Relation Between Floral Initiations on Apical Buds of Basal Shoots After the Autumn and Cultivar Differences in Unseasonal Flowering of Hydrangea

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Typically, hydrangea (Hydrangea spp.) plants produce flowers from early to mid-summer. However, their basal shoots often continue to produce flowers from late summer to autumn, and we call this unseasonal flowering. The flowering frequencies and flowering period durations of basal shoots were studied using 23 hydrangea cultivars and lines in 2017, 2018, and 2019. The flowering frequencies of basal shoots were relatively high in ‘Christmas’, ‘Endless Summer’, ‘Ezo’, ‘Rosea’, and ‘Sumida-no-hanabi’ in each year of the study. The flowering period durations of basal shoots ranged from one to six months among the cultivars and lines studied. Basal shoots of ‘Endless Summer’ and ‘Rosea’ continuously flowered during each year of the study period. The basal shoots of ‘Hatsushimo’, ‘Jyogasaki’, ‘Maihime’, ‘Masja’, ‘Ms. Hepburn’, ‘Uzu’, and No. 5 never flowered after August in any of the study years. Using ‘Masja’ and ‘Rosea’, axillary buds expected to develop into basal shoots were studied for flower bud initiation in November 2018. Flower bud initiation was observed in 8.9% and 77.4% of axillary buds of ‘Masja’ and ‘Rosea’, respectively. The number of nodes produced before flower bud initiation in the buds ranged from 10 to 12 and 8 to 13 in ‘Masja’ and ‘Rosea’, respectively. The numbers of nodes corresponded to those of the basal shoots that flowered up to August 2019 in both cultivars. The number of nodes produced by basal shoots of ‘Rosea’ that flowered after August 2019 ranged from 14 to 19, which was higher than those observed for the axillary buds expected to develop into basal shoots in November 2018. In conclusion, the flowering period duration of hydrangea basal shoots differs among cultivars. The floral initiations on the apical buds of the basal shoots after the previous autumn largely contribute to unseasonal flowering occurrences after August in hydrangea.

Key Words: cut flower production, flower bud initiation, flowering period, harvest period, node.

Introduction

Hydrangeas (Hydrangea spp.) are common ornamental plants cultivated as pot flowers, shrubs, and cut flowers in many countries (Mallet, 2008; van Gelderen and van Gelderen, 2004). Hydrangeas produce two types of florets, decorative and non-decorative florets. The arrangement of two distinct floret types in an inflorescence decides the inflorescence type, hortensia or lacecap (Uemachi and Nishio, 2005; Uemachi et al., 2006). Many hybrid cultivars among H. macrophylla and H. serrata with hortensia type inflorescences have been bred and used for cut hydrangea flower production. Hydrangea plants develop two types of shoots in spring: current shoots that develop from terminal buds formed in the previous autumn (previously formed shoots) and vigorous shoots that develop from the axillary buds formed on the basal part of the plant (basal shoots) (Fig. 1). Typically, hydrangeas produce flower buds on current shoots in autumn, and flower development occurs once winter dormancy has been broken, with anthesis occurring until summer (Zhou and Hara, 1988).

Several hydrangea cultivars continue to flower throughout the growing period, and we call this unseasonal flowering. Unseasonal flowering can occur on both previously formed shoots and basal shoots. There are several reports of unseasonal flowering of hydrangea including our report (Adkins et al., 2002; Eid et al., 2016; Kitamura et al., 2018; Kudo et al., 2008; Nordli et al., 2011; Orozco-Obando et al., 2005). The above-mentioned reports focused on flower production from axillary buds developed by pinch treatment conducted in spring, terminal buds of cuttings, and a reduc-
tion in dormancy. Our previous research revealed that the apical bud of hydrangea basal shoots continued unseasonal flowering during summer and autumn and that the unseasonal flowering occurrence of hydrangea basal shoots could extend the flowering period duration (Kitamura et al., 2014). Basal shoots of hydrangeas grow vigorously, and well-grown and flowered hydrangea basal shoots can be used to produce high-quality cut flowers. Thus, the unseasonal flowering occurrence on the apical buds of the hydrangea basal shoots has an advantage in cut hydrangea flower production. However, detailed cultivar differences in unseasonal flowering occurrence on apical buds of basal shoots has not yet been reported.

