The European Blueberry (*Vaccinium myrtillus* L.) and the Potential for Cultivation. A Review

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ABSTRACT

Blueberries belong to the genus *Vaccinium*, a widespread genus with more than 200 species of woody plants. In Northern Europe, the European blueberry (EB), also called bilberry, is one of the most important wild berries. EB (*Vaccinium myrtillus*) is very demanded by the processing industry, due to its delicious taste and high dietary value. However, to our knowledge there has been made no efforts of domestication of the species, and it is still harvested in forest fields without any cultivation. The successful management of the sweet lowbush blueberry (*V. angustifolium*), which in many ways is similar to the EB, suggests that there are opportunities to increase yield and decrease the significant yearly variation in EB yield, by practices including fertilization, irrigation, cutting trees, and weed control. The fruit yield in wild stands of EB is very variable, but the potential is probably close to 2 tons per hectare. Results from literature on growth of the EB, development and ecology are discussed in relation to possibilities for domestication.

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INTRODUCTION

The European blueberry (EB) is a deciduous woody dwarf shrub, typical and abundant especially in spruce- and pine-dominated heath forests of medium fertility in the northern hemisphere (**Fig. 1**).

EB also grows in marginal types of forests, and above the tree limit up to high altitudes. Typically, it grows on areas of better-drained acid soils. The tiller (individual shoot from the rhizome) develops into an axis (a system of annual shoot increments formed by the branching of the original tiller or subsequently, by the branching of a shoot arising from the lower part of this; of limited longevity) from approximately 5 to 90 cm high depending on climate and nutrient availability (Flower-Ellis 1971). The bush, consisting of abundant tillers, is perennial and deciduous, and leaves are notably bright green, 1-3 cm long, slightly toothed and not leathery. Tillers and leaves are hairless and
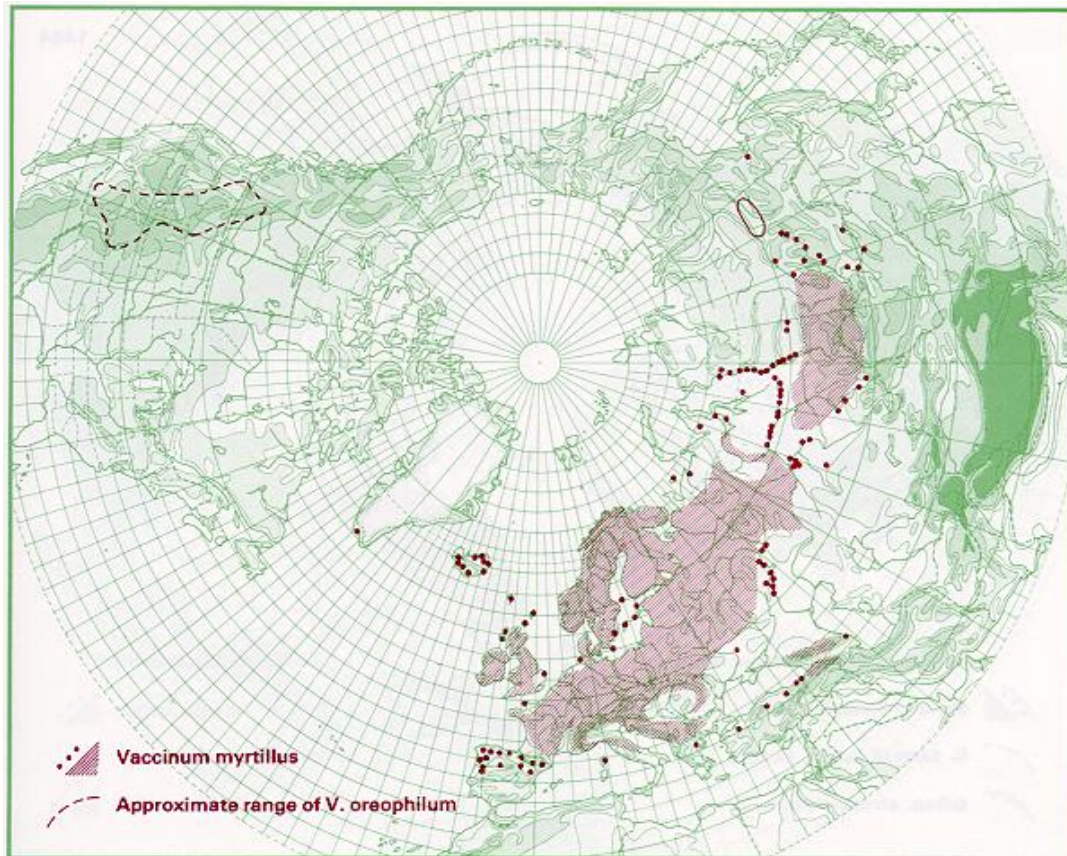
Invited Review

Fig. 1 Distribution of EB in the Northern hemisphere (Hultén and Fries 1986), with the kind permission of Sven Koeltz (Dnr 70-79/1998).

can by this be distinguished from other members of the heather family or any other moorland or mountain shrub even without flowers and fruit. It plays a significant role for a number of other species, particularly of birds and mammals, and its abundance has been used as an indicator of biodiversity within the forests. The EB has long had an important role in human cultures; the nutrient rich berries providing food, and used as a herbal remedy for digestive problems, diabetes and to strengthen capillaries in the circulatory system. The juice of the berries has also been used as a dye, providing a blue colour for both linen and paper (Featherstone 2002).

Cultivation of *Vaccinium* spp. is not a new approach within horticulture. Blueberry cultivation is thought to have started when Native Americans burned wild stands of lowbush blueberries (*V. angustifolium* Ait. and *V. myrtilloides* Michx.) to tend them and to increase production (Strik 2006). More advanced blueberry domestication began in New Hampshire in 1908 by the United States Department of Agriculture (Janes and Percival 2003). Since the 20th century American blueberry species and varieties have been spread to Europe (Nyström 1932; Kühn and Vang-Petersen 1991; Gough 1996; Hjalmarsson 2006). Some of the knowledge achieved from the very successful domestication of highbush blueberry species, could be transferred to the potential cultivation of the European blueberry (EB). However, the approaches and associated technologies developed with the sweet, lowbush blueberry (*V. angustifolium*) in North America, may present an increased likelihood of success. This plant is comparable in many ways to *V. myrtillus*, with similar growth, morphological characteristics (e.g., extensive root and rhizome system), berry size, coloration and good winter hardiness.

Domestication of the lowbush blueberry began in Maine in the 19th century, and the blueberry industry has since undergone a significant increase. In 1990, the industry had over 1000 producers and the lowbush blueberry acreage and production were respectively 113 000 ha (Kinsman 1993) and 12 700 tons, compared to 477 tons in 1951. In 2008 the

production was increased further and was approximately 113 000 tonnes (Percival 2010 pers. comm.). The size of individual producer operations varies from one to over 10 000 ha. Most commercial fields have been developed from abandoned farmland and woodlands that were deemed to have substantial lowbush blueberry plants present after tree removal. Although lowbush blueberry cultivars have been developed, the crop in Maine, the Canadian Maritimes, and Quebec is almost entirely produced by genetically diverse wild clones (Aalders *et al.* 1979; Hall 1979; Chen *et al.* 1998). To make a similar success history in an industry based on the EB may be difficult, as EB are a dwarf shrub that produce single or paired berries on the bush instead of clusters, and consequently have relatively low yields. However, the demand for quality fruit of EB is strong due to a high content of valuable biological compounds (Halvorsen *et al.* 2002; Riihinen *et al.* 2008).

