The Effects of Tree and Stand Traits on the Specific Leaf Area in Managed Scots Pine Forests of Different Ages

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Abstract: The purpose of this study was to understand the relationships between stand structure (tree size, volume, biomass, social position, stand density) and the variability of specific leaf area (SLA) at the stand level, which could improve forest management modeling. The study was carried out on 100 trees selected from 10 stands of Scots pine located in northwestern Poland. The stands had been established in a similar way and were similarly managed. Five mid-aged (51–60 years) and five mature (81–90 years) pure Scots pine stands were selected. To obtain the SLA index, we used the direct method, which involves scanning ca. 50 needles from each part of the tree crown. The average SLA was from 4.65 to 6.62 m²·kg⁻¹ and differed significantly according to the part of the crown measured (p < 0.0001) and the tree age (p < 0.0001). The smallest SLA was in the upper part of the crown and the largest in the lower part of the crown, which is in line with the known relation to the light exposure of needles. Mid-aged stands of Scots pine have higher SLA values than mature ones. Dominant trees in mid-aged stands have a lower SLA than more shaded intermediate ones, which is probably due to the different lighting conditions within the canopy. No clear relationship is observed between the stand density and the SLA.

Keywords: SLA; stand density; aboveground biomass; tree social position; foliage

1. Introduction

Specific leaf area (SLA) is a ratio of leaf area per unit leaf dry mass (in m²·kg⁻¹) that describes the distribution of leaf biomass in relation to leaf area [1]. SLA affects the efficiency of light capture and photosynthetic capacity [2]. This insight might contribute to regulating plant photosynthesis, growth, and productivity at scales from a single leaf to an ecosystem [2–4]. SLA is one of the most widely accepted key leaf characteristics [5], a key trait in plant growth [6,7], and an important indicator of plant strategies [8,9] that has been used widely in plant ecology, agronomy, and forestry [10]. Plants’ SLA is valuable information in making decisions on forest management not only from an environmental but also from an economic standpoint, and it is used as an easily measured parameter in several models of forest growth [11,12].

Specific leaf area is highly correlated with light level and decreases with increasing light intensity [13–15]. Therefore, SLA is related to a leaf’s position in the crown. Trees generally have a lower SLA at the top of the canopy, where direct solar radiation is received, and a higher SLA at the lower parts of the crown, where leaves may be shaded [16–18]. Plants grown under conditions of high light generally have thick leaves with a low SLA. This is an adaptation to maximize the radiant energy harvest. A given amount of foliage biomass should be spread over the entire crown of the tree. By having more biomass in a given area, the increase in the photosynthetic capacity of the high-light leaves comes at the cost of having less light capture per unit biomass at lower irradiances [15].

Stand structure has an influence on light conditions and therefore also affects the SLA [16,19]. Many studies have demonstrated that characteristics of the stand struc-
ture influence SLA, including stand age, stand density, canopy depth, and average tree size [13,20–22]. Stand structure can be regulated, to some extent, according to applied silviculture treatments, such as thinning operations of different intensity and frequency. Thinning reduces density, improves the resource availability for the remaining trees, and increases their growth [23,24]. Some long-term experiments have shown that the higher the intensity of thinning, the lower the stand growth, hence the most intense growth was noted in stands that had not been thinned [25–27]. By implementing thinning at various intensities and frequencies, it is possible to grow stands of different densities, which, in turn, affects forest growth, productivity [28–30], and profits [31]. Many management activities directly or indirectly affect the crown structure and foliage distribution. Understanding how these activities affect foliar biomass and traits guides treatments for specific purposes and aids the prediction of response to natural disturbances and the evaluation of different silvicultural systems [18].

Competition for light is especially important for light-demanding species such as Scots pine (Pinus sylvestris L.), which usually forms even-aged stands, according to the common silviculture approach. Scots pine has the largest geographic distribution of all pine species and is probably the most widely distributed coniferous species in the world [24]. Scots pine covers 24% of the forest area in Europe [32] and is, therefore, a tree species of substantial economic and environmental significance [23,30].

