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Comprehensive Analysis of Flowering Patterns in One-Year-Old Long Shoots of Apple Cultivars with Contrasted Bearing Habits

Ayşe Nilgün Atay[1,*]

[1]Burdur Mehmet Akif Ersoy University, Food Agriculture and Livestock School, Department of Crop and Livestock Production, Horticulture Program, Burdur, Türkiye

HIGHLIGHTS

- There is a significant difference in the quality of floral buds among apple cultivars in shoot zones.
- "Amasya' shoots exhibited a gradual increase in floral bud quality as they extended towards the distal zone.
- In 'Braeburn' and 'Granny Smith,' floral bud quality variables remained stable along the shoot.
- The properties of spur leaves along the shoot have been found to be crucial for maintaining consistent productivity.

Abstract

Before developing orchard management strategies, it is crucial to conduct architectural analysis at the shoot level for the specific type of fruit to be grown. The objective of this study was to analyze flowering patterns in 1-year-old long shoots of three apple cultivars ('Amasya,' 'Braeburn,' and 'Granny Smith') with different bearing behaviors. This analysis aimed to gain a better understanding of their growth dynamics and reproductive activities. The shoot was divided into three consecutive zones (proximal, median, and distal) based on node number. When comparing the number of floral and vegetative buds in the three zones along the shoot, less contrast was observed between alternate-bearing ('Amasya') and regular-bearing cultivars ('Braeburn' and 'Granny Smith'). However, a notable difference in floral bud quality variables was evident in shoot zones between biennial-bearing and regular-bearing cultivars. In 'Braeburn' and 'Granny Smith' with a regular bearing habit, floral bud quality variables remained stable along the shoot. In contrast, 'Amasya' shoots exhibited a gradual increase in floral bud quality from the proximal zone towards the distal zone. 'Amasya' had the fewest spur leaves per inflorescence, both in the proximal zone (0.89) and the median zone (2.87) of one-year-old long shoots, whereas they were nearly equal for 'Braeburn' (5.67 and 6.09, respectively) and 'Granny Smith' (5.55 and 6.59, respectively). In the proximal zone, 'Amasya' had a spur leaf size of 0.48, while 'Braeburn' and 'Granny Smith' exhibited similar spur leaf sizes of 3.39 and 3.59, respectively. This study underscores the significance of floral bud quality, especially the properties of spur leaves along the shoot, in ensuring optimal and consistent productivity. Finally, with the exception of internode length, morphometric traits did not significantly differ between cultivars when considering the entire shoot. However, these differences became apparent when examining successive zones along the shoot.

Keywords: branching; floral quality; tree architecture; reproductive; bearing behaviors

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Corresponding Author E-mail: anatay@mehmetakif.edu.tr

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1. Introduction

In temperate fruit trees, understanding branching and bearing behaviors is crucial due to their crucial agronomic and economic implications. Tree architectural analysis, which allows for the quantification of form and shape, has the potential to characterize growth and branching patterns, as well as flowering and fruiting habits (Halle et al. 1978; Costes et al. 2006). However, these patterns represent complex processes, the mechanisms of which are not yet fully understood, particularly in perennial species characterized by a succession of growth units (Tromp 2005; Hanke et al. 2007; Lauri and Corelli-Grappadelli 2014). Consequently, such an analysis is not easily comprehensible due to the intricate nature of perennial woody plants.

Several classifications have been applied in the architectural characterization of apple trees based on their growth habits (spur and standards, from upright to weeping) (Dennis et al. 1996; Lane et al. 1996), tree forms (columnar, upright, spreading, drooping, and weeping) (UPOV 1982), and fruiting habits (Types I to IV) (Lespinasse 1977), as well as the position of the scaffold branches along the trunk (Lespinasse 1992). In addition, a more detailed modeling approach to architectural traits has been studied in apples (Costes and Guédon 1997; Costes and Guédon 2002; Renton et al. 2006; Wang et al. 2020). These models mainly focused on branching patterns, which have the potential to affect training, pruning, and orchard management efficiency.