The EB is a calcifuge plant that is circumboreal in distribution. It occurs in Europe, the northern parts of Asia, including Japan, and also in Greenland (**Fig. 1**) where it is thought to be introduced from Europe, possibly in Viking times (Featherstone 2002). In Europe it is still harvested in rural areas by the local population (Pardo de Santayana *et al.* 2005; Konovalchuk and Konovalchuk 2006; Coudun and Gegout 2007) for household consumption and recreational purposes (Kangas and Markkanen 2001), and is one of the economically most important wild berry species in Finland, Norway and Sweden (Kangas 2001). For the industry in Sweden, Finland and some Central and East European countries EB are hand harvested by combing the plants in cut forestland. Intensive forestry with clear-cuttings and soil preparation has been observed to give a more even distribution of the different age classes and to decrease the coverage of EB (Kardell and Eriksson 1995; Miina *et al.* 2009). On the contrary, Nielsen *et al.* (2007) found that EB production and growth decreased with increased forest maturity. Therefore, for a stable and possibly increasing supply of berries to the EB industry, there is a need to develop an improved and more scientifically based production system

Table 1 The systematic link between European and American blueberries.

Order	Ericales		
Family	Ericaceae		
Subfamily	Vaccinioideae		
Tribe	Vaccinieae		
Genus	*Vaccinium*	**Section**	**Important species of section**
		Batodendron, Brachyceratium, Bracteata, Calcicolus, Ciliata, Cinctosandra, Conchophyllum, Cyanococcus, Eococcus, Epigynium, Hemimyrtillus, Herpothamnus, Myrtillus, Neurodesia, Oarianthe, Oxycoccoides, Oxycoccus, Pachyanthum, Polycodium, Pyxothamnus, Vaccinium, Vitis-idaea.	*Myrtillus* *V. myrtillus* *Cyanococcus* *V. corymbosum* *V. angustifolium* *V. myrtilloides* *V. virgatum (ashii)* *V. darrowi*

in which consistent, high yielding crops of EB with excellent quality attributes are produced with manageable input costs (e.g. harvesting costs, cost for transportation and logistics). Several aspects need to be taken into consideration in developing an improved production system, either growing EB on abandoned farmland, or by half-cultivation on cut forestland.

To our knowledge, there have been no prior systematic examinations of how to domesticate the EB by half-cultivating forest fields or by growing on farm land. There are however, numerous publications discussing the biology and ecology of EB in forest ecosystems, and how its distribution is affected by natural disturbances and forest cultivation. The objective of this paper is to present an overview of relevant work dealing with EB, and relate it to possibilities for cultivation. The sweet lowbush blueberry will be the benchmark model used since it is highly domesticated and has been thoroughly examined for reactions to environmental conditions (Kinsman 1993; Jeliazkova and Percival 2003b).

VACCINIUM – SYSTEMATICS

The genus *Vaccinium* consists of woody, perennial shrubs in the heath family (*Ericaceae*) and contains, among other species, both the European and the American blueberry (**Table 1**). Although the EB is often referred to as the bilberry, this includes several species of low-growing shrubs in the genus *Vaccinium* that bears fruit. The term European blueberry (EB) will be used throughout this article since it points directly to *V. myrtillus* and defines it as a blue berry which is mirrored in most European languages. Other names are blåbær (Scandinavian), blaeberry (Britain), whortleberry (Britain), whinberry (or winberry, Britain), wimberry, myrtle blueberry, heidelbeere (Germany), blaubeere (Germany), fraughan (Ireland), myrtilli (Italian) and other names regionally (Lid 1963; Tirmenstein 1990; Featherstone 2002; Wikipedia 2009a). The European and the American blueberry species belong to different sections, and while the EB belongs to the section *Myrtillus* together with 11 other species of minor importance, the American blueberries belong to the section *Cyanococcus* (**Table 1**). The EB is a shrub varying in size from approximately 5 to 90 cm, and chromosome number is 2n=24 (Hagerup 1928; Hedberg and Hedberg 1961; Tirmenstein 1990; Vander Kloet and Dickinson 1999; Featherstone 2002). The American blueberries vary in size from approximately 10 to 400 cm with the smaller species known as "lowbush blueberries" (typically less than 1 m in height) and the larger species as "highbush blueberries". The flowers of both sections are bell-shaped, white, pale pink or red, sometimes tinged greenish. However, while the EB grow one (rarely two) flower from a leaf axil bud, the American blueberries can produce an inflorescence containing a cluster of berries from a leaf axil bud. Highbush and lowbush blueberries develop relatively large clusters of berries mainly on one-year-old wood but also some on two and three year old wood, producing greater yields than huckleberries. Western huckleberries are in different taxonomic sections (*Myrtillus*, *Vaccinium*, and *Pyxo-*

thamnus) than highbush and lowbush blueberries (*Cyanococcus*). Sections *Vaccinium* and *Pyxothamnus* each contain one species. Some species are found not only in North America, but also in Europe, Asia, and Greenland (Barney 2008). The two species *V. uliginosum* (Bog bilberry) and *V. vitis-idaeus* (lingonberry) grow frequently under the same environmental conditions in the north of Europe as EB, and belong to the sections *Vaccinium* and *Vitis-idaea* respectively.

PLANT CHARACTERISTICS

Rhizomes and roots

The characteristics and growth pattern of EB are well documented in the work of Flower-Ellis (1971). EB growth pattern is rhizomatous and it usual forms open colonies or patches in the vegetation that can be as large as 15 m in diameter (Ritchie 1956). A characteristic form of the bilberry stand is that of an irregular, approximately circular patch, with an increase in rhizome age from the distal of the stand to the centre (Flower-Ellis 1971). The growth direction of rhizomes is mainly centrifugal, but soil factors strongly affect rhizome growth directions so density and rhizome growth and diameter growth is not necessarily correlated. Rhizomes up to 5.5 m long have been found, with an average length of 2.0 m (Albert *et al.* 2003), and one single clone may occupy several square meters (Flower-Ellis 1971). The branching of the rhizome is sympodial and the aerial shoot disposition is reflected by this. Typically, from their originating point two rhizomes extend 20-30 cm underground without branching before dividing, ideally into two, occasionally into three or more, of which the middle one is the most vigorous. This middle rhizome turns upwards and develops a green shoot or continues its growth underground. After a further 20-30 cm it divides into a group of shoots which corresponds morphologically with the green aerial shoot. Thus the rhizome in EB ends in a green shoot or in a corresponding group of rhizomes. Further growth is continued by two side branches. Along a segment of rhizome, aerial shoots tend to arise at intervals of 20-30 cm (Flower-Ellis 1971). EB rhizomes can live for up to 34 years, although rhizomes older than 15 years rarely produce new aerial shots or rhizomes. A concern that has sometimes surfaced in wild blueberry growth is stagnation of growth caused by a lack of rejuvenation of the rhizome system (Percival 2010 pers. comm.).

