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Irregularity at the edge: Developmental dynamics of leaf margins in six temperate tree species

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Abstract: Leaf teeth are marginal structures that play an important role in early-season gas exchange and have significance for both functional ecology and paleobotanical reconstructions. This study examined the dynamics of leaf margin development during early leaf expansion in six temperate tree species (*Acer platanoides, Betula pendula, Carpinus betulus, Corylus avellana, Salix caprea,* and *Sorbus aucuparia*). Leaf sampling was conducted in a temperate mixed forest near Zielona Góra, Poland. Leaves were collected from sun-exposed and shaded conditions over a 50-day spring period and analyzed using image-based software. Primary traits such as leaf area, perimeter, width, length, and the height and width of each tooth were recorded. From these, five derived variables were calculated: 1) leaf blade irregularity index (perimeter/area), 2) relative irregularity index (based on consecutive measurements), 3) compactness index (perimeter^2/area), 4) shape index (width/length), and 5) simplified tooth area (tooth height × tooth width / 2).

The results demonstrated a rapid decline in leaf margin irregularity during the first 20–30 days of development, after which it stabilized. This pattern was consistent across all species, regardless of their ecological preferences, indicating a universal developmental trend in analyzed woody plants. Among the tested variables, the leaf blade irregularity index (perimeter-to-area ratio) correlated most strongly with actual tooth area and was selected for further analysis. While shade leaves generally exhibited slightly higher irregularity values, no significant differences were detected after adjusting for leaf size. The findings support the hypothesis that margin serration enhances early photosynthetic efficiency, with its relative contribution diminishing as leaves expand. This study contributes to our understanding of species-independent developmental plasticity in leaf morphology and underscores the importance of standardized sampling in ecological and paleobotanical research.

Keywords: leaf teeth; irregularity index; sun – shade leaves; morphometric analysis; temperate trees

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Introduction

Leaves play a crucial role in the growth, development, and survival of plants. They capture light, transport water along with mineral nutrients and assimilates, and are responsible for gas exchange, heat dissipation, and defense against herbivores and pathogens (Nicotra et al., 2011). These multifunctional roles, combined with varying environmental conditions, contribute to the remarkable diversity in leaf shape and structure (Nicotra et al., 2011; Chitwood et al., 2016; McKee et al., 2019). Among plant groups, angiosperms have evolved the most diverse leaf forms. Their morphology, growth, and development are closely tied not only to the species' evolutionary history but also to developmental stages and environmental influences (Nicotra et al., 2011; Yang et al., 2015).

The structures forming the serrated edges of the leaf blade are known as leaf teeth. In this study, teeth are defined as vascularized extensions of the leaf margin incised less than one-quarter of the distance to the midvein, following the definition by Ellis et al. (2009). Understanding the dynamics and environmental determinants of leaf teeth is essential, particularly in the context of paleobotany. A well-established positive correlation exists between the proportion of entire-margined woody dicotyledonous species and higher mean annual temperatures-an observation first noted in the early 20th century (Bailey & Sinnott, 1915, 1916). This correlation forms the basis of leaf physiognomic methods used to infer past climatic conditions from fossil plant assemblages (Wolfe, 1979; Greenwood, 2005; Chen et al., 2014, 2025; Xiao et al., 2023). However, in cooler regions (mean annual temperature around 5 °C or lower), this relationship often breaks down (Peppe et al., 2011), and in the case of European woody flora, an even opposite pattern has been observed (Iszkuło et al., 2024). This cannot be fully explained by the greater abundance of evergreen, snow-covered shrubs in such climates, which typically possess entire leaf margins (Peppe et al., 2011).

It has been observed that developing leaves have disproportionately large teeth compared to mature leaves (Baker-Brosh & Peet, 1997; Feild et al., 2005). This may result from hormonal and genetic regulation, as well as the earlier cessation of activity in the marginal meristem (Kawamura et al., 2010; Bian et al., 2018; Wang et al., 2021). The marginal meristem actively shapes the leaf edge during early development but ceases its function once the final leaf shape is established, while other meristems continue contributing to further expansion (Tsukaya, 2017, 2021). Consequently, leaf teeth in species from genera such as *Ulmus*, *Carya*, and *Acer* are thicker and bright green, indicating high photosynthetic activity, while the remaining parts of the blade are thinner and less pigmented. In juvenile leaves of *Ulmus* species, teeth exhibit well-developed spongy mesophyll, further suggesting more intense gas exchange compared to the central blade area (Baker-Brosh & Peet, 1997; Nicotra et al., 2011). This pattern is supported by studies on *Quercus rubra* (Zwieniecki et al., 2004) and *Liquidambar styraciflua* (Baker-Brosh & Peet, 1997). However, apart from these species, little is known about how leaf blade irregularity changes during early spring development in other taxa. Modern digital methods for analyzing leaf morphology using specialized software now allow researchers to investigate such patterns in detail.

