# Modelling Cowberry (*Vaccinium vitisidaea*) and Bilberry (*Vaccinium myrtillus*) Yields from Mineral Soils and Peatlands on the Basis of Visual Field Estimates

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This study presents new models for predicting bilberry and cowberry yields from site and stand characteristics. These models enable one to evaluate the future states of forests in terms of berry yields. The modelling data consisted of visual field estimates of site and tree stand characteristics, as well as berry yields from 627 forest stands. Berry yields were estimated using a scale from 0 to 10. Using these data, models were prepared which predict the berry yield scores from those site and stand characteristics which are usually known in forest planning calculations. The model predictions correlated positively and often quite strongly with earlier models. The results were in line with previous studies on the effects of site and tree cover on berry production. According to the models, sites of medium and rather poor fertility produce the highest bilberry yields. Increasing tree height increases, and the basal area of spruce and proportion of deciduous trees decrease, bilberry yield. With mineral soils, cowberry yields are best on poor sites. A high proportion of pine improves cowberry yields. The yields are the highest in open areas and very young stands, on the one hand, and in sparsely populated stands of large and old trees, on the other hand. In pine swamps, the yields are best on rather poor sites. Increasing basal area of deciduous trees decreases cowberry yields.

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# 1 Introduction

In Finland, berry yields of different forest and peatland site types have been studied since the 1970s (e.g. Raatikainen 1978, Jaakkola 1983, Raatikainen and Raatikainen 1983, Raatikainen et al. 1984, Jäppinen et al. 1986). In some other countries of the boreal vegetation zone, research began a little earlier (e.g. Yakovlev 1971, Belonogova and Kuchko 1979, Eriksson et al. 1979, Kardell and Carlsson 1982, Belonogova and Zaitseva 1989). Thus, there is plenty of general information on the yields of wild berries.

At the end of the 1980s, Jäppinen and Hotanen (1987) suggested that berry yield research should be aimed at creating predictive models. However, until now only a few models applicable to the conditions of boreal forest belt have been prepared (e.g. Sepponen 1979, Raatikainen et al. 1984, Pukkala 1988, Belonogova and Zaitseva 1989, Muhonen 1995, Ihalainen et al. 1999). All these models have been created for mineral soil sites, with the exception of the model of Sepponen (1979), which was a preliminary attempt to predict berry yields for different peatland site types. One reason for the lack of prediction models is insufficient modelling data. Many factors affect the quantity of berry yields, such as site and stand characteristics, weather, and the state of the ground vegetation. In addition, both spatial and temporal variation in berry yields are very high (e.g. Salo 1999, Wallenius 1999). So, the development of reliable prediction models for wild berries is quite problematic.

In order to develop accurate models, a high amount of predictors may be considered (Jäppinen and Hotanen 1987). However, the prospective use of the model determines the reasonable set of predictors. Belonogova and Zaitseva (1989) presented a formula which predicts bilberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitisidaea*) yields from a short-term view (annual yield predictions). In this model, the number of blooms per square meter, the average percentage of ripe berries of blooms and the average weight of one berry were used as explanatory variables. Models like this are mainly used for advising collectors to localise sites which are worthy of berry collection during a certain year.

If berry yield prediction models are developed

for forest planning purposes, the site and stand characteristics are the most reasonable predictors (Pukkala 1988). The planners and decision makers like to know how alternative ways of managing the stands and the forest will affect future berry yields. In forest planning, the site and stand characteristics are known, and the future stand characteristics can be predicted using the current models. In principle, berry yield prediction models for forest planning can be created by means of two different methods. Firstly, models can be based on empirical measurements of berry vields and site and stand characteristics. The models of Pukkala (1988), which were devised for the most common forest berries in Finland. cowberry and bilberry, are an example of this kind of modelling. Raatikainen et al. (1984) developed models for the same berry species but used not only site and stand characteristics, but also characteristics of the berry vegetation as explanatory variables, such as the height of berry plants. Unfortunately, the models of Raatikainen et al. (1984) are not applicable to forest planning because the future states of berry vegetation are unknown.

