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Condition, Potential Recovery Rate, and Productivity of Lichen (*Cladonia* spp.) Ranges in the Finnish Reindeer Management Area

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ABSTRACT. The focus of the work was to investigate dependency between reindeer density and lichen (*Cladonia* spp.) ranges in the Finnish semidomesticated reindeer management area. Secondly, we formed a model on the recovery rate of ungrazed woodland lichen ranges (29 sites) after forest fires to evaluate the potential productivity and time needed for Finnish lichen ranges to recover at optimal production. During 1974–95, 59% of the variation in mean semidomesticated reindeer density (range: 0.7–3.0 reindeer/km^2 of the total land area) among the reindeer herding districts in Finland was explained by the proportion of land area covered by lichen ranges in these districts. Reindeer densities were highest in the districts where lichen ranges covered 20% to 30% of the area. Reindeer density on the total land area did not explain the condition of lichen ranges, but 58% of the condition was explained by the reindeer density on the lichen ranges. A condition level for lichen ranges of 1000 kg dry matter per hectare (d.m./ha) of lichen biomass can be considered adequate to ensure survival of reindeer and continued production of lichen. To maintain this level within the sedentary Finnish grazing system, winter reindeer densities on lichen ranges must remain below 5–7 reindeer/km^2. According to our model, the maximum amount of living lichen in the woodland lichen stand at the climax stage is on average about 7000 kg d.m./ha. The maximum annual yield of lichen (175 kg d.m./ha) is produced by lichen stands that contain 2600–2800 kg d.m./ha of living lichen. Using our model and our 1995–96 data, we calculated that the average lichen biomass on lichen ranges in the Finnish reindeer management districts was 13.0% of this optimum, and the average lichen production was 36% of the possible maximum annual yield. Our model indicates that the Finnish lichen ranges would have to remain ungrazed for an average of 18 years to recover to maximum production levels. However, the average time needed for the lichen ranges to recover to the level of 1000 kg lichen d.m./ha, would be only about 7 years.

Key words: *Rangifer*, reindeer, *Cladonia*, lichen, pastures, condition, recovery, productivity

RÉSUMÉ. Ces travaux portent tout d'abord sur l'étude de la dépendance existant entre la densité du renne et les grands pâturages de lichen (*Cladonia* spp.) dans le secteur finlandais de gestion du renne semi-domestique. Ensuite, on a conçu un modèle en se fondant sur le taux de récupération, après des incendies de forêt, d'étendues naturelles (29 emplacements) de lichen forestier non pâturées, en vue d'évaluer la productivité potentielle et le temps nécessaire aux grands pâturages de lichen finlandais pour récupérer à une production optimale. De 1974 à 1995, 59 p. cent de la variation dans la densité moyenne du renne semi-domestique (fourchette de 0,7 à 3,0 renne/km^2 de superficie totale des terres), parmi les districts où se trouvent les troupeaux de rennes en Finlande, s'expliquaient par la proportion du territoire qui était couvert par des pâturages de lichen dans chaque district. La densité du renne était la plus élevée dans les districts où les pâturages de lichen couvraient de 20 à 30 p. cent du territoire. La densité du renne sur l'ensemble du territoire n'expliquait pas la qualité des pâturages de lichen, mais 58 p. cent de cette qualité s'expliquait par la densité du renne sur les pâturages de lichen. On peut considérer qu'un niveau de qualité de 1000 kg l'hectare de matière sèche (m.s./ha) de biomasse lichénique est suffisant dans les pâturages pour assurer la survie du renne et la production continue de lichen. Afin de maintenir ce niveau au sein du système de pâturage finlandais sédentaire, les densités hivernales du renne sur les grands pâturages ne doivent pas dépasser 5 à 7 renne/km^2. Selon notre modèle, la quantité maximale de lichen vivant dans le peuplement de lichen forestier au stade climax est en moyenne de 7000 kg de m.s./ha. La production annuelle maximale de lichen (175 kg de m.s./ha) vient de peuplements de lichen qui contiennent de 2600 à 2800 kg de m.s./ha de lichen vivant. En nous servant de notre modèle et de nos données recueillies en 1995 et 1996, nous avons calculé que la biomasse lichénique moyenne sur les grands pâturages des districts finlandais de gestion du renne était de 13,0 p. cent de cet optimum, et que la production moyenne de lichen représentait 36 p. cent de la production annuelle maximale possible. Notre modèle révèle que, afin de récupérer à leurs niveaux de production maximaux, les grands pâturages de lichen finlandais ne devraient pas être pâturés pendant une moyenne de 18 ans. La durée moyenne nécessaire aux grands pâturages pour récupérer au niveau de 1000 kg de lichen de m.s./ha ne serait toutefois que de 7 ans.

