Key note adress:

Reindeer lichen productivity: Problems and possibilities

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Abstract: Reindeer lichens are important in the structure and function of tundra and taiga ecosystems, as exemplified by cover values, biomass, mineral content, and effect on other ecosystem components. They are particularly important for winter ecology of reindeer and caribou which largely really on them. Growth measurement is difficult due to the very slow rate and the methods that have been used are not sufficiently documented, precise, or appropriate. Use of carbon dioxide exchange models, coupled with models of lichen microclimate and water relations, based on microclimatic data are suggested as alternatives for land managers. The assumptions of such models are discussed and the performance of mixed species lichen mats and of the lichen CO_2 environment and its effect on lichen CO_2 exchange.

Key words: pastures, growth

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The importance of reindeer lichens

Many studies from tundras and taigas have shown that reindeer lichens are very important ecosystem components in terms of their biomass and nutrient store. Rencz and Auclair (1978) and Auclair and Rencz (1982) have shown that 20% of the biomass, 25% of the nitrogen, and 12% of the phosphorus of and open lichen woodland in northern Quebec is to be found in a lichen mat which covers 97% of the forest floor. Tundras may have equally high lichen biomass values as lichen woodlands. In a range survey of the Seward Peninsula, Alaska, Swanson et al. (1985) found up to 760 g m^{-2} of live lichen biomass on lichen lowland tundras and up to 1436 g m^{-2} on upland lichen slopes. The total biomass amount is obviously dependent on a varitety of factors including microclimate, time since burn, and grazing history, but it is clear that in terms of biomass and nutrients, the reindeer lichen can dominate the ecosystem.

Reindeer lichens may also strongly control the fluxes of energy and matter in the ecosystem. It has been shown (Kershaw and Rouse 1971, Kershaw and Field 1975, Cowles 1984) that the lichen mat significantly reduces soil temperature while increasing soil water retention by reflecting much of the incident solar radiation. Lichens may signigicantly affect the nutrient dynamics of the ecosystem by forming a filter between above and below ground system components and thus perhaps both reduce the rate of nutrient release and intercept some of the released nurients before they reach the soil (Cowles 1984). Lichens have also been purported to inhibit growth of neighboring vascular plants through the release of allelopathic chemicals (Brown and Mikkola 1974) but Cowles (1984) demonstrated that the overall effect of the lichen mat in northern Quebec on black spruce growth was positive while seedling establishment was negatively affected. Clearly, reindeer lichens can be considered significant controllers of ecosystem fluxes.

However, it is as reindeer/caribou winter forage that the importance of reindeer lichens is best recognized. The winter forage availability appears to be the most significant factor affecting herd size. The availability of the forage is primarily a function of snow characteristics and forage biomass. In a comprehensive literature study Eriksson et al. (1981) cite many studies demonstrating that lichens constitute a significant portion of the winter diet of reindeer/caribou wherever there are any lichens available. These studies, which are based on composition of fecal pellets, stomach contents, fistula samples, and visual observations of foraging animals indicate that lichens account for 15% to 90% of the food. Further it is held that animal condition is improved with access to lichens. Spectacular fluctuations in reindeer/caribou population numbers have often coincided with range depletion and weather hazards, such as the population crash of reindeer on St.Matthew Island, Alaska in 1964 (Klein 1968).

Most important reindeer forage lichens are fruticose, either growing on the ground, such as the genera *Cladonia*, *Cladina*, *Cetraria*, and *Stereocaulon* or as epiphytes on trees such as the genera *Usnea*, *Bryoria*, and *Alectoria*. Management of these lichens is important as they are susceptible to overgrazing (Swanson et al. 1986) which may result in reduced total lichen availability and changes in lichen species composition to less paltable ones (Klein 1968, Oksanen 1978). The lichen mat is also brittle when dry and is therefore sensitive to trampling by animals (Pegau 1970) and vehicles (Carstairs 1976). Finally, fires often destroy the lichen mat, leading to a long successional sequence with a horn lichen phase preceding the reindeer lichens (Swanson et al. 1985). Important winter range can thus be damaged in various ways and needs to be managed properly if reindeer/caribou management is desired.

Growth measurements

For management to be successful the lichen growth rate needs to be known and its relationship to extrinsic and intrinsic factors needs to be established.

