Benzyladenine Increases Branching but Reduces Root Growth of Herbaceous Perennial Liners

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Abstract. The objective of this study is to evaluate the branching effect of benzyladenine (BA) on herbaceous perennial plants during the production of rooted cuttings (liners) and to examine and quantify the root growth of these liners using multiple methods of root evaluation. Five crops were studied: Agastache Clayt. Ex Gronov. ‘Purple Haze’, Gaura lindheimeri Engelm. & A. Gray ‘Siskiyou Pink’, Lavandula xintermedia Emeric ex Loisel. ‘Provence’, Leucanthemum xsuperbum (Bergmans ex J.W. Ingram) Bergmans ex Kent. ‘Snowcap’, and Salvia xhybrida L. (pro sp.) ‘May Night’. After rooting but before transplant, BA was applied to rooted cuttings as four treatments: controls (0 mg L⁻¹), one application of 300 mg L⁻¹, two applications of 300 mg L⁻¹, or one application of 600 mg L⁻¹. Results varied by crop; all crops except Salvia had increased branching as measured as either increased lateral or basal branches and/or increased leaders at 3 to 4 weeks after initial treatment. Four crops showed reduced root growth, whereas Gaura was unaffected. Root dry weight was found to be highly correlated with root surface area and root volume. After transplant and growing out, branching of the finished plants was increased in Gaura and Lavandula, unaffected in Salvia and Leucanthemum, and decreased in Agastache. Treating rooted cuttings with BA before transplant increased branching but the effects were not long lasting, which suggests that additional applications at or after transplant may improve finished plant quality. Reductions in root growth noted in rooted cuttings did not affect the growth of finished plants. Chemical names: N-(phenylmethyl)-1H-purine-6-amine (benzyladenine, BA).

To meet the challenges of producing plants for sale, growers frequently use plant growth regulators (PGRs) to control plant height, branching, and flowering. BA is a PGR that increases branching in floriculture crops when sprayed on containerized plants (Carey et al., 2009; Farris et al., 2009; Martin and Singletary, 1999). The addition of BA, a synthetic cytokinin, increases the ratio of cytokinin to auxin in the plant, disrupting apical dominance (Cline, 1991). This results in more basal and/or lateral branching and fuller plants. The effects of BA vary with cultivar: of 10 Hosta (Funkia K. Spreng; Niobe Salish) cultivars treated with 1250 to 3750 mg L⁻¹ foliar sprays of BA, five cultivars had an increased number of offsets (Garner et al., 1997).

Chemical PGRs are often used during plug and rooted cutting (liner) production but must be used with care for efficacy and to prevent unwanted effects such as phyto- toxicity or delayed flowering. These PGR applications are typically made at 2 to 4 weeks after liners have been transplanted, when plants are established and in active growth (Albrecht and Tayama, 1992). However, we are interested in testing the use of BA at an earlier stage of plant production on liners before transplant. Because liners are still in smaller cells, they are easier to treat with PGRs than plants that have already been transplanted into larger containers and less chemical is required per plant, so growers can save money by spraying earlier in the plant production cycle. Some commercial producers of liners have reported reduced root mass in plants treated with BA (personal communication). BA has been shown to reduce root growth in in vitro Arabidopsis seedlings (Auer, 1996). Sedum leaf cuttings treated with BA at concentrations of 8 to 500 mg L⁻¹ exhibited reduced root growth and increased shoot growth at all concentrations (Boe et al., 1972). Other research has shown BA has no effect on the root growth of treated plants (Khosh-Khui et al., 1978; Leclerc et al., 2006; Richards and Wilkinson, 1984).

However, application of BA to unrooted cuttings of Verbena ×hybrida Voss, which had already initiated adventitious root formation, had no effect on root growth, whereas low rates of BA (30 mg L⁻¹) applied to cuttings before initiation of adventitious root formation increased root dry weight of liners at 12 d after treatment (Svenson, 1991).

