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The water economy of the bilberry (Vaccinium myrtillus) under winter conditions

PAAVO HAVAS

Department of Botany, University of Oulu, Oulu, Finland

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Abstract

HAVAS, PAAVO (Botany Dept., Univ., Oulu, Finland) The water economy of the bilberry (Vaccinium myrtillus) under winter conditions. REP KEVO SUBARCTIC RES STAT 8. 41—52. Illus. 1971. — The wintertime ecology, particularly the water economy and associated problems of a typical species of the boreal coniferous forest zone have been investigated. The water content of the aerial shoots decreases, and the osmotic values and cold resistance increase in the autumn until around the turn of the year when a permanent snow cover is achieved. After that there is a change in the ecophysiology: adaptation to summer conditions begins as early as this. Bilberry is sensitive to the weather and for this reason it is not easy to observe permanent regional differences of the ecotype character. It can be observed though, that ecophysiological changes take place at different times in different regions in accordance with the regional temperature. Even the aerial parts of the shoots are capable of absorbing water directly, for example from melting snow. It is true that water uptake is slow in low temperatures, but it is ecologically significant at least in that it saves the shoots from possible crises due to lack of water in winter and early spring. In addition, when the shoots get sufficient water without risk of damage (no danger of dying from cold) they can prepare for the summer when still under the snow.

1. Introduction

In winter there are two markedly different ecological horizons in the forests of the boreal forest zone (taiga). The trees and shrubs which rise above the surface of the snow are exposed to great variations of temperature and water conditions. The plants covered by a thick layer of snow, on the other hand, are in much more stable conditions as regards temperature and water economy. It is never very cold under the snow, and the water relations of the plants are usually good. Thus the typical species of the field layer in the boreal coniferous forests consist of chamaephytes, in the same way as in the oceanic regions of Europe. The conditions prevailing under the snow could be described as "oceanic".

The following is a survey of the wintertime water economy of one chamaephyte, viz. bilberry (*Vaccinium myrtillus* L.) Bilberry is an exceptional chamaephyte in that it is a tropophyte — i.e. sheds its leaves for the winter. In terms of production in the growing season this is naturally disadvantageous, but the situation is alleviated by the fact that even the aerial parts of the stem are capable of photosynthesis. However this type of stem structure is bound to make the winter water economy more difficult, and it "forces" the plant to seek the shelter of snow. Bilberry is, as is well known, chionophilic and relatively cold sensitive (cf. e.g. PISEK 1952; GJAEREVOLL & BRINGER 1965: 257—268; HAVAS 1965; SONESSON 1969: 507).

2. Material and methods

Live shoot material — aerial parts — was collected in different parts of Finland during the years 1965—1968. In the investigations the shoots were generally divided into two groups: the parts of shoots which had grown during the previous summer (young parts), and the older parts. The material collected in Oulu (approx. 65° N) provided the most reliable results, as the measurements could be made more or less immediately after the sample had been collected. Some measurements on material brought straight from the growing site were also made in Kuusamo (approx. 66°30' N). On the other hand the material collected in Lapland (Utsjoki, Kevo, approx. 69°30' N) and southern Finland (Helsinki and Turku, appr. 60°30' N) is not as reliable, since transportation of the material to the laboratory (Oulu) usually took about a day, during which time the water content of the shoots may have changed. The samples were transported to Oulu in Dewar containers, and an attempt was made to keep them as near the temperature at which they were collected as possible.

To determine the water content, the parts of shoots were weighed fresh and re-weighed after dehydration at 80—100°C. As the shoots in question were, in most cases, more or less dormant, and the dry substance content of such shoots probably does not change very much during the winter, fresh and dry weight measurements were considered sufficient, without measuring water content at full turgor (cf. BARRS 1968: 241—253; CHANEY & KOZLOWSKY 1969: 1407).

Experiments on the water uptake of bilberry shoots were made by using the staining, weighing and heavy water methods. The material included both shoots with roots and excised, i.e. rootless, shoots. They were allowed to dry in a cool place before watering, so that the water content of the shoots became low. In the case of the weighing method presented in figure 4, the water content was approx. 169 % in the young parts and approx. 124 % in the old parts before watering. In the heavy water watering (see table 1), the initial water content of the shoots was only 80—85 %. The watering took place in a plant growth chamber in which the temperature, humidity and lighting could be controlled.

In the staining methods the lightly dried shoots were allowed to take in neutral red stained H_2O, after which the possible staining of their tissues was examined in microscope preparations.

When ordinary water was used for watering (so-called weighing tests), the experiment was carried out in the following conditions: temperature 0—+5°C, relative humidity 80—90 %, and illumination very weak. This was an attempt to eliminate the possible changes in the dry weight of the shoots due to respiration and photosynthesis. Moreover, the test conditions did not differ much from the ecological conditions at the time of snow melt. The watering was done either by sprinkling water on the shoots from time to time, or by immersing (as in the case presented in figure 4) the shoots in water at intervals (the cut surfaces of the shoots were waxed to prevent water from entering there). In the case presented in figure 4 the shoots were watered four times daily. They were weighed twice a day, approx. 1.5 hours after the previous watering, when the surface of the shoots had already dried or at least become drier during the treatment preceding the weighing.

When D_2O was used for watering, different conditions were used in different tests (further details in table 1). The temperature of the shoots — except for the root parts — was the same as that of the water. Throughout the experiment 2—5 cm of each shoot was kept in a bent plastic tube which contained D_2O. The watering continued for about 24 hours, and the experiments took place during the periods 24.—25. 11. 1970 and 30. 11. —2. 12. 1970. The amount of water was measured with a mass spectrometer (*Hitachi Perkin—Elmer RMU-6E*) as soon as possible (1—5 hours) after the watering was discontinued (after the watering the shoots were kept in closed test tubes until the water content was measured). The pieces of shoot to be measured (1—3 cm long) were first washed with distilled water and dried to remove the heavy water left on the surface of the shoots. The amounts of heavy water (DHO and D_2O) were compared with the amounts of H_2O the same shoots were found to contain, which were marked as 100. Of the DHO values half was included in the final percentage. This was added to the obtained D_2O percentages which were naturally taken as such.