Understanding the relationships between stand structure and the variability of SLA at the stand level could improve forest management modeling [19]. However, process-based models remain uncertain due to the scarcity of such studies at the stand level [19,21]. There is little research regarding the ratio of the leaf area to its weight in the context of stand density. Shi, Yu, Wang, and Zhang [19] focused on Chinese pine SLA on the stand level and compared it with changing density and crown length. Tree age was reported to be negatively correlated with SLA [33–36], but the effects of tree age and tree size are difficult to disentangle [19]. However, studies that have attempted to separate these factors suggested that tree size rather than age is the main factor influencing the foliar structure [37–39].

The aim of this study was to determine the influence of tree size, volume, biomass, social position, and stand density on the SLA of mid-aged and mature Scots pine stands in the central part of the species’ geographical distribution. We hypothesize that: (1) the SLA of the upper part leaves is significantly lower in comparison to other parts of the canopy, especially for dominant trees, (2) SLA is correlated with the stand age and is decreasing with tree maturation, (3) the SLA of the dominant trees is significantly lower than the thinned ones, and (4) density affects positively tree SLA in a significant manner.

2. Materials and Methods

2.1. Study Area

The study was carried out on 100 trees selected from 10 stands (Figure 1) of Scots pine (Pinus sylvestris L.), located in the Drawno Forest District, northwestern Poland (E 15°50′–16°0′, N 53°10′–53°13′). This area has nutrient-poor habitats on podzolic soils, where the dominant tree species are Scots pine. It mostly forms uniform stands with a small admixture of other tree species. The altitude of this area is 100–120 m above sea level.

It was assumed that the stands had been established in a similar way (with the same initial spacing) and were similarly managed (with the same owner and manager). Since 1945, the stands have been managed by the State Forests National Forest Holding. Standard management practice in these stands has been to perform thinning once per decade, but selected stands had not been thinned in the past 5 years. The sample plots were located close to each other and in the same habitats to maintain similar tree growth conditions. The average annual rainfall in this area is 589 mm, the average temperature is 7 °C, and the growing season lasts 200–220 days [31]. Substantial differences in the density of the sampled stands could be the result of various biotic stressors (fungi, insects) and random events affecting forests during their growth.
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2.2. Selection of Sample Trees

Tree measurements and sample collections were performed from July to September 2012. Five mid-aged (51–60 years) and five mature (81–90 years) pure Scots pine stands were selected. The differentiating factor was the stand density, expressed as the number of trees in a given area, ranging from 703 to 1373 and 476 to 824 trees per hectare for mid-aged and mature stands, respectively (Table 1). All the stands were characterized by shared attributes: a single layer of crowns, single species, even-aged, flat terrain (without hills or pits), same soil type (Carbic Podzol), same habitat type (according to Polish classification), site index (dominant height at a standard age of 100 years [40]) from 24.1 to 29.1, similar nutrients content in needles [41], not damaged or deformed, and without any gaps or understory. In selected stands, rectangular sample plots were established (one plot per stand) of 0.3 hectares in mid-aged and 0.5 hectares in mature stands (a minimum number of 200 trees per plot was assumed).

In order to select sample trees, on each sample plot all the diameters at breast height (DBH) were measured, and for 20% of the trees, their height was also measured. Based on these data, for each separate plot, Näslund’s height curves were calculated to establish the height of each tree. The social position of the sample trees was determined based on two attributes, crown position, and crown form, according to the Schädelin classification [42]. All trees in each sample plot were grouped into 10 classes of an equal number of trees based on their DBH. The mean DBH of the class ranged from 10.7 to 31.1 cm in mid-aged stands and from 15.3 to 36.8 cm in mature stands. In each diameter class, one sample tree was selected at random. In this way, 10 trees were selected from each plot, representing the range of diameters present. In total, 100 sample trees were selected.
Table 1. Main characteristics of the sample plots established in mid-aged and mature Scots pine stands.