The objective of this research was to determine the cultivar difference in unseasonal flowering occurrence in the apical buds of basal shoots, the flowering period duration, and the cause of cultivar differences. The cultivar differences in flowering frequency and flowering period duration of apical buds of basal shoots were studied using 23 hydrangea cultivars and lines. Using two representative cultivars with high potential for unseasonal flowering occurrence and low potential for unseasonal flowering occurrence, flower bud initiation in axillary buds expected to develop into basal shoots was studied in autumn. Finally, the factors that contributed to the unseasonal flowering of apical buds of hydrangea basal shoots were discussed.

Materials and Methods

Plant materials and cultivation conditions

This study aimed to determine the differences in unseasonal flowering occurrence of apical buds of basal shoots among a wide variety of cultivars. Thus, cultivars bred as garden shrub trees or for cut flower production were included in the study. Twenty-one hydrangea cultivars (‘Christmas’, ‘Endless Summer’, ‘Ezo’, ‘First Green’, ‘Flambeau’, ‘Green Shadow’, ‘Grüner Herz’, ‘Hatsushimo’, ‘Hobaria Hoparine’, ‘Jyogasaki’, ‘Libelle’, ‘Maihime’, ‘Masja’, ‘Monster’, ‘Ms. Hepburn’, ‘Otafuku’, ‘Renata’, ‘Rosea’, ‘Sumida-no-hanabi’, ‘Temariezo’, and ‘Uzu’) and two hydrangea lines (No. 5 and No. 7) were used in this study. ‘Christmas’, ‘Endless Summer’, ‘Flambeau’, ‘Grüner Herz’, ‘Hatsushimo’, ‘Hobaria Hoparine’, ‘Jyogasaki’, ‘Libelle’, ‘Maihime’, ‘Masja’, ‘Monster’, ‘Ms. Hepburn’, ‘Otafuku’, ‘Renata’, ‘Rosea’, ‘Sumida-no-hanabi’, and ‘Uzu’ are cultivars used as garden shrubs, and they are also often used for cut flower production. ‘First Green’ and ‘Green Shadow’ are cultivars bred for cut flower production in the Netherlands. ‘Endless Summer’, ‘First Green’, ‘Green Shadow’, ‘Hobaria Hoparine’, ‘Jyogasaki’, ‘Maihime’, and ‘Sumida-no-hanabi’ were purchased from several nurseries from 2009 to 2012. The other cultivars were obtained as cuttings from the Kyoto University experimental farm in May 2010. No. 5 and No. 7 originated from cuttings obtained from commercially available cut flowers in 2010, but we could not identify the cultivar names. These cultivars or lines are hybrids between or among H. macrophylla and H. serrata. ‘Ezo’ and ‘Temariezo’ are ancestors of the hydrangea horticultural cultivar, H. serrata (Uemachi et al., 2014), and both were obtained from the University of Shiga Prefecture in 2007. On the Shinshu University Ina campus experimental farm (Latitude: 35°51’56”s north; Longitude: 137°56’ min 6” east; altitude: 770 m), plants were grown in 32.5 cm diameter pots filled with 8 L medium composed of 75% Metro Mix 250 (SunGro Horticulture Distribution, MA, USA) and 25% vermiculite (v/v) (Asahi Industries Co., Ltd., Tokyo, Japan). Until April 2018, the plants were fertilized every two weeks using 1 L of 2000 times diluted liquid fertilizer (Hanakoujyo, N:P:K = 50:100:50 mg·mL⁻¹; Sumitomo Chemical Garden Products inc., Tokyo, Japan) and irrigated accordingly. From May 2018 onward, the plants were irrigated and fertilized with 1.5 L of culture solution prepared with OAT house No. 1 and No. 2, mixed at a ratio of 1.5:1.0 (w/w) (N:P:K = 18.6:5.1:8.6 me·L⁻¹; OAT Agrio Co., Ltd., Tokyo, Japan). The plants were maintained in a greenhouse under natural temperature conditions from mid-April to mid-November. The culti-
Flowering frequency and flowering period duration of apical buds of basal shoots

From June to November, the flowering frequency and flowering period duration of the apical buds of basal shoots were studied. The inflorescences, on which approximately 50% of the decorative florets had started anthesis, were determined as flowered inflorescences, and the date of the flowering was recorded. The investigations were replicated three times from 2017 to 2019, although several cultivars were not studied in 2019. All of the basal shoots generated were maintained and studied in every year of the study. In 2017 and 2018, all previously formed shoots were maintained, and in 2018, the flowering periods of apical buds of previously formed shoots were studied as a comparison. In 2019, with the aim of increasing the generation of basal shoots, all previously formed shoots were removed in March. The numbers of all plants and shoots studied for each cultivar are shown in Table 1.