The quantity and size of clones (one rhizome and shoots/axis originating from it) may vary significantly, even within the same population (Albert *et al.* 2004). Nutrient mobilization and reallocation typically occurs in the autumn with nutrients mowing from the leaves to the rhizomes, and this is the main time for rhizome growth, along with the spring (Featherstone 2002). New roots are mainly found in late summer and in autumn, and outside this period no important root formation occurs, even in late spring and early summer, when new aerial vegetation develop and flowering take place (Bonfante-Fasolo *et al.* 1981). However, given

Fig. 2 *Vaccinium myrtillus*. The coin is 21 mm in diameter. (Nestby 2009).

the symbiotic nature of the fine roots with mycorrhizal fungi, there is probably always some level of new root growth and development occurring (Percival 2010 pers. comm.).

Aerial shoots

Aerial shots of EB arising from the same rhizome system have similar characteristics and are referred to as ramets that together with the rhizome, originate from and form a blueberry clone (**Fig. 2**). The resulting entity of ramets/axes of one clone, form a bush (Flower-Ellis 1971).

However, EB has high morphological plasticity, and growth habit in terms of e.g. branching can differ greatly between habitats as a response to environmental differences (Tolvanen 1994). EB aerial shoots grow more vertically and have lower branching angles in open habitats compared with the forest. The stems are angled and woody, and the continuous rejuvenation from the abundant bud bank into many annual shoot generations, leads to a complex shoot age structure within ramets. The growth form of EB clones is phalanx rather than guerrilla (Albert *et al.* 2004), implying that clones produce short internodes and closely packed ramets, and to a lesser degree long internodes and widely spaced ramets. Average ramet age is also affected by its habitat, and increases with forest maturity in older stands (Nielsen *et al*. 2007). Old forests have lower light influx, which results in slower growing and older ramets. Most ramets in a forest habitat are younger than 6 years old (Flower-Ellis 1971; Nielsen *et al*. 2007), although 6-12 years is also common, and ramets of 34 years have also been recorded (Flower-Ellis 1971). Shoots on single ramets are a mix of fertile or vegetative shoots. Fertile shoots have a lower dry weight increment than the vegetative shoots (Tolvanen 1994), and alterations of vegetative and fertile periods are present within single ramets (Paakonen *et al*. 1991). The newest part of the stem from the previous year will be green, soft, and highly branched (Ritchie 1956).

An interesting investigation was undertaken in Belgium, identifying 95 clones among 586 samples analyzed. Despite of intra-population variability in the clonal diversity and in spatial structure of the clones, no differences in clonal diversity were detected between the three different studied habitats. A high proportion of genetic variation existed within populations (86%), while the variation was only 14% between populations (Albert *et al.* 2004). For seedlings, the primary rhizome does not appear until the third year at the earliest (Sylven 1906). The present authors, however, found that seedlings on farmland, improved by added natural peat, grew rhizomes the second year, after seed germinating in March and planting in July (Nestby pers. obs. 2009).

BUD DEVELOPMENT AND FLOWER INDUCTION

EB flowers are born singly (rarely in pairs) in the axils of the leaves on one-year old twigs from May to June. The twigs are sitting on aerial shots that are at least three years old (Flower-Ellis 1971; Tirmenstein 1990; Featherstone 2002). However, sexual reproduction starts and peaks earlier in rejuvenated shoots, indicating shortened ageing process in these (Tolvanen 1994). Flower initials are developed the year before flowering and overwinter in a dormant bud.

There are two types of buds; buds enclosing two bracts and one single flower, and buds which bear a single lateral shoot and a flower. These flowering shoots normally drop together with the leaves in autumn. Some buds do not develop flowers and grow as vegetative short shoots (Flower-Ellis 1971). With respect to floral structure, the stamens are closed within the narrow corolla, while pistils stretch out of the corolla. Flower diameter is approximately 4-6 mm (Flower-Ellis 1971; Featherstone 2002). Following the pattern of EB in a ten years period revealed that EB flowered heavily every second year (Kardell and Eriksson 1990; Selås 2000), indicating a biannual flowering pattern.

In the sweet lowbush blueberry the development is similar. During late summer, floral bud development is initiated in the apical meristem of the upright shoot and then proceeds down the axis of the stem in axillary buds located in the leaf axils. However, in contradiction to the EB they carry "clusters" or multiple inflorescences that originate from a compound floral bud. Growers have been able to dramatically increase yields of the sweet lowbush blueberry by pruning the fields on alternate years. This ensures that the fields are comprised of new shoots and thus have a high flower density. Consequently clonal growth is likely to be an important factor that constrains fruit and seed number (Nuortila *et al.* 2002). A similar practice in EB could delay the fruiting with several years since the generative part of the tiller will be removed. It is a question if the shoots sprouting from buds on the remaining long shoot initiate flower buds the first autumn after cutting in the spring as an effect of rejuvenation (Tolvanen 1993). Cutting may delay sexual reproduction because of increased allocation of resources to vegetative growth to replace lost tissue (Sonesson and Callaghan 1991), and it is suggested that new EB ramets do not produce flowers until two or three years after cutting (Tolvanen *et al*. 1993a, 1993b). The effect of cutting is under investigation by the present authors (Nestby *et al*. pers. comm. 2008).

POLLINATION AND FRUIT DEVELOPMENT

As a result of the extent of large EB clones, the rate of selfing through geitonogamy (transfer of pollen between flowers of the same genet) is significant (Albert *et al.* 2008). In northern boreal forests EB is obligately insect pollinated, and the main pollinators (bumblebee queens) make approximately 76 (Nuortila *et al.* 2002) to 90% (Albert *et al.* 2008) of their flights within a distance of only 40 cm. The EB have no mechanisms for avoiding self-pollination or self-fertilization (Nuortila 2007). Flowers have been found to set fruit equally well with self-pollen and cross-pollen (Nuortila *et al.* 2002; Raspé *et al.* 2004), but cross-pollinated flowers matured more seeds and aborted fewer seeds than those that were self-pollinated. Approximately four times as many seeds in cross-pollination were set at 10 m distance when compared to self-pollinated flowers, suggesting pollen limitation (Jacquemart 1997) and an inbreeding depression at the seed stage (Fröborg 1996; Raspe *et al.* 2004; Nourtila 2006; Nuortila 2007). It appears to be a clonal variation in self-fertility (Raspe *et al.* 2004; Nuortila 2007). Berry fresh weight is positively related with the total weight of seeds and the number of seeds (Ranwala 2001; Ranwala and Naylor 2004), meaning that fruit yield would benefit from cross-pollination. Subsequently, for successful fertilization to occur, extensive interphenotype (clone) pollen movement is required in fields. This indicates that for

Table 2 Chemical composition of *V. myrtillus*, and other selected *Vaccinium* species.