In apple trees, there is a significant variability in flowering patterns among different cultivars (Lauri and Lespinasse 1993; Costes and Guédon 2002). This diversity in flowering patterns has significant implications for orchard management strategies, especially for cultivars that display synchronized or desynchronized flowering rates over the years. Understanding the architecture of 1-year-old long shoots, where flowers are located, can greatly assist in the development of effective orchard management strategies for these cultivars. Comprehensive knowledge of flowering patterns and shoot architecture in apple trees is crucial for devising effective orchard management strategies, especially for cultivars that exhibit biennial bearing over time. It's essential to consider the architectural traits of apple trees, such as branch distribution and fruiting positions, as these factors can impact fruit yield and overall productivity. In this study, we conducted a quantitative and qualitative characterization of flowering patterns on 1-year-old long shoots in three apple cultivars ('Amasya,' 'Braeburn,' and 'Granny Smith') that exhibit distinct bearing behaviors.

The aim was to gain a better understanding of their growth dynamics and reproductive activities. To achieve this, we compared 'Amasya,' which demonstrates alternate bearing patterns, with 'Braeburn' and 'Granny Smith,' both known for regular bearing patterns. We examined variables related to vegetative and reproductive bud development and the quality of floral buds along the annual shoots, which we partitioned into three different successive zones, in addition to analyzing the shoot structures.

2. Materials and Methods

The study orchard was established in 2013 with row spacing set at 4.0 m and tree spacing at 1.0 m. It was located at the Egirdir Fruit Research Institute in Isparta, Türkiye (37° 48' 52.16" N, 30° 52' 39.66" E). Following planting, the trees were trained in a trellis spindle system with minimal pruning. Orchard management practices, including irrigation, nutrition, pest and disease control, as well as weed management, were conducted in accordance with local commercial orchards from 2013 to 2019.

For this study, we selected three different apple cultivars, each with unique genetic backgrounds and levels of vigor: 'Amasya,' 'Braeburn,' and 'Granny Smith,' all grafted onto M.9 rootstock. 'Amasya' is characterized by its desirable features such as eating quality and aroma, but it is subject to irregular yield constraints (Atay et al. 2018). 'Granny Smith' and 'Braeburn,' both popular apple cultivars globally, exhibit consistent yields. 'Braeburn' is distinguished by high-density branching and lateral fruiting, while 'Granny Smith' is known for terminal fruiting and a high mortality rate of axillary buds (Lauri et al. 1997; Fumey et al. 2011).

The trees were arranged in a randomized block design with three replications, and each replication consisted of one tree in 2019. We selected twelve shoots (four per tree) per cultivar, which were gathered from four different directions (North, South, East, and West) during the first week of April. The chosen shoots were typically healthy and bearing, with base diameters of the 1-year-old wood exceeding 5 mm, and each shoot's total length exceeded 40 cm (see Figure 1). Nodes were numbered from the proximal to distal end and categorized into three zones (proximal, median, and distal).