The process of liner production has been divided into five stages: Stage 0, before arrival or harvest of cuttings; Stage 1, cutting arrival or harvest and trimming; Stage 2, calusing; Stage 3, root development; and Stage 4, toning the rooted cutting. During Stage 4 the roots are grown enough so that the root ball will hold together when pulled from the plug tray (Dole and Hamrick, 2006). The objective of this study is to evaluate the effects of the application of BA to herbaceous perennial plants during liner production, specifically during Stage 3, on root growth and shoot branching of the finished liners (Stage 4).

Materials and Methods

Five plant species were studied: Agastache ‘Purple Haze’, Gaura lindheimeri ‘Siskiyou Pink’, Lavandula xintermedia ‘Provence’, Leucanthemum xsuperbum ‘Snowcap’, and Salvia xhybrida ‘May Night’. Plants arrived as unrooted cuttings, which were dipped for 10 sec in 1500 mg L⁻¹ indole-3-butyric acid (IBA) rooting hormone (Hortus IBA Water Soluble Salts 20% IBA; Hortus USA Corp., New York, NY) as a basal treatment and stuck into 72 size (height 5.71 cm, volume 35.4 mL) trays filled with a peat moss media with pine bark, perlite, and vermiculite (45%, 25%, 15%, and 15%, respectively; Fafard 3B; Conrad Fafard, Inc., Agawam, MA). Cuttings were allowed to root under mist with bottom heat at 22 °C (72 °F). Twenty-seven to 34 d after sticking, depending on crop, plants were removed from mist and bottom heat. Cuttings received clear water under mist, but after removal from mist received 100 mg L⁻¹ nitrogen with each irrigation using 20N-4.4P-16.6K Peters Professional General Purpose fertilizer (The Scotts Co. LLC, Marysville, OH).

Benzyladenine (Configure; Fine Americas, Inc., Walnut Creek, CA) was applied to liners at least 8 h after removal from mist. This was considered the Week 0 treatment. The BA treatments included: control (0 mg L⁻¹), one application of 300 mg L⁻¹, two applications of 300 mg L⁻¹ (one application at Week 0 and the second application 2 weeks later), or one application of 600 mg L⁻¹. Treatments were applied when roots from cuttings were evident on all four sides of the root ball but liners were not fully rooted and ready for transplant. Treatments were applied as foliar sprays of BA with a CO₂ backpack sprayer (R&D Sprayers, Inc., Opelousas, LA) applying 210 mL m⁻². Plants were grown in a double polyethylene greenhouse located in Blacksburg, VA (lat. 37.23°N, long. 80.42°W) from January through Apr. 2010. Greenhouse light levels averaged 17.8 mol·m⁻²·d⁻¹ and
temperatures averaged 68.4 °F. The experimental setup was a completely randomized design with each plant species conducted as a separate experiment. Experimental units consisted of six plants in a single six-cell pack with four replications of the experimental unit per treatment for each of three destructive harvests for each crop. An additional set of replications was included for evaluation of how the liners grow out as described subsequently.

Data were collected at 0, 2, and 4 weeks after initial treatment (WAIT) on individual plants in each experimental unit (except at 0, 2, and 3 WAIT on \textit{Agastache} as a result of vigorous growth) and included plant height measured from the top of the container, average width, which was the average of the width measured at the widest point of the plant and again perpendicular to this point, number of branches, number of plants in flower, and phytotoxicity. Branches were counted if they were 2 mm long or longer. Based on growth habit, branches counted in \textit{Leucanthemum} and \textit{Salvia} were basal branches, which had no secondary laterals, and in \textit{Agastache}, \textit{Gaura}, and \textit{Lavandula}, leaders (primary branches with secondary lateral branches) and secondary lateral branches were counted.