The osmotic values of the shoots were determined from shoot material fixed by freezing in plastic bags. The shoots were squeezed in a mechanical press, and the liquid thus extracted was immediately decanted into a test tube in a freezer. In 1965 a few fixations were also made by boiling the samples in an airtight jar. Comparison of the osmotic values of samples fixed by boiling and by freezing showed that the boiled samples had somewhat higher values, as can be seen from the material collected in Kuusamo on Sept. 5th 1968:

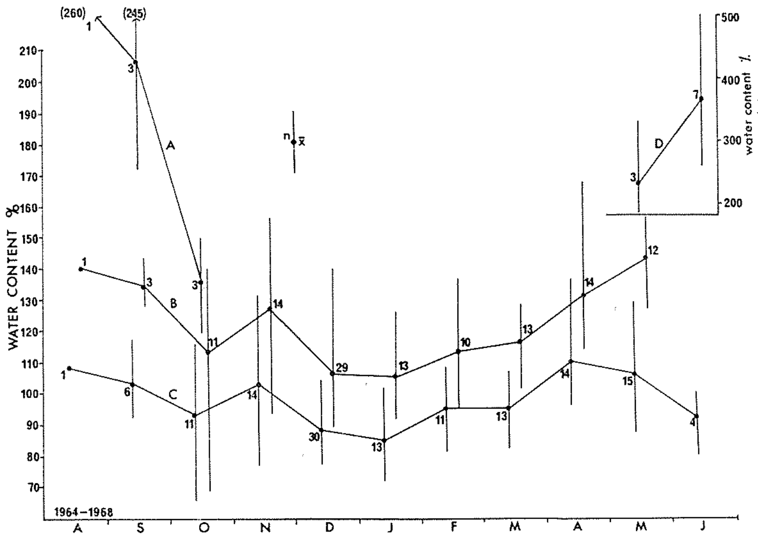

Fig. 1. The water content of bilberry shoots (% of dry weight) in the wintertime under the snow. Oulu 1964—1968, spruce forests of *Myrtillus* and *Vaccinium—Myrtillus* type. A = leaves, B = young (= under one year) parts of shoots (without leaves), C = old parts of shoots, D = bulbs.

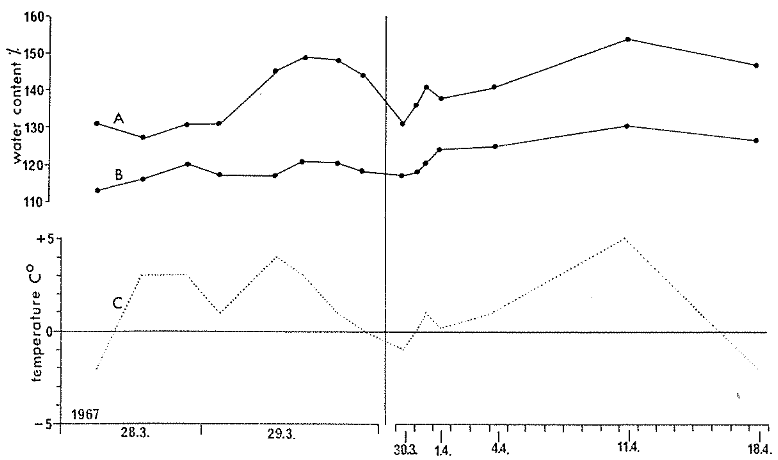

Fig. 2. The water content of bilberry shoots (% of dry weight) under the snow. Oulu 28. 3.—18. 4. 1967, moist pine forest. A = young parts (= under one year) of shoots, B = old parts of shoots, C = temperature above the snow. Depth of snow about 20—30 cm.

	Frozen	Boiled
Leaves	19.24 atm	24.40 atm
New shoots (leafless)	12.88 ,,	15.52 ,,
Shoots of over 1 year (leafless)	15.04 ,,	16.24 ,,

The osmotic values of the extracts were measured in October—December 1968 by using KREEB's (1965) microcryoscopic method. About 0.5 ml of the extract was used for each measurement. The values were calculated according to WALTER's (1931) table, with undercooling corrections taken into account. It was noted that even a long preservation in a frozen state brought about hardly any change in the osmotic values of the extracts.

The cold resistance tests were made in the laboratory by using excised bilberry shoots. They were placed, with their lower ends in water, into dark test chambers whose temperature was slowly decreased for about 6 hours, starting from the temperature the shoots were in before the test. After this the temperature was kept constant for about 2 hours, and then it was slowly raised (for about 6 hours) towards room temperature (cf. e.g. LEVITT 1956: 44—47; TILL 1956: 500—504; PARKER 1961: 374). Four chambers were simultaneously in use, each one having a minimum temperature 2—4° higher than the next. The minimum temperatures were chosen to be such that the cold resistance limit of the shoots was likely to occur between the temperatures of two chambers. After the cold treatment the shoots were placed, with their lower ends in water, in the open laboratory, and their development was observed for several weeks. Notes were made of the browning of the stem and the number of buds that did and did not develop.

3. Water content of bilberry shoots

As is known, plants in cold-winter areas have a lower water content in the winter than in the summer. This annual variation can be seen clearly in figure 1, which shows the variation in the water content of bilberry shoot from Oulu which were covered by snow in winter.

Before the leaves are shed in the autumn their water content decreases very markedly (Fig. 1). Since, however, there still occur changes in the dry matter of the leaves at this stage, the measured changes of water content must be considered only as an indicator.

