Morphological Development of Lingonberry as Affected by In Vitro and Ex Vitro Propagation Methods and Source Propagule

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Abstract. The growth and development of lingonberry (*Vaccinium vitis-idaea* L.) plants propagated either by conventional softwood cuttings or by in vitro shoot proliferation from nodal explants and by shoot regeneration from excised leaves of micropropagated shoots, were studied in cultivars 'Regal', 'Splendor', and 'Erntedank'. Significant differences were observed between the treatments. After 3 years of growth, the in vitro-derived plants produced more stems, leaves, and rhizomes than the conventional cuttings which rarely produced rhizomes. In vitro culture on nutrient medium apparently induces the juvenile branching characteristics that favor rhizome production. This increase in vegetative growth and rhizome yield of in vitro-derived plants over stem cuttings varied among genotypes.

Lingonberry (*Vaccinium vitis-idaea* L.), a high antioxidant-containing medicinal fruit crop (Novelli, 2003; Racz et al., 1962; Stark et al., 1978), is a circumboreal woody, rhizomatous, evergreen dwarf shrub (Luby et al., 1991; Vander Kloet, 1988) which can also be used as a landscape ornamental ground cover (Dierking and Dierking, 1993). Lingonberry products include juice, sauce, preserves, candy, jelly, syrup, ice cream, pickles, wine, and liqueur (Gustavsson, 1997; Holloway, 1981; Lieberman, 1977). The Canadian province, Newfoundland and Labrador, is the largest North American lingonberry producing region (Penney et al., 1997), with about 140,000 kg harvested annually from native stands for processing, mostly for export (Jamieson, 2001).

Since conventional methods of vegetative propagation are unable to supply the large quantities of genetically superior individuals needed by commercial cultivation, new methods are required. In vitro techniques with lingonberry can be used in the future for propagation, germplasm improvement or gene conservation. Used in conjunction with classical breeding methods, an efficient in vitro shoot proliferation system could accelerate cultivar development programs for this species (Debnath, 2000).

Lingonberry is commonly propagated by division, softwood cuttings, and micropropagation. Previous studies indicate that the method of propagation influences the growth habit of the resulting plants. Increased branching and

vigorous vegetative growth are often noted in plants produced through in vitro culture. Tissue-culture-derived strawberries grow more vigorously producing more crowns and runners than conventionally propagated plants (Boxus et al., 1984; Swartz et al., 1981), and micropropagated brambles (*Rubus* sp.) grow vigorously and fruit precociously and heavily (O'Dell, 1989). Shoot growth, cane and lateral branching, and flower production are all greater with tissue culture propagation of thornless blackberry (Swartz et al., 1983). Holloway (1985) reported that softwood and hardwood cuttings of lingonberry failed to produce rhizomes even after the rooted plants had gone through two growth cycles. Similar results were obtained by Lehmushovi (1975, 1977) and Öster (1976). Hosier et al. (1985) reported that micropropagated lingonberry produced a prolific rhizomatous growth habit within 9 months after planting in the greenhouse, and stem cuttings, taken at the time the tissue cultures were initiated, produced plants with less rhizome development. Rhizome production and total plant weight were greater for tissue culture plants than for stem cuttings 'Sanna' lingonberry (Gustavsson and Stanys, 2000). However, Serres et al. (1993) observed that softwood cuttings taken from both division-derived and tissue culture-derived stock lingonberry plants produced plants with as many rhizomes and branch shoots as plants grown from microshoots.

The purpose of this study was to evaluate the performance of lingonberries propagated by stem cuttings with those obtained by axillary shoot proliferation from nodal explants and by adventitious shoot regeneration from excised leaves. Plants propagated by in vitro shoot proliferation have not been compared with those obtained by shoot regeneration from excised leaves of micropropagated shoots in *Vaccinium* species. Propagules of three cultivars grown over three seasons were tested for shoot growth and rhizome production.

