Breaking Dormancy in Red Raspberry with Hot Water Treatment and its Effects on Cold Hardiness

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ABSTRACT. ‘Maurin Makea’, ‘Muskoka’, ‘Ottawa’, and ‘Preussen’ red raspberry (*Rubus idaeus* L.) canes were collected from the field and subjected to different hot water treatments (20, 35, 40, 45, and 50 °C) to determine if endodormancy could be removed by a near lethal stress. Estimation of days for 50% budbreak (DD₅₀) was found useful for describing the state of bud dormancy in the samples. Bud dormancy was broken in ‘Ottawa’ by immersing the canes in 45 °C water for 2 hours, in ‘Maurin Makea’ by treating the canes in 40 °C water, and in ‘Preussen’ by both 40 and 45 °C treatments. The influence of this treatment on dormancy and cold hardiness at different times of the winter was further examined using ‘Ottawa’ raspberry. The treatment removed bud dormancy most effectively in October, when the samples were in deepest dormancy. A slight effect was observed in November, but no effect in January. During ecodormancy in February the treatment delayed budbreak. Hot water treatment reduced cold hardiness of ‘Ottawa’ canes by 8 to 15 °C, and that of buds by 9 to 13 °C during both endo- and ecodormancy. Based on the capacity of buds and canes to reacclimate, recovery from the stress treatment was possible at temperatures ≥4 °C. Loss of cold hardiness was caused by high treatment temperature itself and was not related to breaking of dormancy in samples. This finding suggests that dormancy and cold hardiness are physiologically unconnected in raspberry.

In northern conditions endodormancy of red raspberry usually is broken in December–January (Jennings et al., 1972; Måge, 1975; Palonen and Lindén, 1999; Zrally, 1978). Raspberry frequently suffers winter injury, and it is thought to be prone to injury in late winter, as weakening dormancy diminishes cold hardiness and rehardening capacity. However, maximum cold hardiness is usually observed after dormancy is broken (Palonen and Lindén, 1999; Thorsrud and Hjeltne, 1963; Zrally, 1978). Furthermore, reports on the relationship of dormancy to cold hardiness are somewhat contradictory (Brierley and Landon, 1954; Lamb, 1955; Miles, 1965; Warmund et al., 1989), and cultivars respond differently (Palonen and Lindén, 1999). It is evident that results from the field experiments are confounded with factors that can not be controlled or excluded from the experimental system, such as time of a year or prevailing temperature. If it were possible to artificially remove dormancy from plant samples, dormant and non-dormant tissue could be studied at the same time (e.g., for their cold hardiness).

Endodormancy is regulated by the physiological factors within the dormant structure (Lang, 1987). Under natural conditions endodormancy of woody plants is gradually released by exposure to chilling temperatures. However, different sublethal stresses (e.g., chemical or either high or low temperature) break dormancy in woody plants (Fuchigami and Nee, 1987; Wisniewski et al., 1996). Hot water of 50 °C releases grapevine (*Vitis* L.) cuttings from dormancy (Orffer and Goussard, 1980), and hot water treatment (47 °C) removes bud dormancy in red-osier dogwood (*Cornus sericea* L.) (Shirazi and Fuchigami, 1995; Tanino et al., 1989). Heat stress appears to be more effective, when applied during early and late stages of dormancy than during deepest dormancy (Shirazi and Fuchigami, 1995). In apple (*Malus ×domestica* Borkh.), optimal water temperature for budbreak is 40 to 45 °C (Wang and Faust, 1994). In black poplar (*Populus nigra* L.) heat treatment of 40 to

45 °C releases endodormancy and decreases thermal units needed for budbreak during ecodormancy (Wisniewski et al., 1997). Hydrogen cyanamide (CH₂N₂) removes bud dormancy in red-osier dogwood (Shirazi and Fuchigami, 1995; Tanino et al., 1989) and promotes budbreak in peach trees [*Prunus persica* (L.) Batsch.] (Siller-Cepeda et al., 1992b). Besides woody plants, sublethal low temperature stress has been observed to remove dormancy in overwintering strawberry (*Fragaria ×ananassa* Duch.) plants (Palonen and Lindén, 2001).

