Hot Water Treatment Released Endodormancy but Reduced Number of Flowers in Potted Red Raspberry Plants

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Abstract. Partially released dormancy causes poor and uneven bud break in temperate plant species like red raspberry (*Rubus idaeus* L.). Insufficient chilling may be a problem when raspberries are grown at southern latitudes and in year-round production. Dormancy may be released by sublethal stress in many species. We studied the effect of sublethal stress on endodormancy in red raspberry ‘Glen Ample’ and ‘Ottawa’. Canes growing in pots were treated with either hot water (45 °C, 1 h) or the dormancy-breaking chemical, hydrogen cyanamide (1.04%), after accumulation of 0, 240, 480, 720, 960, or 1200 h of chilling at 1 °C. Bud break, vegetative growth, and number of flowers were recorded during 12 weeks of greenhouse forcing after the treatments. Chilling increased bud break, growth, and dry weight of lateral shoots and number of flowers in both cultivars. During deepest endodormancy (0 and 240 h of chilling), treatment with either hot water or hydrogen cyanamide enhanced bud break and lateral shoot growth but could not completely replace chilling. In ‘Ottawa’, hydrogen cyanamide was more effective than hot water during deepest endodormancy, but hot water treatment broke dormancy effectively when 720 h of chilling had accumulated. For ‘Glen Ample’, hot water was as effective as hydrogen cyanamide in breaking endodormancy. Hot water treatment reduced the number of flowers in ‘Glen Ample’ during late endodormancy (720, 960, and 1200 h of chilling). The chilling requirement for ‘Ottawa’ was fulfilled between 720 and 960 h of chilling. However, in ‘Glen Ample’, 1200 h of chilling was not enough to fully release bud dormancy; bud break remained low and it was increased by dormancy-breaking treatments. Hot water treatment can be used to release endodormancy in raspberries, but treatment conditions need to be optimized to preserve crop potential. Chemical name used: hydrogen cyanamide (Dormex, Hi-Cane, Morgrapes).

The production of raspberry (*Rubus idaeus* L.) in tunnels and greenhouses is increasing in many countries. When cold-stored plants are forced in a greenhouse, endodormancy may become a problem. Partially released dormancy causes poor and uneven bud break, abnormal flower development, and reduces leaf area and flower number (Carew et al., 2000; Erez, 1987). Furthermore, dormancy may restrict elongation of lateral shoots after bud break, resulting in rosette-like growth (Erez, 1999).

Dormancy also limits raspberry production in open fields in low latitudes where natural chilling accumulation is not adequate. Hydrogen cyanamide, H₂CN₂, is commercially available and has been reported to release dormancy in various species (Siller-Cepeda et al., 1992; Snir, 1983; Williamson et al., 2002). Furthermore, sublethal stress caused by hot water treatment seems to be an effective method to break dormancy. Water at 50 °C released dormancy in grapevine (*Vitis vinifera* L.) buds (Orffer and Goussard, 1980). Dormancy of

buds of apple (*Malus domestica* Borkh.) (Wang and Faust, 1994) and hybrid black poplar (*Populus nigra* L.) (Wisniewski et al., 1997) was broken by water at 40 to 45 °C. In four red raspberry cultivars, temperatures of 40 and 45 °C released dormancy in single-node cane pieces (Palonen and Lindén, 2006). Furthermore, hot water treatment (45 °C) can be used to enhance rooting and growth of black currant (*Ribes nigrum* L.) cuttings (Pedersen et al., 2005).

Effects of hot water treatment depend on the stage of dormancy; the treatment enhances bud break during ecodormancy and it is able to induce bud break during endodormancy, whereas at later stages of dormancy, it may injure buds (Wisniewski et al., 1997). However, experiments have mainly been conducted with pieces of shoots or canes, not whole plants. The aim of this study was to examine the influence of treatments with hot water or hydrogen cyanamide on vegetative growth and yield potential of dormant potted red raspberry plants.

Materials and Methods

Plant material. Red raspberries ‘Glen Ample’ and ‘Ottawa’ were used. Bare root ‘Glen

Ample’ plants were received from a commercial nursery (Marja-Suomen taimituotanto, Suonenjoki, Finland) and planted in sandy peat (coarse peat mix; Kekkilä Oyj, Mellilä, Finland) in 3.5-L plastic containers on 16 May 2004. Canes were cut down to soil level and pots moved outdoors. ‘Ottawa’ plants established from root cuttings (Marja-Suomen taimituotanto) were grown in 10 × 10-cm pots (0.8 L vol.) 3 weeks in a greenhouse until 5 June, when they were also planted in 3.5-L plastic containers in the same commercial potting mix. The plants were grown outdoors in the experimental field of the University of Helsinki, Viikki (lat. 60°10' N) and drip-irrigated and fertilized (Peat Superex 12N-5P-27K; Kekkilä Oyj, Eurajoki, Finland) continuously until the end of August. Only one cane per pot was allowed to grow. The growing season was exceptionally rainy (total rainfall 570 mm) and ‘Glen Ample’ plants were infected by raspberry rust, but this did not cause early leaf fall. Plants were grown outdoors until 20 Oct., when they were presumed to be endodormant. At that time, approximately half of the leaves of ‘Ottawa’ and one-third or less of the leaves of ‘Glen Ample’ had been shed.