The other approach to berry yield modelling is to utilize expert knowledge, like Muhonen (1995) and Ihalainen et al. (1999) did. Experts evaluated bilberry and cowberry yields of different forest stands from slides. The site and stand characteristics of each stand were estimated in the field.

Usually the aim of berry yield studies is to define the yields, or yield predictions, for different areas, e.g. forest stands or larger areas, like a given municipality or district (Veijalainen 1982). To estimate berry yields in the field, sample plots have been established from which berries have been collected and weighed. The measured crops are then described as kilograms per hectare.

The size and form of berry sample plots, and the whole sampling method in general, have varied greatly in different studies (e.g. Raatikainen 1978, Eriksson et al. 1979, Sepponen and Viitala 1982a, Jaakkola 1983, Salo 1983). Usually they have been determined instinctively (Sepponen and Viitala 1982b) or on the basis of experience gained from earlier studies (e.g. Raatikainen and Raatikainen 1983, Raatikainen et al. 1984). It is quite problematic to find the right sampling design since wild berries are generally distributed in the field in a clustered manner. One reason for the patchy growth pattern of berry plants is that light does not reach the ground vegetation uniformly because of shading by the crowns of the trees (Laakso et al. 1990). According to Salo (1995), systematic random sampling with small plots always includes many sample plots with no berries at all, resulting in high plot-to-plot variation. High variation results in low precision of the berry inventory.

The problems with empirical berry yield measurements can be overcome with expert modelling, in which experienced collectors or foresters rate different stands according to their berry production. So far, the modelling attempts of this category have employed photographs (slides) of stands (Muhonen 1995, Ihalainen et al. 1999). The problem with slides is that ground vegetation is sometimes difficult to see from the photos, and one photo represents only a small sub-area of a stand which is usually heterogeneous.

In this study, the production capacity of bilberry and cowberry were visually estimated for whole stands during the field inventory of forest stands using a relative scale. It is presumable that any problems resulting from an insufficient view or the patchlike occurrence of berries can be avoided with this method.

In Finland, the total peatland area was originally 10.4 million hectares (or one third of the country's entire land area), of which about 6 million ha have been drained for forestry and agricultural purposes, and 0.84 million ha have been protected (Vasander 1996, p. 6). Although mineral soil sites clearly produce the largest proportion of cowberry and bilberry yields, these berry species also occur on peatlands. In good berry years, the biological yield of cowberry in Finland totals 500 million kilograms, of which 5% (25 million kg) grows on peatlands (Salo 1996). The corresponding figures for bilberry are: total yield 200 million kg, of which 3% (6 million kg) grows on peatlands (Salo 1996). So far, there are no models for predicting the berry yields of peatland sites.

In the present study, relative bilberry and cowberry production of 627 stands, located either on mineral soil sites or on peatlands, were estimated by ocular methods. Since the study material was quite large, it was possible to create prediction models not only for mineral soils but also for different types of peatlands (spruce swamps, pine swamps and open peatlands). The aim was to test a quick method which enables one to produce temporary berry yield prediction models for forest planning purposes. The models are based on expertise and use such site and growing stock characteristics as predictors which are known in forest planning.

# 2 Material and Methods

## 2.1 Estimation of Stand Characteristics and Berry Yields

The study material was collected during the field inventory of forest stands in the summer and autumn of 1999. Three forest planners evaluated stand characteristics and average bilberry and cowberry yields of 627 forest stands located in eastern Finland. The assessments were carried out in privately owned forest holdings so that all stands of the given holding were evaluated.

Before starting the field inventory, the forest planners were instructed to make the berry yield assessments for the present study. It was emphasized that the purpose was to estimate the yields of an average year - not particularly the yields of the study year. Because all the surveyors were experienced foresters and, in addition, interested in berry collection during their leisure time, they were supposed to be experts on berry yields in forests. In other words, they were supposed to have a clear conception about the berry production of different forest stands during an average crop year. The surveyors assessed the berry yields using many indicators such as site and stand characteristics and density of the berry plant vegetation. Therefore, it was possible to assess the berry yields at any time during the growing season.

