Gibberellin- and Cytokinin-induced Growth and Flowering Responses in *Rudbeckia hirta* L.

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Abstract. BA and GA₄₊₇ were applied to vegetative, mature *Rudbeckia hirta* plants at the beginning of long days (LD). There were no synergistic effects, but BA inconsistently affected branching and had no effect on flowering. Floral initiation of the terminal inflorescence was promoted by GA₄₊₇, although axillary inflorescences were not. Increasing GA₄₊₇ levels decreased the time to terminal inflorescence anthesis. However, the interval between the terminal and second axillary inflorescence anthesis was increased. The net result was no significant effect on the time to second axillary inflorescence anthesis. Gibberellins may enhance the LD effect on the apical meristem of *Rudbeckia*, but axillary meristems, which initiate later, remained unaffected. Chemical names used: benzyladenine (BA), gibberellin₄₊₇, (GA₄₊₇).

Cytokinins applied to the apex of plants during noninductive photoperiods can evoke a variety of apical changes, including cell divisions that normally occur early in floral initiation (Bernier and Kinet, 1986). Ogawa and King (1979) reported that cytokinins enhance translocation of the floral stimulus and assimilates from induced leaves, thereby promoting flowering. When applied during floral initiation, BA increased the floret count and capitulum size in the short-long-day plant *Leucospermum cordifolium* (Salisb. ex. Knight) x *L. lineare* R. Br. (Napier et al., 1986) and the flower count of the short-day (SD) plant *Schlumbergera truncata* (Haw.) Moran (Ho et al., 1985; Runger and Poole, 1985). When cytokinins were applied to *Schlumbergera* under noninductive photoperiods, phylloclade (branch) count was increased.

Applications of gibberellins (GA) to long-day (LD) rosette plants under noninductive photoperiods often result in bolting and, occasionally, flowering (Bernier and Kinet, 1986). GA promoted *Gaillardia* x *grandiflora* van Houtte flowering by substituting for and enhancing LD stimuli (Evans and Lyons, 1988). When applied under SD, GA stimulated meristematic cell proliferation in the subapical and central zone, which led to stem elongation and floral initiation in *Rudbeckia hirta* (syn: *R. bicolor*) (Bernier and Kinet, 1986). The sensitivity of *R. hirta* to GA under SD depended on plant age (Kochankov et al., 1987). The pro-

motion of floral initiation using GA, however, is not consistent across genera. Under LD, GA-antagonist growth retardants prevented bolting and flowering in the LD plant *Samolus parviflorus* Raf., but GA applications overrode these effects. In *Silene armeria* L., growth retardants suppressed stem elongation but not flowering, indicating that floral initiation and development and GA levels are unrelated in this species (Bernier and Kinet, 1986).

Combining cytokinins and GA has been effective in increasing the number of pistillate ray florets in *Helianthus annuus* L. (Sladky, 1986). However, when this combination was applied to *Schlumbergera* under inductive SD, GA caused phylloclade elongation, flower bud initiation, and lateral phylloclade development, while reducing the number of flowers produced by BA alone (Ho et al., 1985).

As reported in other species, the potential exists in *R. hirta* for increasing either the number of inflorescences or the number of florets in an inflorescence using cytokinins and gibberellins. The present study was conducted to examine the effects of BA and GA₄₊₇ applied during floral induction on the flowering of *R. hirta*.

Materials and Methods

Seeds of the obligate LD plant *R. hirta* were sown in Sunshine Mix 1 (Fisons Horticulture, Vancouver, B. C.) and grown under SD conditions provided by covering the plants with black cotton cloth from 1700 to 0800 HR. Seedlings were transplanted into the same medium and grown to maturity (14 to 16 expanded leaves) (Orvos and Lyons, 1989) in 1500-cm³ containers. The plants were fertilized weekly during irrigation with 400 mg N/liter from 20N-6.6P-17.6K. At maturity, the plants were moved to LD, which consisted of ambient greenhouse light [623 to 833 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ average photosynthetic photon

flux density (PPFD) at 1200 HR] plus a 4-h night interruption from 2200 to 0200 HR using 60-W incandescent bulbs (3 to 4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD). Treatments were applied at the start of LD and consisted of 0, 20, or 50 μg a.i. BA (ABG-3062, 2% aqueous; Abbot Laboratories, North Chicago, Ill.) and 0, 100, or 200 μg a.i. GA₄₊₇ (ABG-3035, 2% aqueous; Abbot Lab.) in 2 ml aqueous solution pipetted onto the apical meristematic region. Treatments were applied in a randomized complete factorial design with 15 replications.