Plant material and establishment of shoot cultures from nodal explants. Young, actively growing lingonberry shoots of cultivars, 'Regal', 'Splendor', and 'Erntedank' were obtained from plants being maintained in a greenhouse. Shoot-tip cultures, following the method of Debnath and McRae (2001), were established in 175-mL glass jars containing 35 mL BM medium [three-quarter macro-salts and micro-salts of Debnath and McRae's (2001) shoot proliferation medium D] supplemented with (per liter) sucrose (25 g), Sigma A 1296 agar (3.5 g), and Gelrite (1.25 g) (Sigma Chemical Co., St. Louis) and with zeatin (5 μ M). The medium pH was adjusted to 5.0 before autoclaving at 121 °C for 20 min. Culture jars were capped with clear permeable polypropylene caps (Sigma Chemical Co., St. Louis). After explant transfer, jars were sealed with Parafilm, placed upright and maintained at 20 ± 2 °C under a 16-h photoperiod with a photosynthetic photon flux (PPF) density of 30 μ mol·m⁻²·s⁻¹ at the culture level provided by cool white fluorescent lamps.

The vegetative shoots obtained in vitro from the axillary buds were excised 8 weeks following culture initiation and subcultured by transferring the nodal explants (with three nodes, leaves intact) of randomly selected shoots in each vial from the initial culture to fresh BM supplemented with 1 μ M zeatin.

Adventitious shoot regeneration from leaf explants. Adventitious shoot regeneration was obtained from leaf explants of proliferating shoot cultures following Debnath and McRae (2002). Briefly, four almost-fully or fully expanded leaves nearest the apical meristem were excised with a scalpel at the petiole base and five transverse cuts, that did not sever the leaf completely, were made through the midrib. Prepared leaves (8) were transferred to 100 × 25-mm sterilized, disposable petri-plates containing 25 mL of BM plus 2 μ M zeatin with their adaxial side in contact with the medium. Plates were sealed along the rim with two layers of Parafilm. Cultures were incubated in the dark at 20 ± 2 °C for 2 weeks, before transfer to the same photoperiod, light intensity, and temperature employed for multiplication. Buds and shoot clumps from leaf explants were collected 8 weeks following culture initiation and transferred to 175-mL glass vessels (Sigma Chemical Co., St. Louis) containing 35 mL of BM with zeatin (1 μ M). Vessels were capped with polypropylene clear lids and cultured for another 8 weeks for shoot elongation.

Rooting, acclimatization, and evaluation for morphological characters. Rooted softwood stem cuttings (SC), and axillary and adventitious shoots obtained from node (NC), and leaf culture (LC), respectively, were compared for differences in morphology, growth, and rhizome production over three seasons of growth. Eight-week-old in vitro-derived elongated shoots (3 to 4 cm long) were rooted in May 2001 using previously reported techniques (Debnath and McRae, 2001, 2002). Briefly, shoots were excised just above the original explant and planted in 45-cell plug trays (cell diameter = 5.9 cm, cell depth = 15.1 cm) (Beaver Plastics, Edmonton, Alberta,

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Fig. 1. Root and rhizome development from 'Regal' lingonberry: (A) = node culture-derived 4-month-old plant; (B) = node culture-derived 3-year-old plant; and (C) = stem cutting-derived 3-year-old plant.

Canada) containing 2 peat : 1 perlite (v/v). No rooting compound was applied. Trays were placed in a humidity chamber with a vaporizer at $22 \pm 2^\circ\text{C}$, 95% RH at 16-h photoperiod at $55 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF for rooting.