In leafless shoots the changes of water content occur all through the autumn and midwinter in more or less the same way in young and old parts. Usually in sub-snow conditions the youngest parts of the bilberry shoots always contain more water than the older parts of the stem. Bilberry shoots, owing to their thinness, do not have any considerable stores of water in the winter. Variation in the water content is relatively great during the autumn months before snowfall, particularly in October and November. Later on — when the permanent snow cover has come — the situation becomes clearly more stable in this respect.

During the years (1964—1968) when water contents were measured, the average depth of snow in Oulu in January was 30 cm. It can thus be assumed that at that time even the bilberry shoots in the forests, or at least those in the open spaces between the trees, were for the most part covered with snow. The water content curves for January do indeed show a clear bend, with water content beginning to rise gradually. On the average, the water content of the shoots in the Oulu area continues to rise until April, when the same level is reached which prevailed in August and September. It must be remembered, however, that this rise which occurs after the turn of the year is not nearly as distinct in individual cases as the mean value curves suggest. In some cases the water content may even decrease under the snow during the late winter, if the weather stays very cold for a long time.

In April the snow cover around Oulu melts to the extent that bilberry shoots begin to emerge.

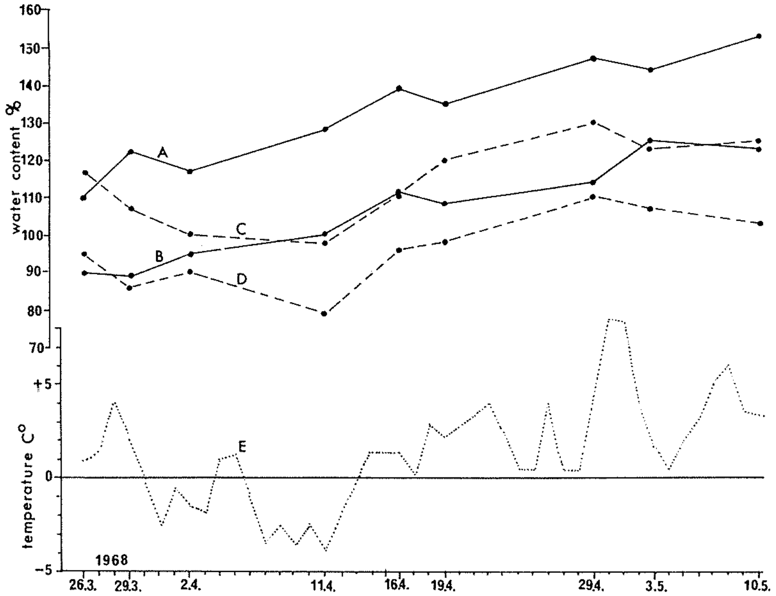

Fig. 3. The water content of bilberry shoots (% of dry weight), spruce forest of *Vaccinium—Myrtillus* type, Oulu 26. 3.—10. 5. 1968. A = young parts (= under one year) of shoots under the snow, B = old parts of shoots under the snow, C = young parts (= under one year) of shoots on snowless site (snow removed 23. 3.), D = old parts of shoots, same place as C, E = temperature (mean) at the meteorogocical station of Oulu.

It can simultaneously be seen that the water content of the old parts of shoots begins to fall. It is likely that at the time when the buds are swelling, little or no further increase takes place in the 1-year-old stem sections of the shoots either, but that the rise of line B in Fig. 1 is mainly due to the great increase of the water content of the buds. When the buds begin to swell, they can not tolerate much decrease in the water content without damage, although they evidently endure considerable drying at midwinter (cf. PISEK 1952: 78).

When the snow cover is thin (Fig. 2) or when there is no snow (Fig. 3, C and D), the temporal variation of the water content of bilberry shoots is geater and more closely related to weather conditions than it is when the shoots are covered with snow. The water content of the shoots rises clearly when the temperature of the air rises, and falls when the temperature falls, both under a thin snow cover and on snowless sites. This, of course, applies only to temperatures around 0°C; if the temperature rises a few degrees during extreme cold, it does not bring about an increase in the water content of the shoots.

The example in Fig. 3 (and many other series of measurements which were made but are not reported here), shows that the water content of shoots uncovered by snow may become critically low after only a few days in natural conditions. In cases of very severe crisis, the water content of the young parts of the shoots may decline to the level of the older parts. In a series of measurements made in Kuusamo during the period April 24—25 1967 it was noted that the water content of the young parts decreased from approx. 185 % to approx. 145 % during 8 daytime hours, and that of the older parts correspondingly decreased from approx. 150 % to 120 % in an area where the snow was removed, and where the soil was frozen but the temperature of the air was about +5°C in the daytime. During the night, however, the water content of these shoots remained relatively constant, with environmental temperature of -5— -7° and humidity of approx. 90 %.

It seems therefore that the crucial factor in the variation of the water content of the shoots is whether the temperature is above or below the freezing point of water.

4. Experiments on the water uptake of bilberry shoots

As indicated above, the water content of the shoots rises in the late winter even under the snow. Could the shoots take up water directly

from the melting snow without absorption through the roots? Methodologically the question is rather difficult to investigate, and the investigations have not yet been completed; as the results obtained so far are interesting, it seems justifiable to present them here.

The first weighing tests were performed by placing bilberry shoots or whole clods of soil with shoots, in snow. Without presenting the numerous experiments that were made, one typical example may be mentioned. The experiment started on March 27, 1968 and ended on April 6, 1968. The temperature of the soil clods was kept suffiently low that the roots remained frozen throughout the experiment. At the beginning of the experiment the water content of the young parts of the shoots was 113 % (of dry weight) and that of the old parts 103 %. By the end of the experiment the water content of the shoots which were kept (except for the roots) in melting snow (+ 0°C) had risen by 19 % in the young parts and by 16 % in the old parts. However in snow whose temperature was -12°C during the experiment, the water content of the shoots had declined slightly: the water content of the young parts decreased by 1.4 % and that of the old parts by approx. 10 %. The experiment can thus be considered to prove that the shoots had absorbed water by their aerial parts from the melting snow. Similar results have also been obtained with excised shoots (whose ends where kept waxed during the experiment).