Applying sublethal stress may provide means for removing dormancy in plant samples, when dormant and nondormant tissue are needed for the experiment at the same time. The aim of this study was to develop a method for breaking endodormancy in raspberry with near-lethal hot water treatment, and to examine the effect of this dormancy breaking treatment on bud and cane cold hardiness.

Materials and Methods

EXPT. 1. DORMANCY BREAKING TREATMENTS. Overwintering canes of three raspberry cultivars (‘Maurin Makea’, ‘Muskoka’, and ‘Ottawa’) were collected from a cultivar trial at the Agri-food Research Finland, Häme Research Station, Pälkäne (lat. 61°20’N), and the cultivar Preussen from a replicated trial in the experimental field of the University of Helsinki, Viikki (lat. 60°10’N) on 9 Nov. 1998, when the plants were presumably in deep endodormancy. Samples were stored overnight in a cold room at 0 °C. From each cane, top portion with five uppermost buds and the base portion were discarded, and the mid-portion of the cane with 15 buds was used in the experiment. Thirty-six canes of each cultivar were randomly assigned to six different treatments. Control samples received no dormancy breaking treatment, and were kept at room temperature (20 °C) during the treatments. The rest of the samples were immersed for 2 h in water with temperature of 20, 35, 40, 45, or 50 °C. One cane was a replicate, thus the experiment had six replicates.

The state of bud dormancy was determined by observing time to budbreak in greenhouse forcing. Immediately after water immersion, sample canes were cut into single-node pieces,

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inserted in perlite and placed under mist in a greenhouse, where temperature was 20 °C, relative humidity 95%, and photoperiod 16 h. The number of broken buds (tips of green leaves separately visible) was recorded three times per week during 6 weeks. At the end of forcing, all the unbroken buds were dissected and the number of dead buds was subtracted from the total number of buds. The state of dormancy was determined as the time in days required for 50% budbreak in the experimental unit of 15 sample buds (DD₅₀). Logit models were used to estimate DD₅₀ values (Lindén et al., 1996).

EXPT. 2. EFFECT OF DORMANCY BREAKING TREATMENT ON COLD HARDINESS. The effect of dormancy breaking hot water treatment on raspberry bud and cane cold hardiness was studied on four different dates during Winter 1999–2000: 19 Oct., 22 Nov., 5 Jan., and 29 Feb. The dates were chosen to reflect different stages in dormancy development. Based on the results obtained the previous winter, dormancy breaking treatment employed in this study was immersion in 45 °C water. ‘Ottawa’ was chosen, because it responded to the treatments most consistently. Each sampling time, 32 canes were collected from the experimental field of the Univ. of Helsinki, and trimmed as described above, so that 16 buds were left on each sample cane. Half of the canes were subjected to a dormancy breaking hot water treatment by immersing them in 45 °C water for 2 h. The rest of the samples served as controls. There were four replicates per treatment each consisting of four canes. Dormancy was determined as described above using eight uppermost buds of each cane (32 buds per treatment and replicate), and the rest of the cane (eight buds) was used for the determination of cold hardiness (see below).

On the first sampling time (19 Oct.), additional 256 canes were collected to study the effect of dormancy breaking treatment on dehardening and rehardening of the samples. One hundred twenty-eight hot-water-treated and 128 control canes were randomly assigned into four different temperature treatments. Canes were loosely packed in black plastic bags to be stored at –3, +4, +11, or +22 °C for 2 weeks. There were four replicates per treatment combination each consisting of eight canes. Bud and cane cold hardiness were determined after 1 and 2 weeks of storage.