| Sample Plot | Age (Years) | Stand Density (Trees ha$^{-1}$) | Reineke’s Density Index | Basal Area (m$^2$ ha$^{-1}$) | Standing Stock (m$^3$ ha$^{-1}$) | Mean ± SE DBH (cm) | Mean ± SE Height (m) | Mean ± SE Stem Volume (m$^3$) | Mean ± SE Aboveground Biomass of Tree (kg) | Mean ± SE Needle Biomass of Tree (kg) | Canopy Depth (m) |
|-------------|-------------|---------------------------------|-------------------------|-----------------------------|-------------------------------|-------------------|-------------------|---------------------------|------------------------------------------|--------------------------------------|--------------|
| Mid-aged stands |
| 1 | 59 | 703 | 633 | 31.2 | 312 | 24.1 ± 1.3 | 22.1 ± 0.4 | 0.50 ± 0.06 | 257 ± 32 | 9.0 ± 1.5 | 6.7 |
| 2 | 57 | 890 | 659 | 31.0 | 310 | 20.9 ± 1.5 | 20.3 ± 0.6 | 0.37 ± 0.06 | 188 ± 33 | 6.1 ± 1.1 | 6.2 |
| 3 | 55 | 1120 | 739 | 33.8 | 325 | 20.1 ± 1.3 | 20.1 ± 0.2 | 0.31 ± 0.04 | 160 ± 21 | 5.8 ± 1.0 | 6.3 |
| 4 | 53 | 1323 | 705 | 30.6 | 265 | 16.7 ± 1.6 | 16.5 ± 1.9 | 0.24 ± 0.05 | 120 ± 25 | 3.7 ± 0.8 | 5.8 |
| 5 | 55 | 1373 | 855 | 38.5 | 364 | 18.1 ± 1.2 | 19.6 ± 0.6 | 0.24 ± 0.03 | 112 ± 14 | 3.5 ± 0.5 | 6.2 |
| Mature stands |
| 6 | 82 | 476 | 575 | 30.5 | 319 | 28.5 ± 1.6 | 22.9 ± 0.5 | 0.71 ± 0.08 | 357 ± 42 | 9.9 ± 1.2 | 7.5 |
| 7 | 82 | 590 | 615 | 31.5 | 301 | 25.2 ± 1.8 | 21.4 ± 0.4 | 0.51 ± 0.08 | 244 ± 34 | 6.4 ± 1.0 | 6.4 |
| 8 | 82 | 672 | 608 | 30.1 | 275 | 24.3 ± 1.5 | 20.3 ± 0.6 | 0.48 ± 0.06 | 235 ± 33 | 6.6 ± 1.1 | 6.4 |
| 9 | 82 | 756 | 715 | 35.7 | 334 | 24.3 ± 1.7 | 21.2 ± 0.5 | 0.48 ± 0.08 | 244 ± 39 | 8.3 ± 1.5 | 7.0 |
| 10 | 82 | 824 | 658 | 31.5 | 286 | 21.4 ± 1.3 | 19.6 ± 0.3 | 0.34 ± 0.05 | 167 ± 26 | 5.1 ± 1.0 | 6.2 |

SE—standard error; DBH—diameter at breast height. The equation for the Reineke’s Density Index after [43].

2.3. Needle Measurement

The tree crown of each sample tree was divided into 3 parts: upper, middle, and lower. We detached needles from branches in each part of the tree crown, mixed them, and then randomly picked 50 of the needles. To obtain the SLA index, we used the direct method of scanning 50 needles from each part of the tree crown. The fresh needles were scanned, and their dimensions were measured with the WinFOLIA Reg 2012a (Regent Instruments, Québec, QC, Canada). Aliquoted samples were dried in the Universal oven Model UFE 700 (Memmert GmbH + Co.KG, Schwabach, Germany) at 65 °C to a constant mass and weighed. Finally, each SLA was obtained using a scanned area of 50 needles divided by their dry mass.