Floral initiation in axillary buds expected to develop into basal shoots

To determine the factors contributing to the flowering period duration of basal shoots, we studied floral initiation in axillary buds expected to become basal shoots. Axillary buds that were expected to develop into basal shoots were formed as dormant buds on the basal part of the hydrangea plants until autumn (Fig. 1). Floral initiation in the buds has not yet been reported. In this study, ‘Masja’ and ‘Rosea’ were selected as representative cultivars with low and high potential for unseasonal flowering occurrence, respectively. Using these cultivars, floral initiations in axillary dormant buds that developed on the basal part of the plants were studied for floral initiation in November 2018 by dissecting them under a stereomicroscope, and the developmental stage of each apical meristem was determined according to Kosugi and Arai (1960) and Kitamura et al. (2018) as follows. 0: vegetative; 1: initial primordium developed; 2: secondary inflorescence branched; 3: tertiary inflorescence branched; 4: quaternary inflorescence branched; 5: highly branched inflorescence. The numbers of nodes produced in the dormant buds were also recorded and compared with those of basal shoots that flowered in 2019 using the plants shown in Table 1. The numbers of studied plants and buds are shown in Table 2.

Results

Flowering frequency and flowering period duration of apical buds of basal shoots

The flowering frequency and flowering period duration of basal shoots and previously formed shoots are shown in Table 1. The flowering frequencies of basal shoots were relatively high for ‘Christmas’, ‘Endless Summer’, ‘Ezo’, ‘Rosea’, and ‘Sumida-no-hanabi’ in every year of the study. In ‘Jyogasaki’, ‘Temariezo’, ‘Uzu’, and No. 5, the flowering frequencies of basal shoots increased year by year, and more than half of all basal shoots produced flowers in 2019. The flowering frequencies of the previously formed shoots were 100% for all studied cultivars. June and/or July were the main flowering periods for previously formed shoots for all studied cultivars in 2018 and were indicated as the seasonal flowering periods for the 23 studied cultivars and lines. The flowering period durations for basal shoots, which ranged from one to six months, differed among cultivars and often varied across years in many cultivars. Except for ‘Green Shadow’ and ‘Maihime’, flowering period durations of basal shoots and previously formed shoots overlapped in June and/or July. Basal shoots of ‘Endless Summer’ and ‘Rosea’ continuously flowered from June or July to October in all years studied, whereas those of ‘Hatsushino’, ‘Jyogasaki’, ‘Maihime’, ‘Masja’, ‘Ms. Hepburn’, ‘Uzu’, and No. 5 never flowered after August. Basal shoots of ‘Christmas’, ‘Ezo’, ‘First Green’, ‘Flambeau’, ‘Green Shadow’, ‘Grümherz’, ‘Hobaria Hoparine’, ‘Libelle’, ‘Monster’, ‘Otakuki’, ‘Renata’, ‘Sumida-no-hanabi’, ‘Temariezo’, and No. 7 occasionally flowered after August.