DETERMINATION OF COLD HARDINESS. Eight buds per cane were used for the determination of cold hardiness as the lethal temperature for 50% of the samples (LT₅₀) in a controlled freezing test. Thirty-two single-node cane pieces per treatment and replicate were packed in plastic bags and placed in a controlled-climate chamber, where temperature was kept at –2 °C overnight to ensure spontaneous ice nucleation in the samples. Next day the temperature was lowered by 5 °C per hour and kept for 30 min at each of the seven test temperatures. The range of test temperatures (between –5 °C and –40 °C) was selected each sampling time based on the expected level of hardiness in the samples. Four samples per treatment and replicate were taken out at 5 °C increments and allowed to thaw at 0 °C. Control samples were kept at 0 °C during freezing treatments. Samples were incubated at room temperature (22 °C) for 10 d and evaluated visually under a dissecting microscope for freezing injury in vascular tissue of canes and in buds, separately.

STATISTICAL ANALYSIS. Values of DD₅₀ and LT₅₀ were estimated using logit models (Lindén et al., 1996) in PROBIT procedure of SAS (SAS Institute, Cary, N.C.). A two-way analysis of variance was performed to test the main effects of hot water treatment and cultivar, and their interaction on the state of dormancy (Expt. 1), and the main effects of hot water treatment and storage temperature, and their interaction on cold hardiness (Expt. 2) in GLM

procedure of SAS. Means were separated using Tukey’s test. In Expt. 2, the effect of hot water treatment on the state of dormancy and cold hardiness was tested with an analysis of variance on each sampling time separately.

Results

EXPT. 1. DORMANCY BREAKING TREATMENTS. The percent budbreak in control samples on 9 Nov. varied from 12.1 to 79.1 (Fig. 1A). The highest percentages of broken buds were observed in ‘Muskoka’ and ‘Ottawa’, and the lowest in ‘Maurin Makea’ and ‘Preussen’. Treatment in 20 °C water decreased budbreak in ‘Muskoka’, ‘Ottawa’, and ‘Preussen’ (Fig. 1B). The highest budbreak for ‘Maurin Makea’ (62.0%) was observed after 40 °C treatment, and for ‘Ottawa’ (95.3%) and ‘Muskoka’ (76.7%) after 45 °C treatment (Fig. 1D–E). ‘Preussen’ had almost equally high percentages of broken buds after 40 and 45 °C treatments (93.8 and 88.6, respectively). The percentage of broken buds during forcing in all treatments varied between 4.4 and 95.3 (Fig. 1). When treated in 50 °C water, all the sample buds died.

Values of DD₅₀ for raspberry cultivars on 9 Nov. varied between 31.8 and 49.6 d in control samples (Table 1). Deepest dormancy was observed in ‘Maurin Makea’ and ‘Preussen’. The state of dormancy (DD₅₀) was affected by dormancy breaking treatment ($P < 0.001$), by cultivar ($P < 0.001$), and by their interaction ($P < 0.001$). Therefore, mean separation was performed for each cultivar separately. In ‘Maurin Makea’, 40 °C water decreased DD₅₀ compared to the control, although this treatment did not differ significantly from the other treatments (Table 1). In ‘Muskoka’, none of the treatments differed significantly from the control. However, the lowest DD₅₀ value was observed after 45 °C water treatment. In ‘Ottawa’, 45 °C water decreased DD₅₀, and in ‘Preussen’ both 40 °C and 45 °C were equally effective in breaking dormancy (Table 1).

EXPT. 2. EFFECT OF DORMANCY BREAKING TREATMENT ON COLD HARDINESS. Hot water treatment (45 °C, 2 h) affected bud dormancy and bud and cane cold hardiness of ‘Ottawa’ raspberry differently at different times of a year (Table 2). The treatment decreased the value of DD₅₀ on 19 Oct. by 17.2 d ($P < 0.001$) and on 22 Nov. by 2.2 d ($P = 0.010$). On 5 Jan., no treatment effect was observed ($P = 0.090$), and on 29 Feb. the treatment delayed budbreak; the value of DD₅₀ increased by 5.3 d ($P < 0.001$). The percentage of broken buds was only increased on 19 Oct. On 5 Jan., the percentage of dead buds recorded at the end of forcing was considerably increased by hot water treatment (Table 2). When unbroken buds were analysed under a dissecting microscope, the layer of brown bud scales was often thicker in hot-water-treated samples compared to the control samples.

