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RESEARCH

The University of West Florida Campus Ecosystem Study: effects of forest vegetation on light availability and soil processes

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Abstract College and university campuses with a notable arboreal component provide unique opportunities for carrying out ecological research. The University of West Florida Campus Ecosystem Study (UWF CES) was established in 2019 as interconnected research to take advantage of the extensive arborescent nature of the UWF campus, particularly concerning longleaf pine (*Pinus palustris*). One of these investigations established permanent plots in forested sites of two contrasting types, one dominated by longleaf pine ("pine site") and the other dominated by hardwoods ('hardwood site'). This study used these plots to examine the influence of forest vegetation on light availability and soil processes. Light was measured as photosynthetically active radiation (and expressed as photon flux density—PFD) with a handheld meter in each plot. Soil was sampled to 5 cm in each plot; texture was measured with the hydrometer method. Identical sampling methods were carried out in a persistent canopy opening to assess light and soil conditions under maximum solar radiation. Mean PFD was ~4× higher in pine stands than in hardwood stands; PFD was 12.8 and 3.5% of full light in the pine and hardwood stands, respectively. All soils were dominated by coarse-textured sands, but silt was significantly higher in pine stand soil and higher still in the canopy opening. Among forest stand plots, sand was negatively related to PFD, whereas clay was positively related to PFD. Across the three sites, silt was positively related to PFD. These relationships are consistent with the importance of solar radiation as one of many drivers of soil weathering.

Keywords Photon flux density · Longleaf pine · Fire exclusion · Soil texture

Introduction

The distinctive urban interface represented by many college and university campuses allows for unique opportunities for ecological research (Turner, 1984), especially those campuses with a significant arboreal component (Cipollini et al., 2019; Cole & Bennington, 2017; Copenheaver et al., 2014; Roman et al., 2017). Copenheaver et al. (2014) carried out a dendroecological analysis of an old-growth forest fragment on the campus of Virginia Tech using the oldest white oak (*Quercus alba*) to identify asynchronous periods of suppression/release. From these results, they concluded that there had once been a closed-canopy forest in the proximity of the current campus. Roman et al. (2017) used a combination of archives and aerial photography to examine urban forest change on the campus of the University of

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Pennsylvania. One of the older campuses in the USA, the University had undergone substantial change regarding trees in the mid-twentieth century under the direction of Ian L. McHarg, Professor of Landscape Architecture, a pioneer of ecology and planning, with a building named in his memory. Several campuses within the natural range of longleaf pine (*Pinus palustris*) have undertaken studies to further understand the unique ecology of that species, with a particular focus on restoration (Cipollini et al., 2019; Cole & Bennington, 2017).

Beginning in the summer of 2019, the University of West Florida Campus Ecosystem Study (UWF CES) was initiated as a series of interconnected research projects to take advantage of the arborescent nature of the UWF campus, especially regarding longleaf pine. Historically, the design of the campus began in 1963, originally on a 405-ha area with several distinct landscape features, e.g., wetlands, hummocks, and a small freshwater bayou. The principal feature of the campus, however, comprised extensive second-growth longleaf pine stands recovering from widespread logging in the Florida Panhandle (Knight et al., 2011). The campus was designed by John E. Jarvis, Jr., who was strongly influenced by the architectural philosophy of Ian McHarg, the Scottish landscape architect and professor at the University of Pennsylvania, having read his well-known book, *Design with Nature* (McHarg, 1995). Jarvis' vision was to maintain, as much as was feasible, all the extant landscape features of the nascent campus. As a result, there was minimal removal of trees, which were predominantly longleaf pine, but also included native oaks (*Quercus* spp.) and magnolias (*Magnolia* spp.), with minimal alterations of original contours (Jarvis, 2008; Marse, 2007). In addition, Jarvis established a network of low-impact, non-paved trails through natural areas as part of the whole campus of UWF.