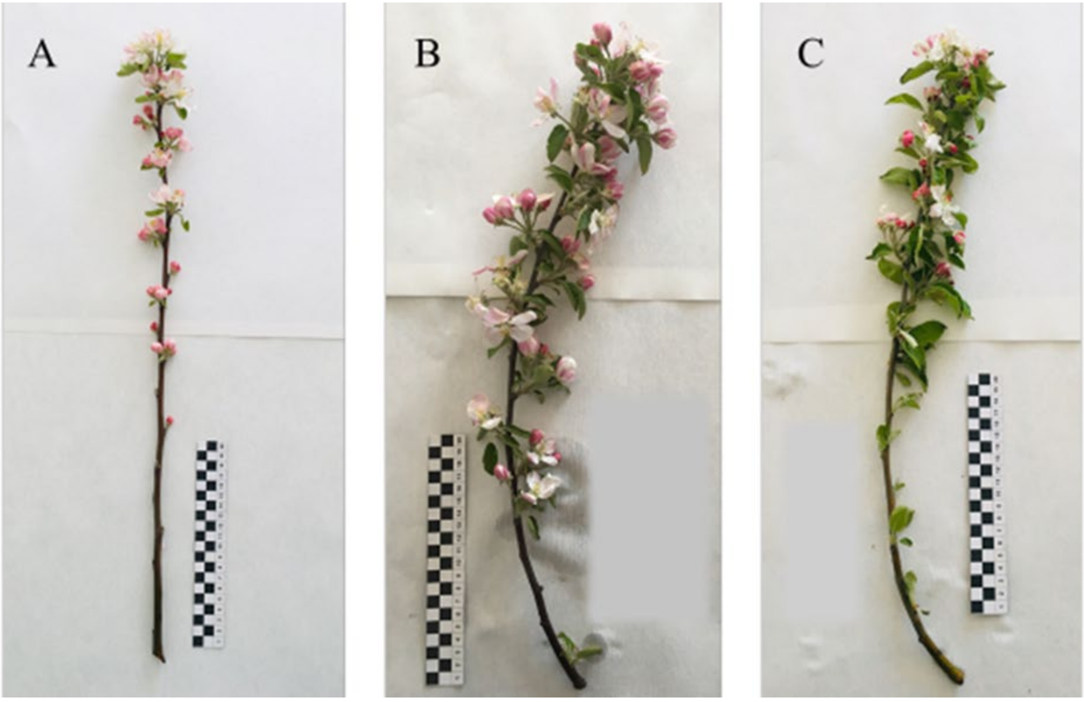

Figure 1. One-year-old long shoots - A: 'Amasya', B: 'Braeburn', and C: 'Granny Smith'

We recorded the nature of buds (whether they were vegetative or generative) node by node along the shoots at full bloom. Full bloom occurred on April 24-26 for 'Amasya' and April 30-May 2 for 'Braeburn' and 'Granny Smith.' We quantified the number of flowers per inflorescence on the flowering buds. Furthermore, we also counted the number of spur leaves per inflorescence. The size of the spur leaves was determined based on a scale ranging from 1 to 5, as previously described in Atay and Atay (2022). In summary, this scale consists of five different intervals: 1) 0-10 cm^2, 2) 11-20 cm^2, 3) 21-30 cm^2, 4) 31-40 cm^2, and 5) >41 cm^2 spur leaf area.

As part of the morphometric traits analysis, we measured the shoot length in cm, from the base to the top, using a fabric tape measure. We used a digital caliper to determine the basal diameter of the shoots in mm. The nodes were counted from the base of the shoots towards the top, and then the internode lengths were calculated for each cultivar on each tagged shoot. We also counted the number of flowering buds per shoot for each cultivar.

Statistical analyses were conducted using R statistical software version 4.1.3 (R Core Team, 2022). The 'ggplot2' package was utilized for graph generation. ANOVA procedures were performed to compare zone effects. Violin plots are recommended for summarizing distributions and displaying all data points effectively, making them a preferable choice for clear communication and visual appeal in presenting important results.

3. Results

Buds on one-year-old wood were individually examined for all cultivars, and assessments were conducted along the shoot zones, from the proximal to the distal end. The number of generative buds in the proximal zone of the shoots was higher for 'Braeburn' compared to 'Amasya' and 'Granny Smith'. The proximal zone was primarily characterized by vegetative buds for 'Amasya' and 'Granny Smith'. In the median zone of the shoots, the average number of generative buds for 'Granny Smith' was relatively lower compared to the other two cultivars. Conversely, in the distal zone on one-year-old long shoots, more than 95% of the nodes for all cultivars were characterized by the presence of generative buds (Figure 2).