Mots clés: *Rangifer,* renne, *Cladonia,* lichen, pâturages, qualité, récupération, productivité

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INTRODUCTION

Ranges of lichens (*Cladonia* and *Cetraria* genera) form one of the most important natural winter pasture resources for wild and semidomesticated reindeer (*Rangifer tarandus*) (Alaruikka, 1964; Skuncke, 1969; Skogland, 1975; Andreyev, 1977). Reindeer lichens (*Cladina* spp.) are the highly preferred winter diet of reindeer (Danell et al., 1994), and one reindeer can consume 2–5 kg of lichen in dry matter per day (Holleman et al., 1979), given sufficient availability. However, under special conditions, as in Svalbard, reindeer compensate for the lack of lichens with other food items (Alendal and Byrkjedal, 1974; Adamczewski et al., 1988).

Growth rates for reindeer lichens are generally low (Igoshina, 1939; Ahti, 1957; Kärenlampi, 1970, 1972; Manseau et al., 1996): estimated production is 11% new lichen biomass per year (Kärenlampi and Kytöviita, 1988). It takes around 100 years for lichen stands to achieve the climax stage (Ahti, 1957; Morneau and Payette, 1989), when the growth rate in the top zone equals the rate of death and decomposition in the bottom zone. Dry reindeer lichen mat is also very vulnerable to trampling during the summer season. Thus a sedentary reindeer grazing system with little or no seasonal migration between winter and summer ranges—typical for Finland—is very damaging to lichen ranges.

The quantity and quality of winter ranges can influence body weight, calf production, and mortality of both wild reindeer (Skogland, 1983, 1985, 1986) and semi-domesticated reindeer (Kumpula and Nieminen, 1992; Kojola et al., 1995; Kumpula et al., 1998). The condition of lichen ranges seems still to form one of the most important economic bottlenecks for semidomesticated reindeer management in northern Finland by affecting stock productivity (Kumpula et al., 1998). The growth and productivity of lichen ranges are therefore an essential part of the economic carrying capacity of reindeer rangeland (see Caughley, 1976, 1979; Caughley and Lawton, 1981; Kumpula, 1999). In their modelling work, Moxnes et al. (1998) observed that to calculate the optimal number of reindeer on pasture area with overgrazed lichen ranges, it was essential to know at which biomass level the maximum production of lichens is achieved.

First, we investigated dependency between reindeer density and lichen ranges in the Finnish semidomesticated reindeer management area. Second, we modelled the recovery rate of woodland lichen ranges to evaluate the potential recovery rate and productivity of lichen ranges in the Finnish reindeer management districts. We based the lichen range model on the recovery rate of ungrazed woodland lichen sites after forest fires. To calculate the standing biomass and annual yield of lichens for lichen ranges of different conditions, we also had to evaluate the dependence of lichen stand biomass on lichen stand volume.

FIG. 1. The semidomesticated reindeer management districts (shaded areas) in Finland. Circles show the location of forest fire sample areas outside the management area in 1996–97: Pyhäntä (5 sites), Rokua (9 sites), Kovdor (7 sites), and Rajajooseppi (8 sites).