There are difficulties in establishing the growth rate of lichens, primarily because they grow so slowly. Accurate changes in lichen diameters of crustose, foliose, or squamulose lichens can be monitored (Hale 1974, Lawrey and Hale 1977), but fruticose lichen mats are more difficult (Andreev 1954). Andreev (1954) reviewed work and methods up to 1952 and suggested a method that has since been widely used (e.g., Scotter 1963, Pegau 1968, Skuncke 1969, Lechowicz 1983). He correctly criticized the method by Tengwall (1928, as cited in Andreev 1954), which was based in changes in lichen height in reference to fixed points above the lichen canopy, pointing out the possibility of snow compressing the mat and of the "fixed " points moving.

Andreev (1954) referred to the method of Gorodkov (1934, as cited by Andreev 1954), which involved measuring growth above a permanent marker of indelible ink or a string but which was discontinued on favor of using "inherent growth markers". The idea of inherent growth markers was proposed by Salazkin (1937, as cited by Andreev 1954) and further developed and modified by Igoshina (1939, as cited by Andreev 1954) and Andreev (1940, as cited by Andreev 1954).

Salazkin's method was based on the assumption that forking of the thallus of *Cladonia* and *Cladina* lichens is a yearly event and therefore can be used as a growth marker (Fig. 1). Salazkin proposed that the yearly production equall-

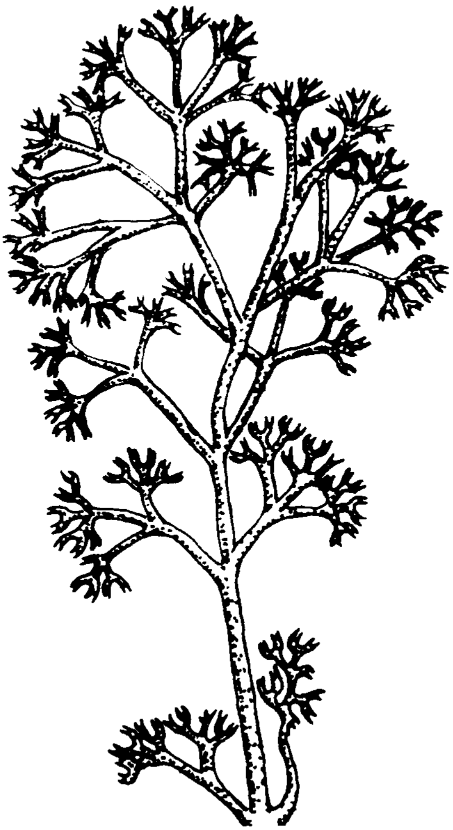

Figure 1. The branching patttern of *Cladina stellaris* (syn. *Cladonia alpestris*). This forking has been assumed to be a yearly event and has been used as an innate growth marker. Adapted from Brehmer in Thomson (1984) and Kärenlampi (1970).

ed the length of the uppermost interval that had stopped elongating, while Igoshina felt that the average of all intervals should be used. Andreev, also used the average interval, but used only the "living" part of the thallus. As results from the marking method of Gorodkin were found to be similar to results from the inherent growth marker method as used by Salazkin, the latter method was considered proven. To cite Andreev (1954), "If branching did not occur every year but (for example) every second year, the amount of annual growth would be half the lenght of a ring that had finished growing. If branching occured more often than once a year, for instance twice a year, the amount of annual growth would be twice as large as the length of a ring. Since experimental data do not disclose such differences, it must be concluded that the podetium of fruticose lichens branches, as a rule, once a year". Note that there is an implicit assumption that branching is a temporally regular event.

There are, therefore, two crucial assumptions on which Andreev's method rests, yearly forking, and a clear demarcation of the live to dead interface. Neither of these can be considered sufficiently demonstrated, although Skuncke (1969) states that Swedish *Cladonias* branched roughly once a year. Andreev specifically states that once growth of an interval has ceased it is no longer alive, rejecting Elenkin's claim (1922, as cited by Andreev 1954) that the fungus may still be alive, without offering experimental proof to the contrary.