A physiological explanation for the relatively large area occupied by teeth in developing leaves may lie in the functional link between serration and elevated early-season gas exchange (Baker-Brosh & Peet, 1997; Wright et al., 2004). The hypothesis of enhanced gas exchange at the leaf margin suggests that serration facilitates early photosynthesis, accelerating assimilate export and delivery in young leaves – particularly when the canopy is still open and light is abundant in the lower strata, combined with high spring water availability (Zohner et al., 2019). Given that margin irregularity decreases as leaves mature, light availability may influence the rate of this change. It has therefore been proposed that shaded leaves exhibit more pronounced margin irregularity. Another proposed function of teeth is the refraction and dispersion of light, which may enhance light penetration to the lower parts of the canopy (Niklas, 1989; Nicotra et al., 2011).

Based on these considerations, the following hypotheses were formulated: 1) the decrease in leaf margin irregularity relative to the rest of the leaf blade with age is a universal phenomenon in woody plant species; 2) shade-type leaves exhibit greater irregularity compared to sun-type leaves; and 3) the reduction in tooth area relative to the rest of the leaf blade occurs more slowly in shade-type leaves than in sun-type leaves.

Therefore, the aim of this study was to investigate the developmental dynamics of leaf margin serration during early leaf expansion in temperate tree species, with particular emphasis on the relative influence of light conditions and developmental time. By quantifying changes in leaf blade irregularity over time in both sun- and shade-exposed leaves, we sought to determine whether margin serration follows a consistent ontogenetic pattern across species and to what extent environmental light conditions modulate this process.

Materials and Methods

The study included six tree species: *Acer platanoides*, *Carpinus betulus*, *Betula pendula*, *Corylus avellana*, *Salix caprea*, and *Sorbus aucuparia*. All species, except for *S. aucuparia*, which produces compound leaves, have simple, undivided leaf blades with serrated margins. For *S. aucuparia*, individual leaflets were treated as separate, complete leaves for the purposes of analysis. These species were selected due to their differing habitat preferences (especially light requirements), variation in margin type (untoothed vs. toothed), and availability within the study area under comparable environmental and light conditions.

Leaf sampling was conducted in a temperate mixed forest adjacent to Campus A of the University of Zielona Góra, Poland (51°94'13"N, 15°53'26"E) during April and May 2017. A total of 1,800 leaves were collected over six sampling periods at ten-day intervals, beginning on 7 April 2017 (sampling days: 0, 10, 20, 30, 40, and 50). For each species, five individuals were selected, and ten leaves were sampled from each: five from sun-exposed shoots and five from shaded shoots. Due to later leaf development in *S. aucuparia*, only five sampling dates were used for this species.

Leaves were dried, pressed, and scanned using an Epson Perfection V700 Photo scanner. Image analysis was carried out using WinFolia software (Regent Instruments Inc.). Prior to analysis, damaged margins were manually corrected, and shadows were removed. The following primary traits were recorded: leaf area, perimeter, width, length, and height and width of each tooth. From these measurements, several derived variables were calculated: 1) leaf blade irregularity index (perimeter/area); 2) relative irregularity index (The relative change in the irregularity index was calculated for each tree within the same species and light condition. It was determined by measuring the difference between the irregularity index values from two consecutive sampling days and dividing it by the earlier value. This calculation was performed separately for each unique combination of species, light condition, and tree number. As this method relies on comparing two consecutive measurements, the first recorded value for each tree does not yield a relative change result); 3) compactness index ($\text{perimeter}^2/\text{area}$); 4) shape index (width/length); 5) simplified tooth area (tooth height × tooth width / 2).

To evaluate the relationship between these calculated variables and the actual area occupied by teeth, manual separation of teeth was performed on 150 leaf scans from the final sampling date (day 50). This step was carried out for four species (*C. avellana*, *C. betulus*, *B. pendula*, and *S. aucuparia*), using five sun-exposed leaves from five individual trees of each species. The separated teeth and remaining blade areas were analyzed in WinFolia to determine the true tooth area.

Correlations were then calculated between the actual tooth area and the following variables: leaf blade irregularity index, shape index, and simplified tooth area. The Shapiro–Wilk test was used to assess the normality of trait distributions. As most traits (leaf area, irregularity index, compactness index, and shape index) did not follow a normal distribution, the non-parametric Wilcoxon signed-rank test was employed to compare sun-exposed and shaded leaves.

All statistical analyses were conducted using JMP Pro 18.0.2 (SAS Institute Inc.).