Quality parameter	V. myrtillus Norway[1]	V. myrtillus references[2]	V. corymbosum references[3]	V. angustifolium references[4]
Berry weight (mg f.w.)	457 ± 81	328 ± 63	1635 ± 346	326 ± 67
Dry matter (g/ 100 g f.w.)	15.0 ± 1.6	15.2 ± 3.2	16.4 ± 4.1	22.1 ± 13.1
Soluble solids content (Brix value in %)	10.8 ± 1.6	9.8 ± 1.1	12.7 ± 2.1	15.4 ± 1.6
pH	2.7 ± 0.1	3.1 ± 0.1	3.2 ± 0.2	2.7 ± 0.1
Titratable acidity (g/ 100 g f.w.)	1.4 ± 0.2	2.4 ± 1.5	1.4 ± 0.6	0.9 ± 0.1
Total anthocyanins (mg/ 100 g f.w.)	275 ± 72	364 ± 189	145 ± 54	181 ± 152
Total phenols (mg GAE/ 100 g f.w.)	612 ± 75	472 ± 164	289 ± 105	546 ± 255
Antioxidants FRAP (mmol/ 100 g f.w.)	5.7 ± 1.2	5.3 ± 2.2	2.6 ± 1.1	9.8
Fructose (mg/ 100 g f.w.)	5290 ± 1027	3687 ± 1092	6171 ± 3150	3900
Glucose (mg/ 100 g f.w.)	5348 ± 1074	3380 ± 988	3296 ± 852	5150
Sucrose (mg/ 100 g f.w.)	578 ± 270	411 ± 187	180	
Citric acid (mg/ 100 g f.w.)	1321 ± 150	683 ± 171	427 ± 168	
Malic acid (mg/ 100 g f.w.)	298 ± 95	261 ± 195		
Quinic acid (mg/ 100 g f.w.)	1703 ± 476	1370	46 ± 73	
Catechins (mg/ 100 g f.w.)	45 ± 24	5.0	5.3 ±	
Chlorogenic acid (mg/ 100 g f.w.)	32 ± 18		59 ± 82	
Ascorbic acid (mg/ 100 g f.w.)	3.0 ± 2.5	18.6 ± 24.6	9.2 ± 3.8	12.1 ± 6.9
Gallic acid (µg/ 100 g f.w.)	834 ± 235	1760		
Quercetin (µg/ 100 g f.w.)	473 ± 262	2263 ± 966	3824 ± 2764	

[1]Based on experimental data from Norwegian trials in 2009 (Nestby *et al.*, unpublished data)
[2]Data compiled from 27 references
[3]Data compiled from 24 references
[4]Data compiled from 4 references

cultivation purposes, it could be useful to expand the "windows of opportunity" by *in situ* rhizomes or seeds or by planting seedlings or advanced clones, to increase the reproductive success and clonal diversity within pollinator flight distances.

FRUIT CHARACTERISTICS

The most significant characteristic of blueberries is their high content of beneficial nutrients and bioactive phytochemicals (**Table 2**). Nutritional compounds comprise carbohydrates and organic acids, which mainly contribute to the taste impression, accompanied by aroma volatiles. The favourable berry aroma from EB shows complex phytochemical patterns based on more than 100 compounds (Rohloff *et al.* 2009), compared to *V. corymbosum* (Parliment and Kolor 1975; Hirvi and Honkanen 1983) and *V. ashei* (Horvat *et al.* 1996).

The nutraceutical quality is recognized by the abundance of natural antioxidants such as proanthocyanidines and anthocyanins (Faria *et al.* 2005) together with the occurrence of other potent flavonoids (Cho *et al.* 2005), other phenols (Taruscio *et al.* 2004; Zadernowski *et al.* 2005), and reasonable amounts of ascorbic acid (Stewart 2004). An obvious difference is the blackish fruit flesh colour of EB compared with the whitish colour of the American blueberries, including *V. angustifolium*, *V. corymbosum* L. (highbush), *V. ashei* Reade (rabbiteye) and *V. myrtilloides* Michx. (sourtop lowbush). Jam made of EB has a more pronounced blueberry-flavour and odour than that of e.g. the *V. corymbosum* cvs. 'Bluecrop' and 'Berkely' (Rødbotten *et al.* 2005). The berries of EB are characterized by 15 anthocyanins according to a Finnish study (Lätti *et al.* 2008). A significantly lower content of the total anthocyanins was observed in berries of the southern regions of Finland compared with the central and northern regions, which is in accordance with observations on latitudinal variation in Norway (Nestby *et al.* 2010, unpublished). Differences in the proportion of anthocyanins were also reported (Lätti *et al.* 2008). In general, berries from EB are characterized by higher levels of total anthocyanins, phenols, and antioxidants, whereas highbush varieties show superior berry weight and thus yield potential (**Table 2**). The study of berry peels and flesh with regard to the *in planta* distribution of bioactive phytochemicals, emphasizes the health-beneficial properties of EB compared to highbush blueberries (Riihinen *et al.* 2008). Recently, resveratrol and

structure-relative compounds that have been reported to show cancer-chemopreventive activities, have been described in *Vaccinium* berries (Rimando *et al.* 2004). Additionally, EB seed oils have been shown to serve as an excellent source for linolenic acid, essential fatty acids, tocopherols and carotenoids (Parry *et al.* 2005).

In order to fully address fruit characteristics, not only the internal quality but also external parameters based on morphological and physiological traits have to be considered. Blueberries from high- and lowbush cultivars show an extended shelf-life and can be freshly stored for periods from 4 to 6 weeks (Krupa and Tomala 2007; Echeverría *et al.* 2009) when using controlled (CA) or modified atmosphere (MA) conditions. Due to their flesh firmness and berry skin properties, they are fitted for long-distance transport for sale on external markets far from the production site. In contrast, berries from EB show a relatively higher degree of vacuolization at full maturation stage, which makes them more suitable for distribution on local markets and fresh consumption rather than long-term storage and/or transport. However, high levels of antimicrobial and bioactive compounds in EB have high potential to suppress bacterial and fungal growth (Koskimaki *et al.* 2009). Postharvest quality of blueberries is clearly reduced due to water loss, lower firmness and shrivelling, as illustrated with *V. ashei* (Schotsmans *et al.* 2007) and *V. corymbosum* (Krupa and Tomala 2007). Whereas levels of anthocyanins and antioxidant capacity decrease over time, the taste parameters of soluble solids and titratable acidity often remain unchanged also after several weeks of storage (Krupa and Tomala 2007). Frozen storage of blueberries as an alternative for quality preservation of whole berries, does not significantly change nutrient and anthocyanin composition even after 4 months (Poiana *et al.* 2008), when suitable freezing conditions are applied.

POTENTIAL OF ENHANCING PLANT DEVELOPMENT AND FRUIT YIELD BY MANAGEMENT

Half cultivation

In Finland, forest owner preferences have changed from an economy based on tree value only, to an evaluation where also berry yields and other non-wood products have to be taken into consideration. This has resulted in the need to assess the effect of silvicultural treatment on berry yields

(Kangas 1998). In Norway, this attitude has not been very apparent. However, there has been a recent and substantial interest in the economical value of resources other than trees in outlying fields. Unfortunately, this has mainly focused on fishing, hunting and tourism. The blueberry resources have been largely overlooked, but should be evaluated as important. Some ecological investigations of forest management including EB, could give inputs to how this resource could be made more easily available for exploitation. In addition to forest management, climate, soil conditions, insects and diseases, browsing animals etc. have an influence on the development of the European blueberry.