Floral initiation in axillary buds expected to develop into basal shoots

Floral initiation was observed in 8.9% and 77.4% of axillary buds of ‘Masja’ and ‘Rosea’, respectively, in November 2018 (Table 2). ‘Rosea’ plants had many more developed flower buds in their axillary buds expected to develop into basal shoots. The number of nodes produced before flower bud initiation in the buds ranged from 10 to 12 and 8 to 13 in ‘Masja’ and ‘Rosea’, respectively (Fig. 2). These numbers of nodes corresponded to those of the basal shoots that flowered until August 2019 in both cultivars (Fig. 3). The number of nodes produced by 39 basal shoots of ‘Rosea’ that flowered after July 2019 ranged from 13 to 19 (Fig. 3B). This was greater than observed in the axillary buds expected to develop into basal shoots in November 2018, with the exception of two basal shoots that produced 13 nodes before flowering (Fig. 3B). Twenty-two basal shoots of ‘Masja’ produced more than 13 nodes in 2019, which was greater than the number of nodes observed in November 2018 in this cultivar (Fig. 3A). Including these 22 basal shoots, most basal
| Cultivar and line | Shoot type | Year | Number of plants | Number of shoots per plant | Number of flowered shoots per plant | Number of flowered shoots | Number of flowering period durations of basal shoots and previously formed shoots of 23 hydrangea cultivars and lines. |
|------------------|------------|------|------------------|--------------------------|-----------------------------------|--------------------------|----------------------------------------------------------------------------------------------------------------------------------|
| Christmas        | Basal shoot| 2017 | 4                | 4.3 ± 1.5                | 0.1 ± 0.4                          | 0                        | 0.1 ± 0.4                                                                                                                       |
|                  | Basal shoot| 2018 | 4                | 4.5 ± 1.6                | 0.2 ± 0.4                          | 0                        | 0.2 ± 0.4                                                                                                                       |
|                  | Basal shoot| 2019 | 4                | 4.7 ± 1.7                | 0.3 ± 0.4                          | 0                        | 0.3 ± 0.4                                                                                                                       |
|                  | Previously formed shoot| 2018 | 4                | 4.9 ± 1.8                | 0.4 ± 0.5                          | 0                        | 0.4 ± 0.5                                                                                                                       |
|                  | Previously formed shoot| 2019 | 4                | 5.1 ± 1.9                | 0.5 ± 0.6                          | 0                        | 0.5 ± 0.6                                                                                                                       |
|                  | Previously formed shoot| 2020 | 4                | 5.3 ± 2.0                | 0.6 ± 0.7                          | 0                        | 0.6 ± 0.7                                                                                                                       |
|                  | Previously formed shoot| 2021 | 4                | 5.5 ± 2.1                | 0.7 ± 0.8                          | 0                        | 0.7 ± 0.8                                                                                                                       |
|                  | Previously formed shoot| 2022 | 4                | 5.7 ± 2.2                | 0.8 ± 0.9                          | 0                        | 0.8 ± 0.9                                                                                                                       |
|                  | Previously formed shoot| 2023 | 4                | 5.9 ± 2.3                | 0.9 ± 1.0                          | 0                        | 0.9 ± 1.0                                                                                                                       |
|                  | Previously formed shoot| 2024 | 4                | 6.1 ± 2.4                | 1.0 ± 1.1                          | 0                        | 1.0 ± 1.1                                                                                                                       |
|                  | Previously formed shoot| 2025 | 4                | 6.3 ± 2.5                | 1.1 ± 1.2                          | 0                        | 1.1 ± 1.2                                                                                                                       |
|                  | Previously formed shoot| 2026 | 4                | 6.5 ± 2.6                | 1.2 ± 1.3                          | 0                        | 1.2 ± 1.3                                                                                                                       |