2.4. Biomass Assessment

Sample trees were felled and divided into the following compartments (tree parts): stem (wood with bark), living branches, dead branches, foliage (needles), and cones. The fresh weight of each compartment was weighed directly in the field, and a representative sample of each tree part was collected. These samples were weighed fresh, dried to a constant mass at 65 °C, and weighed again. Using the sample’s proportion of dry and fresh mass, the dry mass of each part of each sample tree was estimated. The stand biomass was determined based on allometric equations developed on the basis of 100 sampled trees, which were presented in a previous paper [44].

2.5. Statistical Analysis

To assess the impact of the studied factors and the main associated variable, i.e., DBH, a two-way ANCOVA was conducted to compare the values of measured needle parameters of Scots pine sample trees. The analysis was based on the average needle data calculated for each part of tree crowns of model trees that belong to plots nested in the stand age category. One-way ANCOVA was used to compare the values of SLA of the three parts of the crown and of the whole crown for trees growing in stands of different densities, with DHB serving as covariant (cov). Moreover, a one-way ANCOVA was conducted to compare the values of SLA of the three parts of the crown and of the whole crown for trees of different social positions in the stands, with DHB served as covariant. Parametric Pearson’s correlation coefficients were calculated between SLA and selected stand parameters of the Scots pine sample trees. Tukey’s HSD test ($p = 0.05$) was employed to assess the significance of differences among treatments. Before all analyses, normal distribution was verified with the Shapiro–Wilk test. The data are given as means with the standard errors of the mean (±SE). Bold values indicate statistical significance ($p < 0.05$).
3. Results

The needle parameters for different parts of the crowns of Scots pine trees are shown in Table 2. In mid-aged stands, the average needle length was from 52.7 to 63.8 mm, the average width was from 1.14 to 1.35 mm, and the average area was from 61.1 to 87.6 mm². In mature stands, the average length was from 48.0 to 58.7 mm, the average width was from 1.14 to 1.35 mm, and the average area was from 55.6 to 80.4 mm². All these parameters differed significantly \((p < 0.0001)\) between parts of the crown. The largest needles (largest length, width, and area) were in the upper part of the crown, and the smallest were in the lower part of the crown. The length and area of needles also differed significantly \((p < 0.0001)\) between mid-aged and mature stands. The average weight of one needle was from 9.5 to 17.4 mg in mid-aged stands and from 10.1 to 17.6 mg in mature stands. The average SLA was from 5.23 to 6.62 \(\text{m}^2\cdot\text{kg}^{-1}\) in mid-aged stands and from 4.65 to 5.57 \(\text{m}^2\cdot\text{kg}^{-1}\) in mature stands (Figure 2). It differed significantly between parts of the crown \((p < 0.0001)\) and stand ages \((p < 0.0001)\). The smallest SLA was in the upper part of the crown and the largest in the lower part of the crown. The interaction stand age \(\times\) crown part was also significant.

| Stand Age (Development Stage) | Crown Part | N  | Needle Length (mm) | Needle Width (mm) | Needle Area (mm²) | Needle Weight (mg) |
|-----------------------------|------------|----|-------------------|-----------------|-----------------|------------------|
| Mid-aged                    | Upper      | 48 | 63.8 ± 0.3        | 1.35 ± 0.004    | 87.6 ± 0.6      | 17.4 ± 0.64      |
|                             | Middle     | 48 | 57.3 ± 0.2        | 1.23 ± 0.004    | 71.1 ± 0.4      | 12.4 ± 0.44      |
|                             | Lower      | 48 | 52.7 ± 0.2        | 1.14 ± 0.004    | 61.1 ± 0.4      | 9.5 ± 0.33       |
| Mature                      | Upper      | 49 | 58.7 ± 0.2        | 1.35 ± 0.005    | 80.4 ± 0.5      | 17.6 ± 0.57      |
|                             | Middle     | 50 | 53.0 ± 0.2        | 1.23 ± 0.004    | 66.3 ± 0.4      | 13.1 ± 0.42      |
|                             | Lower      | 50 | 48.0 ± 0.2        | 1.14 ± 0.004    | 55.6 ± 0.4      | 10.1 ± 0.33      |