Another method for determining growth rates is monitoring growth of thalli in containers (Kärenlampi 1971, Gaare pers. comm.) or growth of transplanted thalli. The question here is, to what extent the conditions in the containers are known, ecologically meaningful, and extrapolatable. Toxic chemicals in the boxes may reduce growth initially (Goodall pers. comm.), and/or CO_2 concentration around the thalli may be important (Sonesson, pers. comm.) and changed by the presence of the containers insulating the lichen from the ground. Still largely unexplored for growth monitoring purposes, the use of radioactive markers such as strontium and cesium from fallout or experimentally administered should be explored (Feige et al. 1988).

Assuming that both Andreev's growth method (only applicable to *Cladina* and *Cladonia* and other growth methods are valid, they are still not sufficiently precise to allow predictions or evaluate effects of weather changes or habitat conditions (Kärenlampi 1971). As the growth is very slow the time interval must be large (a year) and even year to year fluctuations are difficult to detect. There is consequently a great need for an alternative approach.

Carbon flux

There have been many studies of vascular plant productivity where growth analyses and CO_2 exchange have been used separately or in combination. There is a general agreement or corrrelation between the two methods, but it has proven difficult to measure the natural exchange of all parts and the total flux is generally obtained by extrapolation of laboratory conditions to the field (see Mooney 1972). There have been demonstrations of leaching from foliage, stems, and roots (Barber and Martin 1976, Smith 1976) and fine root turnover is largely unknown (Persson 1978). In spite of these problems, productivity of vascular plants is frequently modeled based on CO_2 exchange of the parts.

Lichens with their relatively simple structure represent in this way a much easier organism to study as they have no below ground parts. Therefore, the exchange of the whole thallus can be assessed together. What then, do we know about reindeer lichen carbon flux? How much of what we know is relevant to reindeer lichen productivity in the field?

In order to be able to model and thus extrapolate the CO_2 exchange data to a variety of weather and habitat condition several assumptions will have to be true.

1. *Carbon dioxide uptake represents the predominant mode of carbon capture; the fungus is not also saprobic.*

The author is not aware of any confirmed reports of saprobic carbon uptake of naturally grown lichenized fungi. Some, normally lichenized fungi, can be grown saprobically isolated from the phycobiont (Ahmadjian 1974), but the nutritional needs of lichenized fungi are assumed to be fulfilled by the phycobiont. Despite the importance of this concern, it has not received sufficient attention and needs study.

2. *There is no significant leaking of organic substances form the thallus or, alternatively, such leaking is quantifiable and can be modeled.*

A study of *Hypogymnia physodes* (Farrar 1976) indicated losses of carbohydrates during the drying/wetting cycles. A study by Cooper and Carroll (1978) identifies the epiphytic lichen *Lobaria oregana* as the major source of polyols in leachates from the canopy of Douglas fir in Oregon. Ribitol was the most abundant ingredient. In an experiment with *Cladina stellaris* (author's unpublished data) exposed to $^{14}CO_2$ there was no leaking of labelled substances; the loss was only through respiration. This type of experimentation needs to be repeated with more reindeer lichen species and losses, if found, must be quantified.

3. *The extrinsic and intrinsic controls of CO_2 flux are well known and quantifiable. Preferably these controlling factors should be few.*

The environmental physiology of lichen thalli is well established and relatively simple. Basically, lichens are metabolically active only when moist. Dry, they are inactive and brittle. Following showers, dew fall, or condensation of upwardly moving soil moisture, activity starts with a burst of CO_2 loss. The thallus starts photosynthesizing if incident radiation allows and the rate is primarily determined by the thallus water content and temperature. As the thallus dries out the photosynthetic rate may first increase until optimum water content is reached and subesquently fall as the internal water potential drops (Fig. 2). The reduction of the photosynthetic rate by supraoptimal water contents has been shown to be caused by increased diffusion resistance of the saturated thallus (Lange and Tenhunen 1981). The rate of drying is purely governed by physical conditions as lichens, lacking roots, do not possess active mechanisms of water uptake, and lacking stomata have no significant dynamic effect on evapotranspiration.