Also in May 2001, terminal softwood cuttings 4 to 5 cm long were taken from new growth of potted plants of each cultivar and planted as above described for rooting of tissue culture-derived microcuttings. Greenhouse-grown plants used for tissue culture provided SC stems for rooting. In July, rooted softwood cuttings and rooted tissue-cultured plantlets were transferred to 10.5 (length) $\times$ 10.5 (width) $\times$ 12.5 (depth) cm^3 plastic pots containing the same medium as used for rooting, and acclimatized by gradually lowering the humidity over 2 to 3 weeks. Hardened-off plants were grown in the greenhouse under natural light conditions at a maximum PPF of $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at $20 \pm 2^\circ\text{C}$, 85% RH. Average day length was 15.3, 14.1, 12.3, 10.5, 9.2, and 8.3 h, for July to December, respectively. Two weeks after transfer, the plants received a solution containing $25 \text{ mg}\cdot\text{L}^{-1}$ N from Peters Azalea Neutral Fertilizer 20N-8P-20K (Plant Products Co. Ltd., Brampton, Ontario, Canada). In subsequent weeks, the fertilizer solution was applied with N concentration raised in $25 \text{ mg}\cdot\text{L}^{-1}$ increments to $100 \text{ mg}\cdot\text{L}^{-1}$. Fertilization was stopped after 5.5 months of the $100 \text{ mg}\cdot\text{L}^{-1}$ N regime. Irrigation was applied when necessary. In January 2002 dormancy requirements were met by maintaining the plants at or below 5°C for 12 weeks. After a second 12-week dormancy period, the plants were grown in the greenhouse until data were taken in December, 2003. Average day length was 13.4, 15.0, 15.5, 15.3, 14.1, 12.3, 10.5, 9.2, and 8.3 h, for the months April to December, respectively in 2002 and 2003.

Data collection and statistical analysis. The experiment was arranged in a completely

randomized block design, with nine plants (replicates) per treatment, and the experiment was repeated three times. The following growth characteristics were measured for each treatment: number of stems, stem branches, and leaves per plant, plant height (cm), plant vigor, number of plants with rhizomes, number of rhizomes and rhizome branches per plant, and rhizome length (cm) and diameter (mm). Vigor was determined by visual assessment, on a scale of 1 (very poor) to 8 (fully normal and healthy shoots with large green leaves and excellent vigor).

Data for all characteristics except plant vigor were subjected to analysis of variance with the SAS statistical software package (Release 8.2; SAS Institute, Inc., Cary, N.C.). The stem and rhizome numbers and their respective branch numbers per plant were transformed to the square root scale, and rhizome formation percentage was submitted to an angular transformation, before the ANOVA to stabilize the variance, and then data for these characteristics were back-transformed for presentation. Unless otherwise noted, statistical F tests were evaluated at $P \leq 0.05$. Differences among treatments were further analyzed using Duncan's multiple range test. Plant vigor was tested by using a categorical data modeling procedure (PROC CATMOD in SAS) and differences between treatment combinations were contrasted using the contrast statement in the CATMOD procedure. This method is appropriate for the analysis of categorical data (Compton, 1994; Grizzle et al., 1969), and allows assessment of both main effects and interaction terms (as in analysis of variance).

Results

In the first growing season after transplanting, all plants did not grow much and produced only 1 to 4 shoots 4 to 6 cm long. However, growth was much more vigorous in the second growing season. The plants produced new shoots from the old shoots plus very vigorous shoots from the base of the plant. Vigorous growth

continued until the end of the experiment.

Both the axillary (NC) and adventitious bud (LC) plants showed appreciable vegetative growth and the canopies became very dense after three growing seasons. Their development with respect to the number of stems, stem branches, and leaves per plant was more advanced than that reached by SC plants of the same age and they could not be distinguished in morphology from each other or from the original clone. Many in vitro-derived plants produced rhizomes after 2 months of growth and within 4 months, two to four rhizomes were produced per plant (Fig. 1A). At the end of year 3, most of the NC and LC plants had elongated rhizomes with rhizomatous shoots (Fig. 1B). However, none of the SC plants produced rhizomes in 2001 and most of them had well developed roots but no rhizome even after three seasons of growth (Fig. 1C).

An interaction between cultivar and propagation method was observed for all characters except plant vigor, percentage of rhizome formation, and rhizome number and diameter (Tables 1 and 2). These two factors affected not only the number of stem and rhizome branches, plant height, leaves per plant, number and frequency of rhizome formation, and rhizome length (Table 1) but also plant vigor ($\chi^2 = 10.82$, $P = 0.0045$ and $\chi^2 = 19.31$, $P < 0.0001$ for cultivar and propagation method, respectively). The induction of shoot and rhizome development was dependent on the propagation type. SC plants produced more vigorous plants but with fewer stems and leaves per plant than those of NC and LC plants. The leaves were generally larger on SC plants than those on NC and LC plants. Both NC and LC plants had similar plant height, but both had less than those of SC plants (Table 1). NC and LC plants produced more rhizome-derived daughter stems than those of SC plants which produced few or no rhizomes after three seasons of growth. After growth in the greenhouse for 3 years, the frequency of rhizome production was least in SC plants (30%, 19%, and 3.7% for 'Regal', 'Splendor', and 'Erntedank', respectively) compared to those produced by NC (89% to 96%) and LC plants