Results

Relationship between actual and simplified tooth area, leaf blade irregularity index, and compactness index

A significant positive correlation was observed between the actual and simplified tooth area in the four analyzed species (*C. avellana*, *B. pendula*, *C. betulus*, and *S. aucuparia*) (Fig. 1). The highest coefficient of determination was recorded in *S. aucuparia* ($R^2 = 0.81$, $P < 0.0001$), and the lowest in *C. betulus* ($R^2 = 0.51$, $P = 0.0006$). The relationship between actual and simplified tooth area is best described by linear functions with the following formulas: $y = 0.3349x + 0.0249$ for *C. avellana*, $y = 0.3071x + 0.0240$ for *B. pendula*, $y = 0.2445x + 0.1966$ for *C. betulus*, and $y = 0.3866x + 0.0498$ for *S. aucuparia* (Fig. 1).

The leaf blade irregularity index (perimeter-to-area ratio) showed a significant negative correlation with the actual tooth area (Fig. 2). The strongest correlation was found in *C. betulus* ($R^2 = 0.80$, $P < 0.0001$), and the weakest in *B. pendula* ($R^2 = 0.61$, $P < 0.0001$). This relationship is best described by linear functions with the formulas: $y = -0.3632x + 1.7149$ for *C. avellana*, $y = -1.8924x + 2.9203$ for *B. pendula*, $y = -0.9295x + 2.2678$ for *C. betulus*, and $y = -2.5698x + 5.4223$ for *S. aucuparia* (Fig. 2).

No statistically significant relationships were found between the leaf blade compactness index and the actual tooth area in any of the studied species (Fig. 3).

Changes in morphological features related to leaf blade irregularity during leaf development

A significant increase in leaf blade area was observed over the study period (Fig. 4, Appendix 1).

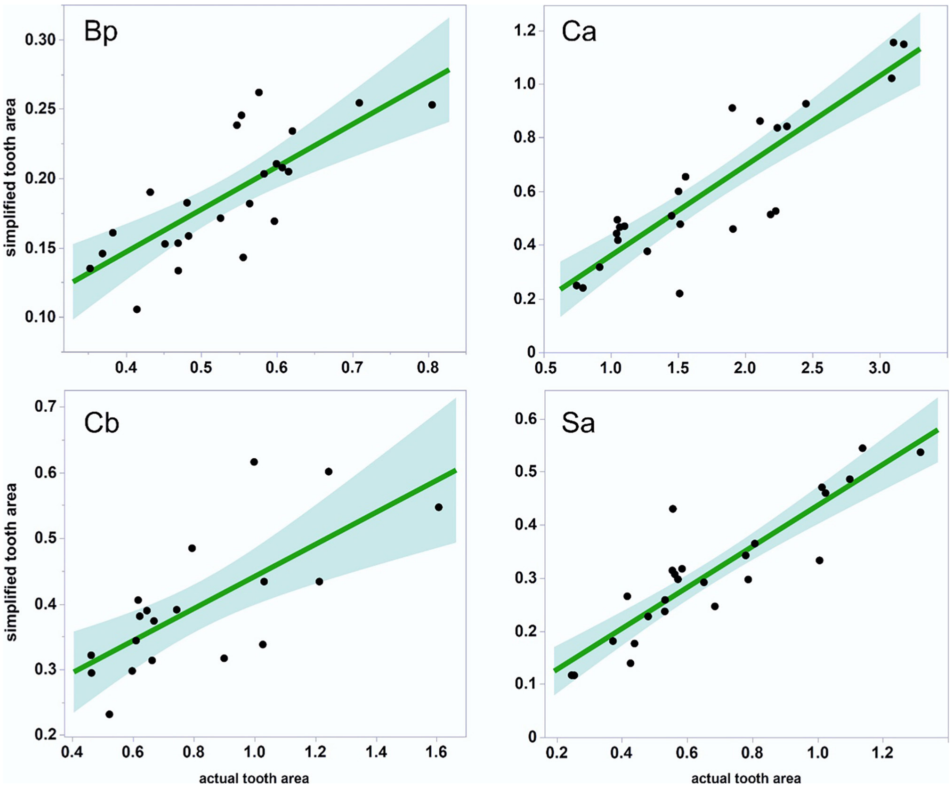

Fig. 1. Relationship between the actual and simplified tooth area in *Betula pendula* (Bp), $R^2 = 0.56$, $P < 0.0001$; *Corylus avellana* (Ca), $R^2 = 0.77$, $P < 0.0001$; *Carpinus betulus* (Cb), $R^2 = 0.51$, $P = 0.0006$; *Sorbus aucuparia* (Sa), $R^2 = 0.81$, $P < 0.0001$; linear fit with 95% CI