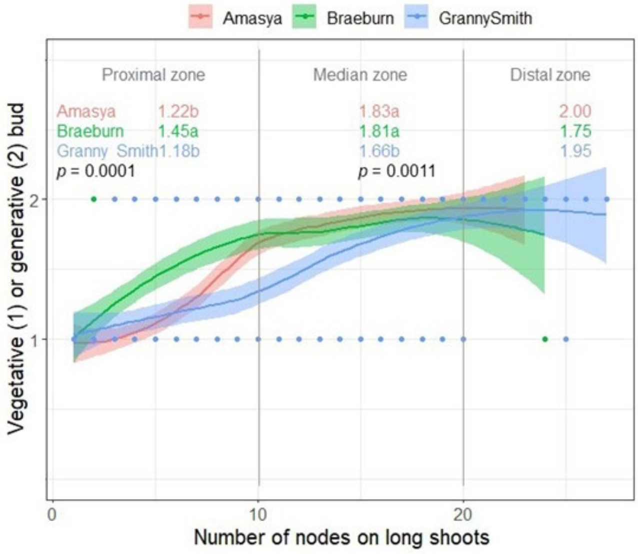

Figure 2. Effect of shoot zone on frequencies of vegetative or generative buds in 'Amasya,' 'Braeburn,' and 'Granny Smith' apples

After the proportion of floral differentiation along 1-year–old long shoots was observed, floral bud quality in the different shoot zones was examined in detail. The number of flowers per inflorescence in 'Amasya' was significantly lower in both the proximal (*p*=0.0001) and median zones (*p*=0.0003) of the shoots compared to the other cultivars (Figure 3). In the distal zone of the shoots, the number of flowers per inflorescence was quite similar for all cultivars, ranging from 4.67 to 5.00 number/inflorescence. This suggests that the number of flowers per inflorescence in 'Amasya' gradually increased towards the distal zone, and the difference diminished in the distal zone of the shoots.

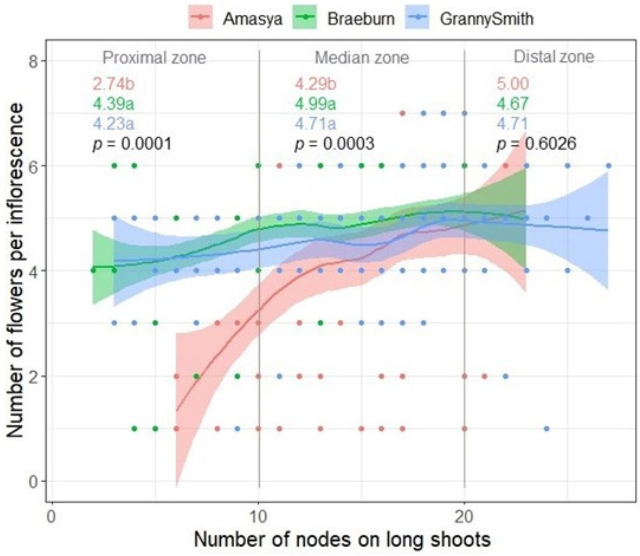

Figure 3. Effect of shoot zone on number of flowers per inflorescence in 'Amasya,' 'Braeburn,' and 'Granny Smith' apples

'Amasya' had the fewest spur leaves per inflorescence, both in the proximal zone (0.89 number/inflorescence) and the median zone (2.87 number/inflorescence) of one-year-old long shoots, whereas they were nearly equal for 'Braeburn' (5.67 and 6.09 number/inflorescence, respectively) and 'Granny Smith' (5.55 and 6.59 number/inflorescence, respectively) (Figure 4). There was no significant difference in the number of spur leaves per inflorescence among all cultivars (6.67, 5.33, and 6.57 number/inflorescence for 'Amasya,' 'Braeburn,' and 'Granny Smith,' respectively) in the distal zone of the shoots.