As is typical of urban interfaces, these natural areas just beyond the main UWF campus have experienced chronic fire exclusion (Francos et al., 2019). Accordingly, much of the UWF CES has focused on the effects of the absence of fire on longleaf pine stands, which are notable by their dependence on fire for maintaining ecosystem structure and function. Results to date have shown that the open physiognomy of fire-maintained stands has transitioned into a closed-canopy forest with southern oaks (e.g., *Quercus virginiana*, *Quercus laurifolia*, *Quercus nigra*) filling in the otherwise open matrix (Gilliam, 2023; Gilliam et al., 2021).

The summer 2022 iteration of the UWF CES identified an area that was devoid of longleaf stems (dominated completely by hardwood tree species) that was adjacent to the more typical longleaf pine stands. That study compared stand composition and soils of the two contrasting stand types, pine versus hardwood (Gilliam et al., 2023). Unsurprisingly, the pine stand was dominated by longleaf pine, whereas the hardwood stand was dominated by flowering magnolia (*Magnolia grandiflora*). As with other studies on UWF campus, live oak (*Q. virginiana*) was ubiquitous in all plots and was the co-dominant in both stand types. The flowering magnolia/live oak association is prominent in Florida (Daubenmire, 1990). In brief, there was generally higher soil fertility in the hardwood stand than in the pine stand (Gilliam et al., 2023).

One variable not measured in that study was light availability reaching the forest floor. This is an important factor in forest ecosystems, especially for understory communities (Neufeld & Young, 2014). Light reaches the forest floor after passing through the overstory canopy and, thus, can be directly influenced by canopy structure (e.g., basal area and stem density), as well as tree species composition (Knapp & Smith, 1982, 1989). This can especially be the case when considering hardwood versus conifer species in the forest canopy, as hardwoods typically have broad, flat leaves in contrast to the needles that are typical of conifers. In addition, solar radiation can have both direct and indirect effects on another component of forest ecosystems, and one that was also not measured in the summer 2022 study—soil texture. Soil texture has important implications for forest ecosystem structure and function, including nutrient supply and hydrology. Whereas most studies on relationships between solar radiation and soil processes have been done in stands of contrasting slope aspect (Beaudette & O'Green, 2009; Gilliam et al., 2014; Rech et al., 2001), our study allows examination of these relationships at the individual plot scale.

For this study, we performed identical sampling (light, soil texture) at a persistent canopy opening that has been used in past studies as a surrogate for conditions prior to the current chronic fire exclusion experienced by the natural areas (Gilliam, 2023; Gilliam et al., 2021). We also acknowledge that it is often difficult to separate the reciprocal effects between plant communities and the soil environment that they occupy. That is plants are often constrained in their distribution by requirements for certain soil characteristics, e.g., fertility and moisture. On the other hand, plants exert profound influences on their edaphic environment, e.g., rhizosphere acidification (Jenny, 1980). This ecological feedback was termed a *circulus vitiosus* by Jenny et al. (1969).

The purpose of this research was to extend sampling on the plots in pine- and hardwood-dominated stands used in Gilliam et al. (2023). Specifically, we addressed these questions: (1) how does light availability vary between stand types? (2) what characteristics of the stand affect light availability? (3) how does soil texture vary between stand types? (4) what is the relationship between solar radiation and the primary soil particles (i.e., sand, silt, clay) comprising texture?

Materials and methods

Study site

This study utilized the permanent plots established by Gilliam et al. (2023), a study that compared forest composition and soils between two distinct stand types: longleaf pine (hereafter, *pine*)-dominated and hardwood-dominated stands. There were 12 circular, 400-m^2 sample plots established within each stand type and located off of trails within the Campus Side Trails area of UWF, Pensacola, Florida (30° 33′ 8″ N, 87° 13′ 29″ W) (Figs. 1 and 2). Mineral soil of these stands is of the Troup series, with deep, excessively drained soils that formed in marine sediments of sandy and loamy textures (Hine, 2013). Troup soils are loamy, kaolinitic, thermic Grossarenic Kandiudults with a high seasonal water table below a depth of 2 m throughout the year (U.S.D.A., 2004). Previous work in forest stands reveals the uniformly acidic nature of soils, regardless of stand type, but with soils of hardwood stands of significantly higher fertility than those of pine stands (Gilliam et al., 2023).