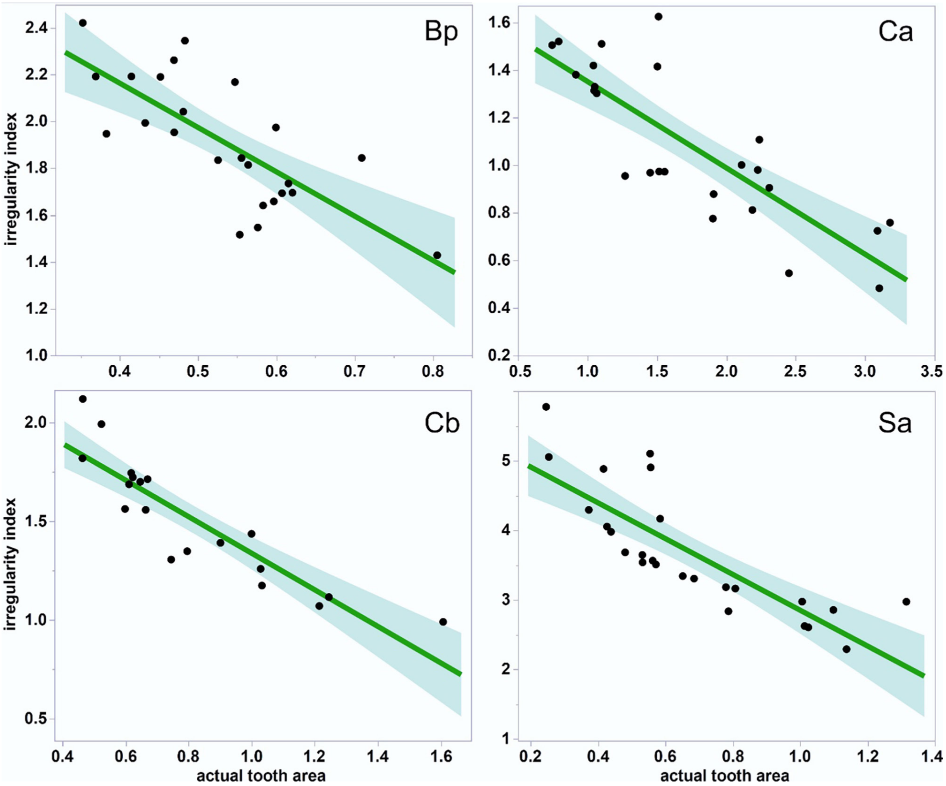

Fig. 2. Relationship between the leaf blade irregularity index and the actual tooth area in *Betula pendula* (Bp), $R^2 = 0.56$, $P < 0.0001$; *Corylus avellana* (Ca), $R^2 = 0.67$, $P < 0.0001$; *Carpinus betulus* (Cb), $R^2 = 0.80$, $P < 0.0001$; *Sorbus aucuparia* (Sa), $R^2 = 0.67$, $P < 0.0001$; linear fit with 95% CI

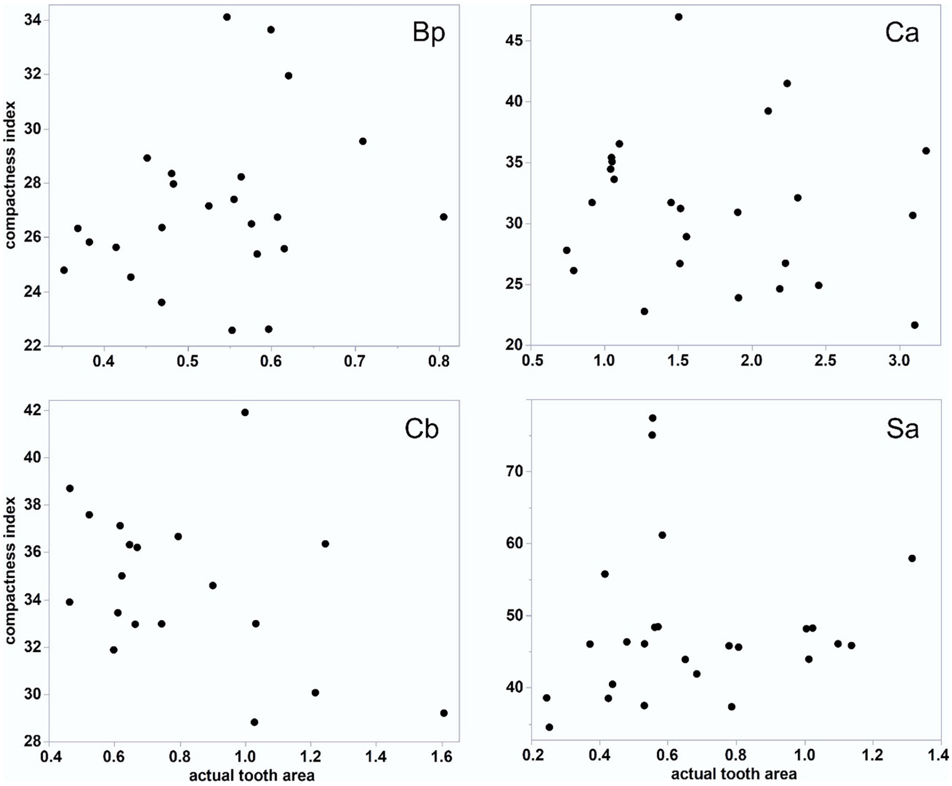

Fig. 3. Relationship between the leaf blade compactness index and the actual tooth area in *Betula pendula* (Bp), $R^2 = 0.06$, $P = 0.231$; *Corylus avellana* (Ca), $R^2 = 0.01$, $P = 0.573$; *Carpinus betulus* (Cb), $R^2 = 0.17$, $P = 0.078$; *Sorbus aucuparia* (Sa), $R^2 = 0.01$, $P = 0.593$