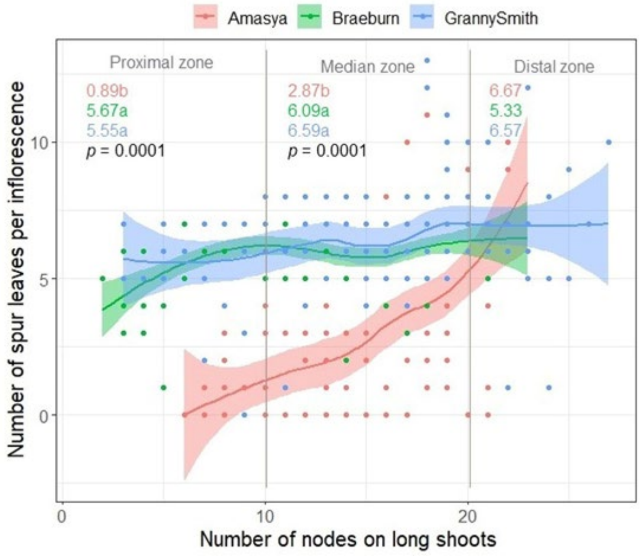

Figure 4. Effect of shoot zone on the number of spur leaves per inflorescence in 'Amasya,' 'Braeburn,' and 'Granny Smith' apples

In addition, the spur leaf size in the proximal and median zones of 'Amasya' shoots was significantly smaller than that of 'Braeburn' and 'Granny Smith' (Figure 5). In the proximal zone, 'Amasya' had a spur leaf size of 0.48, while 'Braeburn' and 'Granny Smith' exhibited similar spur leaf sizes of 3.39 and 3.59, respectively. Among the cultivars, the highest spur leaf size in the median zone was observed in 'Granny Smith' (4.15), followed by 'Braeburn' (3.80). 'Amasya' had relatively smaller spur leaf size in the distal zone of shoots compared to the other two cultivars, but there were no significant differences among these cultivars. The spur leaf size per inflorescence for 'Amasya' gradually increased from the proximal zone to the distal zone, while the sizes for 'Braeburn' and 'Granny Smith' remained more stable along the shoot.

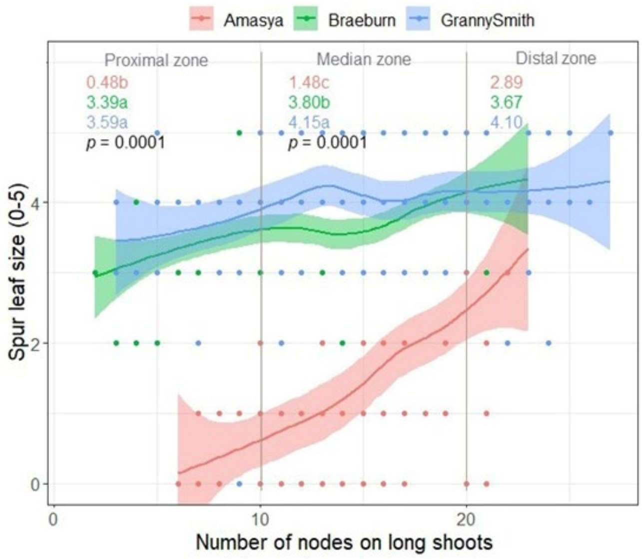

Figure 5. Effect of shoot zone on spur leaf size in 'Amasya,' 'Braeburn,' and 'Granny Smith' apples