During the field inventory, the surveyors evaluated bilberry and cowberry yields for the present study so that each surveyor assessed approximately the same number of the stands (Table 1). The evaluations were made on a scale of 0-10, where '0' indicates very poor bilberry/cowberry yield, or no berries, and '10' a very abundant

**Table 1.** Numbers of study stands representing various fertility classes of mineral soil, spruce swamp, pine swamp and open peatland. Site type numbers (used in modelling) corresponding to the fertility classes are given below each fertility class.

Fertility	Very rich	Rich	Medium	Rather poor	Poor	Very poor	Total
	1	2	3	4	5	6	
			Surve	eyor 1			
Mineral soil	-	24	58	30	2	-	114
Spruce swamp	-	7	21	-	-	-	28
Pine swamp	-	-	4	24	14	12	54
Open peatland	-	-	-	-	-	2	2
			Surve	eyor 2			
Mineral soil	4	56	62	40	-	-	162
Spruce swamp	-	1	6	-	-	-	7
Pine swamp	-	-	-	29	4	1	34
Open peatland	-	-	-	-	-	-	-
			Surve	eyor 3			
Mineral soil	1	84	99	35	-	-	219
Spruce swamp	-	-	4	-	-	-	4
Pine swamp	-	-	-	3	-	-	3
Open peatland	-	-	-	-	-	-	-
			То	tal			
Mineral soil	5	164	219	105	2	-	495
Spruce swamp	-	8	31	-	-	-	39
Pine swamp	-	-	4	56	18	13	91
Open peatland	-	-	-	-	-	2	2

yield. The yield estimations were made on the basis of a general impression; only a few minutes were spent per stand for making both bilberry and cowberry yield assessments. Most of the assessments were made during the summer time when berries were not yet ripe.

The stand characteristics were estimated using an ocular standwise forest inventory. It is a standard method to collect field data for forest management planning carried out at the forest owner level. The field data for a stand included, among others: the stand basal area or, in young stands, the number of stems per hectare, the mean tree age, the mean height and the basal area median diameter. These stand characteristics were measured separately for different tree species and canopy layers. Sites were divided into four categories: mineral soil, spruce swamp, pine swamp and open peatland, and the category of each stand was recorded. In addition, mineral soil and peatland sites were classified into site types representing different fertility classes (Lehto and Leikola 1987, Hotanen and Tonteri 1990).

## 2.2 Description of the Forest Stands

The field data were input into a forest management planning software Monsu (Pukkala 1988) which was used to compute a number of variables for each stand. The variables calculated for each stand were used as explanatory variables in regression analyses. Most of the variables were computed not only for the whole tree population of the stand but also separately for pine (*Pinus sylvestris*), spruce (*Picea abies*), birch (*Betula pendula*, *Betula pubescens*) and other deciduous trees (Table 2). The deciduous trees other than

Table 2. Some variables used as potential predictors in bilberry and cowbern	y yield
modelling. Variables marked with * were computed for all trees and separa	tely for
1) pine, 2) spruce, 3) birch and 4) other deciduous trees.	

Variable	Mean			Unit
	Mineral soil	Spruce swamp	Pine swamp	
Dominant height	15	16	12	m
Total basal area *	17	19	14	m²/ha
Mean diameter of all trees *	16	16	13	cm
(weighted by tree basal area)				
Mean age of all trees *	44	51	50	year
(weighted by tree basal area)				-
Total volume *	129	138	81	m <sup>3</sup> /ha
Pine volume	70	31	74	m <sup>3</sup> /ha
Spruce volume	36	64	2	m <sup>3</sup> /ha
Birch volume	19	40	5	m³/ha
Volume of other deciduous trees	4	3	0	m <sup>3</sup> /ha

birch included aspen (*Populus tremula*), alder (*Alnus incana, Alnus glutinosa*), mountain ash (*Sorbus aucuparia*) and willow (*Salix spp.*).

Most of the inventoried stands were located on mineral soil sites (Table 1). About 15% of the stands were pine swamps and 6% were spruce swamps. Only two stands represented open peatlands. On mineral soils, rich (*Oxalis-Myrtillus* type, OMT), medium (*Myrtillus* type, MT) and rather poor (*Vaccinium* type, VT) fertility categories were well represented. Very rich (*Oxalis-Maianthemum* type, OMaT) and poor (*Calluna* type, CT) mineral soil sites were rare. Spruce swamps were represented by two site types, representing rich and medium site fertility. The fertility of the pine swamps varied from medium to very poor.