Field sampling

Available light to the forest floor was measured as photon flux density (PFD) with a Phantom PHOTOBIO Advanced Quantum PAR meter. Days for measurements were limited to cloudless days which were infrequent during the study period of summer 2023, with a total of three days of measurements during this period: 25 May, 24 July, and 27 July. Previous PFD measurements from the persistent opening indicated a time window of ~three hours at maximum high solar radiation during which time net radiation does not change significantly. Furthermore, Way and Pearcy (2012) found that sunflecks were less dynamic at full sun overhead. Accordingly, all of our light measurements were taken during a <2-h period at full sun and cloudless days. For a given sampling date, PFD was taken at a 1.5-m height at each of nine random/repeated locations within each plot. Light availability for a given plot was calculated as the average of all nine measurements. Values did not vary significantly between sample dates and were significantly correlated among plots. Accordingly, for all data analyses involving PFD, individual plot means were calculated as means across all three sample dates. In addition, PFD was measured at four locations along three transects in the canopy opening, for a total of 12 measurements.

For soil texture analysis, mineral soil was taken to a 5-cm depth within each plot with a hand trowel. This depth was chosen to comport with previous sampling for soil microbial communities and fertility, as it is the depth within which fine root density is highest. Five samples were taken randomly from throughout the plot and combined in sterile polyethylene Whirl-Pak® bags to yield a single composite sample per plot. Sampling was repeated at the 12 locations used in the canopy opening to measure PFD.

Laboratory analyses

Following sampling, soil samples were oven-dried to a constant weight at 38 °C for quality-controlled, long-term storage (Gilliam et al., 2023). Primary soil particles (sand, silt, clay) were quantified via the hydrometer soil texture method (Bouyoucos, 1951).

Data analysis

Means for PFD and soil particles were compared among sample sites (two stand types and canopy opening) via analysis of variance and least significant difference tests, with significant differences