Forest cutting

The EB is severely affected by clear-cutting with substantial reductions in vegetative growth, shoot survival, ground cover and fruit production, and an increase in shoot phenol content. This was confirmed in a study by Atlegrim and Sjöberg (1996) who reported a reduced ground cover and a more patchy spatial distribution after selective cutting. Interestingly, the vegetative investment and shoot survival after cutting did not differ from zero cutting (Atlegrim and Sjöberg 1996). This suggests that percentage cover of EB is highest in established old forest. A study on different age classes of *V. myrtillus* in Polish pine stands strengthen this theory. It was shown that percentage cover- area and weight of aerial shots were highest in 40-80 years old stands (Kalinowski 2004). Similarly, in a pine forest of Kola, 200 years old stands of *V. myrtillus* had the highest production and vitality (Maznaya 2001). This is in agreement with Kardell and Eriksson (1995), who found that percentage cover of EB increased with forest maturity, and that clear cutting reduced percentage cover with 80%, and that the recovering was very slow.

There is suggested a negative connection between EB cover and irradiance; the cover was poorest at clear cutting and greatest at intermediate irradiance, which coincided with high crown forest stands (Parlane *et al.* 2006) and forest regularly thinned (Kardell and Eriksson 1995). However, under Norwegian conditions the effect of clear cutting was the opposite, and the average performance of EB decreased with increased forest maturity and larger tree biomass. This experience could be caused by the use of relatively small clear cuts in Norwegian forests (Tolvanen 1994; Nielsen *et al.* 2007).

Climate

Besides forest management, climate has a decisive impact on the development of the EB. *Vaccinium* grow wild in the temperate zone and stretches into the arctic climatic zone. This environment has typical changes in seasons with relatively warm summers and long days followed by colder autumns and winters with abundant and persistent snowfall and short days. These changes have made it necessary for the blueberry to stop growth in late autumn, to avoid resumption of growth too early in the spring, and to develop avoidance (snow cover) and tolerance to low temperature stress (Rowland *et al.* 2004). This implies that moving types of EB from northern areas to southern areas or vice versa probably will be unsuccessful.

In the last decades the winters have generally been milder and the snow cover more unstable, at least at low altitudes in Scandinavia. The importance of snow cover was notified by Gjærevoll (1949), giving that snow cover is an important factor which determines the altitudinal distribution of EB. In the absence of a protective layer of snow, plants are vulnerable to cold winter temperatures and may be killed (Hall *et al.* 1971), though it is moderately buffered against frost in late winter and early spring (Tolvanen *et al.* 1997). In a winter five degree warmer than average in NE Sweden during 1991-1992, *V. myrtillus* suffered lethal injuries. It was suggested that this was connected to a considerable decrease in solute content during winter (Ögren 1996).

Closer examinations including experiments with infrared heating lamps run with or without soil warming cables, confirmed the effects of winter warming. After a simulated one week long extreme winter warming event in early March, *Vaccinium myrtillus* had delayed bud development by up to 3 weeks in the following spring (June) and reduced flower production by more than 80% (Bokhorst *et al.* 2008).

Later this was more carefully scrutinized and tissue water in the shoots was observed in winter compared with spring and early summer. Soluble solids tended to decrease from December to February under snow cover, while remaining constant under artificial gray and transparent cover (roofing), indicating an enhanced demand for synthesis of proteins, including dehydrins that protect against drought (and freezing) under conditions without snow cover. Also increases of metabolism in early spring were less or absent in plants that wintered without a snow cover. This can be explained by a delayed activation of metabolism resulting from multiple stresses (LT, drought, light) that acted simultaneously on the EB plant (Tahkokorpi *et al.* 2007). However, it should be noticed that blueberries have dormancy mechanisms that are present and functional during the winter. The lowbush blueberry need temperatures of less than 4°C for 1600 hours for dormancy to be broken, which in Nova Scotia typically occurs in February (Percival 2010 pers. obs.). Lack of chilling could give reduced bud burst mistaken as winter injury. Also, nutrition would influence winter hardiness, and Taulavuori *et al.* (1997) concluded that winter hardening and glutathione status in the EB seems to be sensitive to nitrogen fertilization, and not affected by elevated CO_2 and O_3.

In a domestication strategy breeding EB-clones for winter hardiness could be an objective. Little is known of inheritance of this character. In highbush blueberries, cold hardiness is controlled largely by additive, multiple and largely dominant gene effects. These genes are dehydrins (bbdhnd1-bbdhn5) (Arora *et al.* 2000; Rowland *et al.* 2004). Though it is not examined, probably similar mechanisms are prevalent in the EB. However it may be anticipated that the genes that regulate hardiness at least to some degree are different from those found in highbush blueberries.

Another aspect worth noting is the vulnerability of flowers to be injured by frost in late spring/early summer. This has happened more frequently the last decades in both lowbush and EB due to milder winters and earlier resumption of growth in the spring. This frost injury can be as rate limiting as winter injury, and changes with the developmental stage of the plant. The pattern observed in a ten year period that EB flowered heavily every second year, could partly be a result of this, but also due to the physiological effects associated with biennial bearing. During registrations over three years in central Finland, fruit yield varied from zero to 130 kg ha^{-1}, and in a Swedish 15 year study, yields varied from 0 to 450 kg ha^{-1} depending on site and year. The years with almost zero yields always had a history of frost during bloom (Kardell and Eriksson 1990, 1995). An examination in the Arkangels region of Russia illustrated that profuse flowering during fairly warm weather with rain showers after the late spring frost (mid-June), and enough moisture in July and August, secured high fruit yields. These conditions typically occurred every fourth year. In a typical good year the yield averaged from 171 to 341 kg ha^{-1} (Puchnina 1996).

Plant reactions that can reduce LT injury were observed in cranberry uprights (*V. macrocarpum* Ait.) and fruit. Workmaster *et al.* (1999) suggested that ice nucleation of leaves performed by ice penetration via stomata located on the abaxial surface, and that the thick cuticle present on the adaxial surface was an effective barrier to intrinsic nucleation. Only frozen moisture at the calyx end of the fruit in the remnant nectary could induce fruits to freeze, most likely through stomata. If a similar appearance is present in EB it would be a valuable trait preserving the fruit quality by supercooling in short periods with warm freezing temperatures in the autumn.

Soil and nutrition

The EB is one of the dominating dwarf shrubs in forest habitats with low nutrient availability due to its clonal growth habit, the symbiosis with ericoid mycorrhiza (Bonfante-Fasolo *et al* 1981; Kasurinen and Holopainen 2001) and the ability to take up organic nitrogen (Näsholm *et al.* 1998).

The optimal conditions for EB growth, development and fruit yield, according to Svalestad (1983), occurred in Norway under conditions of high humidity and minimal shade. In addition he found that mineral nutrition increased the fruit yield at sites where the EB was a dominating species, especially when water was sufficient.

Similarly, in other studies, mineral nutrition was an important factor for plant productivity. In the northern Apennines, total community net primary production (NPP) of three communities was closely related to nutrient availability. NPP of *V. myrtillus* peaked in the most fertile habitat, and within this the N to P ratio in the whole plant as well as in the leaves reflected the soil phosphate concentration with foliar N to P ratios of less than 16 in the poorer sites. The responses showed by other species in the same habitat suggest that the response of EB is individualistic in response to the nutrient availability, and that the growth is P-limited (Gerdol 2005). A study of Kardell and Eriksson (1995) over 15 years showed that fertilization with 150 kg ha^{-1} of ammonium nitrate the second year after establishment of trial plots, and again before the 10th year, gave varying reactions between field trials situated in the south and north of Sweden. Generally, however, fruit yield increased the first years after implementation of fertilizer, but was reduced gradually towards the second application of fertilizer. After the second application a new increase in fruit yield occurred followed again by a slow decline, but not as significant as after the first application. The best results were achieved when fertilization and thinning of trees were combined.