Treatments. Plants were randomly divided into six groups that were exposed to 0, 240, 480, 720, 960, or 1200 h of chilling (ch) at 1 °C. After the different chilling exposures, the plants were subjected to dormancy-breaking treatments. The first group (0 ch) was treated on 20 Oct. 2004 and the following groups (240 ch, 480 ch, 720 ch, 960 ch, and 1200 ch) at 10-d intervals thereafter. Treatments included two dormancy-breaking methods: hot water immersion (45 °C, 1 h) and a 1.04% solution of hydrogen cyanamide as well as two control treatments: 19 °C water immersion (1 h) and an untreated control. One hour before the treatments, plants were moved from cold storage into room temperature (19 °C).

Both water treatments (45 and 19 °C) were carried out simultaneously in two identical 550-L pools of water. In the hot water treatment, water was constantly running into the pool, and its temperature was kept at 45 ± 1 °C by a thermostat. In the 19 °C water treatment, the pool was filled with water 1 d before the treatment so the temperature stabilized at 19 ± 1 °C overnight. Plant pots were supported upside down above the pool and canes immersed in water for 1 h. Thus, the root system was not treated.

For hydrogen cyanamide treatment, the commercial dormancy-breaking chemical, Dormex (a.i. hydrogen cyanamide 520 g·L⁻¹; Degussa Ag, Trostberg, Germany) was diluted to a 1.04% solution of the a.i. Canes were sprayed to runoff with a hand sprayer inside a fume hood. However, the chemical was not allowed to enter the soil. After the treatments, plants were transferred to a greenhouse for forcing. The untreated control plants were transferred from cold storage into room temperature (19 °C) for a few hours before transfer to the greenhouse.

Hot water and hydrogen cyanamide treatments caused abscission of leaves in those

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plants that still had some green leaves from the previous growing season after storage. At 0 ch and 240 ch, any remaining leaves were manually removed from the plants after both control treatments (19 °C water and untreated control).

Forcing conditions. After the treatments, plants were forced for 12 weeks in a greenhouse (day length 16 h, temperature 18 °C, irradiation 180 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). They were drip-irrigated and fertigated as described previously. Plants were sprayed twice against powdery mildew with penconazole (Topas; Syngenta Co.) and kresoxim-methyl (Candit; BASF Ag.) and once against spider mites with abamectin (Vertimec; Syngenta Co.).

Measurements. During forcing, bud break was scored twice a week and percentage of bud break calculated. A bud was considered broken when all the single leaflets of the first leaf were separately visible. Shoot length (greater than 1 cm) was measured from the base of the lateral shoot to the base of the youngest growing leaf once a week. During anthesis, the number of flowers per plant was recorded twice a week. The onset of flowering was determined as opening of the first flower in a plant. After 12 weeks of forcing, leaf area per plant was measured (LI-3000A; LI-COR, Lincoln, NE). Dry weight of lateral shoots was determined after drying at 70 °C for 7 d.

Experimental design and statistical analysis. The experiment was carried out as a factorial experiment with eight single-plant replications. The main effects of dormancy-breaking treatment (four levels) and the number of chilling hours (six levels) as well as their interaction were analyzed by two-way analysis of variance (SAS 9.1.3 GLM-procedure; The SAS System, Cary, NC). Bud break data values were square root transformed before analysis. Differences between treatment means were separated with Tukey's test at $P < 0.05$. Cultivars were analyzed separately.

Results

Bud break. Both cultivars were in deep endodormancy on 20 Oct. when the experiment was initiated, and removal of old leaves did not enhance bud break. In plants that received no chilling (0 ch), very few buds broke during 12 weeks of forcing in the control treatments until 960 ch (Table 1) (Palonen et al., 2008). There was an interaction between the length of chilling and the dormancy-breaking treatments on bud break in both cultivars (Table 2).