Of the numerous weighing tests that were made, one may be presented (Fig. 4). The experiment shows that the weight of the shoots watered daily increased by 5—10 % of the initial weight. The increase in weight did not stop until 4—5 days after the beginning of the experiment (the decrease in weight noted during the period April 21—23 is probably a "mistake" due to the experimental technique). When the shoots were not watered, their weight decreased rapidly despite the fact that the humidity of the air was relatively high (80—90 %) during the experiment. Commencing on the fifth day after the beginning of the experiment these slightly dried shoots were watered on two days. A very rapid increase of weight was then recorded. This test arrangement was repeated, as Fig. 4 shows. It is naturally difficult to say, whether and how much "exess" watering water there was on the surface of the shoots during the weighing — despite drying. It is probable, however, that its amount could not increase as the watering proceeded, in the same way as the weight increased.

In the kind of weighing tests described above it is naturally impossible to find out how much water the plants may absorb, through which channels it is conveyed, and where it finally goes. Preliminary answers to these questions have been sought for example by staining tests, but it was difficult to see the distribution and amount of the stain (neutral red) in the tissues of the shoots. There are often small wounds, scars etc. on the surface of the shoots, through which the stain easily penetrates. Generally the stain could be noted only in the surface parts, mainly the epidermis. So far we have not been able to elucidate the channels of stain penetration sufficiently well.

Heavy water was used for watering in an attempt to find out the amount of water passing through the surface of the shoots, and its variation in different test conditions, besides being simultaneously used to check the amount of direct uptake of water into the shoots calculated in the weighing and other experiments. As can be seen from table 1, the amount of water originating from D_2O varies greatly, and the amount of material is very small, for which reasons no definite results can be presented yet. It can be seen, however, that a relatively great

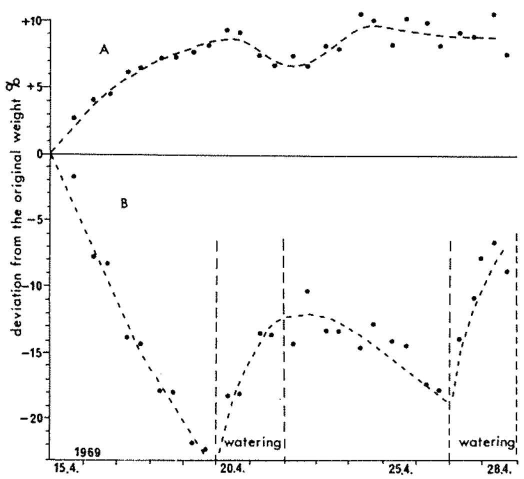

Fig. 4. The watering experiment with bilberry shoots, Oulu 15.—28. 4. 1969. A = the deviation (%) of shoots from the original weight under continuous watering, B = the same, with watering only 20.—21. 4. and 27.—28. 4. See text on page 42!

amount of heavy water has passed into the shoots after watering for about one day. In the extreme cases the parts of shoots kept directly in D_2O contain very nearly twice as much water originating from D_2O as ordinary water. Outside the watering points the amounts of heavy water were naturally much smaller, but even there this water was found. It can be noted further that the amount of water taken up depends particularly on the temperature in which the experiments were made: the warmer it was, the more heavy water passed into the shoots. The material is not sufficient to show the possible effects of other factors. In order to find out whether water had been conveyed as far as the central tissues of the shoots, the measurement was performed also on shoots whose surface parts had been entirely removed before the measurement. In this case the interior parts were found to contain 32.7 % water originating from D_2O (in the part watered with D_2O, temperature +20°C).

5. Osmotic values of bilberry shoots

5.1. Temporal variation of osmotic values in Oulu

As would be expected, the osmotic values of bilberry shoots were clearly higher in the winter than in the summer. The osmotic values of the shoots in Oulu were around 10—15 atmospheres in the summer, but in the winter they often reached a level of over 25 atmospheres. The osmotic values in the winter as in the case of the water content depends particularly on the snow cover. Osmotic values rise in the autumn before the permanent snow cover comes, reaching their peak values at the turn of the year (Fig. 5). The mean values do not reveal any clear regular difference between the osmotic values of the young and the old parts of shoots, and thus they have not been presented separately in Fig. 5. This probably means that the young parts which contain more water than the old (cf. Fig. 1), have a higher concentration of cell sap than the old parts. It can be noted, furthermore, that in the autumn the highest osmotic values often occur in the young parts of shoots, while at midwinter the highest values are generally recorded in the old parts. In the same way as the water content, the osmotic values show conciderable variation in the early winter before snowfall.

In sub-snow conditions the osmotic values begin to fall from the turn of the year towards the spring. During the late winter it is often noted that the peak values again occur in the young parts, but the mean values do not show any essential difference between the young and the old parts at this time. It may be worth noticing, on the other hand, that bilberry in dry pine forest (Fig. 5. line B) shows lightly higher osmotic values throughout the spring period than bilberry in spruce forests (line C). Because of the water situation, bilberry shoots in dry pine forests probably have slightly higher osmotic values than those in moist spruce forests, even in the summer.