On the contrary to the above mentioned studies Nordin *et al.* (2006) reported no effect on growth of EB after fertilizing a boreal forest under storey vegetation with ammonium and nitrate in the range 12.5 to 50.0 kg N ha^{-1}.

The uptake of nutrients in *Vaccinium* is facilitated by symbioses with ericoid mycorrhiza, which provide the hosts with access to soil-nutrient resources that would otherwise be largely unavailable to the plant (Read 1980). Mycorrhizal formation is also contributing to the success of EB in nutrient stressed environments, and Bonfante-Fasolo *et al.* (1981) found that nearly all root hairs examined were mycorrhizal, although infection intensities varied at different times of the year. A heavy fungal infection takes place within new root formation in late summer and autumn, decrease during winter and increase gradually again towards late summer. The mycorrhizal colonization of *Vaccinium* roots take place in the cortical cells where the fungi differentiate typical intracellular hyphae coils, which characterize the symbiotic association between ericaceous plants and their symbions (Harley Smith 1983; Jeliazkova and Percival 2003a, 2003b).

In a forest several factors influence nutrient availability of the EB. At clear-cut it is important to prevent leaching and surface erosion of nutrients through the presence of vegetation that retains nutrients in the ecosystem. In a mixed forest dominated by Norway spruce (*Picea abies* L.) in eastern Finland, the biomass of EB significantly decreased after clear cutting. However, it remained a marked nutrient sink, and the biomass returned to initial levels soon after clear cutting as did the nutrient contents of ground vegetation (Palvainen *et al.* 2005). The fast recovery of *V. myrtillus* in this study is in contradiction to the findings of Kardell and Eriksson (1995) in a 15 years study, who found that *V. vitis-idaea* had a better recovery than *V. myrtillus.*

The uptake of nutrients is also dependent on soil pH, and it is shown that there is an effect on pH of type of dominating tree species on blueberry land. Soil pH was higher under birch (4.7) than under spruce (4.1), while the C/N

ratio was lower under birch (17) than under spruce (23), in a podzol and humus type moor soil. Microbial biomass, C and N, net N mineralization and net nitrification were all higher under birch than under spruce, per unit organic matter (Smolander *et al.* 2005).

Insects

An injury of an insect may be affected by interactions of other factors in the environment. By example the 'Winter moth' larvae (*Operophtera brumata*, *Lepidoptera*) may feed heavily on EB. At the individual level, altered food plant quality due to repeated infection by the fungus *Valdensia heterodoxa*, had no effect of the larval performance in laboratory experiments, but both survival to the adult stage and adult weight were positively affected by N fertilization. In addition exclusion of insectivorous birds increased the frequency of larval damage to EB shoots, indicating higher larval densities, and there was an indication of higher bird predation in fertilized plants. The results suggest that top-down effects (in this case birds) are more important for larval densities than bottom-up effects (e.g. nitrogen, fungus), and that bird predation may play an important role in population regulation of 'Winter moth' in boreal forests (Strengbom *et al.* 2005). Also *Agriopsis aurantiaria* feed on the leaves of EB in the lowland south in Norway. 'Autumnal moth' (*Epirrita autumnata*) and 'Winter moth' are often found together, and both may occasionally de-leaf the birch (*Betula pubescens* Ehrh.) and EB totally (Fjelddalen 2009; Wikipedia 2009b).

It is shown that the wood ant (*Formica aquiloni*) is beneficial for the EB. Close to ant nests herbivore damage to the EB was reduced and proportion of flowers succeeding to berries was increased. It was therefore suggested that distance to wood ant nests and thereby reduced predation from ants, affect herbivore damage to the EB and its reproductive success. However, vegetative growth and reproductive investment was not affected by distance to ant nests, indicating that the EB can also compensate for losses due to herbivore injury (Atlegrim, 2005). It should however be noted that the red ant may feed on the blueberry flower. This was observed in Norway. However, it seem like the injury is mainly on the corolla and not on the pistil or unripe fruit, since the berries developed normally (Nestby 2008 pers. obs.).

This suggests that when methods to improve the yield of the EB are implemented it should be strongly considered not to override the natural defence mechanisms, but rather try to strengthen these or at least not weaken them.

Diseases

Leaf damage caused by diseases is often observed in EB fields. The most common is *Valdensia heterodoxa.* The interaction between this parasitic fungus and its host plant the EB, was affected by nitrogen additions over 5 years in a boreal forest in northern Sweden. Disease incidence on leaves increased following N addition and the effect was stronger in large than in small plots (ranging 1 to 5000 m^2), and disease incidence was also positively correlated with precipitation. High summer precipitation enhanced the N effect, suggesting that precipitation may modify the effects of N deposition on plant-parasite interactions. Parallel to this it is observed in lowbush fields of Nova Scotia that N increases canopy biomass, this lengthens canopy wetness duration and greatly increases the likelihood of infection (Percival 2010 Pers. comm.). This may complicate predictions of future effects of N deposition as precipitation patterns are expected to change as a result of climate change. The results suggests that small scale fertilization experiments may underestimate future large-scale effects of N-deposition, and indicate the need for increased awareness of the problems (Strengbom *et al.* 2006). N-induced changes in the constitutive levels of soluble conjugated amines did not seem to explain the increased parasite (*Valdensia hete-*

rodoxa) susceptibility of the EB under N enrichment. Generally, the concentration of free diamines and insoluble conjugated putrescine were higher in diseased than in healthy shoots, suggesting parasite-induced accumulation of diamines. Free spermine seemed to accumulate in unfertilized, diseased plants, but in fertilized plants this induction was dampened, suggesting that N-induced alterations in spermine metabolism may promote the spread of parasites on the EB under N-enrichment (Witzell *et al.* 2005).

Mummy berry disease (*Monilia vaccinii-corymbosi*) is one of the most important plant pathogenic fungi on blueberries in America and the first verified detection in Europe (Austria) was in 2002. The fungus was likely introduced to Europe years ago and is present in other blueberry plantings, but has not been identified due to possible unfavourable weather conditions (like low temperature) for the fungus or confusion with similar fungi (e.g. *Botrytis cinerea*). It remains to be seen how this disease will affect the EB, which has some resistance to this pathogen (Gosch 2006).

Weeds

Weed pressures are different in established old forests compared with a clear cut sites. These pressures are also more prevalent under birch (*Betula pubescens*) because of differences in light penetration to the ground, than under Norway spruce (*Picea abies*). Birch impose cascading effects on both above- and below-ground communities, soil chemical and physical properties and ecosystem processes. Compared with heather (*Calluna vulgaris*) plant species richness decreased and the vegetation composition changed under birch, with lower cover of grasses and EB (Mitchell *et al.* 2007).

When using applications of N fertilizer in EB, problems could be encountered as a result of heather responding positively to N-application (Britton and Fisher 2008). Similar effects were observed in clear cut areas of Norway spruce forest during 2009, with 'wavy hairgrass' [*Deschampsia flexuosa* (L.) Trin.] and 'fireweed' (*Epilobium angustifolium*) competing strongly with the EB (Nestby 2009 pers. obs.). Also 'Birch' (*Betula pubescens*) sprouting from stubs and 'European Rowan' (*Sorbus aucuparia*) may be a problem if caution is not taken to prevent these to develop (Nestby 2009 pers. obs.).