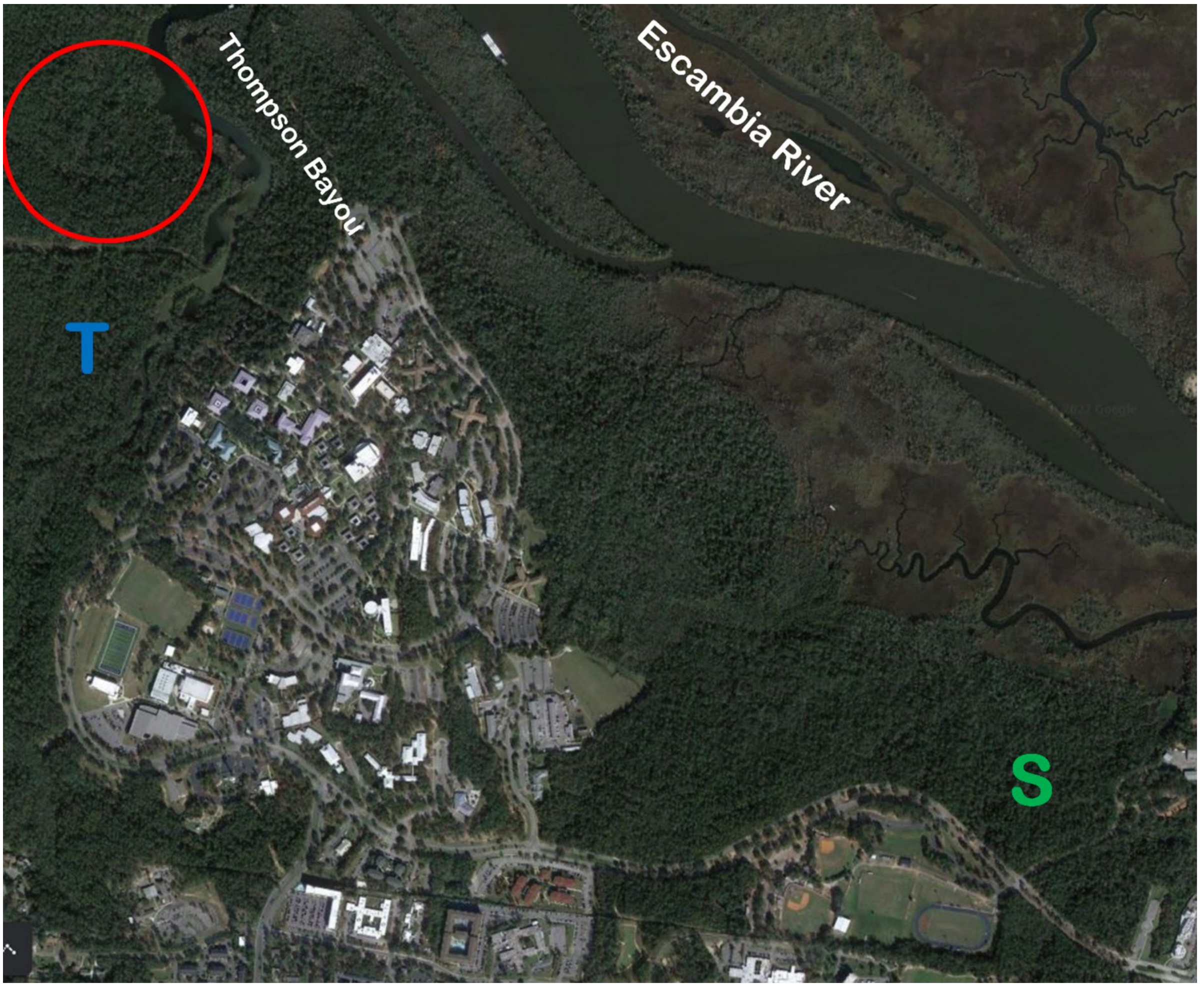

Fig. 1 Map of the campus of the University of West Florida. "T" and "S" denote sampling areas of previous studies (Gilliam et al., 2021; Gilliam et al., 2023), with the circle indicating the general area for sample plots of the present study. Figure from Gilliam et al. (2023); used by permission

accepted at $P<0.10$ (Zar, 2009). Potential relationships between solar radiation and primary soil particles were assessed in two ways. First, linear regression was run on individual plot values of PFD versus sand/silt/clay for forest sites alone. Second, linear regression was run on two-dimensional means for ln-transformed PFD and texture components for the two forest types and the canopy opening. All statistical analyses were performed using Statistix 9, Analytical Software, Tallahassee, FL.

We are aware that the field and statistical designs of our study comprise simple pseudoreplication, a situation that is common for field studies encompassing large areas, such that each stand type represents a sample size of one (Hurlbert, 1984); thus, our data should be interpreted with caution. Our contention, however, is that differences reported herein regarding soil variables are stand-driven, not based on pre-existing differences among sites, as these soils are of the same series (Troup series) and derived from identical parent material (Hine, 2013).

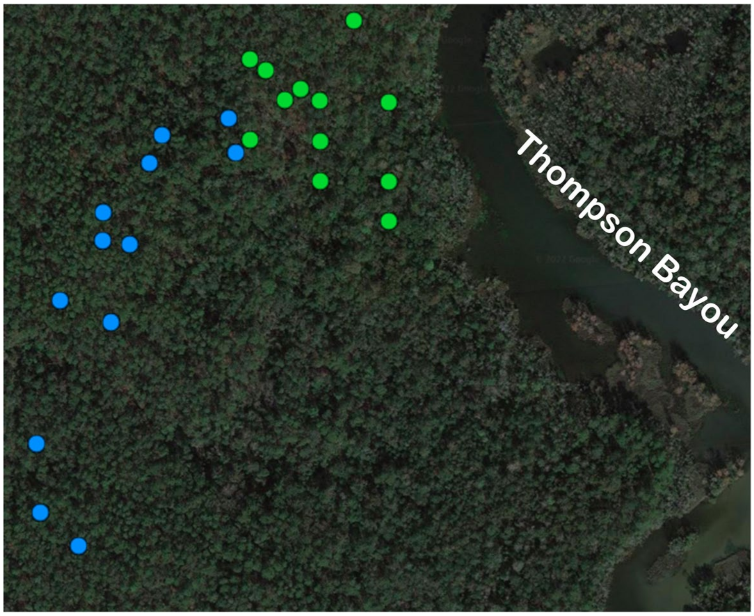

Fig. 2 Map depicting locations of 400-m^2 circular plots for sampling of hardwood-dominated (green) and longleaf pine-dominated (blue) stands. Figure from Gilliam et al. (2023); used by permission