Hot water treatment decreased cold hardiness of both buds and canes on all sampling times ($P < 0.001$ for both tissue types and all sampling times) (Table 2). Bud hardiness was diminished by 9.1 to 13.4 °C, and cane hardiness by 8.4. to 15.1 °C. In hot-water-treated samples, injury caused by low temperature during freezing test was visible as distinct browning of the vascular tissue in bud base. This was not observed in control samples, where injury was shown as even browning of the whole bud base or damage to flower initials.

When samples were stored at different temperatures after the hot water treatment, there were main effects of dormancy breaking treatment ($P < 0.001$ for buds and canes) and storage temperature ($P = 0.050$ for buds and $P = 0.008$ for canes), and their interaction ($P < 0.001$ for buds and canes) on cold hardiness after 1 week

Fig. 1. The effect of different dormancy breaking hot water treatments applied on 9 Nov. 1998 on the cumulative percentage of budbreak in four raspberry cultivars during 6 weeks of forcing. Sample size for each treatment was 90 buds.

Table 1. The effect of different dormancy breaking hot water treatments applied on 9 Nov. 1998 on the state of bud dormancy (DD_{50}) in four raspberry cultivars.

Cultivar	DD_{50} (d)				
	Control	20 °C water	35 °C water	40 °C water	45 °C water
Maurin Makea	49.6 a ²	45.4 ab	42.1 ab	37.5 b	42.5 ab
Muskoka	38.5 ab	54.1 a	42.6 ab	40.7 ab	27.8 b
Ottawa	31.8 b	56.9 a	34.3 b	29.6 b	16.6 c
Preussen	45.9 a	49.9 a	36.3 b	26.7 c	24.4 c

²Values are means of six replicates. Mean separation in rows by Tukey's test at $P < 0.05$.

of storage, and after 2 weeks of storage, as well ($P < 0.001$ for all effects and both tissue types). When stored at -3 °C, control samples cold acclimated, whereas cold hardiness of hot-water-treated samples remained unchanged (Fig. 2). At 4 and 11 °C, cold hardiness of control samples remained unchanged or slightly increased, while hot-water-treated samples cold acclimated, especially during the first week. At 22 °C, control samples slowly deacclimated, whereas cold hardiness of hot-water-treated samples first increased and then slightly decreased, but still remained at a higher level than in the beginning of storage.

Based on DD_{50} and percent budbreak, deepest dormancy was observed in 'Maurin Makea' and 'Preussen', and the most shallow dormancy in 'Muskoka' and 'Ottawa' (Fig. 1, Table 1). Differences observed in DD_{50} may also reflect cultivar differences in thermal units required for budbreak. However, per cent budbreak reflects status of chilling requirement satisfaction. No earlier information on the chilling requirement of the raspberry cultivars studied here is available. In Norwegian conditions, 'Preussen' has a relatively long dormant period compared to several other cultivars (Måge, 1971; Thorsrud and Hjeltne, 1963).

Although endodormancy of woody plants is usually released by exposure to chilling temperatures, different sublethal stresses may also break dormancy (Fuchigami and Nee, 1987). Usually temperatures of 40 to 47 °C have been used to artificially break dormancy, and moist heat has been found to be more effective than dry heat (Wisniewski et al., 1996). In raspberry, bud dormancy was broken by 40 or 45 °C water (Fig. 1, Table 1). However, the response was cultivar dependent. Interestingly, treatment in 20 °C water increased dormancy and almost totally inhibited budbreak in 'Muskoka', 'Ottawa', and 'Preussen' (Fig. 1). Only 4% to 16% of buds broke in these cultivars after immersing the canes in 20 °C water for 2 h. The reason for this is unclear, but it could be caused by so called negation of chilling. For example, in peach the effects of chilling can be negated by temperatures ≥ 21 °C (Erez et al., 1979), and in apple by temperatures of 15 to 30 °C (Young, 1992). In our study, the effect was caused by water immersion; control samples were exposed to similar temperatures, but not immersed in water. Possibly hydration intensified the influence of chilling negating temperature.

