Gibberellin, Light, and Low-temperature Effects on Flowering of *Aquilegia*

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Abstract. *Aquilegia xhybrida* 'Bluebird' and 'Robin', grown as greenhouse pot plants, initiated flower buds before cold exposure (4.5C) under supplemental high-pressure sodium lamps in mid-December, 5.5 months from sowing. Low temperature was the primary environmental factor that affected floral development in 'Bluebird'. As the length of the cold exposure increased, the time between appearance of visible buds, anthesis, and petal shattering decreased, as did inflorescence number and total flower number per plant. Gibberellic acid (GA₃) at 100 or 200 mg-liter⁻¹ accelerated the appearance of visible buds during forcing in treatments without cold exposure. Soil drench applications of GA₃ 2 weeks before cold treatment accelerated floral development more than GA₃ applied after cold exposure. Inflorescence number and total flower number per plant were reduced by 4 or 8 weeks but not by 2 weeks of exposure to cold. The developmental rate of "Robin", i.e., appearance of visible buds and anthesis, was quicker in plants with 18 to 20 leaves than in those with 12 to 14 leaves.

Aquilegia, a well-known garden perennial, has potential as a year-round greenhouse cut flower or pot plant crop if provided the proper environmental and chemical management. Vernalization is believed to be the primary natural environmental factor required for flower induction in *Aquilegia* (Weiler and Shedron, 1985). *Aquilegia* responded most readily to cold after they reached a critical size (Shedron and Weiler, 1982). Holding at 4 to 5C for 10 weeks was sufficient for 100% flowering of 'McKana's Giant' plants that were at the 12- to 15-leaf stage, whereas only 50% of seven- to eight-leafed plants flowered. No plants of 'Fairylend' or 'Crimson Star' with seven to eight leaves flowered. 'Fairylend' flowered 100% with 15 leaves and 4 weeks at 4 to 5C, while it took 8 weeks at 4 to 5C for 15-leafed plants of 'Crimson Star' to flower 100%. Long photoperiods slightly advanced flowering but caused excessive petiole elongation. Damin-oxide sprays reduced petiole elongation. GA₃ induced flowering in some plants receiving insufficient cold but also caused weak growth (Shedron and Weiler, 1982).

New cultivars of *Aquilegia* have been bred and selected for larger flowers, shorter stature, and more uniform growth than older cultivars. The new cultivars may be adaptable to year-round potted plant culture; how-

ever, we found no reports detailing their response to gibberellin, light, or cold. The objective of this study was to determine the effects of gibberellin, light, and low temperature on flowering of nonvernalized Weddle's Songbird series *Aquilegia* cultivars used for greenhouse pot plant culture.

Seeds of Weddle's Songbird series 'Bluebird' and 'Robin' were sown in late July 1986 and shipped from Colorado to Pennsylvania on 7 Oct., when they had four to five leaves. They were transplanted to 7.5-cm (250-cm³) round pots on 14 Oct. 1986 and grown in the Pennsylvania State Univ. greenhouses using high-pressure sodium (HPS) lamps at 10.9 mol·day⁻¹·m⁻² to provide supplemental irradiation of 200 μmol·s⁻¹·m⁻² and extending the photoperiod to 18 hr as natural daylengths shortened. Thermostats were set at 21/16C (day/night). The potting medium was 1.6 vermiculite : 1.6 sphagnum peat :

1 soil (by volume), plus dolomitic lime (4.3 kg·m⁻³), superphosphate (341 g·m⁻³), KNO₃ (568 g·m⁻³), and fritted trace elements (71 g·m⁻³). Plants were fertilized at each irrigation. Pipron was applied weekly to control powdery mildew. Seedlings at either the 12- to 14-leaf stage on 28 Jan. 1987 (age 1) or at the 18- to 20-leaf stage on 26 Feb. (age 2) were held at 4.5C for various durations and/or exposed to GA₃ treatments.