The mean shoot length was slightly longer in 'Braeburn' (54.08 cm) and 'Granny Smith' (53.75 cm) than in 'Amasya' (47.83 cm), with no statistically significant differences (Figure 6A). Mean shoot diameter ranged from 7.87 mm ('Amasya') to 8.37 mm ('Granny Smith') (Figure 6B). 'Granny Smith' shoots had a slightly higher node number (mean: 21.25), but this difference was not statistically significant when compared to the other cultivars (Figure 6C). On the other hand, internode length, as leaf separators, varied depending on the cultivar, with the highest mean internode length found in 'Braeburn' (mean: 2.78 cm), while it was 2.48 cm and 2.53 cm for 'Amasya' and 'Granny Smith,' respectively (Figure 6D). Additionally, the number of flowering buds per shoot did not vary significantly by cultivar, with mean values ranging from 9.83 ('Granny Smith') to 12.08 ('Braeburn') among the one-year-old long shoots of these cultivars (Figure 6E).

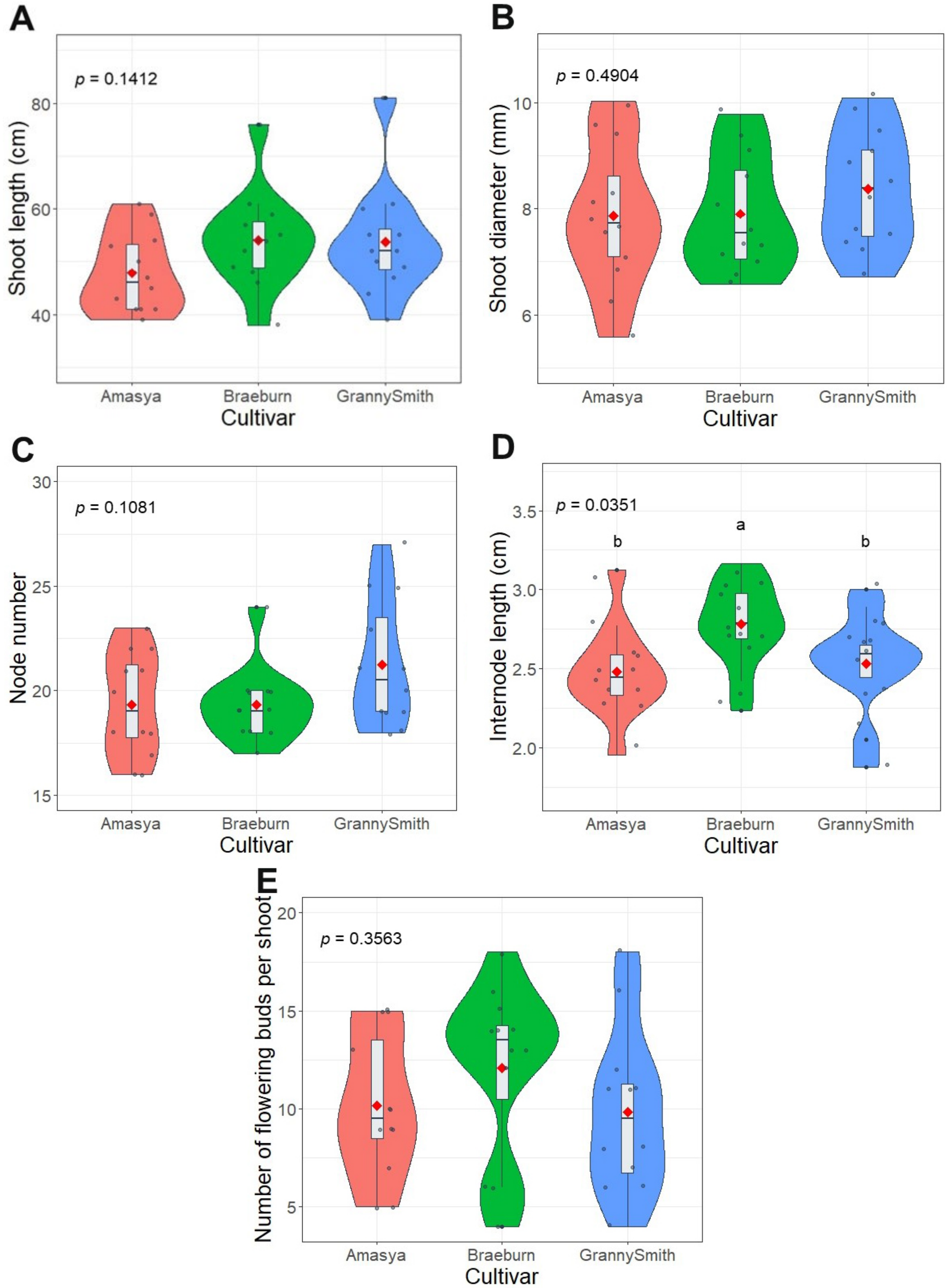

Figure 6. Morphometric traits of one-year-old long shoots in the cultivars 'Amasya,' 'Braeburn,' and 'Granny Smith'. (A) Shoot length (cm), (B) Shoot diameter (mm), (C) Node number, (D) Internode length (cm), and (E) Number of flowering buds per shoot. Different letters indicate statistical significance according to the LSD multiple-range test at $p < 0.05$.

4. Discussion

Three successive zones, comprising the proximal, median, and distal portions, are a common feature in long shoots of fruit trees (Costes and Guedon 2002; Solar et al. 2005; Stanley 2016; Meszaros et al. 2020). In this study, these zones were identified along the 1-year-old shoots of 'Amasya,' 'Braeburn,' and 'Granny Smith,' based on their positions (distance from the base and apex). The number of vegetative and generative buds was estimated for each cultivar in these three zones along the shoots. The distribution of vegetative and generative buds clearly depended on the zone along the shoot. In 'Amasya' and 'Granny Smith,' the proximal zone predominantly contained vegetative buds, forming a pool of buds that enables the