MATERIALS AND METHODS

Dependency between Reindeer Density and Lichen Ranges

The Finnish semidomesticated reindeer management area consists of 56 reindeer herding districts that vary in area from 487 to 5684 km^2 (Fig. 1). The maximum number of reindeer allowed to be kept during winter in these districts has varied from 500 to 13 000 reindeer; thus, reindeer density has varied between 0.8 and 3.3 reindeer/km^2 (Association of Finnish Reindeer Herding Cooperatives, 1976–96).

The winter pasture resources of the Finnish reindeer management area were investigated in 1995–96, both through fieldwork and by remote sensing (Kumpula et al., 1997; see also Colpaert et al., 1995). Altogether, 5392 homogenous field sites [minimum size = 2 ha] were studied in the field in the whole management area. First, we asked the local reindeer herders to identify the locations of the most important winter range areas in each district. Then topographic maps and satellite images were used to plan survey routes in the field. Along these routes, we studied one field site on each separate lichen-dominated vegetation community, as well as some sites on other vegetation communities. Some of the field site data were then used to map the most important vegetation communities in each area by the supervised maximum likelihood classification of Landsat-5 images (Kumpula et al., 1997). The accuracy of the classification of lichen ranges for the whole management area was 86% when cross-checked against the field site data. The land area (ha) and the quantity of lichen ranges in each district were calculated using ARC/INFO software. According to the classification, the average proportion of lichen-dominated ranges varied between districts from 3% to 52% of the total land area.

Using the field site data, we estimated the average volume (dm^3/m^2) of the lichen stand formed by the four most important lichen species (*Cladina stellaris*, *C. mitis*, *C. rangiferina* and *Cladonia uncialis*) on lichen ranges in each reindeer management district. On average, 28 sites on lichen ranges were studied per district. Only the living part of lichens was considered when classifying and measuring the percentage cover and height of lichens at each field site. According to the field data, the average volume of a lichen stand on lichen ranges varied between districts from 0.6 to 18.6 dm^3/m^2 (mean: 5.4 dm^3/m^2).

For each district, we calculated the mean densities of reindeer winter stock (reindeer/km^2) from 1974 to 1995, both on the total land area and on lichen ranges, using statistics from the Association of Finnish Reindeer Herding Cooperatives (1976–96). First we tested the dependence of mean reindeer density (on total land area) on the proportion of lichen ranges on the land area in the districts. Of the models fitted, nonlinear regression yielded the highest regression coefficient. We then tested the dependence of the average lichen volume on lichen ranges on both reindeer density on land area and reindeer density on lichen ranges, using linear and nonlinear regression models.

A Model for the Recovery Rate of Lichen Ranges

We studied 29 forest fire sites of different ages in the coniferous forest area outside the Finnish reindeer management area in 1996–97. Of these sites, 14 were located in the Rokua and Pyhäntä areas of Finland and 15 in the Rajajooseppi and Kovdor areas of Russia (Fig. 1). All the sites in Russia were located in the northern boreal zone, and those in Finland were in the middle boreal zone. Very few wild or semidomesticated reindeer (or none) have inhabited these areas over the last hundred years.

All the study sites were over two hectares in size and were located in dry or very dry Scots pine (*Pinus sylvestris*) forest types. Possible forest fire sites were first identified by fire scars on the trunks and stumps of the Scots pines. The youngest living pines with fire scars were identified and aged by using increment core samples at 1.3 m height (see Lehtonen and Huttunen, 1996; Lehtonen et al., 1996). Five to eight of the oldest living pines with no fire scars were then aged in the same way, and these latter age estimates were used to determine the age of the forest fire. We expected that the oldest Scots pines were first rooted at each site within three years of the forest fire. The number of internodes between branches in the trunk (one internode is a one-year shoot) was used to estimate the age of younger Scots pines. However, all the forest fire sites on the Finnish side were also dated from the historical records of fires kept by the Finnish Forest and Park Service.