Cold exposure and light source with 'Bluebird' (Expt. 1). Age 1 'Bluebird' plants were moved into a 4.5 ± 0.5C cold storage room and held there 0, 2, 4, or 8 weeks, starting on 28 Jan. 1987. A 24-hr photoperiod with 5.9 mol·day⁻¹·m⁻² (irradiance 68.3 μmol·s⁻¹·m⁻²), produced by 215-W cool-white fluorescent lamps (FL), was used in the room. After the cold treatment, one-half of the 192 plants was moved to a greenhouse with an 18-hr photoperiod, produced by a combination of natural daylength and 10.9 mol·day⁻¹·m⁻² supplemental HPS irradiance (168.2 μmol·s⁻¹·m⁻²), while the other half was placed in a growth room with an 18-hr photoperiod, and 11.6 mol·day⁻¹·m⁻² (179 μmol·s⁻¹·m⁻²) irradiance produced by 215-W FL. Experiment 1 was in a split-plot design with cold exposure as the main plot and light source as the subplot. There were four replications with three plants per treatment.

GA₃ cold exposure, and light source with 'Bluebird' (Expt. 2). The cultivar and environmental conditions were the same as those used in Expt. 1. However, only 0 or 2 weeks of cold exposure were used. On 28 Jan. 1987, at the start of cold exposure, GA₃ was applied as a soil drench using 25 ml/pot at 0, 100, or 200 mg-liter⁻¹. After cold exposure, the two light sources and forcing locations as in Expt. 1 were used. The experiment was in a split-plot design with GA₃ as the main plot, cold exposure as the subplot, and light source as the sub-subplot. There were four replications with three plants for each treatment.

Plant age and cold exposure with 'Robin' (Expt. 3). This experiment consisted of the

Table 1. Effects of light source and holding at 4.5C on floral development of *Aquilegia* 'Bluebird' (Expt. 1).^a

Time at 4.5C (weeks)	VB ^b (days)	VB-A ^c (days)	A-S ^w (days)	Inflorescence ht (cm)	Inflorescences (no.)	Total flowers (no.)
<i>Fluorescent lamps in growth room</i>						
0	18.6	10.3	61.7	23.3	7.4	19.2
2	21.8	12.4	57.5	21.9	7.2	19.8
4	41.5	11.5	36.9	20.3	5.4	11.3
8	69.8	11.0	21.6	21.9	4.5	7.2
Significance ^z	LQ	NS	L	NS	L	L
<i>High-pressure sodium lamps in greenhouse</i>						
0	14.8	10.8	61.3	21.0	6.8	21.1
2	21.2	12.1	53.0	23.8	5.9	17.1
4	49.3	16.7	33.2	31.2	3.3	7.7
8	71.2	13.8	33.5	23.6	2.3	6.8
Significance	LQ	NS	LQ	NS	L	L

^aNS, L, LQ: nonsignificant, linear, linear and quadratic regression significance at *P* = 0.05, respectively.

^bVB: days from the beginning of treatments to first visible bud appearance.

^cVB-A: days between appearance of visible buds and anthesis.

^wA-S: days between anthesis and shattering.

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Table 2. Effects of GA₃, cold, and two light sources/growing locations on floral development of *Aquilegia* 'Bluebird' (Expt. 2).

Time at 4.5C (weeks)	GA ₃ (mg·liter ⁻¹)	VB* (days)	VB-A* (days)	A-S* (days)
<i>Fluorescent lamps in growth room</i>				
0	0	18.6	10.3	61.7
	100	11.3	9.1	60.7
	200	9.8	9.2	61.0
Significance		L	NS	NS
2	0	21.8	12.4	57.5
	100	21.3	10.8	61.8
	200	21.5	11.3	54.6
Significance		NS	NS	NS
GA × CD ^w		**	NS	NS
<i>High-pressure sodium lamps in greenhouse</i>				
0	0	14.8	10.8	61.3
	100	9.6	11.3	61.1
	200	9.3	10.8	63.4
Significance		L	NS	NS
2	0	21.2	12.1	53.0
	100	19.9	11.9	60.8
	200	23.2	12.0	49.6
Significance		NS	NS	Q
GA × CD		**	NS	**

*VB: days from the beginning of treatment to first visible bud appearance.