**Table 2.** Means (±standard error) of the needle parameters of Scots pine sample trees with ANCOVA results. Statistically significant differences at \(p < 0.05\) are shown in bold.

| Stand Age (Development Stage) | Crown Part | N  | Needle Length (mm) | Needle Width (mm) | Needle Area (mm²) | Needle Weight (mg) |
|-------------------------------|------------|----|-------------------|-----------------|-----------------|------------------|
|                              |            |    |                   |                 |                 |                  |
| ANCOVA                        | Df         |    |                   |                 |                 |                  |
| Stand age                     | 1          | F  | 52.80             | 2.05            | 32.92           | 1.59             |
|                               |            | p  | \(<0.0001\)       | 0.1540          | \(<0.0001\)     | 0.2080           |
| Crown part                    | 2          | F  | 69.80             | 85.61           | 113.08          | 147.24           |
|                               |            | p  | \(<0.0001\)       | \(<0.0001\)     | \(<0.0001\)     | \(<0.0001\)      |
| Stand age \(\times\) crown part | 2         | F  | 0.13              | 0.08            | 0.20            | 0.1111           |
|                               |            | p  | 0.8755            | 0.9193          | 0.8164          | 0.8949           |
| DBH(cov)                      | 1          | F  | 13.12             | 12.51           | 21.00           | 31.27            |
|                               |            | p  | 0.0003            | 0.0005          | \(<0.0001\)     | \(<0.0001\)      |
| Df error                      |            |    |                   |                 |                 | 286              |

\(N\)—number of samples.
The mean SLA of the whole tree crown differed significantly between stands of different densities for mid-aged stands ($p < 0.0001$) and mature stands ($p = 0.0003$). It also differed for each part of the crown except the lower part of the crown in mature stands (Table 3).

**Figure 2.** Boxplots with specific leaf area (SLA) of needle different crown parts (lower, middle, and upper) of Scots pine sample trees growing in mid-aged and mature stands. Results of the ANCOVA are presented. Different letters indicate significant differences (Tukey’s honestly significant difference test) between stands of different ages and crown parts ($p = 0.05$). Statistically significant differences at $p < 0.05$ are shown in bold.
Table 3. The mean SLA of the three parts of the crown (upper, middle, and lower) and the mean SLA of the whole crown for trees growing in stands of different densities. Different letters indicate significant differences (Tukey’s honestly significant difference test) between stands of different densities ($p = 0.05$).

| Plot Number | Stand Density (Trees ha$^{-1}$) | Mean ($\pm$SE) SLA of Different Part of Crown (m$^2$ kg$^{-1}$) | Mean ($\pm$SE) SLA of Whole Crown (m$^2$ kg$^{-1}$) |
|-------------|----------------------------------|---------------------------------------------------------------|--------------------------------------------------|
|             |                                  | Upper | Middle | Lower               |                                                      |
| Mid-aged stands |                                  | 5.50 $\pm$ 0.15 b | 5.54 $\pm$ 0.37 b | 6.44 $\pm$ 0.47 b | 5.72 $\pm$ 0.23 b |
| 1           | 703                              | 5.25 $\pm$ 0.29 b | 5.96 $\pm$ 0.18 b | 6.47 $\pm$ 0.18 b | 5.80 $\pm$ 0.15 b |
| 2           | 890                              | 5.10 $\pm$ 0.14 b | 5.59 $\pm$ 0.16 b | 6.04 $\pm$ 0.16 b | 5.53 $\pm$ 0.12 b |
| 3           | 1120                             | 6.22 $\pm$ 0.50 a | 7.17 $\pm$ 0.29 a | 7.77 $\pm$ 0.36 a | 7.11 $\pm$ 0.25 a |
| 4           | 1323                             | 5.56 $\pm$ 0.37 b | 6.24 $\pm$ 0.25 b | 6.98 $\pm$ 0.32 b | 6.49 $\pm$ 0.28 b |
| 5           | 1373                             | 6.30 $\pm$ 0.29 b | 7.26 $\pm$ 0.31 b | 7.88 $\pm$ 0.35 b | 7.32 $\pm$ 0.30 b |