tree to respond to damage, pruning, and aging by developing epicormic shoots (Gordon et al. 2006; Atay and Koyuncu 2012). It was observed that 'Braeburn' exhibited bearing behavior in every zone along the shoot, although it was relatively lower in the proximal part, consistent with the findings of Costes et al. (2003) in their description of the architectural development of 'Braeburn'.

The median zone was primarily composed of generative buds for 'Amasya,' while it consisted of vegetative buds for 'Granny Smith'. The third (distal) zone was identified as the floral zone, containing a significant number of associated generative buds for all cultivars. Indeed, the frequency of generative buds varies with terminal bearing behavior in apples, depending on cultivars, shoot type, and length (Lauri and Corelli-Grappadelli 2014; Pallas et al. 2018). The nature of the terminal bud and other buds near the apex on 1-year-old shoots was consistently determined as generative buds in all the cultivars studied. Given the higher light levels, photosynthetic capacity, and hormonal activity in this region, a greater intensity of flowering can be expected in the distal zone (Ferree 1989; Barritt et al. 1991; Tromp 2005; Gottschalk and van Nocker 2013).

The relationship between bud position and fate along the annual shoots determines the flowering patterns, which are associated with bearing habits (e.g., regular or biennial) (Guedon et al. 2001; Costes et al. 2006; Pallas et al. 2018). However, in our study, we observed less contrast between biennial bearing and regular bearing cultivars when comparing these vegetative and generative buds in the three zones along the shoots. 'Amasya,' with irregular bearing patterns, displayed a similar generative bud rate to 'Braeburn' or 'Granny Smith,' characterized as regular cultivars in each zone. This suggests that there is no simple relationship between flowering patterns and regular bearing capacity. Hormonal equilibrium may have a more significant impact than the number of flower buds (Tromp 2005; Bangerth 2006; Hanke et al. 2007).