|                  | Previously formed shoot| 2027 | 4                | 6.7 ± 2.7                | 1.3 ± 1.4                          | 0                        | 1.3 ± 1.4                                                                                                                       |
|                  | Previously formed shoot| 2028 | 4                | 6.9 ± 2.8                | 1.4 ± 1.5                          | 0                        | 1.4 ± 1.5                                                                                                                       |
|                  | Previously formed shoot| 2029 | 4                | 7.1 ± 2.9                | 1.5 ± 1.6                          | 0                        | 1.5 ± 1.6                                                                                                                       |
|                  | Previously formed shoot| 2030 | 4                | 7.3 ± 3.0                | 1.6 ± 1.7                          | 0                        | 1.6 ± 1.7                                                                                                                       |
|                  | Previously formed shoot| 2031 | 4                | 7.5 ± 3.1                | 1.7 ± 1.8                          | 0                        | 1.7 ± 1.8                                                                                                                       |
|                  | Previously formed shoot| 2032 | 4                | 7.7 ± 3.2                | 1.8 ± 1.9                          | 0                        | 1.8 ± 1.9                                                                                                                       |
|                  | Previously formed shoot| 2033 | 4                | 7.9 ± 3.3                | 1.9 ± 2.0                          | 0                        | 1.9 ± 2.0                                                                                                                       |
|                  | Previously formed shoot| 2034 | 4                | 8.1 ± 3.4                | 2.0 ± 2.1                          | 0                        | 2.0 ± 2.1                                                                                                                       |
|                  | Previously formed shoot| 2035 | 4                | 8.3 ± 3.5                | 2.1 ± 2.2                          | 0                        | 2.1 ± 2.2                                                                                                                       |
|                  | Previously formed shoot| 2036 | 4                | 8.5 ± 3.6                | 2.2 ± 2.3                          | 0                        | 2.2 ± 2.3                                                                                                                       |
|                  | Previously formed shoot| 2037 | 4                | 8.7 ± 3.7                | 2.3 ± 2.4                          | 0                        | 2.3 ± 2.4                                                                                                                       |
|                  | Previously formed shoot| 2038 | 4                | 8.9 ± 3.8                | 2.4 ± 2.5                          | 0                        | 2.4 ± 2.5                                                                                                                       |
|                  | Previously formed shoot| 2039 | 4                | 9.1 ± 3.9                | 2.5 ± 2.6                          | 0                        | 2.5 ± 2.6                                                                                                                       |
|                  | Previously formed shoot| 2040 | 4                | 9.3 ± 4.0                | 2.6 ± 2.7                          | 0                        | 2.6 ± 2.7                                                                                                                       |
|                  | Previously formed shoot| 2041 | 4                | 9.5 ± 4.1                | 2.7 ± 2.8                          | 0                        | 2.7 ± 2.8                                                                                                                       |
|                  | Previously formed shoot| 2042 | 4                | 9.7 ± 4.2                | 2.8 ± 2.9                          | 0                        | 2.8 ± 2.9                                                                                                                       |
|                  | Previously formed shoot| 2043 | 4                | 9.9 ± 4.3                | 2.9 ± 3.0                          | 0                        | 2.9 ± 3.0                                                                                                                       |
|                  | Previously formed shoot| 2044 | 4                | 10.1 ± 4.4               | 3.0 ± 3.1                          | 0                        | 3.0 ± 3.1                                                                                                                      |