*VB-A: days between appearance of first visible bud and anthesis.

*A-S: days between anthesis and shattering.

^wGA × CD: GA₃ by cold interaction.

NS,*,**Nonsignificant or significant at *P* = 0.05 or 0.01, respectively.

two plant ages noted earlier and four periods of cold exposure. 'Robin' plants were put into cold storage as described in Expt. 1, also for 0, 2, 4, or 8 weeks. The design had age as the main plot and duration of cold exposure as the subplot.

Plant age and GA₃ with 'Robin' (Expt. 4). Plants were exposed either 0 or 2 weeks to 4.5C. GA₃ was applied at 0 or 100 mg·liter⁻¹ to 'Robin' plants of each of the two age groups just before moving them to a greenhouse with natural photoperiods where they remained until flowering. Age was the main plot and GA₃ the subplot.

Cold exposure, plant age, and GA₃ with

'Robin' (Expt. 5). Plants were exposed 2, 4, or 8 weeks to 4.5C. GA₃ was applied to 'Robin' plants of each age group at 100 mg·liter⁻¹ weekly for 4 weeks, starting either before exposure to 4.5C or after 2 weeks of such treatment. Cold exposure was the main plot, plant age the subplot, and GA₃ treatment the sub-subplot.

Data collected were the dates of the appearance of visible buds (VB) and anthesis (when stamens could be seen), and the last flower shattering (all the petals and sepals had fallen off); inflorescence height (from the top of the crown to the tip of the highest inflorescence); and total number of flowers per plant. Peduncle and flower number were also recorded periodically over the entire flowering period.

Cold exposure and light source with 'Bluebird' (Expt. 1). Flowers had initiated before being exposed to cold, thus low temperature was not required for induction. Cold exposure delayed flower development (Table 1). There were linear and quadratic responses to increasing weeks of cold exposure for each light source. Flower development (total crop time minus days exposed to cold) between treatment and first VB appearance was delayed by exposure to 4 or 8 weeks of cold compared to 0 or 2 weeks of cold. Plants exposed to 4 or 8 weeks of cold needed 12 to 14 days to develop a VB, but with 2 weeks of cold, only 7 days were needed. There was a linear decrease in inflorescence and total flower number per plant with increasing cold exposure for each light source (Table 1).

All plants flowered in every treatment. Flowering response to duration of cold exposure was very similar under the FL and HPS lamps (Table 1). Cold exposure delayed floral development from treatment to VB and to anthesis but not from VB to anthesis under FL or HPS, except with 4 weeks of cold exposure. The longer plants were exposed to cold, the slower flower buds developed. Cold exposure did not significantly affect the time from VB to anthesis, but the longer the cold period, the shorter the time from anthesis to shattering.

GA₃, cold exposure, and light source with 'Bluebird' (Expt. 2). Buds appeared sooner on GA₃-treated noncooled plants without significantly reducing inflorescence height or total number of flowers for both FL- and HPS-treated plants (Table 2). Visible buds also appeared significantly sooner on plants not exposed to cold or GA₃ than on those treated with GA₃ at 200 mg·liter⁻¹ or 100 mg·liter⁻¹ (Table 2). Thus, GA₃ shortened the time interval between initiation and VB, but not between VB and anthesis nor between anthesis and shattering of buds for noncooled plants with either light source.

There was a significant interaction between GA₃ and cold exposure within light sources (Table 2). Noncooled plants treated with GA₃, under FL or HPS lamps, had a linear decrease in days to VB as GA₃ concentration increased. Plants exposed to 2 weeks of cold developed VB about equally rapidly at all GA₃ concentrations. Flower color was more intense and flower development was more uniform (data not presented) with FL in the growth room.