For root measurements and root and shoot dry weights, all six plants from the experimental unit (cell pack) were pooled. Media was washed off of roots by hand using a screen to prevent loss of roots. Roots were washed randomly by experimental unit. To better understand BA’s effects on root growth and development, roots were scanned at each harvest using WinRhizo (Regent Instruments Inc., Quebec, Canada) and analyzed to determine root surface area and root volume. Root surface area and volume were determined by first washing all media off roots by hand and then scanning roots using WinRhizo. Root and shoot dry weights were determined after drying roots and shoots at 66 °C (150 °F) for 48 h. Root:shoot dry weight ratio was calculated on an experimental unit basis using total shoot dry weight (shoot plus flowers, when present). Although the WinRhizo allowed detailed measurement of root growth characteristics, the process was very time-consuming. To facilitate future research, we evaluated the correlation between root dry weight and the root surface area and root volume data from the WinRhizo analysis. Root dry weights of BA-treated and untreated plants at all times of measurement (0, 2, and 3 to 4 WAIT) were compared with root volume and root surface area for each species studied.

After data were collected at 4 WAIT, eight plants of each treatment were randomly selected from the remaining replications, potted into quart-sized plastic pots (1.1 L) filled with Fafard 3B medium, and grown out for a period of 4 additional weeks to assess liner treatment effects on the finished plant. These plants were arranged as single plant replications in a completely randomized design for each crop. On finished plants, data measurements included height, width, and numbers of leaders and lateral or basal branches as applicable and the number of plants flowering.

Data were analyzed by analysis of variance and subjected to least significant difference means separation (P ≤ 0.05) using SAS Version 9.2 by SAS Institute Inc. (Cary, NC) and JMP®9.0 ©2010 SAS Institute Inc. Correlation of root dry weight to root volume and surface area was performed by bivariate analysis and linear regression in JMP®9.0.

\section*{Results}

In all plants, measurements were taken at 0 WAIT to ensure uniformity. At this time, there were no significant differences between control plants and plants treated with BA in plant height, width, numbers of leaders and lateral branches or basal branches, root or shoot dry weights, root surface area, root volume, or root:shoot ratio (data not presented). None of the cuttings were flowering. No significant phytotoxicity was noted in plants at any data collection times.

\textit{Agastache 'Purple Haze'}. At 2 WAIT, all plants treated with BA showed significant increases in the number of lateral branches as compared with control plants (8.8 to 12.4 vs. 2.5), although there were no significant differences in height, width, the number of leaders, or shoot dry weight (data not presented). Root surface area and volume measurements were lower than control plants only in plants treated with one application of 300 mg L⁻¹, whereas plants assigned to the two applications of 300 mg L⁻¹ BA had greater root volume than controls. Because these plants had not yet been treated the second time, this suggests significant variability in the root growth response. There were no significant differences in root dry weights but the root:shoot ratio was significantly lower than controls in plants treated with one application of either 300 or 600 mg L⁻¹ BA (data not presented).

At 3 WAIT, although plant height, width, and number of leaders were unaffected, all BA-treated \textit{Agastache} liners showed an increase in the number of lateral branches as compared with control plants (Table 1). Although shoot dry weight was unaffected, all BA-treated plants had less root dry weight, root surface area, and root volume than control plants, resulting in lower root:shoot ratios relative to control plants. Root growth of \textit{Agastache} liners treated with two applications of 300 mg L⁻¹ or one application of 600 mg L⁻¹ had the greatest reductions in root dry weight.

On finished plants, height and width of BA-treated plants were not different from control plants but plants treated at the higher BA concentrations (two applications of 300 mg L⁻¹ or one application of 600 mg L⁻¹) had fewer leaders and lateral branches than control plants or those treated with a single application of 300 mg L⁻¹ BA (Table 2). There were no differences between BA-treated and untreated plants in the number of plants flowering (data not presented).

\textit{Agastache} liners treated with BA showed increased lateral branches and decreased root growth at 3 WAIT; however, finished plants treated with the higher treatment concentrations in the liner stage had fewer lateral branches.