In the late winter the osmotic values in plants above the snow (Fig. 5, line A) are a few

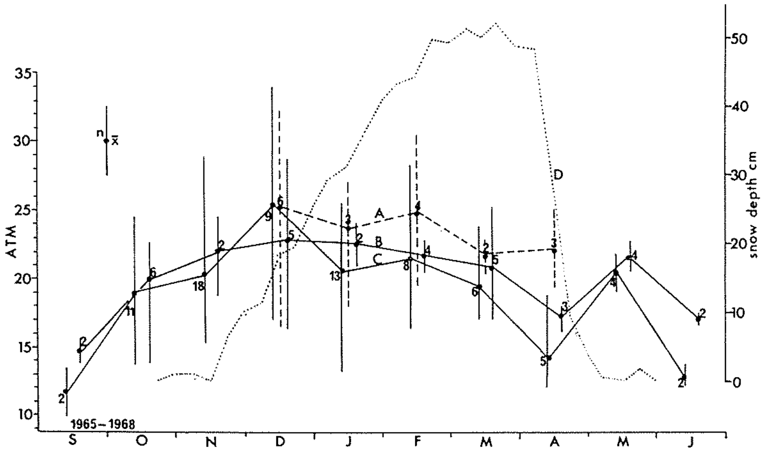

Fig. 5. Osmotic values (extremes and mean) of bilberry shoots, Oulu 1965—1968. A = shoots above the snow, B = shoots under the snow, pine forest of *Empetrum—Vaccinium* type, C = shoots under the snow, spruce forest of *Myrtillus* and *Vaccinium—Myrtillus* type, D = depth of snow 1965—68 (mean) at the meteorological station of Oulu.

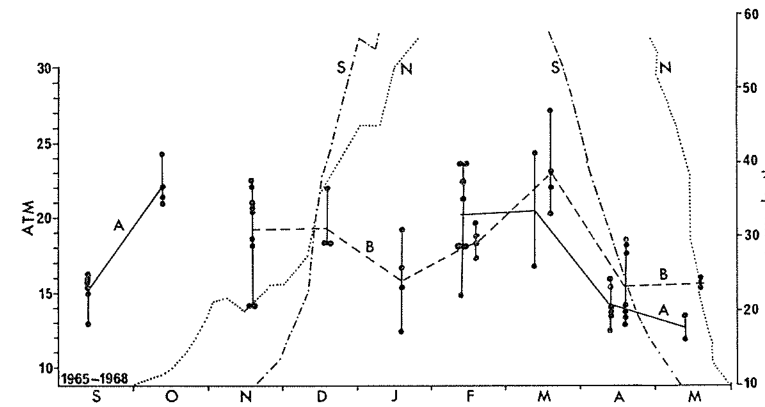

Fig. 6. Osmotic values (1 spot = 1 value) of bilberry shoots, 1965—68. A = Values from northern Finland (Utsjoki and Kuusamo), B = values from southern Finland Helsinki and Turku), N = depth of snow 1965—68 (mean) at Utsjoki and Kuusamo, S = depth of snow 1965—68 (mean) at Helsinki and Turku.

atmospheres higher than in those under the snow. All these measurements apply only to live shoots. An interesting feature of the values recorded in Oulu is the rise in osmotic value which occurs in the bilberries of both pine and spruce forests in May. It can be seen in both the old and the young parts of shoots. As has been explaned above, the water content of the old parts of shoots from Oulu decreases around this time, while no decrease takes place in the young parts. Consequently, the May peak in the osmotic values of the young parts of shoots is probably not due only to a water deficit after emergence from the snow, but is partly active, i.e. osmotically effective substances accumulate in the shoots. The spring situation is of special interest when different regions are compared (cf. below).

Thus the variation in osmotic values throughout the winter is partly correlated with the variation in the water content of shoots, but not entirely so, as indicated above for May. It was also noted that the November increase in water content does not show significantly in the osmotic values, and that the marked December increase in the osmotic values of plants from spruce forests cannot be detected in the variation in the water content of the same shoots.

5.2. Regional variation in osmotic values

The values measured from the shoot material collected in other parts of Finland unfortunately cannot be compared directly with the values from Oulu (cf. p. 42). Since, however, the few measurements that have been made provide indication of some interesting phenomena, the measurements made on material collected in both northern Finland (Utsjoki and Kuusamo) and southern Finland (Helsinki and Turku) are presented together in Fig. 6.

From Fig. 6 it can be seen that in Lapland (line A) at least the osmotic values increase early in the autumn and rise more sharply than in Oulu (cf. Fig. 5) or in southern Finland (line B in Fig. 6). In the late winter however, from March onwards the northern values are lower than the southern. In the late winter the snow cover begins to melt as early as March in southern Finland, and in Lapland about a month later.

It would seem therefore, that there are two peaks in the osmotic values of southern Finland: one in the autumn before snowfall, the other in the spring in March and April when the snow melts. The double peak is of the same type as that in Oulu, but it occurs at a different time due to the melting of the snow. Moreover, the spring peak in southern Finland is perhaps higher and lasts longer than that in Oulu. In Lapland there is probably no spring peak — at least not a clear one — for there is still snow in May, and after that, summer-like conditions follow directly.

6. Cold resistance of bilberry shoots

6.1. Temporal variation of cold tolerance in Oulu

It is naturally difficult to determine the cold resistance of the shoots accurately. The results are affected not only by the length of the cold treatment but also by the structure of

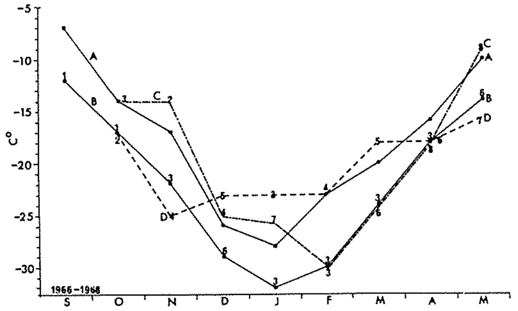

Fig. 7. The average monthly temperatures in which the bilberry shoots under the snow died. (Figures = the numbers of cold tests). Material collected in spruce forests (Oulu, Helsinki, Turku, Kuusamo) and in birch forests (Utsjoki), 1966—68. A = shoots from Oulu kept in temperatures below this will not develop further, B = more than 50 % of the shoots from Oulu will turn brown after the cold test, C = same as B, material from southern Finland (Helsinki and Turku), D = same as B, material from northern Finland (Kuusamo and Utsjoki). See text on page 43!

the shoots (e.g. thickness), number and position of buds, etc. Fig. 7 (line B) shows the means of the temperatures at which shoots, collected from Oulu under the snow at different times during the winter, are damaged so badly that more than half of their area turns brown. With bilberry this situation usually means that no buds subsequently develop. It can be said in general that buds begin to develop only in temperatures 2—5°C higher than this mean (Fig. 7, line A).