Although, there are concerns (Green and Snelgar 1981, Lange and Tenhunen 1981) over experimental methods in which CO_2 drawdown analysis is used (e.g. Larsson and Kershaw 1975), there are several other data sets de-

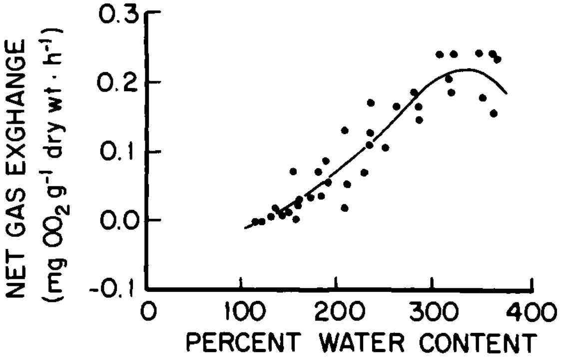

Figure 2. Net photosynthesis in relation to thallus water content in *Cetraria cucullata* from the Seward Peninsula. The measurements were made at optimum temperature and saturating irradiance.

monstrating the multivariate response surfaces of lichen photosynthesis (e.g. Carstairs 1978, Lechowicz 1978, Kappen and Redon 1978). One possible complication to the extrapolations of such data sets to natural condition, is the unknown CO_2 lichen environment and the scarce information of the interaction of CO_2 and other extrinsic and intrinsic factors. Clearly, there is a need to characterize reindeer lichen CO_2 environments and analyze lichen CO_2 gas exchange responses to these.

Lichens do not appear to be nutrient limited (Skuncke 1969, Carstairs 1978) as application of fertilizers did not result in change in growth or photosynthesis. Intrinsically, there are seasonal changes in CO_2 exchange of thalli (e.g. Carstairs 1978) and thalli of different size classes (ages?) have different rates of net CO_2 exchange (Sveinbjörnsson 1987). The exact mechanisms for these have not been fully explored.

4. *The lichen environment can be characterized and related to macroclimatic conditions with appropriate transfer functions.*

Reindeer lichens may be found scattered or in mats of varying expanse, thickness, and composition. These habits profoundly affect their environment as do other physiognomic features of the vascular plant vegetation and the general landscape topography. The thickness of the lichen mat, with dead lichen mulch below the coherent lichen, affects, as mentioned above the intrinsic CO_2 exchange capacity. It also profoundly influences the operational environment of individual thalli (Fig. 3).

Considering lichen mats as reindeer winter ranges, it is perhaps not very relevant to understand the functioning of the thickest mats with much attached dead lichen tissue and mulch as these represent underutilized degenerating range stanges (Andreev 1954) which would not exist with prudent management. However, even small amounts of attached dead tissue can significantly moderate the rapidity and severity of the drying/wetting cycles. On cool clear nights with little wind, infrared radiation loss from thallus tips reduces their temperature, while warmer moist air from the soil and the

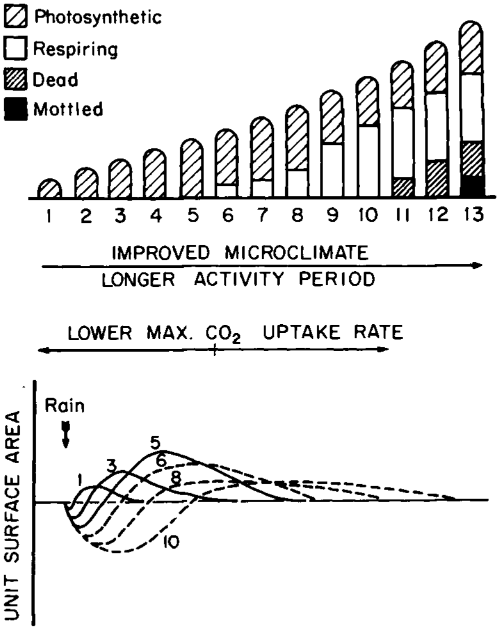

Figure 3. A hypothetical change in net CO_2 flux of lichen mats of different developmental stages. As the lichen mat gets thicker it improves it's own microclimate. Thus, the photosynthetic periods become more prolonged while the maximum rate of photosynthesis starts decreasing once the photosynthetic zone has reached maximum size.

ground rises through the mat. As it diffuses through the upper parts of the lichen thalli, the water condenses on them increasing their tissue water content significantly and rendering them capable of greater photosynthetic rates in the early morning hours. This phenomenon has been found both on low peat mounds on Nunivak Islands (Fig. 4) and in paper birch/white spruce forests in south central Alaska, but would logically be expected to occur most frequently in habitats with little wind movement. This upward movement of water, beneficial as it is to the lichen photosynthesis, which takes place in the uppermost part of the thallus, is not without costs. As mentioned above thicker mats have lower maximum rates than thinner ones, pressumably because they contain attached nonphotosynthetic tissue (Kärenlampi 1970, Carstairs 1978, Sveinbjörnsson 1987) (see Fig.3).