The number of flower organs, flower size, the number of flowers per inflorescence, as well as the area and number of leaves of bourse shoots, have been proposed for analyzing floral bud quality in apples (Lauri et al. 1996; Ferree et al. 2001; Jackson 2003). The number of flowers per inflorescence remained relatively stable across all zones in 'Braeburn' and 'Granny Smith.' There was a gradual increase in the number of flowers per inflorescence toward the distal zone of shoots in 'Amasya.' This trend was also observed in the number of spur leaves per inflorescence and spur leaf size for 'Amasya.' In fact, both the number and size of spur leaves per inflorescence were limited in the proximal and median zones in ‘Amasya’, whereas they were more similar to those of 'Braeburn' and 'Granny Smith' in the distal zone. Generally, the size of reproductive buds (leaf number) differs along apple shoots in one-year-old shoots (Lauri 2007). However, this trend was only obvious in ‘Amasya’, which has irregular yield constraints, in our study. Floral bud quality variables showed stability along the shoot in 'Braeburn' and 'Granny Smith,' which exhibit a regular bearing habit. In contrast to the number of vegetative or generative buds, there was a clear difference in floral bud quality variables in shoot zones between biennial bearing and regular bearing cultivars studied. These findings confirm that floral bud quality, especially spur leaf properties, is strongly associated with the bearing capacity of apples (Ferre and Schmid 2004; Elsysy and Hirst 2017; Atay and Atay 2022). A sufficient amount of spur leaves in apples is crucial for long-term productivity due to its effect on photosynthetic performance, carbohydrates, phytohormones, and nutritional status (Ferree et al. 2001; Wertheim and Schmidt 2005; Madail et al. 2012; Atay and Atay 2022).

In general, differences in the morphometric traits of 1-year-old long shoots between cultivars are expected, possibly due to different growth habits (Lauri and Lespinasse 1993; Costes and Guédon 2002). However, in the present study, there were no differences in shoot length, shoot diameter, node number, and flowering bud number between cultivars when considering the entire shoot scale. These results confirm that weak genetic control may appear in morphological traits when bud position and growth units along the shoot are not taken into account (Verheij 1996; Costes 2003; Sadok et al. 2015). Therefore, no significant effects could be observed in whole shoot traits between cultivars. One possible cause of these finding could be that the shoot age in perennial plants has a greater impact than branching behavior (Costes 2003). In our study, we used 1-year-old long shoots with a similar crop load, and this stability in the studied shoots may have influenced these findings.

Interestingly, internode length appeared to be significantly impacted by the cultivar effect in the present study. A similar result was found for some horticultural crops by Da Silva et al. (2014) and Sadok et al. (2015), demonstrating that internode lengths were mainly genetically controlled. The internode lengthening process plays a crucial role in maintaining water conductance, light interception, hydraulic efficiency, and mechanical stability as it affects the stiffness of shoots and the number and size of the leaves (Cochard et al. 2005; McCulloh and Sperry 2005; Sadok et al. 2013). Therefore, internode lengthening traits are suggested as one of the most important architectural components for achieving high productivity (Sadok et al. 2015). Since our study was conducted on only three cultivars trained with the same system, further analysis of different cultivars in various growing systems, under different environmental and orchard management conditions, would be relevant.

5. Conclusions

In conclusion, the results demonstrate differences in flowering patterns along the three successive zones (proximal, median, and distal) on the 1-year-old shoots of 'Amasya,' 'Braeburn,' and 'Granny Smith.' There was less contrast observed between alternate bearing ('Amasya') and regular bearing cultivars ('Braeburn' and 'Granny Smith') when comparing the number of vegetative or generative buds in these three zones along the shoot. However, a clear difference in floral bud quality variables was evident in shoot zones between biennial bearing and regular bearing cultivars studied. Floral bud quality variables remained stable along the shoot in 'Braeburn' and 'Granny Smith,' which have a regular bearing habit, while there was a gradual increasing trend from the proximal zone towards the distal zone in 'Amasya' shoots. The results of this study highlight the importance of floral bud quality, especially spur leaf properties along the shoot, in ensuring optimal and consistent productivity.

Author Contributions: The author has read and agreed to the published version of the manuscript.

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