Neither light source, GA₃, cold exposure, nor age of plants at time of treatment significantly affected the time interval between VB and anthesis. However, for each light source, with 2 weeks of cold exposure, the time between anthesis and petal shattering was least at 0 or 200 mg and greatest at 100 mg·liter⁻¹ GA₃. Light source, duration of cold exposure, or GA₃ did not significantly influence inflorescence height or the total number of flowers.

Plant age and cold exposure with 'Robin' (Expt. 3). Older plants developed flowers faster than younger plants (Table 3). Cold exposure time delayed the appearance of VB and anthesis at each plant of age 1 and 2; as the length of the cold period increased, buds appeared later, with a significant quadratic response. There was a significant quadratic response with more flowers on age 1 plants as cold exposure time increased but not with age 2 plants. Age 1 plants had more inflorescences without cold exposure, while age 2 plants had longer inflorescences with no cold exposure. Time to VB was 5 days for age 2 plants, but 20 days in age 1 plants.

Plant age and GA₃ with 'Robin' (Expt. 4). When treated with GA₃ at 100 mg·liter⁻¹, age 1 plants developed VB and reached anthesis after fewer days of forcing than age 2 plants. The interval from VB to anthesis was longer in age 2 plants than age 1 plants. Age 2 plants' inflorescences were shorter, but number of inflorescences and flowers were fewer in age 2 than in age 1 plants. GA₃ had no effect on days to VB, total number of flowers and inflorescences, or on inflorescence height regardless of plant age. However, plants of age 2 not treated with GA₃ reached VB in ≈15 days, whereas others required between 22 and 30 days (difference significant at *P* = 0.05).

Cold exposure, plant age, and GA₃ with 'Robin' (Expt. 5). GA₃ treatment applied before cold exposure accelerated the development of floral buds to VB more than when applied after cold exposure, but did not sig-

Table 3. Effects of plant age and holding at 4.5C on floral development of *Aquilegia* 'Robin' (Expt. 3).

Plant age ^z	Time at 4.5C (weeks)	VB* (days)	Inflorescence ht (cm)	Inflorescences (no.)	Total flowers (no.)
1	0	24.8	29.9	3.7	22.7
	2	57.7	23.4	2.0	10.9
	4	59.6	27.0	2.5	11.0
	8	86.7	23.0	2.2	5.7
Significance ^x		LQ	NS	L	LQ
2	0	15.2	26.8	1.4	5.2
	2	42.2	19.5	2.4	10.1
	4	46.0	18.1	2.2	6.7
	8	61.0	---	---	---
Significance		LQ	L	NS	NS
AGE × CD ^y		**	*	*	**

^zAge 1: 12–14 leaves (28 Jan. 1987); Age 2: 18–20 leaves (26 Feb. 1987)

*VB: days from the beginning of treatment to first visible bud appearance.

^xNS, L, LQ: nonsignificant, linear, linear and quadratic regression significance at *P* = 0.05.

^y---; anthesis not observed by termination of experiment.

^wAGE × CD: age by cold interaction.

NS,*,**Nonsignificant or significant at *P* = 0.05 or 0.01, respectively.

Table 4. The effect of GA₃ application time and duration of holding at 4.5C on percentage of plants that flowered for two ages of *Aquilegia* 'Robin' (Expts. 4 and 5).

	Treatments		Flowering	
	GA ₃ (mg·liter ⁻¹)	Time at 4.5C (weeks)	Age 1 (%)	Age 2 (%)
GA ₃ and age ^z	0	0	100	81.3
	100	0	100	87.5
	0	2	62.5	75.0
LSD 5%			10.5	6.2
GA ₃ and cold ^y	Before 4.5C	2	100	87.5
	After 4.5C	2	75.0	87.5
	None	4	68.8	62.5
	None	8	75.0	31.3
LSD 5%			12.0	10.5

^zGA₃ was applied after cold exposure and just before moving to a greenhouse.

^yGA₃ concentration was 100 mg·liter⁻¹ applied as a soil drench.

nificantly affect the time between VB and anthesis (Table 4). No other significant effects were associated with the time of GA₃ application.