Within each site, we estimated the average percentage cover (%) and the average height (mm) of a lichen stand formed by the four different lichen species (*Cladina stellaris*, *C. mitis*, *C. rangiferina*, and *Cladonia uncialis*). In this article we call these species "reindeer lichens," although *Cl. uncialis* is not taxonomically included in the same group as the other three. Percentage cover and height estimates in a lichen stand were based on the *living part* of lichens only. All estimates at each site were done within five randomly chosen squares (3 m × 3 m). The average volume of the lichen stand (dm^3/m^2) was then calculated for each site, using the average percentage cover and the average height. Regrowth of a reindeer lichen stand after a forest fire was analyzed by fitting and testing several nonlinear regression models to the data.

Calculating Standing Biomass, Potential Recovery Rate, and Productivity of Lichens in a Stand

We evaluated the standing biomass and productivity of lichens in a stand on the basis of 55 sample plots (0.25 m^2) of lichens collected in 1993 and 1995. First, percentage cover and height of the lichen stand formed by "reindeer lichens" were estimated inside the plots. Then lichens were collected and cleaned, dried at room temperature (21˚C) for five days, and weighed. After the air-dried (a.d.) biomass was weighed, the samples were oven-dried for 24 hours at 105˚C, and the dry matter biomass (d.m.) was weighed. However, samples collected from 16 plots in 1993 were not oven-dried, so the d.m. estimates for these samples had to be calculated on the basis of the average weight loss of lichens from a.d. to d.m. biomass in the 1995 samples.

Dependence of the d.m. biomass of lichens on the volume of lichens in a stand was then calculated according to a quadratic regression model. Equation (1) calculated the d.m. biomass of lichens (kg/ha) in a lichen stand by the percentage cover (%) and the height (mm) of lichen cover. Equation (2) used the dependence of d.m. biomass of lichens in a stand on lichen volume and the growth curve of lichen volume after forest fire to calculate the development of a lichen stand as a lichen biomass (kg d.m./ha) after a forest fire. Equation 2 was modified to Equation 3 to calculate the number of years since a lichen stand with a certain biomass had experienced a forest fire. Equations (2) and (3) were then used to evaluate the potential recovery rate and productivity of lichen ranges in the Finnish reindeer management area.

RESULTS

Reindeer Densities and Lichen Ranges in the Finnish Grazing System

According to the fitted regression model (Lorenzian peak), the variation in the mean winter stock density of reindeer on total land area during 1974–95 was 59% explained by the proportion of lichen ranges on the land area within the Finnish reindeer management districts ($R^2 = 0.59$, N = 55, $p < 0.0001$, Fig. 2). When fitting this model, we excluded one exceptional reindeer management district where the proportion of lichen ranges was 52% and the mean winter density of reindeer on land area 2.6 reindeer/km^2. The variation in the condition of lichen ranges was poorly explained by the mean winter stock density of reindeer on total land area. In fact, according to the linear regression model, it seemed, paradoxically, that the higher the mean winter stock density over total land area, the larger the volume of lichen on lichen ranges within the districts ($R^2 = 0.09$, N = 56, y = 1.92x + 2.08, $p = 0.02$).

On the other hand, condition of lichen ranges was explained relatively well by the mean winter stock density of reindeer on lichen ranges over the past 20 years. The model that best fit the data was the sigmoidal decay model (Y-axis intercept = the volume of lichens) representating an ungrazed climax-stage lichen stand (78 dm^3/m^2). When we eliminated three outliers from the data, this regression model explained 58% of the variation in the volume of lichens on lichen ranges between the districts ($R^2 = 0.58$, N = 53, $p < 0.0001$) in terms of the mean winter stock density of reindeer on lichen ranges (Fig. 3).