Results

Light availability

Not only was mean PFD significantly higher in the pine-dominated stand, but it was also ~four times that of the hardwood-dominated stand (Table 1). Using mean PFD of the canopy opening as maximum light, the amount of light reaching the forest floor for pine- versus hardwood-dominated stands was 12.8 versus 3.5%, respectively, of full light.

Across all plots combined, PFD was significantly ($P<0.0001$), negatively related to stem density (Fig. 3A). By contrast, there was no significant relationship between PFD and basal area.

The potential effect of overall species composition on availability of light reaching the forest floor was assessed by correlating the results of canonical correspondence analysis (CCA) on the overstory communities of both stand types previously performed by Gilliam et al. (2023). Because axis scores reveal gradients of species composition, regressions of measured plot variables with CCA scores assess whether those variables vary with species composition. Linear regression revealed a significant ($P<0.001$) relationship between PFD and CCA axis 1 score (Fig. 3B), the axis that explains the most variation in species composition.

Soil texture

All soils analyzed in this study were >80% sand (Table 1). There were significant differences between forest stand types, with hardwood soils higher in sand and lower in silt than pine stands. Standard soil texture triangles revealed that hardwood soils would be

Table 1 Means (±1 SE) for photon flux density (PFD) and percent content of sand, silt, and clay for the two forested sites and the canopy opening. Texture was determined by soil texture triangle (Troeh & Thompson, 1993). Means with the same superscript are not significantly different at $P<0.10$

Site	PFD μmol m^{-2} s^{-1}	Sand %	Silt %	Clay %	Texture
Hardwood	53.5 ± 6.5^{c}	87.6 ± 0.8^{a}	4.9 ± 0.5^{c}	7.5±0.8	Sand
Pine	196.1 ± 30.9^{b}	84.5 ± 0.9^{b}	6.7 ± 0.7^{b}	8.8±0.9	Loamy sand
Opening	1533.3 ± 29.9^{a}	84.1 ± 1.3^{b}	9.6 ± 0.8^{a}	6.4±1.0	Loamy sand

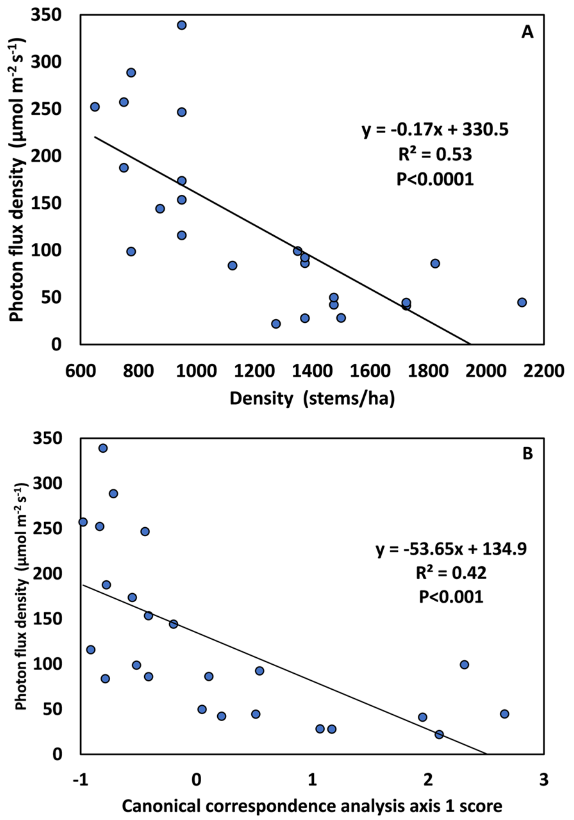

Fig. 3 **A**. Linear regression of PFD versus stem density for all forest sample plots. Equation for the line is $y = -0.17x + 330.5$, $r^2 = 0.53$, $P<0.0001$. **B**. Linear regression of PFD versus axis 1 scores from canonical correspondence analysis for all forest sample plots. Equation for the line is $y = -53.65x + 134.9$, $r^2 = 0.42$, $P<0.001$