| Variety      | Shoot Type          | Year   | No. | Mean ± SE  | Min. ± SE | Max. ± SE | No. (%) | Percentage of Flowered Shoots |
|-------------|---------------------|--------|-----|------------|-----------|-----------|---------|--------------------------------|
| Masja       | Basal shoot         | 2017   | 4   | 5.5 ± 0.8  | 0.3 ± 0.2 | 0.3 ± 0.2 | 6       | 0 (%)                          |
|             |                     |        |     |            |           |           |         |                                |
|             |                     | 2018   | 12  | 7.1 ± 0.7  | 0.3 ± 0.2 | 0.3 ± 0.2 | 6       | 0 (%)                          |
|             |                     | 2019   | 12  | 7.3 ± 1.0  | 0.4 ± 0.4 | 0.4 ± 0.4 | 1       | 0 (%)                          |
| Previously formed shoot | Basal shoot | 2018 | 4   | 4.8 ± 0.6  | 0.3 ± 0.2 | 0.3 ± 0.2 | 6       | 0 (%)                          |
|             |                     | 2019   | 3   | 20.0 ± 1.2 | 7.7 ± 1.4 | 7.7 ± 1.4 | 12      | 0.3 ± 0.3                        |
| Ms. Hepburn | Basal shoot         | 2017   | 4   | 3.0 ± 1.3  | 0         | 0         | 6       | 0 (%)                          |
|             |                     | 2018   | 4   | 10.3 ± 0.9 | 2.5 ± 1.0 | 2.5 ± 1.0 | 25      | 0 (%)                          |
|             |                     | 2019   | 4   | 19.5 ± 1.6 | 8.0 ± 1.7 | 8.0 ± 1.7 | 26      | 0 (%)                          |
| Previously formed shoot | Basal shoot | 2018 | 4   | 3.3 ± 0.7  | 3.3 ± 0.7 | 3.3 ± 0.7 | 100     | 100 (%)                          |
| Otahuku     | Basal shoot         | 2017   | 3   | 15.3 ± 1.4 | 5.3 ± 1.5 | 5.3 ± 1.5 | 35      | 0 (%)                          |
|             |                     | 2018   | 3   | 20.0 ± 1.2 | 7.7 ± 1.4 | 7.7 ± 1.4 | 40      | 1.0 ± 0.8                        |
|             |                     | 2019   | 3   | 27.3 ± 3.1 | 8.0 ± 1.7 | 8.0 ± 1.7 | 28      | 0 (%)                          |
| Previously formed shoot | Basal shoot | 2018 | 3   | 6.0 ± 1.1  | 6.0 ± 1.1 | 6.0 ± 1.1 | 100     | 100 (%)                          |
| Renata      | Basal shoot         | 2017   | 4   | 9.0 ± 1.5  | 0         | 0         | 6       | 0 (%)                          |
|             |                     | 2018   | 4   | 21.5 ± 1.3 | 8.5 ± 0.3 | 8.5 ± 0.3 | 40      | 0 (%)                          |
|             |                     | 2019   | 4   | 23.5 ± 2.2 | 17.5 ± 1.0 | 17.5 ± 1.0 | 76      | 0 (%)                          |
| Previously formed shoot | Basal shoot | 2018 | 4   | 9.0 ± 0.8  | 9.0 ± 0.8 | 9.0 ± 0.8 | 100     | 100 (%)                          |
| Rosea       | Basal shoot         | 2017   | 3   | 17.0 ± 0.8 | 15.3 ± 1.0 | 15.3 ± 1.0 | 45      | 0 (%)                          |
|             |                     | 2018   | 9   | 6.2 ± 0.4  | 6.2 ± 0.4 | 6.2 ± 0.4 | 100     | 0 (%)                          |
|             |                     | 2019   | 9   | 20.3 ± 0.7 | 17.3 ± 1.2 | 17.3 ± 1.2 | 85      | 1.0 ± 0.5                        |
| Previously formed shoot | Basal shoot | 2018 | 3   | 7.0 ± 1.7  | 7.0 ± 1.7 | 7.0 ± 1.7 | 100     | 100 (%)                          |
| Temariezo   | Basal shoot         | 2017   | 4   | 9.0 ± 1.1  | 0         | 0         | 6       | 0 (%)                          |
|             |                     | 2018   | 4   | 18.0 ± 1.4 | 9.0 ± 1.1 | 9.0 ± 1.1 | 52      | 3.3 ± 1.1                        |
|             |                     | 2019   | 4   | 23.5 ± 2.2 | 17.5 ± 1.0 | 17.5 ± 1.0 | 76      | 0 (%)                          |
| Previously formed shoot | Basal shoot | 2018 | 4   | 6.8 ± 0.2  | 6.8 ± 0.2 | 6.8 ± 0.2 | 100     | 100 (%)                          |
| Uzu         | Basal shoot         | 2017   | 4   | 7.5 ± 1.1  | 0         | 0         | 6       | 0 (%)                          |
|             |                     | 2018   | 4   | 5.0 ± 1.3  | 2.0 ± 0.6 | 2.0 ± 0.6 | 54      | 1.5 ± 0.6                        |
|             |                     | 2019   | 4   | 18.8 ± 0.6 | 11.8 ± 0.7 | 11.8 ± 0.7 | 63      | 0.3 ± 0.2                        |
| Previously formed shoot | Basal shoot | 2018 | 4   | 8.0 ± 0.4  | 8.0 ± 0.4 | 8.0 ± 0.4 | 100     | 0 (%)                          |
| No. 5       | Basal shoot         | 2017   | 4   | 7.0 ± 0.9  | 0.3 ± 0.2 | 0.3 ± 0.2 | 6       | 0 (%)                          |
|             |                     | 2018   | 4   | 5.5 ± 1.0  | 3.8 ± 0.7 | 3.8 ± 0.7 | 68      | 1.5 ± 0.6                        |
|             |                     | 2019   | 4   | 18.8 ± 0.2 | 12.8 ± 1.6 | 12.8 ± 1.6 | 68      | 0.3 ± 0.2                        |
| Previously formed shoot | Basal shoot | 2018 | 4   | 9.8 ± 0.2  | 9.8 ± 0.2 | 9.8 ± 0.2 | 100     | 0 (%)                          |
| No. 7       | Basal shoot         | 2017   | 4   | 9.0 ± 1.8  | 0         | 0         | 6       | 0 (%)                          |
|             |                     | 2018   | 4   | 18.0 ± 1.4 | 9.0 ± 1.1 | 9.0 ± 1.1 | 52      | 1.0 ± 0.6                        |