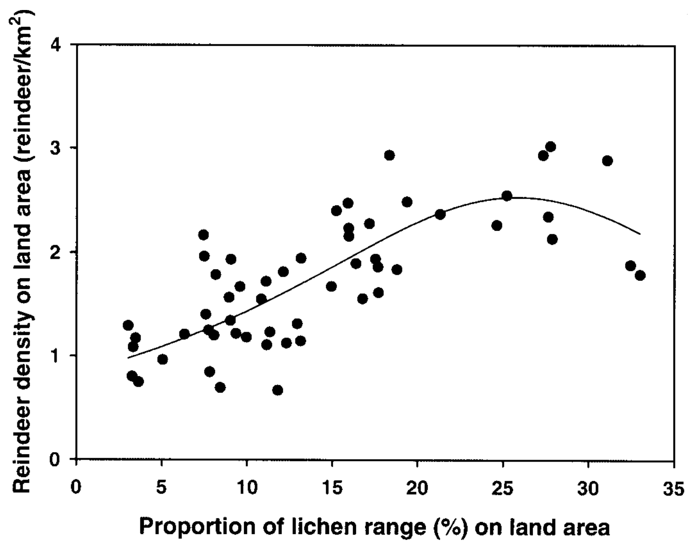

FIG. 2. The dependence of the mean density of semidomesticated reindeer in Finland (measured on total land area in winter, 1974–95) on the proportion (%) of lichen ranges on the land area ($R^2 = 0.59$, N = 55, y = 2.54/(1+((x-25.82)/18.10)^2), $p < 0.0001$).

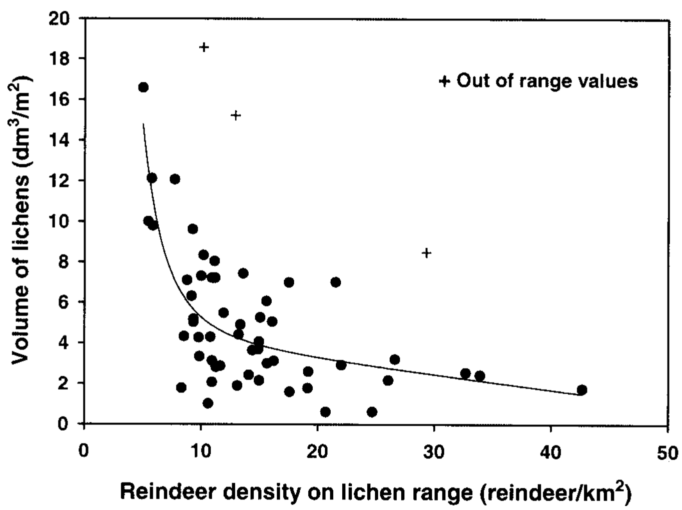

FIG. 3. The dependence of lichen range condition (volume of lichens, dm^3/m^2) on the mean density of semidomesticated reindeer on lichen ranges, measured in winter 1974–95 in Finland ($R^2 = 0.58$, N = 53, y = 4.60 + 0.58·(73.86-x)/(0.58 + (x/3.37)^3) -0.07x, $p < 0.0001$).

Recovery of a Lichen Stand after Forest Fire

The increases in the coverage, height, and volume of reindeer lichens in a lichen stand after forest fire best follow asymmetric sigmoid curves (Fig. 4). Eighty years after a fire, the coverage of a lichen stand is roughly 90% and its height is 80 mm, which means 70 dm^3 of lichen/m^2.

Standing Biomass, Potential Recovery Rate and Productivity of Lichen Ranges in Finland

The mean weight loss of reindeer lichens from a.d. to d.m. biomass was 11.26% (SD = 3.114, SE = 0.50, N = 39). Biomass (d.m.) of reindeer lichen was significantly dependent on lichen volume ($R^2 = 0.80$, N = 55, $p < 0.0001$, Fig. 5). This dependence was the basis of Equation (1), which calculates d.m. lichen biomass per hectare for lichen stands from estimates of the percentage cover (%) and height (mm) of reindeer lichens in the stand. According to Kumpula et al. (1997) and Equation (1), lichen biomass on lichen ranges in the Finnish reindeer management districts ranged from 38 to 1272 kg d.m./ha (mean: 349 kg d.m./ha).

$$LB_{d.m.} = (0.6134 \cdot LC \cdot LH) + (0.000038075 \cdot LC^2 \cdot LH^2) \quad (1)$$

where $LB_{d.m.}$ is the dry matter biomass of reindeer lichens in a stand (kg d.m./ha); LC is the average percentage cover (%) of reindeer lichens in a stand; and LH is the average height (mm) of reindeer lichens in a stand.