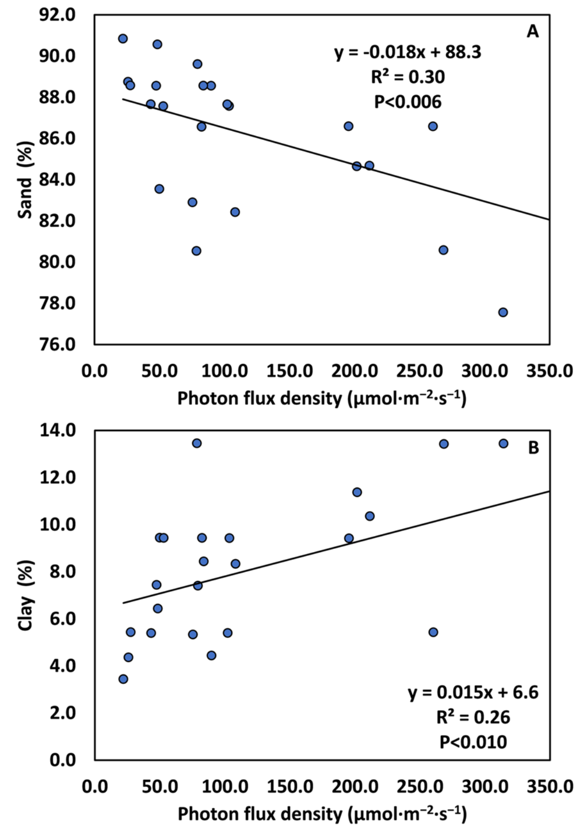

Fig. 4 **A**. Linear regression of sand fraction versus PFD for all forest sample plots. Equation for the line is $y = -0.018x + 88.3$, $r^2 = 0.30$, $P<0.006$. **B**. Linear regression of clay fraction versus PFD for all forest sample plots. Equation for the line is $y = 0.015x + 6.6$, $r^2 = 0.26$, $P<0.010$

classified as sand, whereas pine soils would be classified as loamy sand. Such contrasts were even sharper when considering soils from the canopy opening. These soils were significantly higher in silt fraction than soils from both forest sites, 50% higher than pine soils and essentially twice that of hardwood soils (Table 1).

Solar radiation/soil texture relationships

Our data for PFD allow us to test for solar radiation/soil texture relationships, using PFD as a surrogate for solar radiation. We did this on two contrasting scales—plot and site. At the plot scale, we regressed sand, silt, and clay content per plot on plot means of PFD for both forested sites combined. At the site scale, we regressed means per site of sand, silt, and clay versus site means of PFD.

Although PFD and silt varied significantly between stand types, the regression of silt versus PFD was not significant. Sand, however, was significantly negatively related to PFD (Fig. 4A), whereas clay was significantly positively related to PFD (Fig. 4B). Neither sand nor clay was significantly related to PFD. Silt, however, was significantly positively related to PFD (Fig. 5).