Fewer days from beginning of treatment to VB were needed when GA₃ was applied before rather than after cold exposure for both age 1 and age 2 plants. Age 1 plants treated with 100 mg GA₃/liter before cold exposure plus 2 weeks of cold formed visible flower buds after forcing 27 days, but after only 15 days in age 2 plants. In contrast, when GA₃ was applied after 2 weeks of cold exposure, age 1 plants formed visible flower buds after 48 days of forcing, but after only 29 days in age 2 plants. Regardless of age or time of application, buds appeared sooner when plants were treated with GA₃. GA₃ had no effect on days to VB, total number of flowers and inflorescences, or on inflorescence height regardless of plant age or time of GA₃ application. However, age 1 plants treated with GA₃ after 2 weeks of cold exposure reached VB in ≈27 days. Those treated before cold exposure reached VB in ≈48 days, and those without GA₃ in ≈58 days (differences significant at *P* = 0.05). Age 2 plants treated with GA₃ after cold exposure reached VB in ≈15 days. Those treated before cold exposure reached VB in ≈29 days, and those without GA₃ in ≈42 days (differences significant at *P* = 0.05).

Flowering percentage of two ages of 'Robin' during forcing (Expts. 4 and 5). A higher percentage of age 1 than age 2 plants

flowered when exposed to 4 or 8 weeks of cold but not treated with GA₃ (Table 4). Age 1 'Robin' flowered 100% with no cold exposure, with or without GA₃, and with 2 weeks of cold exposure with 100 mg GA₃/liter applied before cold exposure.

Floral initiation and development. The floral initiation and vernalization requirements of *Aquilegia* used in this study contradicted previous studies (Shedron and Weiler, 1982). As a general rule, herbaceous perennials need a period of low-temperature exposure for flowering. According to those authors, a cold treatment is required in most, but not all, *Aquilegia* × *hybrida* seedlings.

Some selections either did not need chilling to flower or they might have a reduced vernalization requirement that could be partially replaced by GA₃ and/or high irradiance and long-day conditions. The ability to cause or prevent flower initiation at a selected date can be a very useful technique when developing year-round schedules for flowering pot plants.

Some genotypes may differ in their requirement for day/night temperatures or red/far red (R/FR) light balance and high irradiance to initiate flowers. The R/FR ratio of light reaching the leaves is of special interest. Red light stimulates the synthesis of gibberellins and auxins and reduces the endogenous ABA content, but far red stimulates the synthesis of abscisins and in that way enhances bud inhibition (Tillberg, 1985). The R/FR balance of the FL or HPS lamps

might have induced floral initiation in Weddle's Songbird series *Aquilegia* that were not vernalized.

Aquilegia selections that initiated floral buds without vernalization may differ genetically from the types studied by Shedron and Weiler (1982). Weddle may have selected for an annual flowering habit. There may have been unidentified stress conditions that substituted for cold exposure and influenced floral initiation. Further studies are needed to determine if stress alone can cause floral initiation in these newer *Aquilegia* selections.

Exposure to cold delayed the floral development on the plants that had already initiated flowers; the longer the cold exposure, the shorter the time from anthesis to flower shattering, thus shortening the postharvest life of the flowers. Increasing the duration of cold storage of *Aquilegia* 'Bluebird' that had previously initiated flower buds reduced the shelf life (using the time interval between anthesis and petal shattering as a measure of shelf life, Table 2). Longer periods of cold exposure also reduced flower number. Therefore, it was not necessary to provide vernalization conditions once the plants had initiated flowers.

Weddle's Songbird series nonvernalized plants should be placed in long-day conditions or be treated with GA₃ to hasten flower development to visible bud during forcing. GA₃ did not significantly affect inflorescence height, inflorescence number, or flower number. GA₃, applied before cold exposure, accelerated floral development during forcing when plants were exposed for 2 weeks to 4.5C. On plants that had initiated flowers, the effect of GA₃ might be reduced by longer cold exposure (4 or 8 weeks) when GA₃ is applied before cold exposure. Supplemental light positively affected floral development after cold exposure.

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