By fitting Equation (1) to the asymmetric sigmoid growth curve of lichen volume (see Fig. 4), Equation (2)

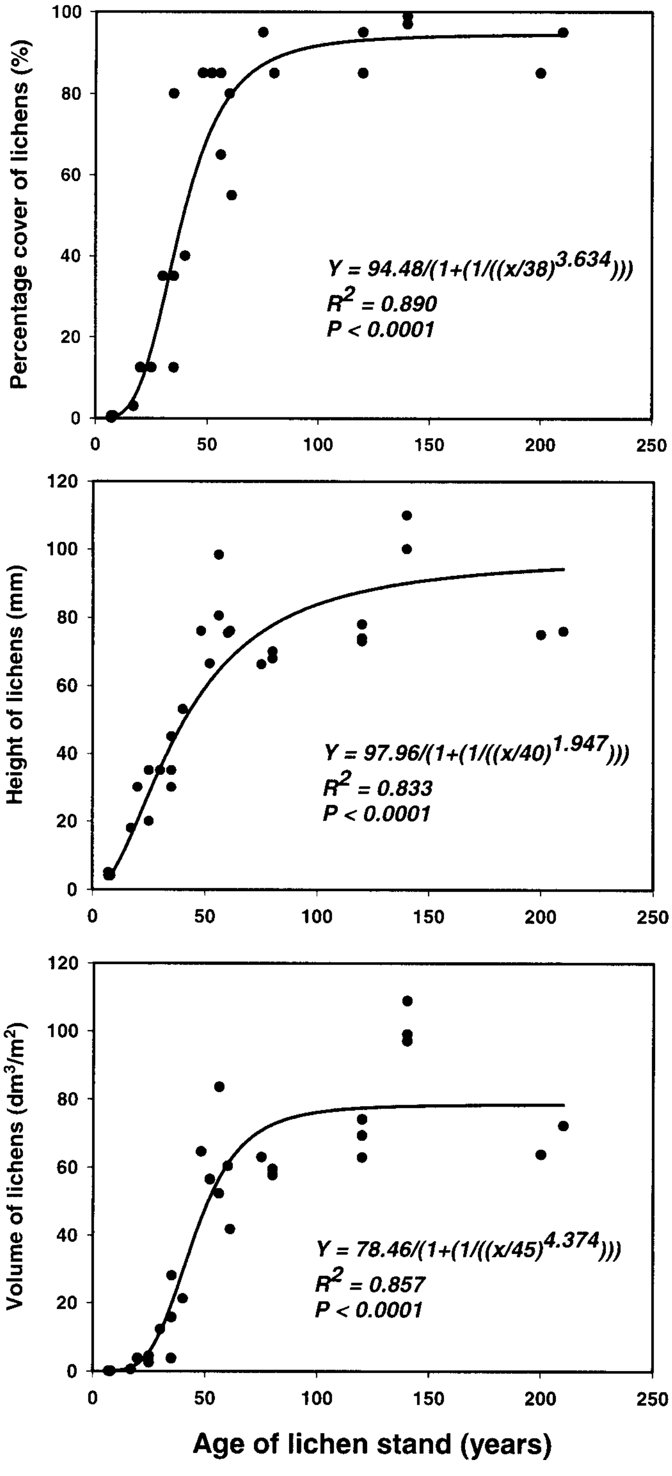

FIG. 4. The growth curves of reindeer lichens fitted to the data representing percentage cover (%), height (mm), and volumetric (dm^3/m^2) growth after forest fire of lichen stands in dry to very dry pine forests.

could be used to calculate the biomass of reindeer lichens (kg d.m./ha) in a stand in each year "n" after a forest fire.