In 'Glen Ample', both hot water and hydrogen cyanamide increased bud break compared with the control treatments until 960 ch (Table 1). Bud break ranged between 51% and 60% in hot water treatment and between 49% to 68% in hydrogen cyanamide treatment after different durations of chilling. After 1200 ch, 38% of the buds broke in the untreated control and 59% to 64% in the dormancy breaking treatments.

In 'Ottawa', hot water treatment did not enhance bud break during deepest endodormancy, whereas hydrogen cyanamide enhanced bud break (Table 1). At 720 ch, both

hot water and hydrogen cyanamide enhanced bud break but after 960 ch, there were no differences between the treatments. At 1200 ch, bud break reached 80% to 92% in all the treatments. Although bud break increased in canes treated with hot water during deepest endodormancy only in 'Glen Ample', the lateral shoots were shorter than in the control treatments in both cultivars (data not shown).

Flowering. There was an interaction between the length of chilling and the dormancy-breaking treatments on the time of flowering

(Table 2). Chilling duration hastened the onset of flowering in the control treatments (Table 3). Hydrogen cyanamide hastened the onset of flowering in 'Glen Ample' at 0 ch and both hot water and hydrogen cyanamide in 'Ottawa' until 480 ch. Increasing duration of chilling increased the number of flowers in both cultivars (Table 2; Fig. 1A–B). Hardly any flowers developed during deepest endodormancy. The number of flowers increased considerably at 720 ch in 'Glen Ample' and at 960 ch in 'Ottawa'. Hydrogen cyanamide treatment

Table 1. The percentage of bud break in raspberry 'Glen Ample' and 'Ottawa' after different treatments and at different stages of dormancy.

Treatment	Number of chilling hours						<i>P</i> value in analysis of variance
	0	240	480	720	960	1200	
Glen Ample							
Hot water 45 °C, 1 h	52 a ^z	60 a	51 a	54 a	55 a	59 ab	NS
Hydrogen cyanamide	49 a	54 a	63 a	66 a	68 a	64 a	NS
19 °C water	6 b	6 b	27 b	29 b	36 b	46 bc	<0.001
Control	7 b	6 b	30 b	33 b	31 b	38 c	<0.001
<i>P</i> value in analysis of variance	<0.001	<0.001	<0.001	<0.001	<0.001	0.002	
Ottawa							
Hot water 45 °C, 1 h	24 b	25 b	48 ab	68 a	85	84	<0.001
Hydrogen cyanamide	58 a	71 a	79 a	79 a	67	80	NS
19 °C water	8 b	36 b	44 b	36 b	74	92	<0.001
Control	4 b	17 b	24 b	33 b	55	84	<0.001
<i>P</i> value in analysis of variance	<0.001	<0.001	<0.001	<0.001	NS	NS	

^zFor each column and cultivar separately, values followed by the same letter are not significantly different by Tukey's test at $P < 0.05$. Bud break data values were square root transformed before pairway comparisons. Values are means of eight single plant replicates.

NS = nonsignificant.

Table 2. Two-way analysis of variance table presenting P values for the main effects of chilling, dormancy-breaking treatment, and their interaction on bud break, time of flowering (days to flower), number of flowers, and lateral shoot dry weight in red raspberry 'Glen Ample' and 'Ottawa'.

	Bud break		Days to flower		No. of flowers		Dry wt	
	Glen Ample	Ottawa	Glen Ample	Ottawa	Glen Ample	Ottawa	Glen Ample	Ottawa
Chilling	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Treatment	<0.001	<0.001	<0.001	<0.001	0.0037	0.027	<0.001	NS
Chilling × treatment	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

NS = nonsignificant.

Table 3. Average time in days to the beginning of flowering in raspberry 'Glen Ample' and 'Ottawa' after different treatments and at different stages of dormancy.

Treatment	Number of chilling hours (ch)						<i>P</i> value in analysis of variance
	0	240	480	720	960	1200	
Glen Ample							
Hot water 45 °C, 1 h	— ^z	40 a	48	48	40	40	NS
Hydrogen cyanamide	44 a	44 a	41	44	37	41	0.007
19 °C water	84 b	52 ab	43	39	36	37	<0.001
Control	84 b	66 b	44	40	36	36	<0.001
<i>P</i> value in analysis of variance	<0.001	0.011	NS	NS	NS	0.036	
Ottawa							
Hot water 45 °C, 1 h	54 a	47 a	46 a	40	40	41	<0.001
Hydrogen cyanamide	46 b	44 a	43 a	46	45	43	NS
19 °C water	—	81 b	65 b	49	42	43	<0.001
Control	—	79 b	63 b	49	43	43	<0.001
<i>P</i> value in analysis of variance	0.028	<0.001	<0.001	NS	NS	NS	

^zNo flowers developed.