Table 1. Mean values of the main effects across all treatments for combined effect of propagation method (SC = stem cutting, NC = node culture, and LC = leaf culture) and cultivar for leaf and shoot characteristics in lingonberries grown over three seasons.^z

Treatment	Stems (no./plant) ^y	Stem branches (no./plant) ^y	Plant ht (cm)	Leaves (no./plant)	Plant vigor (scale 0–8) ^x
Cultivar (C)					
Regal	4.9 a ^w	9.8 a	8.9 b	230 b	4.5 b
Splendor	4.6 a	8.9 ab	10.9 a	213 b	5.1 ab
Erntedank	5.0 a	7.9 b	11.3 a	271 a	5.6 a
Propagation method (PM)					
SC	1.3 c	8.3 b	12.6 a	164 c	5.8 a
NC	8.1 a	8.4 b	8.6 b	256 b	5.1 b
LC	5.5 b	10.0 a	9.9 b	295 a	4.2 c
Significant effects ^v	PM, C × PM	C, PM, C × PM	C, PM, C × PM	C, PM, C × PM	C, PM

^zData were collected after three seasons of growth.

^yData for number of stems and stem branches per plant were transformed to the square root scale and back-transformed for presentation.

^xVigor was assessed visually based on plant appearance using a scale from 1 = very poor to 8 = fully normal and healthy shoots with large green leaves and excellent vigor.

^wMean separation within columns and factors for stem number and branches, plant height and leaf number per plant by Duncan's multiple range test, and for plant vigor by categorical analysis (CATMOD procedure in SAS). Means with different letters indicate differences at $P \leq 0.05$.

^vSignificant effects ($P \leq 0.05$).

Table 2. Mean values of the main effects across all treatments for combined effect of propagation method (SC = stem cutting, NC = node culture, and LC = leaf culture) and cultivar for rhizome characteristics in lingonberries grown over three seasons.^z

Treatment	Rhizome formation (%) ^y	Rhizomes (no./plant) ^x	Rhizome branches (no./plant) ^x	Rhizome length (cm)	Rhizome diam (mm)
Cultivar (C)					
Regal	65 ab ^w	2.7 c	9.9 b	33 a	1.1 a
Splendor	69 a	3.4 b	8.7 b	32 a	1.1 a
Erntedank	57 b	4.6 a	21.6 a	24 b	1.2 a
Propagation method (PM)					
SC	17 c	1.3 c	9.9 b	23 b	1.4 a
NC	93 a	3.8 b	20.7 a	48 a	1.2 b
LC	82 b	5.1 a	8.7 b	14 c	1.1 b
Significant effects ^v	C, PM	C, PM	C, PM, C × PM	C, PM, C × PM	PM

^zData were collected after three seasons of growth.

^yPercentage data were transformed to angles and back-transformed to percentage for presentation.

^xData for number of rhizomes and rhizome branches per plant were transformed to the square root scale and back-transformed for presentation.

^wMean separation within columns and factors by Duncan's multiple range test, $P \leq 0.05$, whereby means associated with different letters signify significant differences.

^vSignificant effects ($P \leq 0.05$).

(74% to 93%). However, SC plants which were rhizome bearing had fewer but thicker rhizomes than those of NC and LC plants (Table 2).

Significant differences were observed between NC and LC plants for shoot and rhizome characters (Tables 1 and 2). The NC plants, which arose through axillary shoot proliferation, produced more stems and rhizome branches and longer rhizomes but fewer stem branches, leaves, and rhizomes than the adventitiously produced LC plants. Shoot vigor and frequency of rhizome formation were better in NC plants than in LC-plants (Tables 1 and 2).

