Dormancy, Cold Hardiness, Dehardening, and Rehardening in Selected Red Raspberry Cultivars

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ABSTRACT. Canes and flower buds of selected red raspberry cultivars (*Rubus idaeus* L. ‘Maurin Makea’, ‘Muskoka’, and ‘Ottawa’) were sampled from a field (latitude, 61°20’N; longitude, 24°13’E) at 1-month intervals during Winter 1996–97 to study the interaction of dormancy and cold hardiness, hardiness retention, and rehardening capacity. One set of canes was subjected to dehardening (3 days) and two sets to dehardening + rehardening (3 and 7 days) treatments before cold hardiness determination. Maximum midwinter hardiness occurred in January, after breaking of endodormancy. Cold hardiness of canes and buds reached –28.6 to –37.2 °C and –24.2 to –31.6 °C, respectively. Throughout the winter, raspberry canes were hardier than buds. Endodormancy had a greater influence on dehardening and rehardening in buds than in canes, and cultivars differed in their response. Dehardening of ‘Maurin Makea’ canes and buds, and ‘Muskoka’ buds was slightly enhanced by breaking of dormancy, whereas dehardening in ‘Ottawa’ was not affected by dormancy. Raspberry canes and buds could reharden even after dormancy release. Reharden capacity was affected by the state of dormancy only in ‘Maurin Makea’ buds. Changes in dormancy status failed to explain cultivar differences regarding dehardening and the capacity to reharden suggesting other factors may be involved.

Red raspberry (*Rubus idaeus*) plants frequently suffer winter injury in northern climates. This injury usually occurs from midwinter until freezing temperatures end in April or May. Symptoms include tip dieback with injured buds on the living part of the cane (Nestby, 1992). Red raspberries develop sufficient cold hardiness in autumn, but the capacity to retain cold hardiness during intermittent short periods of warm weather and to reharden are crucial for their winter survival (Brierley and Landon, 1946; Zatylny et al., 1996). As little as 4 h daily for 2 d at 4 °C caused deacclimation of ‘Latham’, and –3 °C was needed to maintain hardiness (Brierley et al., 1952). In another study, hardiness was lost in raspberry cultivars exposed to 5 °C for 48 h at the end of January (Thorsrud and Hjeltne, 1963). Cultivar differences in dehardening have also been detected; cold hardy ‘Latham’ maintained hardiness longer and lost it more gradually than the sensitive ‘Malling Promise’ (Pacholak, 1978).

In northern latitudes (40°N to 64°N), red raspberry endodormancy usually lasts through December (Bailey, 1948; Brierley and Landon, 1946; Jennings and Carmichael, 1972; Måge, 1975; Zraly, 1978). Maximal cold hardiness has been reported to occur in January (Thorsrud and Hjeltne, 1963) or in February, 2 months after the breaking of endodormancy (Zraly, 1978). Hardiness has been positively correlated with the length and depth of endodormancy (Bailey, 1948; Jennings, 1964; Thorsrud and Hjeltne, 1963).

Reports on dormancy in relation to cold hardiness in raspberry are somewhat contradictory. Lamb (1955) found that dormant ‘Latham’ buds maintained their hardiness when exposed to 15.5 °C for 2 or 4 d, but after breaking of dormancy, both treatments caused deacclimation. In contrast, Miles (1965) found no differences in loss of hardiness of ‘Latham’ and ‘September’ at two dates during and after the endodormant period. ‘Latham’ raspberry canes dehardened in early winter, retained capacity to

reharden, if bud development did not occur (Brierley and Landon, 1954). Warmund et al. (1989) observed an effect of endodormancy on deacclimation of generative and vegetative tissues of *Rubus* ‘Cherokee’ blackberry. During dormancy, floral primordia and xylem were hardier and did not deacclimate as rapidly at 16 °C as after dormancy release. The phloem was also hardier during dormancy than afterwards, but the rate of deacclimation in the phloem was not affected by the state of dormancy. Stem tissues were able to reharder during endodormancy. After the breaking of endodormancy, only the xylem had the capacity to reharder.