On the mineral soil sites, pine was the most common tree species since its standing volume was more than half of the total volume (Table 2). Spruce accounted for almost a third of the total volume, and the proportion of birch was about one sixth. On the spruce swamps, spruce was the dominant tree species; its standing volume was nearly half of the total volume. Birch and pine were also common on spruce swamps. Pine swamps consisted almost entirely of pine.

The average stand volume of the forest stands was quite high on mineral soils and spruce swamps (129 m<sup>3</sup>/ha and 138 m<sup>3</sup>/ha, respectively) (Table 2). However, all stages of stand develop-

ment were well represented in both categories. The average stand volume of the pine swamps was considerably lower (81 m<sup>3</sup>/ha). The mean ages for the 91 stands representing pine swamps were not uniformly distributed: 60% of the stands belonged to the age class 40–60 years.

### 2.3 Statistical Analysis

The berry yield prediction models were formulated by means of linear regression analysis. The distributions of berry yield assessments were skewed for most site categories: the proportions of zero and small values were emphasised in the data. Site categories in which the bilberry or cowberry yield evaluations consisted entirely of zeros were excluded from regression analyses.

In order to enable the skewed distributions of the berry yield evaluations to resemble a normal distribution, several potential transformations of the response (y) were tried. In this study, logarithms were found to be the best form of transformation. To avoid taking logarithms of zeros, one was added to the yield estimate. Thus, in regression analyses the predicted variable was ln(y + 1).

The next step was to test whether the relationships were different in different site categories. If this was the case, a model of its own was created for each category. Or, alternatively a common model was formulated for several categories.

When the foresters assessed the berry yields, it is probable that they established different criteria for assigning ratings. For someone a rating of 'three' may indicate a medium berry yield whereas for someone else it may indicate a low yield. This fact was taken into account by dummy variables when creating the models. Every surveyor was given his own dummy to account for the scale differences between surveyors. In addition, site types were included in the regression analyses by other dummy variables. Some transformations of original predictors were used as additional potential predictors (e.g. squared mean height).

## **3** Results

#### 3.1 Prediction Models for Bilberry Yield

A common model was devised for bilberry yields on mineral soils, spruce swamps and pine swamps. In the two stands representing open bogs, the field estimate of the bilberry yield was zero. The regression analysis resulted in the following prediction model for the bilberry yield:

$$\ln(y_b + 1) = 0.243 + 0.594 D_1 + 0.0016 h^2 - 0.0137 G_s - 0.189 \text{ dec}$$
(1)  

$$R^2 = 0.40$$
  
RMSE = 0.54

where

 $y_b$  = bilberry yield

- $D_1 = \text{site dummy:}$   $D_1 = 0, \text{ if site type is } 1, 2, 5 \text{ or } 6 \text{ (Table 1)}$   $D_1 = 1, \text{ if site type is } 3 \text{ or } 4 \text{ (Table 1)}$  h = arithmetical mean height (m)  $G_s = \text{basal area of spruce } (m^2/\text{ha})$
- dec = proportion of deciduous trees of the total

volume (ranges from 0 to 1)

According to the model, site types of medium and rather poor fertility, i.e. sites 3 and 4 in Table 1, produce the best bilberry yields on mineral soil sites, spruce swamps and pine swamps. Fig. 1 indicates the same fact. A good bilberry yield may be found in a mature stand which is not



Fig. 1. Predicted bilberry yields for the study stands representing mineral soil sites, spruce swamps and pine swamps as a function of the mean diameter of the trees. The predictions were calculated by using Equation (1). ◆ site types 1, 2, 5 and 6 △ site types 3 and 4 (see Table 1).

dominated by spruce and deciduous trees. The priority of mature stands over younger ones with regard to bilberry yield can be concluded both from Equation (1), in which the coefficient of the square of arithmetical mean height is positive, and from Fig. 1, in which the mean diameter of trees correlates positively with bilberry yield. There were no differences in the bilberry yield assessments arrived at by the different surveyors.