The cultivars in this study differed significantly in their shoot proliferation and rhizome development potential for all characters except stem number and rhizome diameter (Tables 1 and 2). Across propagation methods, 'Erntedank' produced the most vigorous plants with more leaves, rhizomes, and rhizome branches than 'Regal' and 'Splendor'. 'Regal' plants were shorter but had more stem branches than 'Erntedank'. While 'Splendor' had the maximum frequency of rhizome formation, 'Erntedank' rhizomes were the shortest (Table 2). It appears that plant vigor and rhizome number were inversely correlated with stem branches and rhizome length (Tables 1 and 2).

Discussion

Tissue culture (NC and LC) plants produced many stems and rhizomes during the first three seasons of growth and consequently provided a larger framework for shoot production during the experiment than did plants produced by stem cuttings. As reported earlier for *Vaccinium* species (Gustavsson and Stanys, 2000; Hosier et al., 1985; Morrison et al., 2000), this could be the result of the in vitro hormonal treatment (cytokinin), which can induce an increased number of shoots per plant. Blueberry plants produced by micropropagation produced more vigorous shoots than plants produced from conventional cuttings (Smagula and Lyrene, 1984), and consistently yielded more fruit during the first three seasons after field establishment (Read et al., 1988, 1989). These improved yields are due to the high numbers of branches formed on micropropagated plants. It is possible that, supernumerary branching and rhizome formation in plants resulting from in vitro culture could be a symptom of their rejuvenation. Woody plants recently derived from in vitro culture may retain the effects of rejuvenation ex vitro when they are grown and propagated conventionally. Plants derived from reversion from mature to juvenile characteristics may be a general phenomenon

in plant tissue culture. The cause of juvenile reversion effects in lingonberry node and leaf cultures is unknown.

Presumably the increase in vegetative growth with respect to the number of stems, stem branches, and leaves per plant contributed to the increase in rhizome yield of NC and LC plants of lingonberry. Whether the useful agronomic traits observed in the first three seasons of these plants are stable has to be ascertained in subsequent years and in field trials. The morphological differences observed in the present study can at least partly be attributed to the different conditions of propagation. In tissue culture, shoots grown from nodal explants or from leaves are proliferated in vitro by the use of cytokinin. This promotes the proliferation or regeneration of shoots and suppresses root formation. Only when planted into a peat-perlite medium in the greenhouse do these shoots start to form roots. When cuttings are planted into the same rooting medium, they start to form shoots and roots at the same time (data not shown).

Comparison of tissue culture and cutting propagation has also been made for 'Sanna' lingonberry and other *Vaccinium* species, leading to similar findings as in the present study. Although Grout et al. (1986) reported more basal branches and lateral shoots on micropropagated

plants of highbush blueberry than on those propagated by stem cuttings, and Read et al. (1988) obtained more flower buds and higher yields on micropropagated highbush cultivars, micropropagated lowbush blueberries produced fewer flower buds than did conventionally propagated plants (Morrison and Smagula, 1986). However, in contrast to present study, Serres et al. (1993) observed that softwood cuttings produced a rhizomatous growth habit soon after rooting. This differential response might be due to different genotypes and/or culture condition used for propagation. Micropropagated ginger plants had significantly reduced rhizome yield in the first generation of ex vitro growth (Smith and Hamil, 1996).

Both axillary and adventitious shoot plants derived from node and leaf culture, respectively of three lingonberry cultivars grew vigorously and significant differences were found for growth and morphology between two kinds of source propagule. This might be due to two explant sources used for propagation as was also reported by Shen et al. (1996) in chinese gooseberry.

The genotype often profoundly affects growth and development. The advantage of increased rhizome production of in-vitro-derived plants over stem cuttings varied among genotypes. This result is reported in other studies on *Vaccinium angustifolium* (Morrison et al., 2000).

Genetic variation has frequently been observed in plants regenerated from tissue cultures (Larkin and Scowcroft, 1981). The degree and type of variation is affected by several factors, including genotype (Lee and Philips, 1988). No obvious variant plants were observed in the present study.

In conclusion, this study showed the economic benefit of using tissue culture plants compared with traditional stem cutting plants. The enhanced vegetative growth and rhizome yield of tissue-culture-derived lingonberry plants should prove to be beneficial to lingonberry growers concerned with rapid establishment of plants for early fruit production and an improved return on their investment.

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