The temporal variation in the cold resistance of aerial bilberry shoots is relatively great. In the summer the shoots are damaged by temperatures of only about -10°C, while at midwinter they tolerate temperatures of about -30°C when covered by snow. It seems that shoots with low water content which have been hardened above the snow may tolerate still lower temperatures, but the measurements made on them are not numerous enough to provide reliable results.

A distinct change of trend can be seen in the cold resistance at midwinter in January, in the same way as in the water content and osmotic values.

It seems that the cold resistance of bilberry shoots depends particularly on the water content. By drying the shoots artificially before the cold treament, it is possible to increase the cold resistance in the wintertime by several degrees. The results presented in table 2 provide an example of this. When the shoots were kept dry for a few days before the cold treatment (temperature +5 — +10°C) — during which time their water content became very low (but not too low) — they tolerated temperatures more than 10°C colder than those tolerated by shoots which had received water before the experiment. It should be noted that the cold resistance of the shoots was not affected at least not crucially by any other kind of pretreatment which normally contributes to hardening (such as low temperature). In the summer it is naturally impossible to decrease the water content of the shoots to the same degree without causing damage to the shoots.

6.2. *Regional variation in cold resistance*

Fig. 7 shows that there are regional differences in the cold resistance. It should be noticed that the shoot material collected from other parts of the country probably not fully comparable with the material from Oulu, as the long transportation may have decreased the cold resistance of shoots, but presumably the material from northern and southern Finland can be compared. The temporal variation of cold resistance is smallest in Lapland, where the maximal resistance is already reached late in the autumn (before thick snow cover comes). In Oulu and southern Finland the difference between summer and winter is much greater than in Lapland. The maximum is reached around the turn of the year in Oulu, and as late as February in southern Finland. In May the situation is reversed: the shoots from Lapland are most resistant and those from southern Finland most sensitive to cold. Yet, when the buds was being observed (in Fig. 7 this has been presented only for Oulu), it was noted that the buds of the shoots from Lapland were as resistant as those from southern Finland, although the shoots from Lapland turned brown more easily in the winter. In the summer of 1964 live shoots were brought from different parts of the country (Helsinki, Oulu, Kuusamo) to the Botanical Garden of the University of Oulu. Some cold resistance tests were made with this material during the late winter 1965. The shoots had all been in the same conditions in Oulu and sheltered by the snow in the winter. It turned out that the bilberry shoots collected near Helsinki were slightly more resistant

than those collected in Kuusamo (Maanselkä area). The shoots brought into the garden from near Oulu fell between the shoots of Helsinki and Kuusamo in their cold resistance. It can be assumed, therefore, that in southern Finland (where the snow cover is often relatively thin) the shoots are adapted to tolerate cold better than in Kuusamo, where there is usually a great deal of snow in the winter.

Table 1. The amount of heavy water as a percentage of the amount of H_2O (=100) in bilberry shoots watered with D_2O.

Temperature of the roots 1) (C°)	Temperature of D_2O (C°)	Light (lux)	The parts of shoots kept in D_2O				Samples taken outside the parts of shoots kept in D_2O 3)			
			DHO (%)	D_2O (%)	Water from D_2O (%) 2)	Number of buds	DHO (%)	D_2O (%)	Water from D_2O (%) 2)	Number of buds
-5	+2	1.000	—	—	—	—	1.1	0.0	0.6	0
-5	+2	1.000	—	—	—	—	5.6	0.0	2.8	3
+2	+2	1.000	—	—	—	—	1.5	0.0	0.8	1
+2	+2	1.000	—	—	—	—	5.5	0.0	2.8	3
—	+2	1.000	—	—	—	—	3.1	0.0	1.6	0
—	+2	1.000	72.0	16.0	52.0	3	1.8	0.0	0.9	3
—	+2	1.000	70.0	16.0	51.0	3	12.4	1.4	7.6	0
—	+4	10.000	137.8	83.7	152.6	1	18.3	4.6	13.8	1
-5	+5	10.000	140.3	97.3	167.5	3	22.7	2.3	13.7	1
-5	+10	10.000	117.6	54.1	112.9	3	19.0	2.0	11.5	1
—	+10	10.000	107.0	40.6	94.1	3	43.0	5.5	27.0	2
—	+10	10.000	155.0	135.0	212.5	1	43.3	9.1	30.7	3
—	+10	1.000	149.6	130.2	205.0	1	54.5	9.4	36.7	1

1) The roots of the shoots were kept in H_2O during the watering fest. A dash (—) in the column indicates that excised shoots without roots were used.

2) Methods of calculation are given on page 42.

3) Generally 1—3 cm away from the parts watered with D_2O.

Table 2. Cold resistance of pretreated bilberry shoots.

Time of the experiment	Duration of pretreatment (days)	Conditions prevailing during the pretreatment 1)	Water content (%) of the shoots at the beginning of cold treatment	Cold resistance 2) (°C)
3.—8. 11. 67	5	The lover ends of the shoots kept in water	127	-5—-10
"	"	The shoots kept dry	49	-20
1.—4. 12. 67	3	The lower ends of the shoots kept in water		-4—-8
"	"	The shoots kept dry		> -20
8.—11. 3. 68	3	The shoots kept under snow (temp. ± 0°C and -15°C)	122	~ -10
"	"	The lower ends of the shoots kept in water		-8—-13
"	"	The shoots kept dry	54	~ -20

1) During the pretreatment some of the shoots were kept in varying temperature (during the day about +20°, during the night about +5°C, some in stable temperature (about +25°C). Part of the shoots were exposed to light for 12 h/day, part were kept in darkness all the time. The humidity of the air also varied in different samples of shoots. These factors did not, however, clearly affect the cold resistance, for which reason they are not specified here.