On spruce swamps, site 3 includes, among others, oligo-mesotrophic paludified spruce forest and *Vaccinium myrtillus* spruce swamp (Hotanen and Tonteri 1990). Type 4, such as *Vaccinium vitis-idaea* spruce swamp, was not represented in the study material. On pine swamps, types 3 and 4 contain, among others, paludified pine forest and spruce-pine swamp (Hotanen and Tonteri 1990). All peatland site types mentioned above are such on which bilberry occurs in the field layer, usually as a dominant species (Laine and Vasander 1990). The other spruce and pine swamp site types which belong to types 3 and 4 are free of bilberries.

#### 3.2 Prediction Models for Cowberry Yields

A separate model was created for cowberry yields



Fig. 2. Predicted cowberry yields for the study stands representing mineral soil sites as a function of the mean diameter of the trees. The predictions were calculated by using Equation (2). A: ◆ fertile sites △ poor sites. B: evaluations given by different surveyors for fertile sites: ■ surveyor 1 △ surveyor 2 ○ surveyor 3.

on mineral soils and pine swamps. The yield estimations were always zero both for spruce swamps and open peatlands. So, no model was prepared for these sites. In the case of mineral soil sites, the prediction model was as follows:

$$ln(y_c + 1) = 0.311 + 0.192 S_2 - 0.141 S_3 + 1.699 D_2 + 0.518 pine - 0.0224 G + 0.0048 t_g - 0.626 D_2 ln(h + 1) + 0.0499 D_2 h R^2 = 0.62 RMSE = 0.44$$
(2)

where

- $y_c$  = cowberry yield
- $S_i$  = surveyor dummy:
  - $S_i = 1$ , if surveyor is *i*; otherwise  $S_i = 0$
- $D_2$  = site dummy:  $D_2$  = 0, if forest site type is *Myrtillus* type or more fertile (1–3 in Table 1)  $D_2$  = 1, if forest site type is *Vaccinium* type or poorer (4–5 in Table 1)
- pine = proportion of pine of the total volume (ranges from 0 to 1)
- $G = \text{stand basal area} (\text{m}^2/\text{ha})$
- $t_g$  = mean age of all trees (a)
- h = arithmetical mean height (m)

Equation (2) and also Fig. 2 indicate that forests of *Vaccinium* type or poorer produce the best cowberry yields. The most abundant yields can be found, on the one hand, in recently clear-felled open areas and in young seedling and sapling stands (zero or small mean diameter) and, on the other hand, in old forests (Fig. 2). Pine volume has a positive effect on cowberry yields. However, a stand suitable for cowberry collection should not be too dense.

The regression coefficients of Equation (2) indicate that each of the three surveyors had used the scale from 0 to 10 in a different way when they evaluated cowberry yields on mineral soil sites. The estimates given by surveyor 2 were somewhat higher than those given by surveyor 1. The assessments of surveyor 3 were lower than those of the two other surveyors (Fig. 2).

In the case of pine swamps, the prediction model for cowberry yields was as follows:

$$ln(y_c + 1) = -0.0178 + 0.512 S_2 + 0.381 D_3 - 0.0541 G_{dec}$$
(3)  

$$R^2 = 0.52$$
  
RMSE = 0.36

where

 $y_c$  = cowberry yield  $S_i$  = surveyor dummy

- = surveyor dummy as in Equation (2)
- $D_3$  = site dummy:  $D_3 = 0$ , if site type is 3, 5 or 6 (Table 1)  $D_3 = 1$ , if site type is 4 (Table 1)

 $G_{dec}$  = basal area of deciduous trees (m<sup>2</sup>/ha)

According to the model, only the site type and the

amount of deciduous trees affect cowberry yields on pine swamps. Site type 4, which includes, for example, paludified pine forest and spruce-pine swamp (Hotanen and Tonteri 1990) produces the best cowberry yields. In these peatland site types, cowberry appears in the understory (Laine and Vasander 1990). The other types, that belong to site type 4, have no cowberries. The basal area of deciduous trees has a negative effect on cowberry yields. Equation (3) also indicates that the evaluations given by surveyor 2 were considerably higher than those of the other surveyors.