Monospecific lichen mats have been characterized in terms of boundary layer resistance as a function of wind speed as well as internal thallus resistance to water loss (Lechowicz 1976, Collins and Farrrar 1978, Green and Snelgar 1981, Link et al. 1985). Light penetration in such mats has also been studied (Kershaw and Harris 1971). Humidity, temperature, and drying rates all have been monitored in lichen woodland mats (Carstairs 1976, Kershaw and Field 1976). But just as different species have different gas exchange and water relations it is logical to assume that mixed mats may not simply be the sum of the parts. As an example, the dark brown, *Cetraria islandica* absorbs more solar radiation than the faintly yellow *Cetraria cucullata*, and as resistance characters are identical in these species,the former dries out faster than the latter (Sveinbjörnsson and Resnick *in prep.*). It does not necessarily have to be that these differences persist in mats of these two species as they may be differentially exposed to radiation and as thermal conductance and convection may be different depending on exact composition of the lichen canopy.

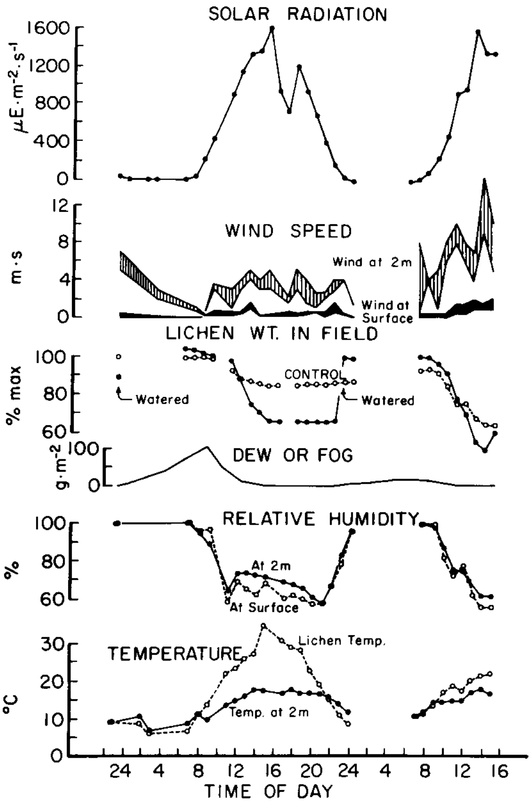

Figure 4. Microclimatic conditions and lichen water content on a peat mound edge near the airport on Nunivak Island, Alaska. Note the high humidity and dew deposition at night and early morning in spite of considerable wind speeds.

Models of lichen biophysics (Hoffman and Gates 1970) and physiology exist; some are simply regression models based on laboratory or field data (Lechowicz 1976, Lange et al. 1977, Paterson et al. 1983), while others attempt to take a more synthetic mechanistic approach (Link et al. 1985). A mathematical model of lichen mats biophysics also exists (e.g. Lechowicz 1976), although it has not been verified in situ. Thus, the framework exists for a combined model of lichen biophysics and physiology based on laboratory and field measurements. The use of well constructed models, with robust transfer functions relating macroclimate and lichen condition coupled with existing physiological models, can be used to evaluate the productivity of lichen ranges following verification in the field.

The lichen resource is utilized by the reindeer/caribou both in accordance within their behavioral constraints, and in intensive management, the directions of the manager. Lichen-reindeer interactions have been modeled (Bunnell et al. 1973) but with more behavioral and management input these models may now be improved. The time is ripe for a concerted effort to join these parts into one realistic model with range management as a guiding goal. Thus, the range manager may be provided with a tool to maximize use and minimize abuse of this valuable resource.

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References

Andreev, V.N.1954. Growth of forage lichens and methods to improve it. - *Geobotanica* 9:11-74. (English translation).