The retention of cold hardiness once attained and the capacity to reharder after a warm period are possibly the most crucial factors for winter survival of raspberry. The objective of this research was to determine the interrelationship of endodormancy and cold hardiness, and to observe hardiness retention, and rehardening capacity in canes and flower buds of ‘Maurin Makea’, ‘Ottawa’, and ‘Muskoka’ red raspberry.

Material and Methods

PLANT MATERIALS. One-year-old canes of ‘Maurin Makea’, ‘Ottawa’, and ‘Muskoka’ red raspberry were collected from a cultivar trial at the Agricultural Research Centre of Finland, Häme Research Station, Pälkäne (latitude, 61°20’N; longitude, 24°13’E). The planting was established in 1992 on a loam soil as a randomized complete block design with three blocks. Canes were sampled on seven dates during Winter 1996–97; 7 Oct., 7 Nov., 1 Dec., 6 Jan., 3 Feb., 3 Mar., and 10 Apr. Very low temperatures occurred at the end of December, and a warm period followed by low temperatures occurred in February (Fig. 1).

To determine dormancy status, three replicate whole-cane samples per cultivar and block were sampled. To study cold hardiness and de- and rehardening, sample canes (seven or eight canes per cultivar and block) were sectioned into 15- to 20-cm-long pieces, except for the terminal and basal 20 to 30 cm of each shoot, which was discarded, packed in polyethylene plastic bags, and placed on ice in styrofoam boxes. The treatments were initiated on the sampling day.

DETERMINATION OF DORMANCY STATUS. Apical buds were removed from nine raspberry canes per cultivar, and canes were

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Fig. 1. Mean, minimum, and maximum temperatures as averages of 5-d periods recorded at the Agricultural Research Centre of Finland, Häme Research Station, Pälkäne, during Winter 1996–97.

inserted into perlite and placed in a greenhouse in a mist propagation bench. Relative humidity was 85% to 95%, and temperatures were $20 \pm 2^\circ\text{C}$. Canes were subjected to natural photoperiod and irradiance since dormancy release in raspberry is independent of photoperiod (Heide, 1993). The number of broken buds was recorded three times each week for 6 weeks. Dormancy status was determined as the average time (days) to budbreak for the first five buds per cane. When fewer than five buds broke, the value 42 d (the observation time) was assigned to the unbroken buds.

DEHARDENING AND REHARDENING TREATMENTS. Fifteen to 20-cm-long cane samples were placed in polyethylene bags and randomly assigned to four temperature pretreatments before cold hardiness of the samples was determined by controlled freezing. Pretreatments were 1) no pretreatment, direct determination of hardiness, 2) dehardening at 10°C for 3 d, 3) dehardening at 10°C for 3 d followed by short rehardening including 1 d at -3°C , 1 d at -5°C , and 1 d at -10°C , and 4) dehardening at 10°C for 3 d followed by long rehardening including 1 d at -3°C , 1 d at -5°C , and 5 d at -10°C . Three replications were sampled for each cultivar, pretreatment, and freezing temperature.

DETERMINATION OF COLD HARDINESS. Cane samples were wrapped in moist paper towels to ensure ice nucleation and repacked in plastic bags. This was done before initiating rehardening in pretreatments 3 and 4. Samples were placed in a controlled-climate chamber (Weiss 2600/45...5 Du-Pi, Weiss Umwelttechnik, Reiskirchen, Germany). Starting from the prevailing field temperature in treatment 1, from 0°C in treatment 2, and from -10°C in treatments 3 and 4, chamber temperature was lowered $5^\circ\text{C}\cdot\text{h}^{-1}$, and maintained for 30 min at each of seven test temperatures. The range of test temperatures (between -5 and -45°C) was selected each sampling time based on the expected level of hardiness in samples. Three replicate samples of each cultivar were removed at 5°C increments and allowed to thaw overnight at 0°C in closed styrofoam boxes. Control shoots were maintained at 0°C during the freezing treatments.