2) The shoots were placed for appr. 20 minutes into chambers in each of which the temperature differed about 5°C from the temperature of the other chambers. After the cold treatment the degree of brownness of the shoots and the develpment of buds were observed. Cold resistance was estimated as a enough average of the observations made.

7. Discussion

As would naturally be expected, a definite temporal variation was noted in the water content, osmotic values, and cold resistance of bilberry shoots. The actual growing season of bilberry ends as early as July (according to our IBP-investigations) in *Hylocomium-Myrtillus* type spruce forests in Kuusamo (HAVAS 1970: 9). In September, at the time when the plants begin to shed their leaves, the water content of the shoots begins to decrease, and the osmotic values and cold tolerance simultaneously begin to increase. Later in the autumn, however, the range of variation of water content and osmotic values is relatively great. Since the autumn can be rainy in Finland, and the relative humidity of the air is generally high, plants must apparently have an ability to decrease "actively" the water content of their shoots (cf. BANNISTER 1964: 492; WEISER 1970). It is likely that the decrease in water content is not due to any increase in the dry substance of the shoots, as the amount of photosynthesis probably remains small during the dark, cold autumn. It seems more probable that water uptake is related to the environmental temperature, as has often been indicated by the water uptake of roots. The experiments presented in this study show that the aerial parts of the shoots are also capable of direct water uptake in the winter, but even in this case the effectiveness of water uptake seems to depend more on the temperature than anything else.

In the autumn the osmotic values of the youngest parts of the shoots are approximately as high as those of the older parts — occasionally even higher. This is so, despite the fact that the young parts have a higher water content than the old. High osmotic values may have positive significance for the winter survival of the young parts of shoots with buds. Yet the cold resistance of bilberry shoots seems to depend mainly on their water content. As has been shown in table 2, cold resistance of the shoots can be affected easily by changing their water content. Rather than going further into the ecophysiological background of this question, reference can be made to the wiews of WEISER (1970) on the changes in the water penetration of the cells of woody plants in connection with hardening.

Thus when winter comes, bilberry shoots have no great stores of water to use as do the thick stemmed trees (cf. e.g. MICHAELIS 1934 a, b; PISEK & LARCHER 1954; TRANQUILLINI 1957; LARCHER 1963; WARDLE 1968). Under the protecting snow cover water storage is not important. On the contrary, when there is a permanent snow cover, the environment provides the shoots with water. Around the turn of the year the water content of the shoots begins to rise gradually, while the osmotic values begin to fall and cold tolerance decreases. Thus the situation is different from that of for example the phanerophytes of long-winter areas, in which the water content continuous to decrease often long into the spring (cf. e.g. WARDLE 1968: 489), the cold resistance remains high, and the winter dormancy relatively deep. It must be noted, however, that long periods of extreme cold or thaw do also affect the subsnow conditions. Similarly, the frost condition of the soil probably also affects the winter ecophysiology of bilberry shoots.

TILL (1956) has noted that the cold tolerance of the aerial parts of chamaephytes does not sow as clear a regional variation as that of northern phanerophytes. TILL has not measured the cold resistance of bilberry, but all the Central European chamaephytes and hemicryptophytes he has investigated have a maximal cold resistance (op.cit.: 533) wich is less than the cold resistance of Finnish bilberry shoots. It may be, however, that within Finland regional differences do occur, but in such a way that in areas with plenty of snow (e.g. Kuusamo) the cold resistance of the shoots is lower than in areas with little snow (e.g. Oulu and Helsinki). It is quite obvious that the coming of winter affects the regional differences noted in cold resistance (Fig. 7). The early, thick snow cover of Lapland accounts for the lesser cold resistance of the shoots there, and the attainment of maximum resistance as early as the autumn. As bilberry reacts easily to changes in the ecological conditions however the possible regional differences in ecotype character are hidden behind this "weather sensitivity".

According to THREN (1934) the osmotic values of bilberry shoots in Central Europe at midwinter were somewhat lower (normal winter value 17 atm.) than those measured in Oulu, where the winter values are 20—25 atm. WALTER (1929) reports values of the same order of magnitude as those measured in Oulu. This may, however, be due to differences in fixing methods (cf. p. 43).

On sites with little snow (under trees, on hummocks, etc.) the water economy and cold resistanse of bilberry shoots during the late winter may be critical even more so than that of phanerophytes, which are better adapted to an absence of snow. The snow cover or its absence thus affects the location of species in the boreal forest zone, both on a small scale and in the regional distribution of vegetation (cf. e.g. HAVAS 1965).

In the present study special attention has been paid to the increase in water content of the shoots under the snow in the late winter. It seems that the shoots are capable of taking up water not only through their roots but also directly, without the help of the roots, and the more effectively this is the greater is their water deficit. When the snow begins to melt in the spring, the heat of the sun upon the dark shoots causes the snow around them to melt very early. At that time the shoots are often covered by a thin layer of water, and the humidity of the air is very high in this kind of snow cavity. Yet it seems that bilberry shoots are hardly capable at all of taking up water from the water vapour of the air. The direct water uptake of the shoots apparently takes place very slowly at low temperatures, but increases in speed as the temperature rises. Only sufficiently long periods of thaw bring about the necessary changes in the water content of the shoots. This is good, of course, since it prevents the shoots from reacting too easily to temporary climatic changes. Naturally, as the spring proceeds, the soil thaws as well, and water uptake through the roots also begins. The ecological significance of the direct water uptake of the shoots probably lies merely in the fact that it prevents drying catastrophes. Thus bilberry could be considered a kind of "winter epiphyte". The increase of water content is greatest in the young parts, and especially in the buds. It is a known fact that some plants in certain conditions are able to absorb water by their aerial parts (KRAUSE 1935; ARVIDSSON 1951; EISENZOPF 1952; STONE 1957; VAADIA & WAISEL 1963 and the literature mentioned by them). From time to time views have been expressed in the literature that direct water uptake would be possible even in winter condition (GATES 1914: 484; MICHAELIS 1934a: 225—229; 1934b: 360; CARTELLIERI 1935: 467; BANNISTER 1964: 494; WARDLE 1968: 494; ROUSCHAL 1939: 151).