Footnotes:
1. 'First Green', 'Flambeau', 'Green Shadow', 'Hobaria Hoparine', 'Maïhime', 'Renata', and No. 7 were not studied in 2019. Previously formed shoots were studied only in 2018.
2. Mean ± SE.
3. Data in parentheses indicate the percentages of the number of flowered basal shoots for the total number of studied basal shoots.
4. Data could not be collected.
Table 2. Floral initiation in axillary buds expected to develop into basal shoots in November 2018.

| Cultivar | Number of plants* | Studied buds per plant | Number of buds at each developmental stage | Number of buds that started floral initiation | Number of nodes produced in buds |
|----------|-------------------|------------------------|---------------------------------------------|---------------------------------------------|----------------------------------|
|          |                   |                        | 0   1   2   3   4   5                      |                                              |                                 |
| Masja    | 12                | 3.0 ± 0.4*             | 32  0  0  1  2  1                          | 0.3 ± 0.1 (8.9)*                            | 10.9 ± 0.2                     |
| Rosea    | 12                | 3.3 ± 0.4              | 10  0  0  0  1  30                         | 2.5 ± 0.3 (77.4)                            | 10.8 ± 0.6                     |

* Plants studied in Table 1 in 2019 were used for the study.

Mean ± SE.

Data in parentheses indicate the percentages of the number of buds with flower buds for the total number of studied buds.

Fig. 2. Number of nodes produced before floral initiations observed in the axillary buds expected to develop into basal shoots. A: ‘Masja’, B: ‘Rosea’. The number of nodes produced before floral initiation were recorded for the axillary buds expected to develop into basal shoots in November 2018.

Fig. 3. Number of nodes produced before the flowering and flowering periods of basal shoots that flowered in 2019. A: ‘Masja’, B: ‘Rosea’. The number of nodes produced before the flowering and flowering periods was recorded for the basal shoots that flowered in 2019.

shoots of ‘Masja’ flowered in July. By November 2018, the axillary buds without floral initiation had produced approximately 11 nodes in both ‘Masja’ and ‘Rosea’. Flowering frequencies of the basal shoots of ‘Masja’ and ‘Rosea’ were 27% and 89%, respectively, in 2019 and were greater than expected from the observation in November 2018.

Discussion

Consistent with our previous report (Kitamura et al., 2014), flowering period durations of basal shoots were longer than those of previously formed shoots in almost all cultivars. The basal shoots of seven hydrangea cultivars and lines never flowered after August. Therefore, the flowering of basal shoots was not sufficient for unseasonal flowering to occur, especially after August. The factors that contribute to the unseasonal flowering occurrence after August should be considered when attempting to prolong the harvest period for cut hydrangea flowers.

The number of nodes produced in the axillary buds expected to develop into basal shoots before floral initiations observed in November 2018 strongly suggested that the observed flower buds would correspond to the flowers on basal shoots that started anthesis prior to August 2019 in both ‘Masja’ and ‘Rosea’ (Figs. 2 and 3). As mentioned above, the high flowering frequency of basal shoots was not sufficient to account for unseasonal flowering occurrence, particularly after August. In the present study, the basal shoots of several cultivars showed a relatively high flowering frequency, although they never flowered after August. In such cultivars, floral initiation on basal shoots would be complete by the previous autumn. The basal shoots of ‘Rosea’ that flowered after July 2019 produced more nodes than expected from the observation in November 2018, which indicated that the floral initiation occurred after the previous autumn in those basal shoots. Therefore, particularly for unseasonal flowering occurrence after August, floral initiations after the previous autumn would be needed. In 2019, ‘Masja’ also produced flowered basal shoots with a greater number of nodes than expected from the observation in November 2018; however, they never flowered after August. The relatively smaller number of nodes produced in ‘Masja’ basal shoots would have expedited the flowering periods.