'Ottawa' buds were presumably in deepest dormancy on 19 Oct., when DD_{50} was ≈ 30 d, and hot water treatment hastened budbreak by 17 d (Table 2). However, even in control samples 69% of buds were able to grow and broke during 6 weeks of forcing. The question is, whether these samples may be considered endodormant at all, since growth was resumed as soon as optimal temperature and moisture were available. Endodormancy is regulated by the physiological factors within the dormant structure (Lang, 1987). Probably dormant condition in 'Ottawa' buds was a combination of eco- (temperature, moisture), para- (apical dominance), and endodormancy, as according to Junttila (1988) often is the case. When intact 'Ottawa' canes were forced under mist on 7 Oct. and 7 Nov. 1996, $<5\%$ of buds broke (Palonen and Lindén, 1999).

On 22 Nov., DD_{50} had diminished to 11 d, and after hot water treatment it was 9 d (Table 2). Dormancy breaking treatments have been reported to be most effective during early and late stages

Table 2. The effect of hot water treatment (45 °C for 2 h) on the state of bud dormancy (DD₅₀), the percentages of broken buds and dead buds after 6 weeks of forcing, and cold hardiness (LT₅₀) of 'Ottawa' raspberry on different sampling times.

Sampling time	DD ₅₀ (d)		Budbreak (%)		Dead buds (%)		LT ₅₀ buds (°C)		LT ₅₀ canes (°C)	
	Control	Hot water	Control	Hot water	Control	Hot water	Control	Hot water	Control	Hot water
19 Oct.	29.5 ^a	12.3	68.8	94.5	0	0	-21.9	-12.5	-23.3	-14.9
22 Nov.	11.0	8.8	100	99.2	0	2.3	-27.5	-15.1	-34.4	-19.3
5 Jan.	10.8	13.3	97.6	94.7	1.6	25.8	-28.7	-15.3	-30.7	-21.6
29 Feb.	5.4	10.7	100	97.5	0.8	4.7	-27.5	-18.4	-32.2	-21.6

^aValues are means of four replicates, except percentages of broken buds and dead buds are based on a pooled sample of 128 buds per treatment.

Fig. 2. Cold hardiness (LT₅₀) of raspberry buds (A) and cane vascular tissue (B) after dormancy breaking treatment applied on 19 Oct. 1999 and stored at different temperatures for either 1 or 2 weeks. C = control, and D = canes immersed in 45 °C water for 2 h. Values are means of four replicates and vertical bars represent SE.

of endodormancy, and less effective during deepest dormancy (Siller-Cepeda et al., 1992a, 1992b; Wisniewski et al., 1994; 1996). However, in our study, hot water treatment was almost equally effective in October (deep dormancy) and November (late dormancy). In the beginning of January, when endodormancy of raspberry is already broken (Jennings et al., 1972; Måge, 1975; Palonen and Lindén, 1999), hot water treatment had no effect on the state of dormancy. At the end of February hot water treatment

delayed budbreak by about 5 d. Dormancy breaking chemical H₂CN₂ inhibits or delays bud break during ecodormancy in crabapple (*Malus sylvestris* L.), red-osier dogwood (Fuchigami and Nee 1987), and in peach trees (Siller-Cepeda et al., 1992b). Heat treatment applied during later stages of ecodormancy in black poplar either inhibited budbreak or killed the buds (Wisniewski et al. 1997). In our study, hot water treatment caused most injury in January, when ≈25% of the treated buds were dead, whereas at the end of February no extensive damage was observed.