Browsing animals and birds feeding on the berries

Moose (*Alces alces*) and deer (different species), which are quite abundant in Norway, are feeding on EB plants (Featherstone 2009). This was confirmed in an examination undertaken in a mature Scandinavian pine (*Pinus sylvestris*) forest. At sites subjected to differing natural intensities of grazing by *Cervus elaphus* (red deer), it was shown that ramet size, abundance and fruit set and invertebrate activity on EB were negatively related to grazing intensity. Even at low grazing intensities the performance of the plant was affected. The effect on fruit production and invertebrate activity indicated that red deer grazing has a negative impact on the population dynamics of the plant (Tømmervik *et al.* 2004; Hegland *et al.* 2005; Melis *et al.* 2006; Parlane *et al.* 2006). The EB have a protective mechanism against heavy feeding of bank vole (*Clethrionomys glareolus*), possibly explained by changes in plant chemistry (Selås 2006). These browsing effects are also confirmed in studies simulating herbivory (Tolvanen *et al.* 1993b; Tolvanen 1994).

EB foliage is highly palatable and it is also an important food source for birds such as red grouse (*Lagopus lagopus*), ptarmigan (*Lagopus mutus*) and black grouse (*Tetrao tetrix*). The capercaillie (*Tetrao urogallus*) in particular depends on EB, and it eats the stems and buds in winter, as well as the leaves in spring and summer (Featherstone 2009). It is well known in Scandinavia that 'Gray thrush' (*Turdus pilaris*) and 'Starling' (*Sturnus vulgaris*) feed on the fruit (Nestby 2009 pers. obs.). Therefore, if the intention is to increase the EB abundance, it may also be important to reduce or some-

how deter the number of browsing animals (Tømmervik *et al.* 2004; Hegland *et al.* 2005; Melis *et al.* 2006; Parlane *et al.* 2006).

Finally, examinations have shown that EB respond negatively in growth performance and age to the disturbance and stress on ski pistes (Rixen *et al.* 2004).

Cultivation on farm land

The main difference from forest fields is that the soil pH often will have to be adjusted by adding sulphur or organic matter of low pH (e.g. compost, natural peat). Also it may be necessary to top-dress the soil with a layer of organic matter at specified intervals. In addition the weed pressure may be different from forest fields, and the protection against light-related stress and wind given by forest trees, will normally be lacking. However, when moving the EB into cultivated land the possibility to adapt the cultivation system to the plant will be more flexible. There is very little experience with this kind of cultivation, and it is necessary to take a broad and sequential experimental approach to build a knowledge base.

REPRODUCTION

Seeds

The reproduction of EB has been widely studied due to the use of EB for re-vegetation purposes and for its significance in forest and heath ecology, where EB is one of the dominating dwarf shrubs. The natural reproductive success of EB in forest ecosystems is contributed to it being a species with a long life span, a mixed breeding system and a high seed dispersal potential (Flower-Ellis 1971). However, the importance of seeds in regeneration of EB seems to fluctuate. EB has been found to be one of two dominant seed-bank species in five boreal forests stands in northern Sweden (Granström 1982). On the contrary moors in Scotland (Ranwala and Naylor 2004) and in a closed temperate forest of Spain (Laskurain 2004) had a complete absence of seeds or seedlings. Interestingly, EB was one of the most frequent shrub species in all these sites, resulting in its clonal growth with subterranean rhizomes being essential for spreading. Local patches of EB have been found to have a shoot density up to 400 reproductive shoots per square meter (Ranwala 2001). Consequently, seedling recruitment in natural populations is possible within stands of established conspecific adults only at "windows of opportunity" (Erikson and Fröborg 1996). "Recruitment at windows of opportunity" (RWO) is likely in EB since substrates suitable for germination, seedling survivorship and juvenile growth occur within the habitat space already occupied by conspecific adults. This strategy provides that seed availability is not limiting, contributing to explain why EB each year produce copious numbers of seeds and at the same time is characterized by an almost total absence of seedlings. RWO may also explain the incidence of genotypic diverse clones represented by only one ramet that may exist within spatially large clones (Albert *et al.* 2004).

The number of seeds per fruit reported in literature for EB fruits range from an average of 25 (Flower-Ellis 1971) to 40 (Ritchie 1956) to 71 (Ranwala and Naylor 2004). Seed number varies greatly in response to pollination treatment with cross-pollinated berries containing a maximum of 120 mature seeds, while self-pollinated berries containing a maximum of 35 (Nuortila *et al.* 2006). Upon examining the seeds at berry maturity, the average number of mature seeds per berry was 66 and 12 in cross- and self-pollinated berries respectively.

Seed germination occurs over the range 15-24°C (Ranwala and Naylor 2004), and has been shown to occur when stratified in the presence of light under cool (15.5°C) temperatures for more than 12 weeks (Baskin *et al.* 2000). The best germination has been obtained by no stratification and 16 weeks of incubation in 12 h light at 25/15°C day/night

temperatures (Baskin *et al.* 2000). EB seeds are probably conditionally dormant at maturity, as the maximum possible germination percentage was not obtained using fresh seeds (Baskin *et al.* 2000). Trials have also shown that germination is poorer in light having a high far-red ratio, as is under a dense tree canopy (Skrindo 2005). Digestion of berries by birds also affected EB seed germination (Honkavaara *et al.* 2007), while digestion by bears did not enhance germination (Skrindo 2005).

There is a considerable variation in EB fruit and hence seed production between years. Depressed berry production has been associated with high temperatures during flower-bud formation in autumn, high temperatures in winter in association with thin snow cover, frost during flowering in spring and low or high amounts of precipitation during berry ripening in summer (Selås 2000). Analyses of a 50-year time series of fruit production in EB showed that the highest production occurred in years with relatively high levels of summer precipitation.

It is suggested that an average temperature increase will reduce seed viability and cause negative implications for the spread of EB in Scotland (Ranwala and Naylor 2004), while it is likely to benefit from a warmer climate in the subarctic (Milbau *et al.* 2009).

Vegetative propagation

While vegetative regeneration by rhizomes is very successful in nature, vegetative propagation for making homogenous plant material for cultivation and research purposes has a low success-rate (Jaakola *et al.* 2001). The EB may be propagated both *in vivo* and *in vitro* and different media have been used. Investigating growth initiation *in vitro* in EB using different concentrations of N^6-isopentenyladenine in the modified MS-medium, Jaakola *et al.* (2001) found that the optimal concentration for the initiation of growth of microshoots *in vitro* was 49.2 μM, compared to 24.6 and 78.4 μM. The treatment undertaken in spring, resulted in 44% growing explants after 8 weeks. Rooting of the EB microshoots *ex vitro* were improved by incubating them in a 2.07 mM solution of a potassium salt of indole-3-butyric acid (KIBA) at a concentration of 0.49 μM for 5 minutes before planting in peat. Then 71.9% of the microshoots rooted after 5 weeks, while 81.3% rooted *in vitro* in a rooting medium containing IBA at 0.49 μM.