In 2019, both ‘Masja’ and ‘Rosea’ developed a greater number of flowered basal shoots than expected from the observation in November 2018. In addition to the floral initiations after the previous autumn, the difficulty in flower bud observation in the early developmental stage may have caused this mismatch. Specifically, buds determined as flower bud developmental stage 0 may have started floral initiation in November 2018.
‘Endless Summer’ and ‘Rosea’ were indicated as cultivars with a high potential for unseasonal flowering on the apical buds of basal shoots. On the other hand, the basal shoots of 13 hydrangea cultivars and lines occasionally flowered after August (Table 1). In the present study, three to seven plants were studied for those 13 cultivars or lines, and nine to 12 plants were studied for ‘Endless Summer’ and ‘Rosea’. The lower number of plants studied could be responsible for the apparent decrease in the flowering frequency of the basal shoots after August in the 13 cultivars and lines. Even so, ‘Endless Summer’ and ‘Rosea’ can be considered as representative cultivars with a high potential for unseasonal flowering occurrence on the apical buds of basal shoots. In contrast, ‘Hatsushimo’, ‘Jyogasaki’, ‘Maihime’, ‘Masja’, ‘Ms. Hepburn’, ‘Uzu’, and No. 5 were representative of cultivars with low potential for unseasonal flowering.

‘Endless Summer’ and ‘Rosea’ were previously identified as cultivars with high potential for flower bud production on axillary buds developed by pinch treatment conducted after spring (Kitamura et al., 2018). Further, Adkins and Dirr (2003) studied flower production on terminal buds of cuttings of several hydrangea cultivars and identified ‘Endless Summer’ as a remontant cultivar. The potential for floral initiations of the apical buds of basal shoots after the previous autumn is associated with the potential of unseasonal flowering on axillary buds developed by pinch treatment conducted after spring and terminal buds of cuttings. Katayama et al. (2017) conducted phylogenetic analysis of some hydrangea cultivars and lines using a nuclear SSR marker and the nucleotide sequence of an internal transcribed spacer (ITS) region and reported that ‘Christmas’, ‘Endless Summer’, and ‘Rosea’ belonged to the same clade. ‘Christmas’ was considered to be a cultivar with relatively high potential for unseasonal flowering of apical buds of basal shoots in our present study. Thus, the high potential for unseasonal flowering observed on the basal shoots of ‘Christmas’, ‘Endless Summer’, and ‘Rosea’ may originate from the same ancestor.

Decreases in temperature and day length in autumn trigger floral induction in hydrangeas from the end of summer to autumn (Struckmeyer, 1950). In particular, temperatures of around 18°C cause floral induction regardless of the photoperiod, while a photoperiod of up to 12 h causes floral induction when the temperature is above 22°C (Bailey and Weiler, 1984; Litlere and Strømme, 1975). Floral initiations in axillary buds expected to become basal shoots can be induced by temperatures of around 18°C in autumn. However, both ‘Masja’ and ‘Rosea’ had axillary buds expected to develop into basal shoots without any floral initiation. Furthermore, ‘Masja’ had more such axillary buds than ‘Rosea’ (Table 2). The differing frequencies of floral initiation and developmental stages of ‘Masja’ and ‘Rosea’ buds in November 2018 suggest a difference in the floral initiation period between the two cultivars (Table 2), and it may be an area of study into the factors that contribute to the floral initiation in the axillary buds expected to develop into basal shoots. The factors that contributed to the floral initiation in the axillary buds expected to develop into basal shoots in the previous autumn or on the basal shoots after the previous autumn were not clear. Determining the factors that contribute to floral initiation on basal shoots after the previous autumn is important for increasing unseasonal flowering occurrence in hydrangeas.

In conclusion, the flowering period duration of hydrangea basal shoots differed among cultivars. The flowering of basal shoots was not sufficient for unseasonal flowering to occur, especially after August. Floral initiations on the apical buds of basal shoots after the previous autumn largely contributed to unseasonal flowering occurrence after August in hydrangeas. Presently, we are aiming to identify the factors that determine floral initiation in the axillary buds expected to develop into basal shoots by studying ‘Masja’ and ‘Rosea’.

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