## 4 Discussion

In the present study, the average bilberry and cowberry yields of whole forest stands were estimated during the field inventory with the use of a scale of 0-10. The foresters employed in this study formed a general view of the berry yields at the same time as they assessed the growing stock characteristics. An advantage of this data collection method was that errors arising from the patchy growth pattern of berries can most probably be avoided. Another advantage is that visual estimation is quick and cheap. Models devised by means of this method can be used temporarily until more reliable empirical models are available. A similar method may also be used to develop preliminary models for other nonwood forest products.

It was quite surprising to observe that for so many stands the berry yields were estimated at zero. According to the field assessments, about one third of the study stands did not produce bilberries at all. The amount of stands with no cowberry yield was almost 60%. There are several potential explanations for this. There were several stands in which there was no bilberry or cowberry vegetation, or it was scanty. Another reason may be that the surveyors have given the berry yield estimations very cautiously. Finally, the estimations (a great number of zeros and small values) may have been affected by the fact that the field survey was conducted in a poor berry year. In particular, the bilberry yield of the study year was very poor in eastern Finland; the cowberry yield was average. The crops of the study year



Fig. 3. Correlation between the predicted bilberry yields calculated by Equation (1) of this study and the models of A) Ihalainen et al. (1999), B) Muhonen (1995) and C) Pukkala (1988). The predictions were computed for the mineral soil stands of the present study material. □ site types 1, 2, 5 and 6 ▲ site types 3 and 4 (see Table 1).



Fig. 4. Correlation between the predicted cowberry yields calculated by Equation (2) of this study and the models of A) Ihalainen et al. (1999), B) Muhonen (1995) and C) Pukkala (1988). The predictions were computed for the mineral soil stands of the present study material. □ fertile sites ▲ poor sites.

may have affected somewhat the evaluations even though the surveyors were asked to estimate the berry yields of an average crop year.

In this study, the prediction models for bilberry and cowberry yields were formulated for forest planning purposes. Expert knowledge was utilized in modelling, but in a different way than in the studies of Muhonen (1995) and Ihalainen et al. (1999). The models of the present study were not validated with independent data. Instead, the model predictions were compared to previous models, using the stands of our material which represented mineral soil sites (495 stands) (Figs. 3 and 4). The predictions of the models of this study correlated positively with the predictions of previous models (Pukkala 1988, Muhonen 1995, Ihalainen et al. 1999), although the data used for modelling were collected in a different way in each study and the explanatory variables and modelling techniques varied a lot.

The predicted bilberry and cowberry yields computed with Equations (1) and (2) of this study correlated significantly (p-value < 0.01) with the predictions calculated by using the models of Pukkala (1988), Muhonen (1995) and Ihalainen et al. (1999). In the case of bilberry, the correlations with the models of Pukkala (1988), Muhonen (1995) and Ihalainen et al. (1999) were 0.420, 0.244 and 0.797, respectively. In the case of cowberry, they were 0.264, 0.787 and 0.689. In the latter case, it can be seen that the predictions calculated by our Equation (2) correlated more strongly with expert models (Muhonen 1995, Ihalainen et al. 1999) than with a model which is based on empirical measurements (Pukkala 1988). Typical to the models of this study is a very clear effect of site fertility on the berry yields (Figs. 3 and 4).

When considering the prediction model for bilberry yield, it can be concluded that the foresters had used the scale similarly when giving bilberry yield estimations. Contrary to this, the cowberry yield evaluations given for mineral soil sites differed from surveyor to surveyor. When comparing the mean values of the evaluations given by surveyors 1, 2 and 3 (1.40, 2.25 and 0.65, respectively) to the overall mean (1.35), it can be seen that the mean value for surveyor 1 is of the same magnitude as the overall mean. When applying Equation (2) the surveyor dummies may be taken as zero; then the model predictions are near the average score of the surveyors. When considering the cowberry yield prediction model for pine swamps, the estimations given by surveyor 2 were considerably higher than those of the two other surveyors. In this case, the surveyor dummy may be excluded when applying the model.