\textit{Gaura lindheimeri 'Siskiyou Pink'}. At 2 WAIT, BA-treated \textit{Gaura} liners showed no significant differences in height or numbers of leaders or lateral branches as compared with controls (data not presented). Shoot dry weight increased in liners treated with two applications of 300 mg L⁻¹ BA or one application of 600 mg L⁻¹ BA when compared with control plants (data not presented). Root dry weight, surface area, and volume were greater than controls in plants treated with one application of 300 mg L⁻¹ BA (data not presented). Root:shoot ratio was greater than controls in plants treated with one or two applications of 300 mg L⁻¹ BA. Again, because the second application of the 300 mg L⁻¹ BA had not yet been applied, there is some variability in liner response to the 300 mg L⁻¹ BA treatment.

At 4 WAIT, BA-treated \textit{Gaura} liners showed no significant differences in plant height or width as compared with the control plants (Table 1). However, all \textit{Gaura} liners treated with BA had more leaders than the untreated control plants; the number of lateral branches on these shoots at this time was not different from control plants. Shoot dry weight was greater in BA-treated plants than in control plants (Table 1). Root growth was unaffected by BA treatment; there were no significant differences in root dry weight, root surface area, root volume, or root:shoot ratio compared with control plants. In \textit{Gaura} liners, treatment with BA resulted in more shoot growth at 4 WAIT without significantly affecting root growth.

In finished \textit{Gaura} plants, there were no significant treatment effects on plant height or width (Table 2). However, all plants treated with BA had significant increases in the number of leaders and lateral branches relative to the untreated control plants. The branching effects of BA in \textit{Gaura} liners were persistent in the finished plants. There were no differences in the number of plants in flower between BA-treated and untreated plants (data not presented).

\textit{Lavandula ×intermedia 'Provence'}. For \textit{Lavandula} at 2 WAIT, there were no significant differences in BA-treated plants in plant height, width, number of leaders, number of lateral branches, or shoot dry weight as compared with control plants (data not presented). All liners treated with BA had significant reductions in root dry weight, root surface area, root volume, and root:shoot ratio at 2 WAIT as compared with control liners (data not presented).

At 4 WAIT, \textit{Lavandula} liners treated with two applications of 300 mg L⁻¹ or one application of 600 mg L⁻¹ BA were significantly taller than untreated controls (Table 1). Width was significantly increased only with two applications of 300 mg L⁻¹ BA. Only liners treated with one application of 600 mg L⁻¹
BA had increased numbers of leaders and lateral branches as compared with control plants. Shoot dry weight increased with all BA treatments as compared with control liners. Root surface area, volume, and root:shoot ratio were reduced in all BA-treated Lavandula liners relative to controls at 4 WAIT, although root dry weight was significantly reduced only with two applications of 300 mg L\(^{-1}\) BA.

Finished Lavandula plants treated with multiple applications of BA were taller than control plants, but two applications of 300 mg L\(^{-1}\) or a single application of 600 mg L\(^{-1}\) BA reduced plant width as compared with control plants (Table 2). Plants treated with two applications of 300 mg L\(^{-1}\) BA had greater numbers of leaders and lateral branches than control plants. Lavandula did not flower during this study.

At 4 WAIT, BA-treated Lavandula liners showed increased numbers of leaders and lateral branches at the highest BA concentration and decreased root growth with all BA treatments; however, only plants treated with two applications of 300 mg L\(^{-1}\) showed persistent increases in branching in finished plants.

Leucanthemum ×superbun 'Snowcap'. At 2 WAIT, Leucanthemum liners treated with BA were not significantly different from controls in the shoot measurements of plant height, width, number of basal branches, or shoot dry weight (data not presented). However, root dry weight, root surface area, and root volume were significantly less in plants treated with BA as compared with controls (data not presented). Liners treated with one application of either 300 mg L\(^{-1}\) BA or 600 mg L\(^{-1}\) BA had significantly lower root: shoot ratios as compared with control liners (data not presented).