Auclair, A.N.D. and **Rencz, A.N.**1982. Concentration, mass, and distribution of nutrients in a subarctic *Picea mariana - Cladonia alpestris* ecosystem. - *Can. J. For. es.*12:947-968.

Barber, D.A. and **Martin, J.K.** The release of organic substances by cereal roots into soil. - *New Phytol.* 76:69-80.

Brown, R.T and **Mikkola, P.** 1974. The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. - *Acta Forestalia Fennica* 141:1-22.

Bunnell, F., Kärenlampi, L., and **Russel, D.** 1973. A simulation model of the lichen-*Rangifer* interactions in Northern Finland. - *Rep. Kevo Subarct. Rec. Stat.* 10:1-8.

Calkin, P.E. and **Ellis, J.M.** 1984. Development and application of a lichenometric dating curve, Brooks Range, Alaska. - In: Mahany, W.C. (ed.), *Quarternary Dating Methods.* Amsterdam, Elsevier, 227-246.

Carstairs, A.G.1976. Environmental factors affecting net CO_2 assimilation in *Cladonia alpestris* (L.) Rabh. in the subarctic. *M.Sc. thesis, McGill University, Montreal.* 88 pp.

Carstairs, A.G. and **Oechel, W.C.** 1978. Effects of several microclimatic factors and nutrients on net carbon dioxide exchange in *Cladonia alpestris* (L.) Rahb. in the subarctic. - *Arctic and Alpine Research,* 10:81-94.

Collins, C.A. and **Farrar, J.F.** 1978. Structural resistance to mass transfer in the lichen *Xanthoria parietina.* - *New Phytol.* 81:71-83.

Cooper, G. and **Carroll, G.C.** 1978. Ribitol as a major component of water soluble leachates from *Lobaria oregana.* - *Bryologist* 81:568-572.

Cowles, S. 1984. Effects of lichen cover on conifer growth in the northern taiga. - *Ph.D. dissertation, McGill University, Montreal* 132 pp.

Denton, G.H. and **Karlen, W.** 1973. Lichenometry: Its applicatioin to Holocene moraine studies in southern Alaska and Swedish Lapland. - *Arctic and Alpine Research* 5:347-372.

Eriksson, O., Palo, T., and **Söderström, L.** 1981. Renbetning vintertid. Undersökningar rörande svensk tamrens näringsekologi under snöperioder. - *Växtekologiska Studier,* 13, Uppsala, 92 pp.

Farrar, J.F. 1976. The lichen as an ecosystem: observation and experiment. - In: Brown, D.H., Hawksworth, D.L., and Bailey, R.H. (eds.) *Lichenology: Progress and Problems.* Academic Press, London. pp. 385-406.

Feige, G.B., Jahnke, S., and **Niemann, L.** 1988. Tschernobyl belaset uns weiter. - *Essner Universitäts Berichte,* Nr 2:8-14.

Green, T.G.A. and **Snelgar, W.P.** 1981. Carbon dioxide exchange in lichens. Partition of total CO_2 resistances at different thallus water contents into transport and carboxylation components. - *Physiol. Plant.* 52:411-416.

Hale, M.E. 1974. Growth. - In: Ahmadjian, V. and Hale, M.E. (eds.) *The lichens.* Academic Press, New York. pp. 437-492.

Hoffman, G.R. and **Gates, D.M.** 1970. An energy budget approach to the study of the water loss in cryptogams. - *Bulletin of the Torrey Botanical Club,* 97:361-366.

Kappen, L. and **Redon, J.** 1987. Photosynthesis and water relations of three maritime antarctic lichen species. - *Flora (Jena) 179:215-229.*

Kärenlampi, L. 1970. Distribution of chlorophyll in the lichen *Cladonia alpestris*. - *Rep. Subartic Res. Stat.* 7:1-8.

Kärenlampi, L 1971. Studies on the relative growth rate of some fruticose lichen. - *Rep. Kevo Subarctic Res. Stat.* 7:33-39.

Kershaw, K.A. and **Field, G.F.** 1975. Studies on lichen-dominated systems. XV. The temperature and humidity profiles in a *Cladina alpestris* mat. - *Can. J. Bot.* 53:2614-2620.