The following day, each sample was cut into three pieces. A 1 cm long internodal section was cut from each piece for the electrolyte

leakage test (Suojala and Lindén, 1997). Remaining samples were incubated in plastic bags at room temperature (22°C) for 1 week to allow oxidation of the injured tissue, and were evaluated visually under a dissecting microscope for freezing injury in canes and buds. Three cane pieces and three buds were examined per sample. Cane survival was evaluated by removing a thin layer of cortical tissue with a surgical knife and assessing injuries in the vascular regions of the cane. A green color indicated a living sample, and dark brown color indicated that the critical tissues for cane survival were dead. Buds were rated as either living or dead by cutting them longitudinally and assessing internal color changes. A green color indicated a living bud. If the pith and/or the vascular tissues of the bud or the floral primordia were brown, the bud was considered dead. Values of LT_{50} were estimated using logit models (Lindén et al., 1996) in the SAS procedure PROBIT (SAS, 1989).

FIELD OBSERVATIONS. Winter injury to field canes was evaluated visually on an arbitrary scale (0 to 9) on 30 May 1997, after growth had resumed.

STATISTICAL ANALYSIS. Cold hardiness (LT_{50}) of buds and canes after pretreatments 1, 2, 3, and 4 was expressed as $\text{LT}_{50}1$, $\text{LT}_{50}2$, $\text{LT}_{50}3$, and $\text{LT}_{50}4$, respectively. Cold hardiness data (LT_{50}) were tested with a repeated measures analysis of variance (ANOVA) for the main effects of cultivar and time, and their interaction by using the GLM procedure of SAS (SAS, 1989). Means were separated for each sampling time by the S–N–K test (Steel and Torrie, 1980).

Dehardening percentage was calculated as $(\text{LT}_{50}1 - \text{LT}_{50}2) / \text{LT}_{50}1 \times 100\%$ to describe the rate of dehardening. Rehardening capacity was calculated as $\text{LT}_{50}3 - \text{LT}_{50}2$ and $\text{LT}_{50}4 - \text{LT}_{50}2$, in short and long rehardening, respectively. Data on dehardening percentages and rehardening capacities were tested with a repeated measures ANOVA to determine cultivar differences. Correlation analyses between dormancy status and $\text{LT}_{50}1$, $\text{LT}_{50}2$, $\text{LT}_{50}3$, $\text{LT}_{50}4$, as well as dehardening percentage and the rehardening capacities were performed to assess effects of dormancy on cane and bud cold hardiness, dehardening, and rehardening. Pearson correlation coefficients were calculated by using the CORR procedure of SAS (SAS, 1989).

Results

Raspberry flower bud hardiness was affected by dormancy status to a greater extent than cane hardiness. Differences between cultivars also occurred. ‘Maurin Makea’ was particularly susceptible to changes in dormancy status. Cold hardiness of ‘Ottawa’ was least influenced by dormancy.

Deepest dormancy, determined as the longest time to budbreak, occurred in ‘Muskoka’ in October, in ‘Maurin Makea’ in October to November, and in ‘Ottawa’ in November (Fig. 2). Thereafter, dormancy decreased rapidly until January and slowly until the end of the experiment in April. Percentage of budbreak in raspberry canes was 5% to 10% in October and 40% to 80% in April (Fig. 2). In ‘Maurin Makea’, many buds were winter injured in the field, resulting in a lower percentage of budbreak in this cultivar from February onwards.

Cultivar and date effects were significant in most of the hardiness measurements (Table 1). Because of a cultivar $\times$ time

Fig. 2. Dormancy status of three raspberry cultivars on a scale of 0 (least) to 42 (deepest) determined as days to budbreak, and percentage of broken buds in greenhouse forcing at each sampling time during Winter 1996–97. Vertical bars represent $\pm$ SE ($n = 3$).

interaction, cultivar differences in cold hardiness are reported separately for each sampling time (Fig. 3). Raspberry canes were harder than buds (Fig. 3A). Differences in cane cold hardiness between raspberry cultivars were observed in January and February. Cultivar differences in bud cold hardiness occurred January through April; overall, the least hardy buds were found in 'Maurin Makea'.