Our own experiments in cooperation with University of Natural Resources and Applied Life Science, Institute of applied Microbiology in Vienna Austria, with *in vitro* establishment and multiplication, have shown that clones of *V. myrtillus* are successfully established and multiply with a rate of 3-4 shoots per subculture (Laimer pers. comm. 2010). Micropropagated plants have been shown to have a precocious and higher rhizome production compared with plants propagated from cuttings in both lingonberry (*V. vitis-idaea*) (Gustavsson and Stanys 2000; Debnath 2005) and lowbush blueberry (*V. angustifolium*) (Morrison *et al.* 2000). Rhizome production in lowbush blueberry is also affected by the N status (Smagula and Hepler 1980).

Micropropagation is reliable and efficient, especially for the rapid introduction of new cultivars, and large-scale liquid cultures combined with automated bioreactors could be a tool to eliminate most manual handling in micropropagation and reduce production costs significantly. Additionally, molecular markers introduced in *Vaccinium* are powerful tools in the genetic identification of clonal fidelity (Debnath 2009). A combination of advanced micropropagation, including molecular markers, could be valuable in a future establishment of new large plantings of EB on abandoned farm land. However, experiences from the Canadian lowbush industry have shown that the success of advanced cultivars has been limited (Jamieson pers. comm. 2007.). The reason is more political than horticultural, since the production is advertised as exploiting the wild lowbush blueberry growing in half cultivated fields. Anyway, in the effort to domesticate the EB these tools should be integrated in a scientific approach to the objective.

HARVEST AND DELIVERY

It would be a benefit to have a model for prediction of fruit yield. It would provide information to decide fruit retention and harvestability, and if this could be provided to end users prior to harvest, it would assist in determining estimated berry supply. In Finland Pukkula (1988) created a model collecting data on site properties, trees and berry yields. However, this model was dependent of a large number of empirical data over many years and therefore, was easily biased. Models based on expert modelling (Muhonen 1995; Ihalainen *et al.* 2002, 2003, 2005) and on regression analysis, to relate the expert priorities to stand characteristics, seem to be more appropriate. However, according to Kangas and Mononen (1997) expert models can only relieve the acute need for prediction models and produce temporary models for forest planning inexpensively and quickly. To construct models that reliably describe the effect of trees and the site on berry yield, one needs to gather large quantities of empirical data over several years (Belonogova and Kuchko 1979). Recently Miina *et al.* (2009) have constructed generalized linear mixed model techniques predicting yields as a function of site and stand characteristics, using the permanent sample plots of the National Forest Inventory (Finland).

The predictions of the expert based models correlated logically with site and stand characteristics and were in line with earlier models based on empiric data, and were less laborious. According to the model, yield would be positively correlated to tree age and height and the standing volume of pine. Conversely, the yield would be negatively correlated to the stand (tree) basal area, the standing volume of deciduous trees and to a *Vaccinium* site type or poorer (ecological term that defines the combination of tree species and dominating shrub species). These Finish examinations also show that forest stands of medium fertility, but also on rather poor mineral soil, produce the highest EB yield in different parts of Finland. However, these findings are not unique probably because they are subjective, and it may be difficult to distinguish between rather poor and medium soil sites. In addition EB thrives on poorer soil sites in northern Finland than in southern Finland (Ihalainen *et al.* 2005). In Norway it is observed that blueberry yields may be quite high at high altitudes or in the north where birch is dominant forest forming tree species, or above the tree limit (Nestby pers. obs. 2007). This coincide the defined 'Blueberry birch forest' in Norway which is dominated by EB in the undercover (Bendiksen *et al.* 2008). A long-term study conducted in the Kirov Region of Russia showed that average daily air temperatures and quantity of precipitation during spring-summer had the greatest influence on EB fertility. Average long-term yield of EB was highest in the spruce EB forest (41.5 ± 4.1 g m^{-2}) and lowest in the aspen EB forest (21.5 ± 2.6 g m^{-2}).

Also the fruit picking technique can affect the yield, and picking EB fruits with a comb once or twice a year decreased the number of plants growing. In all picking variants including hand picking once and twice a year, mass and area of leaves were smaller than at no picking. However, picking twice a year with a comb increased the reproduction value compared with no harvesting (Kalinowski 2007).

CONCLUSION

Hence, the results and observations referred to in this paper suggest that in situations of nutrient poor environments, blueberry growth and development is reliant upon the mycorrhizal association for nutrient availability. However, given the need to provide sufficient upright stem growth for adequate floral bud induction, initiation and development, low applications of at least nitrogen and phosphorous may be beneficial on the poorest soils. Also, adequate amounts of water during growth and generic development are of

great importance to achieve a good fruit yield, as well as avoidance of frost in the flower. For domestication of the EB it will be of importance to consider the nutritional and mycorrhizal conditions, and search optimal level of fertilization and methods to strengthen the mycorrhizal association dependent on soil conditions, to provide optimal yield, fruit quality and plant health. A system where the ramet is cut every second year, as practised in lowbush blueberry, could contribute to increased fruit yield and effect the second year pattern of EB flowering (biannual flowering), observed by Kardell and Eriksson (1990), and positively contribute to optimal shoot growth and flower bud production in the sprout year. However, there are concerns that EB may react differently, and that the regenerative shoots need more years to develop fertile shoots.

It is indicated that medium or slightly poorer soil sites will have the highest yield potential, and that a selective cutting of trees is recommendable before clear cutting (at least large clear cuttings), because that will prevent a marked reduction in EB phytomass production. Side effect is by removing an extensive amount of forest there may be concerns of removing carbon sinks and subsequently contrib.-uting to greenhouse gas effect. There is presently no recommendation on how EB and forestland can coexist for the EB commercial production. The effects discussed above are based on situations of stands with solely tree production, where there are taken no steps towards weed control which imply that all under vegetation are allowed to grow and compete. By controlling the vegetation giving preference to the blueberries, even richer soil sites could be suitable for blueberry production if the soil pH was not too high (>5.2). It is also a question how the mesomorphic character of the EB can be handled. The EB thrives in shadowy conditions and does not tolerate the desiccating impact of direct sunlight (Raatikainen and Ratikainen 1983; Salo 1995). Also, it is probably a matter of the EB undergoing excessive amounts of photoinhibition (Percival 2010 pers. comm.). Maybe it could be solved by cutting narrow stripes in the forest instead of cutting a larger area leaving trees in a spread pattern. This practice has been successfully used with sweet lowbush blueberry production in Canada, and should be examined in more detail with the EB. However, in Norway growing on clear cuts show good results as well as growing above the tree limit. This indicates that the amount of light is not as much of a problem in EB as the desiccative effect of sun and wind. If the water conditions are sufficient, the EB should grow and produce well even on large open areas. There is probably an optimal size of the open spaces dependent e.g. on topography and altitude, also because it is shown a reduced visit of pollinating insects when the hedge effect of trees is lacking, and the average temperature would also be reduced.

It is important to notice that EB is an important nutrient sink after cutting and that the growth is markedly dependent on P-level in the soils, which implies that the EB could benefit from P-fertilization. However, other plant species are effective nutrient sinks after forest clearing resulting in the EB having to compete with these or use various technologies to minimize these grass and broadleaf weed pressures in commercial production. An effective weed strategy also would positively affect the fruit yield of the EB, as observed in the sweet lowbush blueberry (*V. angustifolium*). Other environmental factors including winter freezing, frost during flowering, low temperatures and low rainfall during flowering and growth and animal browsing have obviously negative effect on fruit yields.

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