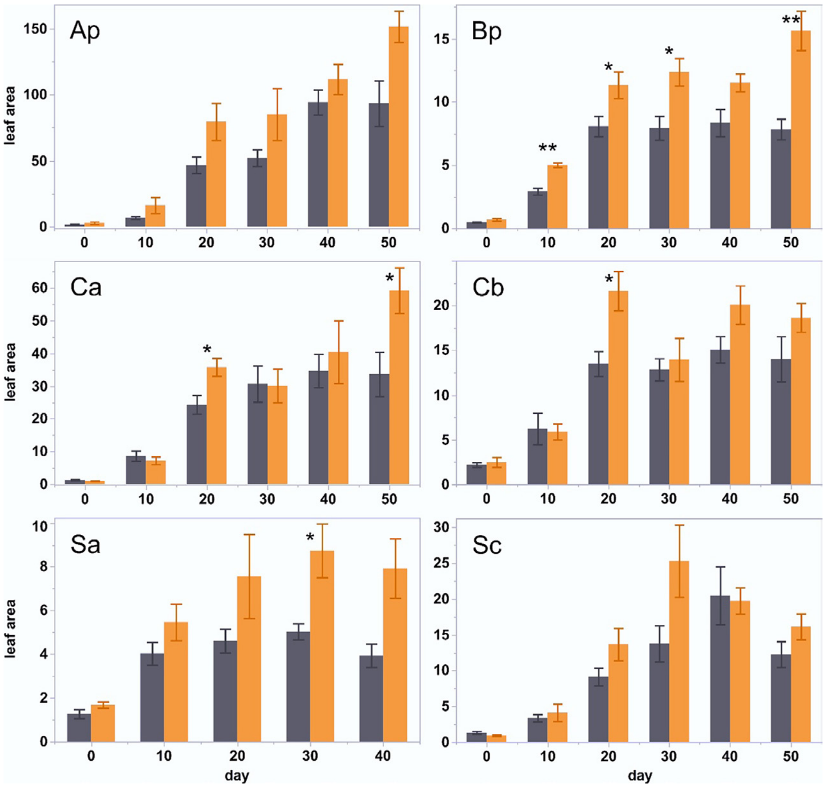

Fig. 4. Average leaf blade area (± standard error) of shade (grey) and sun (orange) leaves in *Acer platanoides* (Ap), *Betula pendula* (Bp), *Corylus avellana* (Ca), *Carpinus betulus* (Cb), *Sorbus aucuparia* (Sa), and *Salix caprea* (Sa) during development. Wilcoxon test for shade and sun leaves: * $P < 0.05$; ** $P < 0.01$)