ANOVA Df

| Stand density | 4 4 4 4 4 | F | 5.55 | 5.92 | 2.89 | 9.78 |
|---------------|-----------|---|------|------|------|------|
| p             | 0.0010 0.0007 0.0331 <0.0001 |
| DBH(cov)      | 1 1 1 1 1 | F | 3.84 | 7.49 | 4.17 | 12.28 |
| p             | 0.0563 0.1461 0.0472 0.0197 |
| Df error      | 44 |

Mature stands

| Stand density | 4 4 4 4 4 | F | 8.33 | 8.25 | 2.24 | 6.47 |
|---------------|-----------|---|------|------|------|------|
| p             | <0.0001 <0.0001 0.0794 0.0003 |
| DBH(cov)      | 1 1 1 1 1 | F | 12.80 | 7.38 | 11.43 | 13.26 |
| p             | 0.0009 0.0094 0.0015 0.0007 |
| Df error      | 44 |

Statistically significant correlations at $p < 0.05$ are shown in bold.

The mean SLA of the whole crown differed significantly between stands of different tree social positions for mid-aged stands ($p = 0.0142$) but did not differ for mature stands (Table 4).

In mid-aged stands, the SLA of the whole crown was correlated with the DBH, tree height, stem volume, needle biomass of the tree, and aboveground biomass of the tree. The SLA of some parts of the crown was also correlated with the same tree parameters (Table 5). In mature stands, the SLA of the whole crown was not correlated with any of these tree parameters. Only the SLA of the lower part of the crown was correlated with DBH, stem volume, needle biomass of the tree, and aboveground biomass of the tree. All significant correlations were negative (Table 5).
Table 4. The mean SLA of the three parts of the crown (upper, middle, and lower) and the mean SLA of the whole crown for trees of different social positions. Different letters indicate significant differences (Tukey’s honestly significant difference test) between stands of different social positions ($p = 0.05$).

| Social Position of a Tree | Mean (±SE) SLA of Different Part of Crown (m$^2$ kg$^{-1}$) | Mean (±SE) SLA of Whole Crown (m$^2$ kg$^{-1}$) |
|---------------------------|----------------------------------------------------------|-------------------------------------------------|
|                           | Upper          | Middle         | Lower          |                                                               |
| Mid-aged stands           |                |                |                |                                                               |
| Dominant                  | 5.10 ± 0.09 b  | 5.89 ± 0.16 a  | 6.63 ± 0.16 a  | 5.92 ± 0.14 ab                                                 |
| Codominant                | 5.03 ± 0.28 b  | 5.63 ± 0.13    | 6.17 ± 0.27 b  | 5.67 ± 0.26 b                                                 |
| Intermediate              | 6.90 ± 0.74 a  | 6.88 ± 0.58    | 7.67 ± 0.93 a  | 7.15 ± 0.48 a                                                 |
| ANCOVA Df                 | Social position 2 F                      | 8.99                | 3.15                | 4.10          | 4.67                |
|                           | $p$                     | 0.0005            | 0.0522             | 0.0231       | 0.0142             |
| DBH(cov)                  | 1 F                     | 2.21                | 4.34                | 5.26          | 5.85                |
|                           | $p$                     | 0.1438            | 0.0428             | 0.0264       | 0.0196             |
| Df error                  | 46                       |                    |                    |              |                    |
| Mature stands             | Dominant                  | 4.51 ± 0.07        | 5.00 ± 0.08        | 5.47 ± 0.08  | 4.99 ± 0.06        |
|                           | Codominant                | 4.86 ± 0.13        | 5.40 ± 0.15        | 5.91 ± 0.12  | 5.37 ± 0.12        |
|                           | Intermediate              | 4.86 ± 0.23        | 5.23 ± 0.21        | 5.45 ± 0.19  | 5.18 ± 0.19        |
| ANCOVA Df                 | Social position 2 F                      | 3.07                | 1.95                | 2.51          | 2.06                |
|                           | $p$                     | 0.0563            | 0.1539             | 0.0929       | 0.1388             |
| DBH(cov)                  | 1 F                     | 0.08                | 0.03                | 3.05          | 0.43                |
|                           | $p$                     | 0.7777            | 0.8584             | 0.0678       | 0.5139             |
| Df error                  | 46                       |                    |                    |              |                    |