At 4 WAIT, Leucanthemum liners treated with BA showed no significant differences in plant height or width relative to controls (Table 1). However, the number of basal branches was significantly increased with all BA treatments as compared with control liners. Shoot dry weight was significantly increased only with two applications of 300 mg L\(^{-1}\) BA. Root growth was significantly affected by BA; root dry weight, root surface area, root volume, and root:shoot ratio were significantly decreased in all BA-treated liners as compared with controls.

Finished Leucanthemum plants treated with BA showed no significant differences in plant height but plants treated with one application of 600 mg L\(^{-1}\) had a 14% reduction in width relative to control plants (Table 2). The number of basal branches on finished plants was unaffected by BA treatments as compared with control plants. Leucanthemum did not flower during this study.

Leucanthemum liners treated with BA had significantly greater basal branching and decreased root growth at 4 weeks after initial treatment when compared with controls, although this branching improvement was no longer evident in the finished plants.

Salvia ×sylvestris 'May Night'. At 2 WAIT, BA-treated Salvia liners showed no significant differences in plant height, width, number of basal branches, or shoot dry weight when compared with control plants (data not presented). Root dry weight, surface area, and volume were significantly reduced in all BA-treated liners as compared with controls. There was no significant difference in root:shoot ratio in BA-treated liners relative to control plants (data not presented).
At 4 WAIT, BA-treated Salvia liners had no significant differences in plant height, width, number of basal branches, or shoot or root dry weight relative to control liners (Table 1). However, root surface area and root volume were significantly reduced in liners treated with a single application of 300 mg L\(^{-1}\) or 600 mg L\(^{-1}\) BA as compared with those of control liners.

Finished Salvia plants treated with BA showed no significant differences in plant height, width, or number of basal branches when compared with control plants (Table 2). Salvia did not flower during this study.

At 4 WAIT, BA treatment did not significantly increase branching of Salvia liners, although root surface area and volume decreased with one application of 300 or 600 mg L\(^{-1}\) BA. After transplant and grow out, there were no differences in the finished Salvia plants.

**Correlations of root measurements.** Root growth of liners is important to growers because adequate roots are necessary to ensure plant establishment after transplant. Because our liners had reasonable root initiation (Stage 3) before BA treatment, we wanted to assess the impact of BA on root growth. We found that root surface area and root volume were each highly correlated (\(P < 0.0001\)) with root dry weight for all five crops (Fig. 1). Coefficients of determination \((r^2)\) of root dry weight to root surface area ranged from 0.7342 for Gaura to 0.876 for Lavandula. Coefficients of determination \((r^2)\) of root dry weight to root volume ranged from 0.7444 for Gaura to 0.9496 for Lavandula. Although the WinRhizo scans allowed measurement of root surface area and root volume, which would have been extremely difficult to collect by hand, the scanning process was very time-consuming. Because the data in this study were highly correlated, roots scans did not provide significantly more information than provided by root dry weight alone.

**Discussion**

Treating perennial plant liners with BA before the transplant stage changed the plants’ growth habits, although the results varied by species, as expected (Basra, 2000). Treatment effects were most noticeable at 4 weeks after initial treatment. At this time, lateral or basal branches and/or leaders, which are measures of a plant’s fullness, showed significant increases in BA-treated liners of all crops studied except Salvia compared with untreated plants. The branching results are similar to those of Martin and Singletary (1999) where 18 herbaceous perennials were screened for response to 1000, 2000, or 4000 mg L\(^{-1}\) BA applied as a foliar spray after transplant; the majority (89%) of the BA-treated plants developed significantly more offshoots than untreated controls but root growth was not assessed. In their study, no additional branching was seen in the higher two concentrations as compared with 1000 mg L\(^{-1}\) BA (Martin and Singletary, 1999), and later studies have used lower concentrations with good success (Carey et al., 2008; Farris et al., 2009). Drench or foliar application of BA at concentrations from 250 to 2000 mg L\(^{-1}\) increased vegetative shoots, reproductive shoots, and flower buds in Coreopsis verticillata L. ‘Moonbeam’; however, plants treated with 1000 or 2000 mg L\(^{-1}\) BA had persistent symptoms of phytotoxicity and a 10-15 delay in flowering as compared with only transient phytotoxicity and a 7-d delay in flowering in plants treated with 250 or 500 mg L\(^{-1}\) BA (Farris et al., 2009).