^yFor each column and cultivar separately, values followed by the same letter are not significantly different by Tukey's test at $P < 0.05$. Values are means of eight single plant replicates.

NS = nonsignificant.

Fig. 1. Number of flowers per plant in raspberry 'Glen Ample' (A) and 'Ottawa' (B) subjected to different dormancy-breaking treatments after different durations of chilling. Values are means of eight single plant replicates. NS, *, **, *** Nonsignificant or significant at $P < 0.05$, 0.01 , or 0.001 , respectively. For each chilling level separately, means with the same letter are not significantly different ($P < 0.05$) by Tukey's test.

increased the number of flowers compared with control in both cultivars until 480 ch. Hot water treatment reduced the number of flowers compared with control in 'Glen Ample' after 720 ch.

Shoot dry weight and leaf area. There was an interaction between the length of chilling and the dormancy-breaking treatments on shoot dry weight (Table 2). In 'Glen Ample', treatment affected shoot dry weight at all durations of chilling except 1200 h (Fig. 2A). Shoot dry weight remained low in both control treatments during deepest endodormancy. Increased chilling duration increased leaf area (data not shown) resulting in higher shoot dry weight. At 0, 240, 480, and 960 ch, shoot dry weight was highest in plants treated with hydrogen cyanamide. Hot water treatment increased shoot dry weight compared with both controls at 0 and 240 ch.

In 'Ottawa', both hydrogen cyanamide and hot water treatment increased shoot dry weight compared with both control treatments at 0 ch and hydrogen cyanamide at 240 ch (Fig. 2B). After longer chilling, there were no differences between the treatments.

Other observations. Leaf removal in the control treatments at 0 and 240 ch did not cause bud break but wounds leaked sap. New shoots emerged in all the plants during forcing. 'Ottawa' sprouted more than 'Glen Ample',

but in both cultivars, growth of root suckers was independent of both the treatment and the length of the chilling period. Malformation of leaves was observed during forcing in hot water-treated plants. At higher levels of chilling, hydrogen cyanamide caused phytotoxic symptoms; cane tips dried and died.

Discussion

Accumulation of chilling enhanced bud break, vegetative growth, and the number of flowers and hastened flowering. This is in accordance with earlier reports for *Rubus* species (Dale et al., 2003; Lopez-Medina and Moore, 1999; Måge, 1971, 1975; White 1999; White et al., 1999). In single-bud shoot pieces of several species, hot water treatment has been observed to release endodormancy (Orffer and Goussard, 1980; Shulman et al., 1983; Wisniewski et al., 1997). Palonen and Lindén (2006) found that depending on the cultivar, water at 40 or 45 °C broke endodormancy of raspberry buds. In our experiment, intact canes of pot-grown plants, excluding roots, were treated with hot water.

Based on our results, the dormancy-breaking treatments comprised of either hot water or hydrogen cyanamide were able to break bud endodormancy but could not com-

pletely replace chilling. Both hot water and hydrogen cyanamide increased bud break and to some extent enhanced vegetative growth in endodormant plants. However, dormancy-breaking treatments could not completely release deepest endodormancy: although bud break increased compared with the control treatments, the lateral shoots remained short.

Chilling requirement differed between 'Glen Ample' and 'Ottawa'. In 'Glen Ample', dormancy-breaking treatments enhanced bud break still after 1200 chilling hours, which indicates that this duration was not enough to fully release bud dormancy caused by endo- and/or paradormancy. Bud break of 'Ottawa' increased considerably between 720 and 960 ch in both control treatments. At the same time, the dormancy-breaking treatments became ineffective. Furthermore, the number of flowers increased after 960 ch. Thus, the chilling requirement for 'Ottawa' was apparently fulfilled between 720 and 960 ch, although additional chilling further increased bud break. However, the problems in determining exact chilling requirements include determination of the time of chilling inception, weighted coefficients for different temperatures, and the end of dormant phase (Warmund and Krumme, 2005). Chilling requirement also depends on the growing conditions in the previous growing season (Heide, 2003).