Discussion

The forest overstory appeared to exert a profound effect on light availability reaching the forest floor. The range of values for pine stands (44–334 µmol

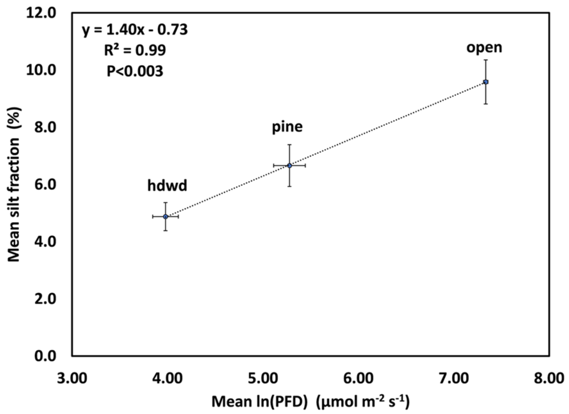

Fig. 5 Linear regression of mean silt fraction versus mean ln(PFD) for the three sample sites. Equation for the line is $y = 1.40x - 0.73$, $r^2 = 0.99$, $P<0.003$

m^{-2} s^{-1}) and hardwood stands (22–99 µmol m^{-2} s^{-1}) were in line with light data reported in other studies (Loik & Holl, 2001; Santiago & Dawson, 2014). On the other hand, these values were generally far below light saturation points for species comprising contrasting functional groups of forest herb communities. Neufeld and Young (2014) found these to be 592 µmol m^{-2} s^{-1} for spring ephemerals, 352 µmol m^{-2} s^{-1} for summer greens, 550 µmol m^{-2} s^{-1} for winter-greens, and 291 µmol m^{-2} s^{-1} for evergreens.

Several factors likely contributed to these pronounced differences in light regimes related to stand type. Longleaf pine was the dominant species in the pine stands, but was completely absent in the hardwood stands (Gilliam et al., 2023). Light availability to the forest floor is largely a function of leaf area index (LAI), and Fassnacht et al. (1997) found that LAI in hardwood stands can be up to five times that of conifer stands. Furthermore, because of the foliar arrangement of longleaf branches, wherein the long needles that give the species its common name are confined only to the ends of branches, LAI of longleaf pine stands is notably low (Sharma et al., 2012).

Patterns of light availability to the forest floor, however, were not simply a function of the presence/absence of longleaf pine. Across all plots combined, PFD was significantly ($P<0.0001$), negatively related to stem density (Fig. 3A). By contrast, there was no significant relationship between PFD and basal area, suggesting that it was the number of stems, but not their size, that was a significant driver in determining light availability to the forest floor.

On another level, overall species composition appeared to influence availability of light reaching the forest floor. Gilliam et al. (2023) performed canonical correspondence analysis (CCA) on the overstory communities of both stand types. Axis scores generated by CCA indicate gradients of species composition (Barbour et al., 1999; Šmilauer & Lepš, 2014). Accordingly, regressions of variables measured with individual plots versus CCA scores determine whether those variables vary with species composition. Typically, axis 1 explains most of the variation in species composition (Šmilauer & Lepš, 2014). Thus, it is notable that regression revealed a significant ($P<0.001$) linear relationship between PFD and CCA axis 1 score (Fig. 3B).

Given that soils of the Troup series (see *Study site*) are characteristically deep and excessively drained, having been formed from parent materials of sandy/loamy-textured marine sediments (Hine, 2013), it is unsurprising that all soils were predominantly sand (Table 1). On the other hand, there were significant differences between forest stand types, with hardwood soils higher in sand and lower in silt than pine stands (Table 1).

Soil texture is an important physical characteristic because it profoundly influences the hydrology and biogeochemistry of terrestrial ecosystems (Jenny, 1980), including the retention of water and nutrients. Soils in this study are high in sand content and thus low in retention of both. Because of the highly drained nature of these soils, however, slight variation in finer particles (i.e., silt and clay) can sensitively alter water and nutrient retention. Silver et al. (2000) found that soil texture greatly exerted significant effects on soil C, N, and P in tropical soils, with fertility generally decreasing with higher sand content. Soil texture also has been used to accurately predict soil water content and availability (Saxton & Rawls, 2006).

Among the several factors that can determine rates of weathering is solar radiation. Egli et al. (2006) found sharp differences in soils of north- versus south-facing aspects of an Alpine site in Italy that they ascribed to higher solar radiation on south slopes. Similarly, Gilliam et al. (2014) found significantly higher acidity, which typically increases with weathering, in soils of southwest- versus northeast-facing slopes in a hardwood forest of West Virginia.