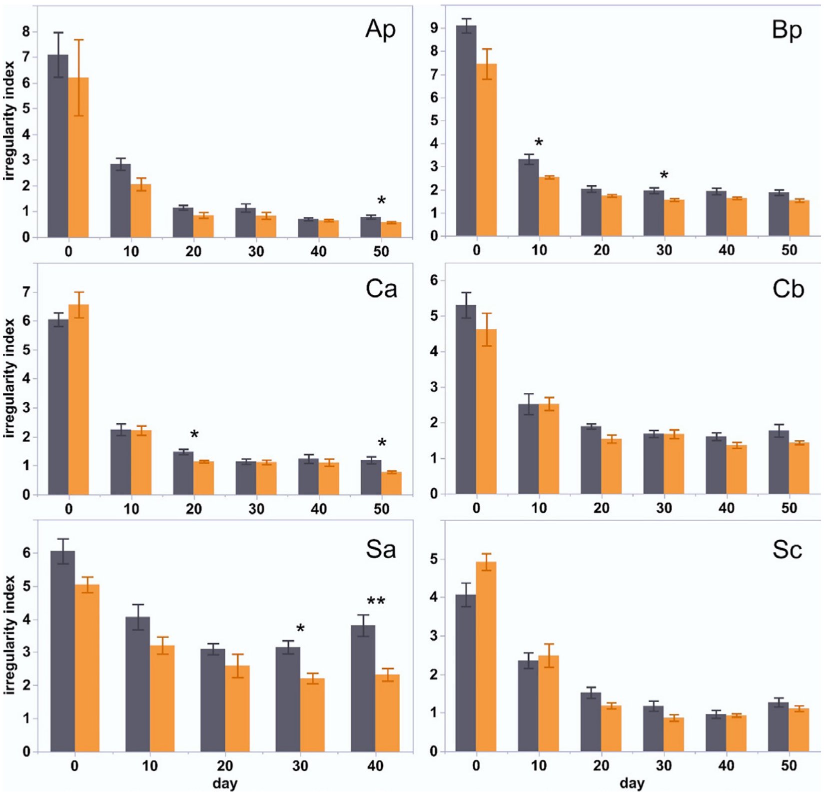

Fig. 5. Average leaf blade irregularity index (perimeter/area ± standard error) of shade (grey) and sun (orange) leaves in *Acer platanoides* (Ap), *Betula pendula* (Bp), *Corylus avellana* (Ca), *Carpinus betulus* (Cb), *Sorbus aucuparia* (Sa), and *Salix caprea* (Sa) during development. Wilcoxon test for shade and sun leaves: * P < 0.05; ** P < 0.01

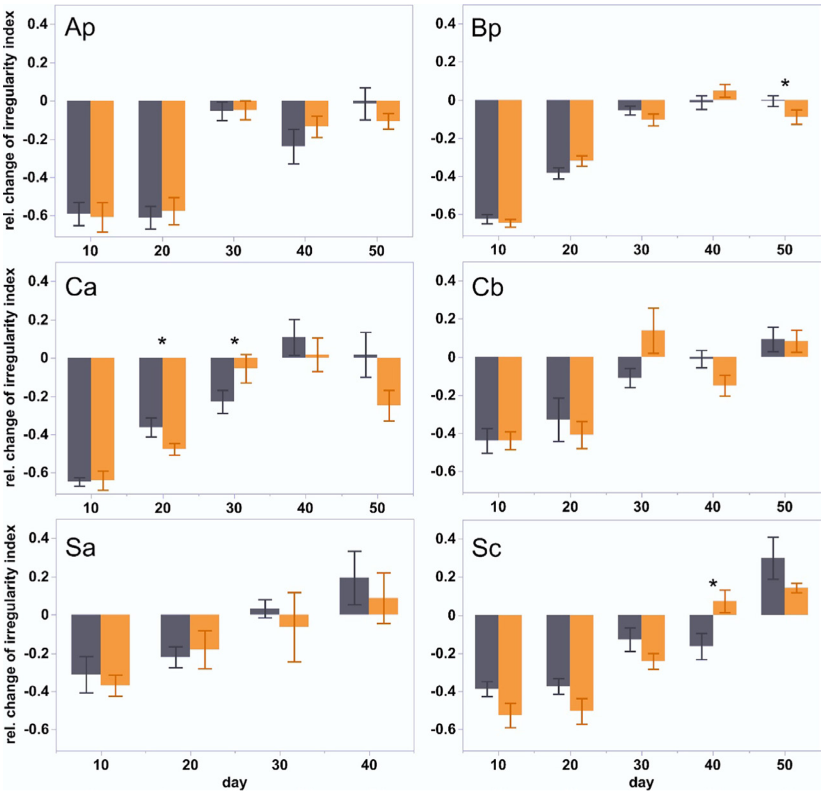

Fig. 6. Relative change of irregularity index (± standard error) of shade (grey) and sun (orange) leaves in *Acer platanoides* (Ap), *Betula pendula* (Bp), *Corylus avellana* (Ca), *Carpinus betulus* (Cb), *Sorbus aucuparia* (Sa), and *Salix caprea* (Sa) during development. Wilcoxon test for shade and sun leaves: * P < 0.05

