of their decay-resistant wood (Meier, 2015)—the observed distribution of the dominant species across the plot suggests competition resulting from growth responses to fine-scale moisture differences and shade tolerance. White oaks and southern shagbark hickory are known for conservative growth patterns, and both invest in a large taproot at the expense of the aboveground parts, often as a result of repeated dieback and resprouting (Johnson et al., 2002). This makes them more competitive on sites with limited soil moisture but less competitive on moist sites, where species like the yellow-poplar, which invest less in root biomass, achieve high aboveground growth. Sugar maple occurred at similar biomass across the landforms but favored moister microsites, as measured by wetness and radiation. Beech was found mostly in the valleys throughout the plot. Sugar maple can grow in a wide variety of soils but grows best on well-drained loams (Godman, 1965) as well as on limestone-based soils, as on our site, all of which is in agreement with what we observed in our data. Beech, however, is rarely found on limestone-rich soils (Tubbs and Houston, 1990), which is why it was absent from the areas where sugar maple was particularly abundant. With beech performing best on alluvial soils and generally being considered sensitive to low soil moisture, it was similarly expected that we found it to occur primarily in the valley landforms. White ash biomass is well-distributed throughout the plot (Fig. 4), which is not unexpected—It is a species that is common in the region, where limestone is the predominant bedrock, and is most competitive on soils with moderate to high calcium content (Erdmann et al., 1979). Its presence, in terms of biomass, was greater in the benches and slopes than in the valleys, where other species likely outcompeted it. The valley landform of our plot is more disturbed, with parts of it subject to flooding, and the yellow-poplar can respond with rapid growth in disturbed areas. In addition to being the fastest growing of the six focus species, it performs especially well on alluvial soils and soils on lower slopes (Beck, 1990). Yellow-poplar is a prolific seed produced whose seeds can survive dormancy for up to seven years (Clark and Boyce, 1964), making it particularly adapted to regenerating on sites experiencing disturbances. The observed distribution of white oak on the plot matched its ecological traits, being a generalist that occupies a wide variety of sites and avoiding all but the most dry (Minckler, 1965) and wettest conditions (Rogers, 1990). Its biomass ranged from 17.5 (in the valleys) to 32.6 $\mathrm{Mg{\cdot}ha^{-1}}$ on the slopes, which was a much smaller amount of variation compared to that of the southern shagbark hickory, whose variation among the landforms was almost 4-fold (from 5.1 in the valley to 19.3 $\mathrm{Mg{\cdot}ha^{-1}}$ on the slopes). While this hickory species does grow best on alluvial soils (Nelson, 1961, 1965), on our plot, it seems to have been outcompeted and excluded from those sites and is found on sites where it may not grow as well, but where it is more competitive relative to its associates.

Aboveground biomass was highly variable across 20 m × 20 m quadrats, varying 25-fold and with standard deviations one-third or more of the mean. Within the dominant species, many quadrats had no biomass, and standard deviations exceeded the mean. Other studies within large plots report high variance across 20 m × 20 m quadrats (Chave et al., 2003; Xu et al., 2015). We also replicated the area of a standard US Forest Service's FIA plot (672 $\mathrm{m^2}$) by testing 25 m × 25 m quadrats and found a standard deviation of 62.8 $\mathrm{Mg{\cdot}ha^{-1}}$, more than a quarter of the mean. The correlations between topography and biomass accounted for a very small portion of the variance, with even significant correlations having r^2 below 0.1. This demonstrates that there are many other drivers of biomass distribution and that many are inherently unpredictable owing to the stochastic nature of tree death. The sampling unit size has a major impact on how we perceive ecological phenomena, and it influences the correlation structure and variance (Bellehumeur et al., 1997). Unpredictability at a small scale highlights that small, FIA-like plots cannot properly capture and describe local variation and underscores the importance of establishing and maintaining large forest inventory plots to supplement them. Both strategies have value, of course, and complement one another by providing answers to questions that neither of the approaches alone can address.

Our investigation into the patterns of variation of forest biomass revealed relationships between its distribution, dominance of several different species on different landforms, and the potential effect of landform, moisture, and solar radiation indices. The forest biomass was greater than that of many forests in the region, though not as high as the biomass in old-growth forests. There was limited variation across the study plot. The biomass of the six most dominant species, however, exhibited a stronger variation among the different parts of the plot and strong associations with topography. The species distributions are in agreement with the ecological expectations for species occurrence. In addition, the two digitally-derived indices, the topographic wetness and potential radiation index, were significant predictors of the biomass of the examined dominant species in the studied landforms. While the indices were all significantly related to species biomass, they did not account for a high proportion of the variation. The simple landform classes were a stronger predictor of dominant species biomass. Finally, we observed that the variation of biomass, especially of the dominant species, is sufficiently high to justify employing large plots to supplement studies of forest ecosystems with more numerous but smaller in size plots.

In order to examine additional environmental variables that may impact tree growth and species distribution, we are at the early stages of conducting soil chemistry work covering pH, nutrients, soil depth, and surface moisture on a fine scale to see if these improve the prediction of local variation of the stand and the species. In addition, we are remeasuring all stems to capture the dynamics of the forest. This will allow us to monitor the impact of currently spreading non-native pests (Morin et al., 2017), such as the emerald ash borer (*Agrilus planipennis*) and beech leaf nematode (*Litylenchus crenatae*), as well as effects of climatic variation. Predicting forest responses will depend on both documenting local variation and how it changes over time.

CRediT authorship contribution statement

Dawn Lemke: Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Luben Dimov:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Helen Czech:** Writing – review & editing, Methodology, Investigation. **Patience Knight:** Writing – review & editing, Validation, Supervision, Methodology, Investigation. **William Finch:** Conceptualization. **Richard Condit:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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