Because light sampled in our study (400–700 nm; photosynthetically active radiation, expressed as PFD) is ~50% of total solar radiation (Davies-Colley & Payne, 2023), our PFD data can be used as a surrogate for solar radiation, which we did at both the plot and site scales. At the plot scale, there was variation among texture classes and relationships with PFD, wherein silt varied significantly, and silt did not. By contrast, sand was negatively related, and clay positively related, to PFD (Fig. 4A, B). Results at the site scale contrasted sharply with those at the plot scale, with neither sand nor clay significantly related to PFD, but silt being positively related to PFD (Fig. 5).

Using a completely different approach, Rech et al. (2001) came to the same conclusion regarding the relationship between solar radiation and weathering as they relate to soil texture. Utilizing cinder cones in east-central Arizona, they compared south- versus north-facing slopes with respect to a variety of soil characteristics, including particle size analysis. They determined that the higher solar radiation of the south-facing slopes enhanced rates of weathering, with higher silt and clay, and lower sand, than north-facing slopes. This conclusion was confirmed by the calculation of weathering ratios using Ca:Zr ratios (Rech et al., 2001).

In addition to the direct effects of solar radiation on soil weathering, however, light can influence soil indirectly via its direct effects on plants. The uptake of nutrients by plants is a naturally acidifying process (termed *rhizosphere acidification*) and one that is driven by PAR (Faget et al., 2013). Indeed, numerous factors interact to determine soil texture, including organisms (especially plants, microbes, and soil invertebrates), parent material, climate, and weathering (Jenny, 1980), with the weathering process resulting in the formation of silt and then clay. Thus, highly weathered soils tend to be clay dominated, and less-weathered soils tend to have high sand content (Troeh & Thompson, 1993), consistent with patterns found in our study.

Conclusions

Our results call to mind the words of Frank Egler, who famously stated: “Ecosystems are not only more complex than we think, but more complex than we can think.” (Egler, 1977). Forest ecosystems are indeed complex in their numerous interactions between abiotic and biotic processes. Data presented in this study demonstrate the influence of forest canopies on solar radiation reaching the forest floor. Although much of that was driven by dominant species, i.e., the long, linear needles of longleaf pine versus the broad, flat leaves of flowering magnolia (Addington et al., 2015), it was also found that both stand structure (i.e., density) and the overall species composition of the stand contributed to influencing the incidence of light reaching the forest floor.

Most studies examining the effects of solar radiation on soil weathering and texture do so by comparing north- versus south-facing slopes (Gilliam et al., 2014; Rech et al., 2001), with south slopes receiving higher solar radiation (Geiger et al., 2003; Tajchman and Lacey 1986; Tajchman et al. 1988). Our approach was at a finer scale, both among individual plots and across closely adjacent sites. Despite contrasting approaches, our findings were consistent with these other studies in that variation in solar radiation contributed to variation in soil texture, with sand content decreasing and clay content decreasing with solar radiation, suggesting solar radiation-mediated weathering of these coarse-textured soils. On the site scale, this was apparent for solar radiation and silt.

Finally, the indirect effects of light on soil texture via direct effects of forest vegetation also must be considered. Indeed, these likely represent synergistic interactions, further adding to the complexity of these ecosystems.

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Availability of data and materials All data from this study are available from FRANK S. GILLIAM upon request.

Author contribution Frank S. Gilliam conceived the research; Alayna L. Currey, Leo P. Young, Brenton C. Davis, and Caden M. Perry collected the field data; Frank S. Gilliam, Alayna L. Currey, Leo P. Young, Brenton C. Davis, and Caden M. Perry collected the laboratory data; Frank S. Gilliam analyzed the data; Frank S. Gilliam, Alayna L. Currey, Leo P. Young, Brenton C. Davis, and Caden M. Perry wrote the paper.

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Declarations

Ethical approval All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

Research involving human participants and/or animals Not applicable

Consent to participate Not applicable

Consent for publication All authors consent for this paper to be published.

Conflict of interest The authors have no conflict of interest to declare.

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