Another important function of the snow cover is that it allows the plants to prepare for the growing season. Preparation for maximum utilization of the growing season as early as possible without risk is very important for tropophytes such as bilberry, especially in areas where the growing season is short (cf. TRANQUILLINI 1957: 659; BILLINGS & BLISS 1959; MOONEY & BILLINGS 1960; WARREN WILSON 1966). The buds begin to swell when still under the snow, particularly in northern Finland, where the snow melts late. The readiness for respiration and photosynthesis also increases under the snow. Possibly photosynthesis even takes place under thin snow cover. According to our observations the ecological conditions make this possible: e.g. the CO_2 concentration of the air may be high under the snow, especially when the soil is not frozen. Bilberry stems have a great number of stomata. Besides, shoots in northern Finland have even more stomata (appr. 200/mm^2) than those in southern Finland (appr. 150/mm^2). Studies on these questions will be presented separately later.

The snow naturally melts at different times in different regions. In southern Finland there seems to be the risk that the snow melts too early even on the growing sites of bilberry, and the situation thus leads to a danger of drying or even freezing (cf. e.g. PISEK 1952; LARCHER 1963; WATSON et al. 1966; HAVAS 1965). In northern Finland the snow cover melts so late that the cold and dry spring period is almost nonexistent. It seems that for example the osmotic values of bilberry shoots reflect these circumstances. In Lapland there is no clear increase in the osmotic values after the snow has melted, as there is in Oulu. In southern Finland, on the other hand, a corresponding spring peak of osmotic values seems to occur as early as March and to be very high. THREN (1934) reports that in Central Europe the peak values in bilberry shoots occur even earlier, i.e. in February and March, and the spring peak is even higher than the autumn peak of December. In Alpine regions (around or above the forest line) no clear spring peak of osmotic values has been reported (PISEK & CARTELLIERI 1934; CARTELLIERI 1935: 472, 475; ULMER 1937). Thus it would seem that as we move from the north to the south and from the alpine regions to the forest zone, the curve which represents the variation in osmotic values becomes double-peaked with the period of mid-winter snow cover falling between the two peaks. ·

Thus the spring peak noted in the osmotic values is apparently actively controlled by the young part of the shoots in which the water content simultaneously increases. The variation of water content and osmotic values thus does not occur in the same way at all times, or in the same way in the young and old parts of shoots (cf. also PISEK et al. 1935).

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Waldgrenzstudien im nördlichen Finnisch-Lappland und angrenzenden Nordnorwegen

FRIEDRICH-KARL HOLTMEIER

Institut für Geographie und Länderkunde der Universität,
44 Münster, Johannisstrasse 1—4, Bundesrepublik Deutschland

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Abstract

HOLTMEIER, FRIEDRICH-KARL. (Inst. f. Geogr. u. Länderkunde, Univ., 44 Münster, BRD). Waldgrenzstudien im nördlichen Finnisch-Lappland und angrenzenden Nordnorwegen Timber-line studies in northern Finnish-Lapland and adjacent northern Norway. REP KEVO SUBARCTIC RES STAT 8. 53—62. Illus. 1971. — The pine forests in the valleys of the Utsjoki, the Kevojoki and the Tanariver are isolated outliers of the continuous boreal pine forest zone. The actual pine forestline is not a real climatic one because it has strongly been influenced by man (reindeer, cattle, forest-fires etc.). The scattered pattern of the pine forest-line is not only caused by these anthropogenous influences but also by difficulties in seed production, increasing to the North and upwards to the mountain region. Furthermore the spreading of pine seeds by the wind is not very effective considering the transport of big quantities of seeds. Natural regeneration of the pine forest decreases to the North of this area and in the vertical plane, too. Strong injuries of young pines by "Frosttrocknis" (dehydration by the wind in winter) in consequence of the unfavourable vegetation period in 1968 are discussed in detail. In contrast to the configuration of the pine forest-line the pattern of the upper birch forest-line is strongly influenced by the local climate. The most important ecological factor is the distribution of the snow cover by the wind in winter.

Nach mehrjährigen Arbeiten an der oberen Waldgrenze in den Alpen führte Verfasser in den letzten drei Jahren Waldgrenzuntersuchungen in Finnisch-Lappland und Nordnorwegen durch. Dieser Artikel befasst sich mit Beobachtungen an den Waldgrenzen im nördlichsten Finnisch-Lappland und im angrenzenden nordnorwegischen Gebiet. Standquartier war die subarktische Forschungsstation Kevo.

1. Die Kiefernwaldgrenze

Die Forschungsstation Kevo liegt inmitten einer weit in die subarktische Birkenwaldzone vorgeschobenen Kiefernwaldexklave nördlich der zusammenhängenden subarktischen Kiefernwaldgrenze. Die geschlossenen und relativ gutwüchsigen Kiefernbestände konzentrieren sich auf die trockenen fluvioglazialen Terrassen des Kevojoki- und des Utsjokitales. An den Talhängen klingen sie allmählich aus. Zwischen Kevo und dem Grenzdorf Utsjoki finden diese Kiefernbestände ihre aktuelle nördliche Grenze. Bei Utsjoki sind nur mehr Einzelkiefern vorhanden. Zusammen mit den spärlichen Kiefernvorkommen im westlichen Tanatal bilden sie Reste eines früher ausgedehnteren, im wesentlichen durch den Menschen eingeschränkten Kiefernwaldareals (Raubbau, Rentiere, Vieh-