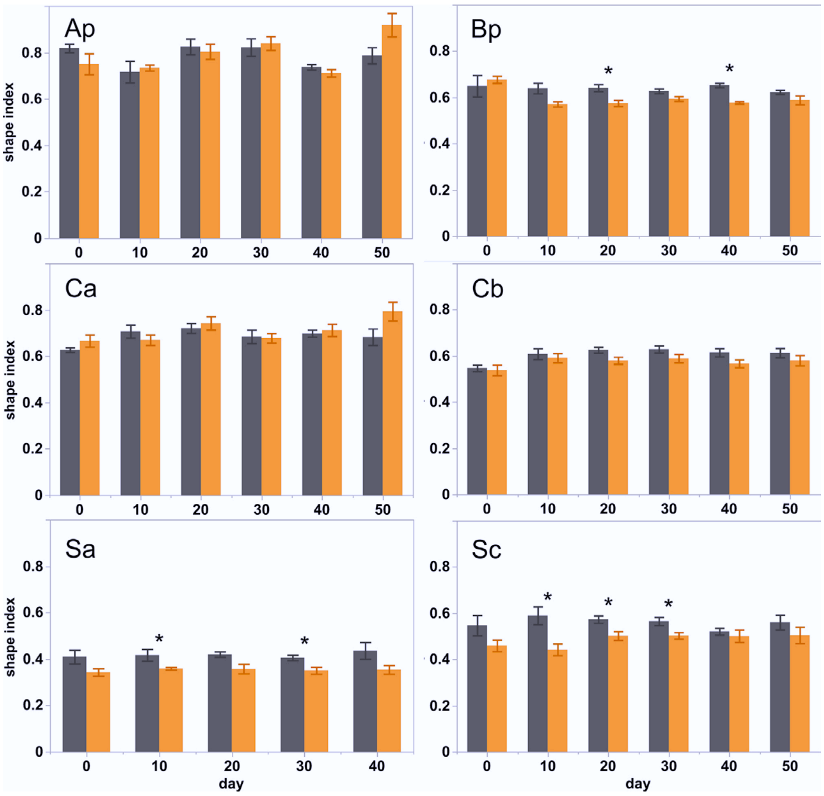

Fig. 7. Average leaf blade shape index (width/length ± standard error) of shade (grey) and sun (orange) leaves in *Acer platanoides* (Ap), *Betula pendula* (Bp), *Corylus avellana* (Ca), *Carpinus betulus* (Cb), *Sorbus aucuparia* (Sa), and *Salix caprea* (Sa) during development. Wilcoxon test for shade and sun leaves: * P < 0.05

The fastest growth occurred within the first 20–30 days of observation, after which the growth rate stabilized. In all analyzed species, sun leaves were generally larger than shade leaves; however, significant differences were particularly evident in *B. pendula*, and at specific time points in *C. avellana*, *C. betulus*, and *S. aucuparia* (Fig. 4).

The irregularity index of the leaf blade decreased within the first 20–30 days of development and then, similar to leaf area, stabilized (Fig. 5, Appendix 1). The most pronounced differences in this parameter occurred between the first and second sampling dates. Differences between shade and sun leaves were observed, with shade leaves generally exhibiting higher irregularity values. Significant differences were recorded in *B. pendula*, *C. avellana*, *S. aucuparia*, and *A. platanoides* (Fig. 5).

By the final sampling date, the highest irregularity index was observed in *S. aucuparia*, followed by *C. betulus*, *B. pendula*, *S. caprea*, *C. avellana*, and *A. platanoides* (Fig. 5).

Since the perimeter-to-area ratio increases with leaf size (reflecting an allometric relationship), a relative change of irregularity index was used to eliminate this effect (Fig. 6). This analysis confirmed the general trend of a decreasing proportion of teeth relative to leaf blade area as leaves aged. No consistent effect of light conditions on this parameter was detected. Significant differences were identified in only four instances: in *C. avellana*, higher values were recorded for shade leaves on day 20 and for sun leaves on day 30; in *B. pendula*, higher values were observed for shade leaves on day 50; and in S. caprea, for sun leaves on day 40 (Fig. 6).

The shape index remained stable throughout the study period (Fig. 7, Appendix 1). Differences according to light regime were observed, with shade leaves exhibiting higher shape index values. Significant differences were recorded in *S. caprea*, *S. aucuparia*, and *B. pendula* (Fig. 7).

Discussion

Parameters determining the actual area of leaf teeth

To identify the parameter most strongly correlated with the actual tooth area, we evaluated the usefulness of calculated variables such as the simplified tooth area, the leaf blade irregularity index, and the leaf blade shape index. These parameters can be derived from leaf scans using specialized software. Among these, both the simplified tooth area and the irregularity index showed strong correlations with the actual tooth area, whereas the relationship between the actual tooth area and the compactness index was statistically insignificant.

Despite the comparable levels of correlation between the actual tooth area and both the simplified tooth area and the irregularity index, only the irregularity index was selected for further analyses. Several arguments supported this decision. Firstly, obtaining accurate height and base values for each tooth frequently required manual correction, as image blur at the leaf edges hindered automated measurements. This process was time-consuming, labor-intensive, and introduced potential measurement errors. Secondly, the simplified tooth area assumes a triangular shape and, therefore, does not fully capture the natural complexity and irregularity of tooth morphology.

The irregularity index, defined as the ratio of leaf perimeter to area, is directly linked to the gas exchange hypothesis and the edge effect described in this context (Baker-Brosh & Peet, 1997; Royer et al., 2008). It is a simple and broadly applicable parameter, even for species with entire leaf blades.

Morphological changes during leaf development

The results of this study confirm the hypothesis that the decrease in leaf margin irregularity relative to the rest of the leaf blade with age is a universal phenomenon among the studied tree species, aligning with previous findings in *Quercus rubra* (Zwieniecki et al., 2004) and *Liquidambar styraciflua* (Baker-Brosh & Peet, 1997). This pattern may reflect the functional significance of leaf teeth in young, developing leaves, where the earlier maturation of marginal tissues enables intense photosynthesis (Givnish, 1979; Baker-Brosh & Peet, 1997; Royer & Wilf, 2006; Royer et al., 2008). From a physiological perspective, gas exchange efficiency is maximized at the leaf margin. Consequently, not only the proportion of tooth area to blade area but, more importantly, the perimeter-to-area ratio emerges as a key indicator of potential gas exchange capacity.