After dehardening treatment, raspberry cane hardiness seldom fell below -20°C (Fig. 3B, Table 2). Depending on the cultivar,

bud hardiness after dehardening treatment fell below this hardiness level during and after February. After the dehardening treatment, cultivar differences in cane hardiness were observed in January and February, and in bud hardiness in November, February, and March. 'Maurin Makea' buds readily lost hardiness after January.

Raspberry canes and buds could reharden when exposed again to low temperatures after dehardening (Fig. 3C, Table 2). After the short rehardening treatment for 3 d, cultivar differences in hardiness were observed for canes in October, February, and March, and for buds from February through April. After January, 'Maurin Makea' lost the capacity to regain the level of hardiness it had before the dehardening treatment. Reharden for 7 d did not alter the results (Fig. 3D, Table 2). Differences in cane cold hardiness between cultivars were smaller

after long rehardening than after short rehardening, whereas differences in bud cold hardiness between cultivars remained unchanged.

Endodormancy and initial cold hardiness were negatively correlated in 'Maurin Makea' canes ($r = -0.532$, $P = 0.013$). 'Muskoka' cane hardiness was negatively correlated with dormancy status after the dehardening treatment ($r = -0.443$, $P = 0.045$) and after the long rehardening treatment ($r = -0.481$, $P = 0.027$). Correlation coefficients between dormancy status and cane hardiness determinations were negative, because the greatest hardiness was achieved after endodormancy was broken.

Bud cold hardiness was related to dormancy status to a greater extent than cane cold hardiness. Momentary cold hardiness in buds was not influenced by dormancy status in any cultivar. In

Table 1. Repeated measures ANOVA for different hardiness determinations (LT_{50}) of raspberry canes and buds from October to April.

Dependent variable	Main effects and interaction	P	
		Canes	Buds
Cold hardiness	Cultivar	NS	0.001
	Time	<0.001	<0.001
	Cultivar $\times$ time	0.002	<0.001
Dehardened	Cultivar	0.002	0.001
	Time	<0.001	<0.001
	Cultivar $\times$ time	0.024	<0.001
Rehardened (short)	Cultivar	0.007	0.018
	Time	<0.001	<0.001
	Cultivar $\times$ time	0.001	<0.001
Rehardened (long)	Cultivar	0.036	0.007
	Time	<0.001	<0.001
	Cultivar $\times$ time	<0.001	<0.001
Dehardening percentage	Cultivar	NS	NS
	Time	0.001	<0.001
	Cultivar $\times$ time	0.014	<0.001
Rehardening capacity (short)	Cultivar	NS	NS
	Time	0.003	0.037
	Cultivar $\times$ time	NS	NS
Rehardening capacity (long)	Cultivar	NS	NS
	Time	<0.001	NS
	Cultivar $\times$ time	0.003	0.004

NSNonsignificant parameter estimate at $P = 0.05$.

'Maurin Makea' buds, hardiness was positively correlated with dormancy after the dehardening treatment ($r = 0.481$, $P = 0.027$), as well as after both rehardening treatments ($r = 0.527$, $P = 0.014$ and $r = 0.512$, $P = 0.018$ in short and long rehardening, respectively). 'Muskoka' bud hardiness was positively correlated with dormancy after dehardening ($r = 0.451$, $P = 0.040$).

When dehardening percentage and rehardening capacities were calculated, no differences between raspberry cultivars were observed, but a cultivar $\times$ time interaction was observed for dehardening percentage and for rehardening capacity in long rehardening (Table 1). Dehardening percentage was negatively correlated with dormancy status in 'Maurin Makea' canes ($r = -0.448$, $P = 0.042$) and buds ($r = -0.543$, $P = 0.011$), and in

'Muskoka' buds ($r = -0.608$, $P = 0.003$). When cultivars were pooled, a negative correlation between dehardening percentage and dormancy status was observed in buds ($r = -0.468$, $P < 0.001$). The capacity to reharden and dormancy status were positively correlated only in 'Maurin Makea' buds ($r = 0.433$, $P = 0.049$ in long rehardening).