$$LB_{yn} = [B / (1+(1/ (LA_{yn} / 45)^{\alpha}))] + [C / (1+(1 / (LA_{yn} / 45)^{\alpha}))^2] \quad (2)$$

where LB_{yn} is the dry matter biomass of reindeer lichens (kg d.m./ha) in the n^{th} year after forest fire in a lichen stand;

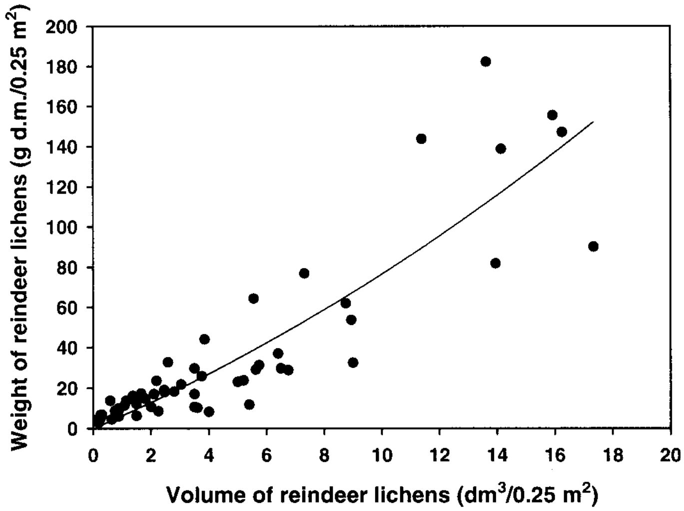

FIG. 5. The quadratic dependence between the biomass of reindeer lichens (g d.m./0.25 m^2) and the volume of lichens (dm^3/0.25 m^2). Volume was calculated from the percentage cover (%) and height (mm) of living lichens in a stand ($R^2 = 0.80$, $N = 55$, $y = 6.13x + 0.15x^2$, $p < 0.0001$).

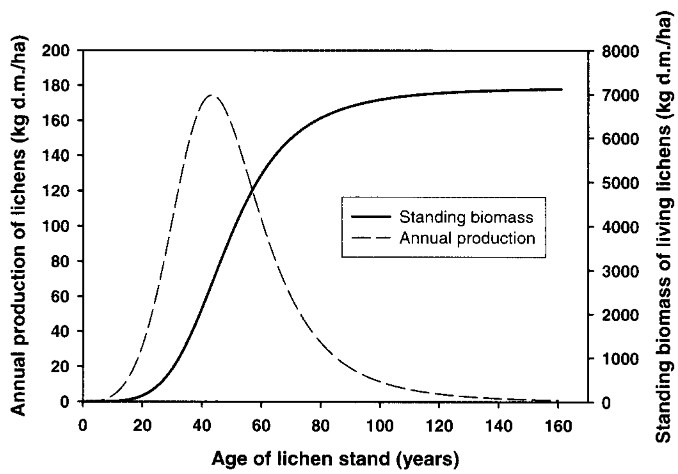

FIG. 6. The development and productivity of a reindeer lichen stand as a living lichen biomass (kg d.m./ha) after forest fire in dry and very dry pine forests.

LA_{yn} is the age of a lichen stand (years) after forest fire (in n^{th} year); $B = 4812.7364$; $C = 2343.8862$, and $\alpha = 4.374$.

Finally, Equation (3) was formed from Equation (2) to calculate the years passed since a forest fire at a lichen stand with a certain lichen biomass. This equation could be used to compare the state of grazed lichen stands in the Finnish reindeer management districts to the developmental stage of an ungrazed lichen stand.

$$LA_{yn} = 45 / \{[(B-2 \cdot LB_{yn})/(2 \cdot LB_{yn})] + [(B/(2 \cdot LB_{yn}))^2 + C/LB_{yn}]^{0.5}\}^{1/\alpha} \quad (3)$$

For explanations, see Equation 2.

According to the growth model of lichen biomass based on Equation (2), the maximum amount of living lichen in woodland lichen regions can average somewhat more than 7000 kg d.m./ha in a climax-stage lichen stand (Fig. 6).