After growing out for 4 weeks, only finished plants of Gaura and Lavandula showed persistent improvements in branching as a result of the BA treatment. Finished Salvia and Leucanthemum plants showed no significant branching effects after growing out, whereas Agastache plants showed less branching at two treatment concentrations.

The persistence of the branching effect of BA varied with species, as seen in results by Latimer and Freeborn (2009) in which the increases in branching in herbaceous perennials treated with foliar sprays of 600 mg L\(^{-1}\) BA after transplant to quart size pots ranged from 2 weeks in Leucanthemum × ‘Alaska’ to 6 weeks in Euphorbia ‘Chameleon’. Plants metabolize BA at differing rates; even different cultivars of the same species are different (Auer et al., 1992). Because plants metabolize BA quickly, in \(\approx 10\) d (Carey et al., 2009), multiple applications over the production cycle may be more effective than a single application.

Plant growth regulators affect root growth as well as shoot growth in plants (Basra, 2000). Low concentrations of BA, 30 mg L\(^{-1}\), applied to unrooted cuttings as foliar sprays immediately or 12 h after sticking, increased root dry weight in Verbena evaluated 12 d later when compared with untreated controls, whereas 300 mg L\(^{-1}\) BA tended to reduce root dry weight (Svenson, 1991). The multiple applications and higher rate used in our studies had greater effects on root dry weight. Furthermore, Svenson (1991) found that BA applications later than 48 h after sticking had no effect on the cuttings. BA at 400, 800, or 1200 mg L\(^{-1}\) applied to seedlings of four cultivars of Coleus blumei benth after transplant increased the number of branches but did not affect root growth (Khosh-Khui et al., 1978). Similarly, in BA-treated Hemerocallis ‘Happy Returns’, the number of divisions per
plant was increased, whereas root fresh weight was unaffected (Leclerc et al., 2006). In their review of the role of cytokinins in adventitious root formation, Van Staden and Harty (1988) concluded that root initiation and root elongation are affected differently by exogenous cytokinins in that root initiation is more sensitive to inhibition by high levels of cytokinins than is root elongation. In our studies, BA was applied during root elongation. Root measurements showed significant reductions in BA-treated Agastache, Lavandula, Leucanthemum, and Salvia liners at 4 WAIT (3 WAIT for Agastache). However, these plants did not show any reduced shoot measurements at this time. Thus, these reductions in root growth did not appear to affect shoot growth. Root:shoot ratio decreased in BA-treated Agastache, Lavandula, and Leucanthemum liners at 4 WAIT (3 WAIT for Agastache). In our studies, BA seemed to encourage shoot growth at the expense of root growth.

Root surface area and volume measurements were highly correlated with root dry weight. These results are similar to those of McPhee (2005) in a study of Pisum sativum L. seedlings in which root dry weight was
highly correlated with root volume and root length. Because the intent of our study was to study the effects of BA on the root and shoot growth of liners, root and shoot dry weight measurements were not taken for plants after transplant and growing out for an additional 4 weeks; however, these measurements would be helpful in future studies in understanding the effects of BA on plants as they grow to marketable size.

Treating plants with BA as liners before transplant resulted in more branching, which produced a liner that appeared fuller at an earlier stage of growth. However, in most of the crops tested, branching of the untreated liners eventually matched that of plants treated with BA, suggesting that multiple applications of BA may be beneficial. Root growth of liners of some crops was reduced by BA treatments but this reduction did not seem to influence the overall growth of the finished plants. In summary, herbaceous perennial plant liner producers may use BA to increase liner size and branching without a major impact on subsequent plant establishment. Finished plant producers should consider applying BA again on responsive plants either in the flat before transplanting or in the finishing container shortly after transplanting.

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