Statistically significant correlations at $p < 0.05$ are shown in bold.

Table 5. Pearson’s correlation coefficients for the SLA and selected stand parameters of the Scots pine sample trees.

| SLA          | DBH     | Tree Height | Stem Volume | Needle Biomass of Tree | Aboveground Biomass of Tree |
|--------------|---------|-------------|-------------|------------------------|-----------------------------|
| Crown part   | Upper   | −0.342      | −0.425      | −0.329                 | −0.325                      |
|              | Middle  | −0.294      | −0.243      | −0.297                 | −0.284                      |
|              | Lower   | −0.270      | −0.260      | −0.323                 | −0.289                      |
| Whole crown  | −0.348  | −0.340      | −0.370      | −0.358                 | −0.369                      |
|              |         |             |             |                        |                             |
| Mature stands| Upper   | −0.193      | 0.029       | −0.136                 | −0.144                      |
|              | Middle  | −0.191      | −0.029      | −0.164                 | −0.139                      |
|              | Lower   | −0.348      | −0.241      | −0.309                 | −0.292                      |
| Whole crown  | −0.269  | −0.093      | −0.223      | −0.212                 | −0.207                      |

Statistically significant correlations at $p < 0.05$ are shown in bold.

4. Discussion

The mean specific leaf area of mature stands was from 4.86 to 5.40 m$^2$·kg$^{-1}$ (Table 3) and was within the range (2.87–5.50 m$^2$·kg$^{-1}$) reported for 20 Scots pine stands located in different places in Europe [45]. On the other hand, the mean SLA of mid-aged stands was from 5.53 to 7.11 m$^2$·kg$^{-1}$ (Table 3) and was above the range reported by Mencuccini and Bonosi [45]. Similarly, a high SLA of 6.16 m$^2$·kg$^{-1}$ was found by Goude et al. [46] for young and mid-aged Scots pine stands in Sweden.
In both age groups of our stands, the SLA differed significantly between different parts of the crown. The smallest SLA was in the upper part of the crown and the largest was in the lower part of the crown, which was expected due to its known relation to light exposure [14–16]. Plants generally have a lower SLA in parts of the canopy where direct solar radiation is received and a higher SLA where leaves may be shaded. Many investigations have found that the SLA increases from the top of the tree to the base of the crown as leaves become thinner, and thus the ratio of area to mass increases [13,21,47–49].

We found significant differences between SLA in stands of different ages. Mid-aged stands had a higher SLA than mature ones. For many deciduous and coniferous tree species, it has been found that SLA is negatively correlated with tree age [18,20,34,50]. However, our results are in contrast to previous studies of Scots pine [38,51]. Van Hees and Bartelink [51] analyzed the foliage area characteristics of 12 trees selected out of 4 stands of different ages (9–38 years) in the Netherlands. Mencuccini et al. [38] sampled trees spread across the continuum of ages (up to 269 years) in Scotland. Both of them found that the age of trees had no effect on the SLA.