This parameter is inherently influenced by allometric relationships, as the perimeter of an expanding leaf increases at a slower rate than its area. Thus, smaller leaves naturally exhibit higher perimeter-to-area ratios. The presence of teeth amplifies this relationship by increasing the perimeter without substantially increasing the overall area. Our study confirms that teeth significantly contribute to an elevated perimeter-to-area ratio in young leaves, particularly during early developmental stages (Zwieniecki et al., 2004). This likely reflects an evolutionary strategy aimed at maximizing marginal gas exchange when leaves are small and light availability is high. The analysis revealed that the proportion of tooth area to total blade area stabilizes between days 10 and 30 of leaf development, indicating that leaf shape and marginal characteristics are established early in development.

Furthermore, despite considerable ecological diversity among the studied species, the observed pattern was consistent across taxa, suggesting a potentially universal developmental trend among woody plants. However, due to the limited number of species examined, broader sampling, meta-analyses, or global comparative studies would be necessary to confirm the generality of this phenomenon.

Interestingly, although *S. caprea* is typically regarded as a species with entire margins, our data revealed clear marginal irregularity at early developmental stages, reinforcing the broader trend identified in this study.

Influence of light on morphological changes in the leaf blade

The study identified differences between sun-exposed and shaded leaves; however, these differences were primarily attributable to variations in leaf size rather than tooth characteristics. This conclusion is supported by the analysis of the relative irregularity index, which accounts for the influence of leaf size on perimeter-to-area relationships. Using this index, no significant differences were found between light conditions, except for four cases at the lower significance threshold ($P < 0.05$). Consequently, the second hypothesis – that shade leaves exhibit greater irregularity than sun leaves – was not supported. Likewise, the third hypothesis – predicting a slower decrease in tooth area relative to blade area in shade leaves – was not confirmed either.

In our study, sun-exposed leaves were generally larger than shaded leaves. Conversely, shade leaves exhibited a higher irregularity index, although this metric is size-dependent and should therefore be interpreted cautiously. After adjusting for size effects using the relative change of irregularity index, the influence of light conditions on tooth development was no longer statistically significant. These findings indicate that while light availability affects overall leaf morphology, particularly leaf area and shape index, it does not substantially impact tooth development.

Our results highlight the high morphological plasticity of leaves in response to varying light conditions (Xu et al., 2008). The literature reports mixed findings regarding the effect of light on leaf area, with studies suggesting species-specific and context-dependent responses. Some studies have found that shade leaves are smaller than sun leaves, while others report the opposite, or no significant difference at all (Isanogle, 1944; Parkhurst & Loucks, 1972; Clendon

& Millen, 1982; Goulet & Bellefleur, 1986; Nicotra et al., 2011; Maslova et al., 2021). These discrepancies may be attributed to species-specific traits, environmental conditions, or the developmental stage of the leaves. For example, in *S. caprea*, shade leaves were larger than sun leaves at the initial observation point, but at later stages, either no differences or larger sun leaves were recorded (Fig. 4). This underlines the importance of standardizing light conditions and sampling fully developed leaves in morphometric studies.

Although the irregularity index was higher in shaded leaves, this may not directly reflect the presence or function of teeth. Instead, it could be influenced by overall leaf shape or the width-to-length ratio (Verwijst & Wen, 1996). Previous studies have suggested that leaf margin traits, including teeth, might facilitate increased light dispersion and gas exchange, potentially benefitting shade-adapted leaves (Gottschlich & Smith, 1982; Niklas, 1988, 1989; Gurevitch & Schuepp, 2006; Leigh et al., 2017; Givnish & Kriebel, 2017).

Conclusions

In conclusion, our findings confirm that the ratio of tooth area to total leaf blade area is established early in leaf development and is a common feature among woody plants. While shaded leaves exhibited higher irregularity when considering the unadjusted irregularity index, this effect disappeared after adjusting for leaf size. Thus, light conditions appear to influence general leaf size and shape more strongly than tooth development itself.

These findings may contribute to a better understanding of the developmental processes underlying leaf tooth formation – a trait commonly used in paleobotanical analyses. Our study indicates that the degree of serration is not significantly influenced by light conditions but rather by the developmental stage of the leaf, suggesting that tooth formation is primarily time-regulated rather than light-driven. Understanding this ontogenetic dynamic can enhance the interpretation of tooth presence in both extant and fossil tree species – especially considering that paleobotanical analyses typically assess only the presence or absence of teeth without reference to the developmental stage of the leaf. Thus, our results may support paleobotanists in better understanding the origin and functional role of this trait, independently of light availability

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