Lower buds in raspberry are in deeper dormancy than upper buds (Måge, 1975). Similarly, there may be differences in cold hardiness along the cane. To ensure that estimates of DD₅₀ and LT₅₀ were comparable between the treatments, we always used upper buds for dormancy determination and lower buds for determination of cold hardiness. Usually sublethal stress that breaks dormancy, also decreases stem cold hardiness (Shirazi and Fuchigami, 1995; Tanino et al., 1989; Wisniewski et al., 1994). Both raspberry cane and bud cold hardiness decreased as a result of the rest breaking treatment (Table 2). Hardiness decline was greatest (15.1 °C in canes and 13.4 °C in buds) as samples were at their hardiest state in midwinter. Raspberry cold hardiness decreased also during ecodormancy, when hot water treatment had no dormancy breaking effect. This suggests that loss of hardiness was not related to breaking of endodormancy, but caused by high treatment temperature or by tissue hydration, although the duration of the treatment was only 2 h. Several scientists have suggested that dormancy and cold-acclimation are physiologically unconnected processes in woody plants (e.g., Arora et al., 1997; Fuchigami et al., 1982; Salzman et al., 1996).

When incubated at -3 °C, control samples cold acclimated, but hot-water-treated samples failed to cold acclimate (Fig. 2). Presumably this low temperature did not allow recovery from sublethal stress, because at higher temperatures (4 and 11 °C) hot-water-treated samples cold acclimated, even close to the level found in control samples. Even at 22 °C, hot-water-treated samples increased in hardiness during the first week, although control samples deacclimated. After 2 weeks at 22 °C, control and hot-water-treated samples had equal hardiness levels. High temperature presumably allowed recovery in samples increasing resistance to freezing stress. Similarly, hot-water-treated red-osier dogwood plants deacclimated at low temperature (5 °C day/2 °C night), while control plants increased in cold hardiness (Tanino et al., 1989). Furthermore, plant dieback of hot-water-treated dogwood samples was observed at low temperature (0 or 5 °C), while at higher temperature (above 10 °C) plants were able to recover (Shirazi and Fuchigami, 1993).

Bud dormancy status is usually assessed by measurement of their growth rate or developmental stage under forcing conditions. The dormancy status is expressed as the mean number of days to budbreak, or as either the mean percentage of budbreak or the mean developmental stage of buds after a predetermined time (e.g., Hauagge and Cummins, 1991; Latimer and Robitaille, 1981;

Rinne et al., 1997). In our study, the dormancy state of raspberry buds was determined by estimating the time required for 50% budbreak (i.e., the DD₅₀ value). Hauagge and Cummins (1991) used a similar approach for quantification of bud dormancy status (D50) in apple (*Malus* Mill.). They considered estimations of D50 as more precise and illustrative than either budbreak percentage or bud development stage after forcing. Hauagge and Cummins (1991) employed quadratic models for estimation of days for 50% budbreak, whereas we used the logit model, which is appropriate for modelling binary response variables (e.g., budbreak/no budbreak) (Collett, 1991). The DD₅₀ values and their standard errors were easily calculated using logit model parameters.

In conclusion, endodormancy of raspberry could be broken by 40 or 45 °C water treatment. The response was cultivar dependent. Based on the capacity of buds and canes to cold acclimate, recovery from the stress treatment was possible at temperatures ≥4 °C. The deacclimating effect of this treatment was observed during both endo- and ecodormancy, and was presumably due to high treatment temperature or tissue hydration, and not due to removal of dormancy. Therefore, this method can not be used to study the relationship of dormancy to cold hardiness. However, this finding suggests that dormancy and cold hardiness are physiologically unconnected in raspberry. Moreover, as incomplete budbreak due to inadequate chilling is often a problem when raspberry is grown in mild winter climates or in a greenhouse, hot water treatment might offer a simple means to overcome dormancy in these plants.

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