Discussion

Dormancy status had a greater influence on dehardening and rehardening of raspberry buds than canes. Moreover, cultivars differed in their response; cold hardiness characteristics of 'Ottawa' were not related to dormancy status, whereas 'Maurin Makea' responded to changes in dormancy, 'Muskoka' being intermediate between these cultivars. Because cultivar differences in hardiness behavior could not be explained by differences in dormancy status, other factors may be involved.

Studies on dormancy effects should be conducted from November to January because the greatest changes in dormancy status occur during this period. Endodormancy of 'Maurin Makea', 'Ottawa' and 'Muskoka' raspberry was broken in January, as has been reported for other raspberry cultivars (Bailey, 1948; Brierley and Landon, 1946; Jennings and Carmichael, 1972; Måge, 1975; Zraly, 1978). Under our conditions, the majority of buds were able to grow for ≈ 4 months before weather conditions allowed for summer growth. However, according to White et al. (1999), especially in the lower region of the cane, endodormancy in raspberry buds is replaced by paradormancy, which suppresses growth, until further chilling leads to full removal of endodormancy. In our experiment, apical buds were removed before forcing to suppress the effect of apical dominance. However, for more accurate determination of dormancy status, the canes should be cut into one-node sections before forcing, as was done by Måge (1975).

Maximal cold hardiness of raspberry cultivars occurred after dormancy was broken, as was observed by Thorsrud and Hjeltne (1963) and Zraly (1978). In contrast, blackberry floral primordia, xylem and phloem are hardier before the breaking of dormancy than after (Warmund et al., 1989). The positive relationship between hardiness of a cultivar and the length of the endodormant period as reported by Bailey (1948), Thorsrud and Hjeltne (1963), and Jennings (1964) was not observed in this study. Field observations in spring (data not presented) revealed that 'Maurin Makea' had suffered more winter injury than 'Ottawa' or 'Muskoka' and was the least hardy cultivar. Damage had probably occurred at two times; at the end of December (minimum temperature -26.6°C), and in February, when below -20°C occurred after a warm period (Fig. 1). Throughout the winter, raspberry canes were harder than buds. This agrees with the findings of Doughty et al. (1972) and Hummer et al. (1995). The rehardening treatments demonstrated that raspberry canes have a higher capacity to acclimate than buds, possibly due to different survival mechanisms.

Loss of hardiness caused by dehardening treatment was greater in midwinter, when initial hardiness was greater (Table 2). After dehardening treatment, canes were consistently hardy to about -20 to -25°C . Dehardening of 'Maurin Makea' canes and buds, and 'Muskoka' buds was enhanced slightly by the breaking of dormancy, whereas dehardening in 'Ottawa' was unaffected by dormancy status. Consequently, factors other than dormancy must be involved. This may explain some contradictory reports. Lamb (1955) found that breaking of dormancy had an effect on

Fig. 3. Cold hardiness (LT_{50}) of buds and canes of three raspberry cultivars (A) in the field, (B) after dehardening, (C) after dehardening + short rehardening, and (D) after dehardening + long rehardening. Legend in A applies to all figures. For each sampling time separately, values with the same letter (canes in upper case, buds in lower case) are not significantly different at $P = 0.05$ according to S-N-K test. Letters are presented only where significant differences occurred between cultivars.

Table 2. Change in raspberry cane and bud cold hardiness as a consequence of dehardening (10 °C, 3 d) and rehardening (short: -3 °C, 1 d; -5 °C, 1 d; -10 °C, 1 d; and long: -3 °C, 1 d; -5 °C, 1 d; -10 °C, 5 d) treatments.