Kershaw, K.A. and **Harris, G.P.** 1971. A technique for measuring the light profile in a lichen canopy. - *Can. J. Bot.* 49:609-611.

Kershaw, K.A. and **Rouse, W.R.** 1971. Studies in lichen dominated systems. I. The water relations of *Cladonia alpestris* in spruce-lichen woodland in northern Ontrio. - *Can. J. Bot.* 49:1389-1399.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. - *J. Wildlife Mgmt.* 32:350-367.

Lange, O.L., Geiger, I.L., and **Schulze, E.-D.** 1977. Ecophysiological investigations on lichens of the Negev desert. V. A model to simulate net photosynthesis and respiration of *Ramalina maciformis*. - *Oecologia* 51:426-429.

Lange, O.L. and **Tehunen, J.D.** 1981. Moisture content and CO_2 exchange of lichens. II. Depression of net photosynthesis of *Ramalina maciformis* is caused by increased thallus carbon dioxide diffusive resistance. - *Oecologia* 51:426-429.

Larson, D.W. and **Kershaw, K.A.** 1975. Measurement of CO_2 exchange in lichens: a new method. - *Can J. Bot.* 53:1535-1541.

Lawrey, J.D. and **Hale, M.E.** 1977. Natural history of Plummers Island, Maryland. XXIII. Studies of lichen growth rates of Plummers Island, Maryland. - *Proc. Wash. Biol. Soc.* 90:698-725.

Lechowicz, M.J. 1976. Environmental response structure of Cladina lichens from contrasting habitats. - *Ph.D. dissertation, University of Wisconsin, Madison.* 189 pp.

Lechowicz, M.J. 1978. Carbon dioxide exchange in Cladonia lichens from subarctic and temperate habitats. - *Oecologia* 31:225-237.

Lechowicz, M.J. 1983. Age dependence of photosynthesis in the caribou lichen *Cladina stellaris*. - *Plant Physiol.* 71:893-895.

Link, S.O., Driscoll, M.F. and **Nash III, T.H.** 1985. CO_2 exchange in lichens: Towards a mechanistic model. - In: Brown, D.H (ed.), *Lichen physiology and cell biology.* Plenum Publishing Co. pp. 77-91.

Mooney, H.A. 1972. The carbon balance of plants. - *Annu. Rev. Ecol. Syst.* 3:315-347.

Oksanen, L. 1978. Lichen grounds of Finnmarksvidda, northern Norway, in relation to summer and winter grazing by reindeer. - *Rep. Kevo Subarct. Res. Stat.* 14:64-71.

Paterson, D.R., Paterson, E.W., and **Kenworthy, J.B.** 1983. Physiological studies on temperate lichen species. I. A mathematical model to predict assimilation in the field, based on laboratory responses. - *New Phytologist* 94:605-618.

Pegau, R.E. 1970. Effect of reindeer trampling and grazing on lichens. -*J. Range Mgmt.* 23:95-97.

Persson, H. 1978. Root dynamics in a young Scots pine stand in central Sweden. - *Oikos* 30:508-519.

Rencz, A.N. and **Auclair, A.N.D.** 1978. Biomass distribution in a subarctic *Picea mariana-Cladonia alpestris* woodland. - *Can. J. For. Res.* 8:168-176.

Scotter, G.W. 1963. Growth rates of *Cladonia alpestris, C. mitis,* and *C. rangiferina* in Taltson River region, N.W.T. - *Can. J. Bot.* 41:199-1202.

Skuncke, F 1969. Reindeer ecology and management in Sweden. - *Biol. Pap. Univ. Alaska, no.8,* 81 pp.

Smith, W.H. 1976. Character and significance of forest tree root exudates. - *Ecology* 57:324-331.

Sveinbjörnsson, B. 1987. Reindeer lichen productivity as a function of thallus thickness. *Arct.Alp. Res.* 19:437-441.

Swanson, J.D., Schuman, M., and **Scorup, P.C.** 1985. Range survey of Seward Peninsula reindeer ranges, Alaska. USDA. - *Soil Conservation Service,* Anchorage, Alaska.

Thomson, J.W. 1984. *American arctic lichens. I. The macrolichens.* - Columbia University Press, New York, 1984. Illustrations by Brehmer, B. pp. 163.