In 'Glen Ample', percentage of bud break clearly increased already between 240 and 480 ch. However, number of flowers in the control treatments increased only at 720 ch. After 1200 ch (7 weeks of chilling), only 38% of buds broke in the untreated control plants, whereas dormancy-breaking treatments enhanced bud break. Earlier, White (1999) and Dale (2008) reported the high chilling requirement of 'Glen Ample'. Although Dale (2008) suggested that 780 ch completed its chilling requirement, Mazzitelli et al. (2007) showed that in whole canes of this cultivar, chilling requirement might be as high as 1900 h. Despite the long chilling period in our experiment, bud break in the middle and lower parts of the cane in 'Glen Ample' was poor. White (1999) stated that paradormancy strengthens toward the base of the cane and inhibits bud break until a sufficient amount of chilling has accumulated. The influence of paradormancy was also shown by Mazzitelli et al. (2007); in intact canes, maximal bud burst was achieved after 1900 ch, but in the middle and base parts of the cane, bud burst was incomplete even after 2500 ch, whereas endodormancy of one-bud cane pieces was released after 1400 ch. Furthermore, according to Dokoozlian et al. (1995), hydrogen cyanamide does not increase bud break after chilling requirement is fulfilled in grapevine.

It is probable that physiological changes in the buds are similar both in hot water treatment and during chilling accumulation. Recently, expressed sequence tag (EST) libraries at different phases of dormancy and microarray analysis in red raspberry have revealed that during dormancy release, genes encoding heat shock proteins as well as other stress response and detoxification-related genes are

Fig. 2. Lateral shoot dry weight per plant in raspberry 'Glen Ample' (A) and 'Ottawa' (B) subjected to different dormancy breaking treatments after different durations of chilling. Values are means of eight single plant replicates. NS, *, **, *** Nonsignificant or significant at $P < 0.05$, 0.01 , or 0.001 , respectively. For each chilling level separately, means with the same letter are not significantly different ($P < 0.05$) by Tukey's test.

expressed (Mazzitelli et al., 2007). Furthermore, Walton et al. (2009) observed using microarray analysis in kiwifruit [*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson] that several stress-related genes are upregulated after hydrogen cyanamide treatment. Mechanisms of action of dormancy-breaking treatments such as hot water treatment or hydrogen cyanamide are not clear. However, hot water treatment has been used for decades to force cut flowers such as lilac (Dole and Wilkins, 1999; Escher, 1996).

Sublethal stress caused by treatment in hot water (45 °C) for 1 h released endodormancy but apparently injured flower initials, because the number of flowers was reduced. Injuries seemed to become more severe at later stages of endodormancy. Flower initials have been shown to be more susceptible also to frost injuries than leaf initials (Palonen, 1999). Daugaard and Lindhard (2007) observed that strawberry frigo plants subjected to phytosanitary hot water treatment survived 48 °C for 5 min. However, this treatment reduced the number of flowers and to preserve cropping potential, 42 °C treatment for a maximum of 10 min is recommended (Daugaard and Lindhard, 2007).

The effectiveness of hydrogen cyanamide (Snir, 1983) and hot water (Wisniewski et al., 1997) in breaking dormancy has previously

been shown to depend on the stage of dormancy. After adequate accumulation of ch, dormancy-breaking treatments may be harmful and prevent growth (Snir, 1983; Wisniewski et al., 1997). At later stages of endodormancy, hydrogen cyanamide caused drying of cane tips in our experiment. This is apparently related to the phytotoxicity of this chemical, which has been earlier observed, e.g., in blueberries (*Vaccinium* spp.) (Williamson et al., 2001), peach (*Prunus persica* Batsch.), and plum (*Prunus domestica* L.) (Erez, 1987). Snir (1986) reported that whole canes of raspberry died after treatment with hydrogen cyanamide during late dormancy. Furthermore, susceptibility depended on cultivar as was also observed in our experiment, in which 'Glen Ample' was injured but no toxic symptoms were observed in 'Ottawa'. A more sustainable way forward would be to breed cultivars with low chilling requirements.

Our experiment suggests that endodormancy of biennial-type raspberries is restricted to buds and possibly canes, but does not occur in roots. During forcing, new root suckers emerged continuously. Neither chilling nor treatment had any impact on growth of these shoots. However, Carew et al. (2000, 2001) and Takeda (1993) reported that chilling enhances new sucker emergence in primocane fruiting raspberries, whereas Williams (1959)

concluded that only soil temperature restricts shoot growth. Sap leakage from wounds in dormant canes showed that xylem transport continued, which supports the idea that the bud is the actual site of endodormancy in biennial raspberries.

In conclusion, hot water treatment enhanced bud break in raspberry plants, depending on the stage of endodormancy. In 'Glen Ample', it was as effective as hydrogen cyanamide at all stages of endodormancy. In 'Ottawa', only hydrogen cyanamide enhanced bud break during deepest endodormancy, whereas at 720 ch also, hot water treatment enhanced bud break. However, hot water treatment reduced the number of flowers in 'Glen Ample' at later stages of endodormancy. Hot water treatment is a promising method for breaking endodormancy in raspberries, but application time and duration of the treatment need to be carefully optimized to preserve maximum yield potential.

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