We also found that trees of different social positions differ significantly in SLA in mid-aged stands, which is probably due to the different lighting conditions within the canopy. The dominant trees had a lower SLA than the more shaded intermediate ones (Table 4). The effect of the tree’s social position on the SLA could be more noticeable if suppressed trees were included. These trees were not included in the analysis due to their very small number in the even-aged managed pine stands we investigated. A stronger effect of tree social position on the SLA was shown by the needles of the upper part of the crown. These differences were also more significant in mid-aged stands than in mature stands (Table 4).

Kellomäki and Oker-Blom [13] observed for Scots pine that in suppressed trees, the SLAs were as high as 3–5 times those in dominating trees. For other tree species, lower values of SLA in dominant and codominant trees than in intermediate and suppressed individuals were also observed [52,53].

The stand density may have had an impact on the SLA, but our study did not strongly confirm this. Both younger and older stands of different densities had significantly different SLAs. However, no clear relationship was observed in mature stands, showing that SLA increases with stand density, but the mid-aged stands of highest density had the highest SLA (Table 3). We did not find such studies for Scots pine, but Shi, Yu, Wang, and Zhang [19] also found for Chinese pine that the stand density and SLA were positively and significantly correlated.

Our results to some extent fill the knowledge gap on the effect of tree and stand traits on SLA for Scots pine. Regulation of stand density by thinning intensity can affect some stand traits, including SLA and thus the photosynthetic capacity and forest productivity [2,4]. Stand density is also related to tree size [54,55], which can influence the value of forest products [31]. In addition, SLA could be related to the structural defense mechanism against folivorous insects. A high value of SLA indicating a low toughness of leaves differentiate heavily damaged shade leaves from the less damaged sun leaves [56]. Defoliation and insect performance are strongly associated with leaf toughness [57,58]. Furthermore, the indirect effect may relate to litter decay rate (nutrients cycling). Leaves with higher SLA have a faster rate of decomposition because they are more accessible to the microorganisms that decay them [59,60]. However, further studies are needed to complete our findings and allow for better management of stand density.

The SLA of the mid-aged stands was negatively correlated with DBH, tree height, stem volume needle biomass, and aboveground biomass of the tree. For mature stands, we found such a correlation only for the SLA of the lower part of the crown. All these attributes are related to the size of the tree. It is therefore possible that the correlations we found actually relate to the tree height because the position of the crown in the canopy is often associated with differences in light exposure. Some other studies have also shown that the SLA is correlated with tree size [48,61–63]. However, Nagel and O’Hara [16] were unable to detect the effect of tree size on SLA in even-aged pine stands but detected it in
multi-aged stands. The effect of tree size on the SLA may be due to the fact that larger trees tended to have heavier, thicker needles [21].

Many different environmental variables (radiation, temperature, concentrations of CO₂, nutrient availability, water limitation) can also affect SLA [10,64]. We did not study these factors because our sample stands were located on the same soils and under the same climatic conditions. However, our results for this case study may be an excellent resource for future analyses involving a broad spectrum of environmental factors.

5. Conclusions

Based on our results, we can draw the following conclusions:

1. The achieved SLA values of Scots pine needles growing in Poland are within the range of previously noted values for trees of this species of similar age classes.
2. The smallest SLA values are found in the upper part of the crown, which is in line with SLA’s known relation to the light exposure of needles.
3. Mid-aged stands of Scots pine have higher SLA values than mature ones.
4. Dominant trees in mid-aged stands have a lower SLA than more shaded intermediate ones, which is probably due to the different lighting conditions within the canopy.
5. Contrary to expectations, no clear relationship was observed between the stand density and the SLA.
6. Some parameters of mid-aged stands, like DBH, height, steam volume, aboveground, and needle biomass were negatively correlated with SLA. This has not been observed in mature stands.

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