Sampling time	Cultivar	Organ	Initial hardiness LT ₅₀ (°C)	Change in LT ₅₀ (°C)		
				In dehardening	In short rehardening	In long rehardening
7 Oct.	MM ²	Cane	-19.2	+2.5	-5.5	-4.9
		Bud	-15.0	+2.5	-6.7	-5.1
	Ottawa	Cane	-20.8	+1.6	-13.3	-13.3
		Bud	-17.5	+0.9	-5.6	-8.4
	Muskoka	Cane	-17.5	+2.5	-7.5	-6.8
		Bud	-16.7	+0.9	-5.1	-4.8
7 Nov.	MM	Cane	-22.5	0	-7.8	-12.9
		Bud	-19.2	0	-6.6	-9.9
	Ottawa	Cane	-24.2	+0.8	-7.7	-9.4
		Bud	-21.1	+0.3	-6.7	-7.6
	Muskoka	Cane	-26.6	+3.2	-7.4	-9.9
		Bud	-21.7	-0.8	-3.9	-3.1
1 Dec.	MM	Cane	-27.5	+4.2	-10.0	-8.4
		Bud	-21.6	+1.6	-6.7	-8.4
	Ottawa	Cane	-30.3	+5.4	-8.4	-9.3
		Bud	-25.0	+2.5	-6.7	-5.6
	Muskoka	Cane	-28.1	+4.8	-5.6	-6.7
		Bud	-23.3	+3.3	-6.6	-7.5
6 Jan.	MM	Cane	-28.6	+2.8	-11.7	-13.2
		Bud	-24.2	+3.4	-5.0	-7.3
	Ottawa	Cane	-37.2	+7.8	-12.5	-9.0
		Bud	-31.6	+9.1	-6.1	-10.0
	Muskoka	Cane	-34.2	+12.2	-12.2	-13.9
		Bud	-27.4	+8.2	-6.5	-10.0
3 Feb.	MM	Cane	-36.3	+17.9	-7.7	-17.4
		Bud	-24.2	+11.7	-5.0	-3.3
	Ottawa	Cane	-31.6	+9.1	-11.7	-13.8
		Bud	-26.4	+7.2	-7.5	-8.3
	Muskoka	Cane	-28.6	+3.6	-10.9	-10.9
		Bud	-22.5	+4.1	-11.1	-11.6
3 Mar.	MM	Cane	-25.8	+7.6	-2.9	-1.4
		Bud	-16.2	+8.6	-4.9	-5.4
	Ottawa	Cane	-26.4	+2.8	-8.0	-6.4
		Bud	-18.9	-3.6	-1.7	-3.3
	Muskoka	Cane	-26.4	+5.1	-6.2	-6.8
		Bud	-20.8	+4.0	-2.2	-3.2
10 Apr.	MM	Cane	-23.1	+0.9	-4.2	-7.8
		Bud	-5.0	+0.8	0	0
	Ottawa	Cane	-25.6	-0.2	-6.5	-9.2
		Bud	-13.1	+6.5	-7.2	-12.6
	Muskoka	Cane	-23.4	+0.3	-6.4	-10.3
		Bud	-17.5	+10.6	-6.7	-9.5

²MM = 'Maurin Makea'.

dehardening in 'Latham', whereas Miles (1965) reported no difference in the loss of hardiness before or after the breaking of dormancy in 'Latham' and 'September' raspberries. According to Warmund et al. (1989), dehardening of blackberry floral primordia and xylem are affected by dormancy, whereas that of phloem is not.

Both raspberry canes and buds could reharden when exposed once again to low temperatures, even after the endodormant period. Rehardening treatment for 3 d at -3, -5, and -10 °C was sufficient to reharden raspberry canes and buds. Four more days at -10 °C (long rehardening) only enhanced hardiness slightly. Rehardening capacity was affected by the state of dormancy only

in 'Maurin Makea'; buds of this cultivar lost the capacity to regain their original level of hardiness after January. Brierley and Landon (1954) reported that 'Latham' raspberry canes dehardened in early winter (dormancy unspecified) could reharden if buds did not become active. Our study is the first to report that raspberry canes and flower buds have the capacity to reharden even after endodormancy is satisfied. In blackberry (*Rubus* sp.) the capacity to reharden is impaired in the xylem after the breaking of dormancy (Warmund et al., 1989).

Cold hardiness is influenced by numerous endogenous and environmental factors. Changes in dormancy status did not explain why raspberry cultivars had a different ability to maintain

hardiness and to rearden after exposure to warm temperatures. These characteristics might be related to a different minimum temperature requirement for growth in the cultivars, leading to differential bud development and subsequent rise in moisture content of the buds. Biochemical or biophysical examinations, or morphological studies on the rate of bud development might explain cold hardening, dehardening, and rehardening of raspberry buds and canes.

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