The number of days to anthesis of the terminal and second axillary inflorescence, number of distillate ray florets, the terminal and second axillary inflorescence disk diameter, days between anthesis of the terminal and second axillary inflorescence, number of branches, number of leaves on the main stem, and plant height were measured at the time of terminal inflorescence anthesis. The disk floret inflorescence diameter was measured at anthesis of the first row of disk florets because florets continue to initiate over an extended period.

Results

No significant interactions between GA₄₊₇ and BA were found. In addition, there were no significant treatment effects on distillate ray floret count, disk floret inflorescence diameter, plant height, or number of leaves (data not shown). Significant main effects were observed on branch count, days to inflorescence anthesis, and the difference between days to terminal and second axillary inflorescence anthesis.

BA applied at 20 μg significantly reduced branch count (17) in *R. hirta* compared to the control and the 50- μg treatment (20 and 19, respectively; Student–Newman–Keuls test, $P \leq 0.01$). However, the control and 50- μg treatments were not significantly different.

GA₄₊₇ applied at 100 or 200 μg a.i. significantly decreased days to terminal inflorescence anthesis, but had no significant effect on days to second axillary inflorescence anthesis (Table 1). Anthesis of the second axillary inflorescence to flower occurred an average of 5 days after the terminal inflorescence when treated with 200 μg GA₄₊₇, while the control plants flowered only 3 days after the terminal inflorescence.

Table 1. Effects of GA₄₊₇ on the number of days to anthesis of the terminal inflorescence (TI) and second axillary inflorescence (SAI) and days between inflorescence anthesis in *Rudbeckia hirta*.

G A ₄₊₇ (μg a.i.)	Terminal inflorescence (days)	Second axillary inflorescence (days)	TI and SAI difference (days)
0	79 a [*]	82 a	3 b
100	74 b	78 a	4 ab
200	73 b	78 a	5 a

^{*}Mean separation within columns by Student–Newman–Keuls test, $P < 0.05$.

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Discussion

Cytokinins enhance translocation of the floral stimulus and assimilates from induced leaves (Ogawa and King, 1979) and increase flower counts (Ho et al., 1985; Napier et al., 1986). Cytokinins applied at times other than specific initiation stages either have no effect, delay flowering, or increase branching (Rünger and Poole, 1985). BA increased phylloclade (branch) counts in *Schlumbergera* but only when applied before the start of floral initiation (Ho et al., 1985; Rünger and Poole, 1985). In the present study using *R. hirta*, the effect of BA on branching was inconsistently deleterious when applied at the start of floral induction but before floral initiation.

Gibberellins applied under SD simultaneously stimulate cell proliferation in the sub-apical tissues and the central zone of the apical meristem (Bernier and Kinet, 1986). In *Rudbeckia*, stem elongation and flowering are not inextricably linked (Mumek, 1940). Therefore, enhanced flowering in the terminal inflorescence is likely an early promotion of floral initiation. Yet, as is often observed following exogenously applied growth regulators, the response was temporary, and GA₄₊₇ did not enhance axillary inflorescence initiation in *R. hirta*. In this case, apical floral initiation alone, and not subsequent development, was affected

by GA₄₊₇; nor were axillary meristems influenced by the single GA₄₊₇ treatment at the start of LD. Even under SD with GA applied daily for 5 days, Kochankov et al. (1987) observed only apical floral initiation.

These results indicate that BA did not affect flowering in *R. hirta* when applied at the onset of LD. The combination of BA and GA, although effective in increasing pistillate ray floret counts in *Helianthus* (Sladky, 1986), had no effect in *R. hirta*. GA₄₊₇, applied at the onset of LD, promoted floral initiation in the apical meristem of *R. hirta* without lasting effect, leaving axillary meristem initiation unaffected. Flowering has been promoted in another LD bolting plant, *Gaillardia* (Evans and Lyons, 1988), where GA₄₊₇ promoted flowering by substituting for and enhancing the LD stimuli. In *Rudbeckia*, GA₄₊₇ applied at the onset of LD may enhance the effects of LD in the apical meristem. When applied during floral initiation of the apical meristem, GA₄₊₇ did not enhance floral initiation in the axillary meristems. The net result was no increase in either inflorescence size or count.

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