According to the prediction model for bilberry yield, the best crops on mineral soil sites, spruce swamps and pine swamps may be found in a mature stand which is not dominated by spruce and deciduous trees. Consequently, it can be concluded that bilberry thrives best and produces most berries on pine-dominated stands. In the case of mineral soil sites, these conclusions are supported by many earlier studies (e.g. Eriksson et al. 1979, Raatikainen and Raatikainen 1983, Belonogova and Zaitseva 1989). Bilberry is a mesomorphic plant which means that it produces the most abundant yields in quite shadowy conditions and does not tolerate the desiccating impact of direct sunlight (Raatikainen and Raatikainen 1983, Salo 1995). However, a stand suitable for bilberry gathering should not be too dense. According to Raatikainen et al. (1984), the crown density of a tree stand varying between 10 and 50% is most favourable for a good bilberry yield. Thereby, the negative effect of spruce on bilberry yield may be explained by the fact that spruce shades ground vegetation much more than pine, and this shading negatively affects berry production (Laakso et al. 1990). This study indicates that openings and seedling and sapling stands produce the poorest bilberry yields. This is a well-known result when considering mineral soil sites (e.g. Kardell 1980, Etholen 1983, Raatikainen and Raatikainen 1983. Raatikainen et al. 1984). When considering spruce and pine swamps, the result is supported by Salo (1988) who found that clear cutting has a very negative impact on bilberry crops in peatland forests.

The prediction model of this study for bilberry yield very clearly indicates that forests of medium and rather poor fertility (*Myrtillus* and *Vaccinium* types) produce the highest bilberry crops; a result earlier found, e.g., by Eriksson et al. (1979), Raatikainen and Raatikainen (1983), Raatikainen et al. (1984), Belonogova (1988) and Kuchko (1988). Oligo-mesotrophic paludified spruce forests and *Vaccinium myrtillus* spruce swamps also produce bilberries. When considering pine swamps, good bilberry yields may be found in paludified pine forests and spruce-pine swamps. Raatikainen and Raatikainen (1983) have earlier suggested that paludified pine forests and oligomesotrophic paludified spruce forests, in particular, are peatland site types which produce high bilberry yields.

In the case of mineral soil sites, it is obvious that forests of Vaccinium type or poorer are most favourable for producing good cowberry vields. On poor sites, the best vields can be found in gaps and in old forests. These results are similar to many previous studies (e.g. Raatikainen 1978, Etholen 1983, Raatikainen et al. 1984, Belonogova 1993, Ihalainen et al. 1999). According to Belonogova (1993), the period of intensive development and berry production for cowberries in felling areas is limited by young stands formation and, in addition, high cowberry yields are not characteristic for closed stands. These facts were strongly supported by the results of this study. The priority of pine over other tree species with regard to high cowberry yields was found in the present study, as in many previous studies (e.g. Eriksson et al. 1979, Kardell and Carlsson 1982, Raatikainen et al. 1984).

On pine swamps, the best cowberry yields may be found in paludified pine forests and sprucepine swamps on which deciduous trees do not occur, or at least their proportion of the total basal area is small. Raatikainen (1978) has stated earlier that in addition to poor mineral soil sites paludified pine forests produce the best cowberry yields.

This study suggests that spruce swamps are not worthy of cowberry collection during an average berry year. It may be that the conditions of spruce swamps are not advantageous for cowberry production even though cowberry is present on many spruce swamp site types, even as a dominant species in the field layer. Spruce, which is generally a dominant tree species of spruce swamps, shades ground vegetation and by that means creates unfavourable, moist and shadowy, soil conditions and microclimates for cowberries. Being a photophilous plant with xerophyte tendencies it is quite obvious that cowberry does not thrive and produce yield on such conditions.

When applying the models of this study, it is important to keep in mind that the berry yield predictions are for an average berry year. The very high annual variation in berry yields (e.g. Salo 1999, Wallenius 1999) was not accounted for. Salo (1984) observed that during a poor berry year people collect bilberries and cowberries on sites which are not typically advantageous for these berry species. For example, during a very dry summer people who lived in eastern Finland also collected cowberries on spruce swamps, even though only a little. According to Salo (1988), berries which grow on peatlands only seldom suffer from drvness whereas berries occurring on mineral soil sites usually remain small and drop off during dry summers.

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