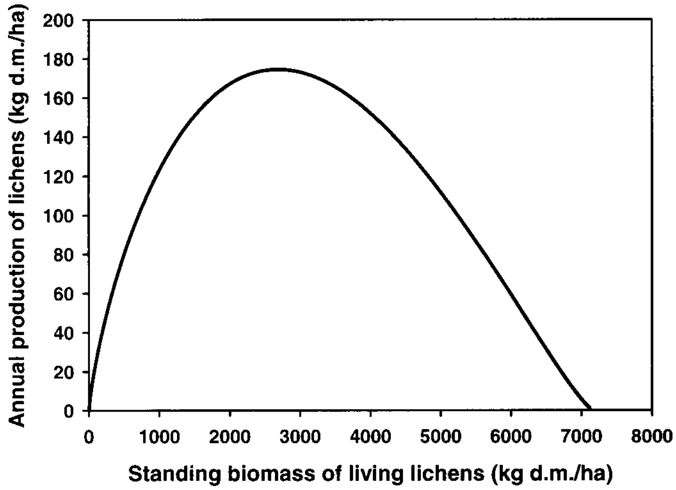

FIG. 7. The annual production of reindeer lichens in a stand at various succession levels after forest fire in dry and very dry pine forests. Standing crop and productivity of lichens were calculated as a living lichen biomass (kg d.m./ha).

The maximum annual yield of new lichen (about 175 kg d.m./ha) is produced by the lichen stands that are 43–44 years old and contain 2600–2800 kg d.m./ha of living lichen (Fig. 7).

According to our model, the average biomass of lichen in lichen ranges within the Finnish reindeer management districts was only around 13% of this optimum biomass, and the average annual productivity around 36% of the maximum. This indicates that Finnish lichen ranges would need to be totally out of grazing from 9 to 28 years (on average 18 years) to recover to the level that gives the highest yield of new lichen per year. Because the model is based on the recovery and growth of ungrazed lichen stands after forest fire, the time needed for grazed lichen ranges to recover could be even longer. However, the average time needed for the lichen ranges to recover to a condition level adequate to sustain lichen production and support winter nutritional needs of reindeer (1000 kg lichen d.m./ha) would be only about 7 years.

DISCUSSION

To interpret the dependency between reindeer densities and lichen ranges in Finland, we must consider the effects on pastures of other land uses, especially forestry. However, the fact that some clear dependence between reindeer densities and lichen ranges was found indicates that reindeer and lichen ranges still dominate this interaction field in Finland.

The proportion of lichen ranges on total pasture land in Finland seems to have greatly affected the long-term densities of semidomesticated reindeer grazing on that land from 1974–95. The optimal portion of total pasture land occupied by lichen ranges lies between 20% and 30%. When the percentage of lichen ranges has been smaller, the mean reindeer density on natural pastures has also been lower. In contrast, when this percentage has risen above 30%, the number of reindeer on natural pastures has decreased, probably because other types of pasture were lacking.

The average animal densities in the Finnish semidomesticated reindeer ranges are much higher than animal densities reported, for example, in the wild reindeer areas of Norway (Reimers et al., 1983; Skogland, 1983). Skogland (1983) reported that the most heavily grazed winter ranges in Norway were located in wild reindeer regions where animal densities were, or had been, over 20 reindeer/km^2 lichen range. Although those regions differed in topography and vegetation from northern Finland, their lichen pastures contained a comparable lichen biomass (calculated from Skogland, 1983). However, according to Skogland (1983), wild reindeer densities were usually much lower (< 1.0 reindeer/km^2 and < 5.0 reindeer/km^2 lichen range) and lichen biomass was several times as high as in the winter ranges in best condition in Finland.

Kumpula et al. (1997) have estimated that, to support the nutritional needs of reindeer relatively well during winter on the most important lichen ranges, lichens should be 30 mm high (volume = 15 d.m.^{3}/m^2) and cover at least 50% of the lichen ranges. According to Equation (1), this means a biomass of approximately 1000 kg lichen d.m./ha. This relationship between the reindeer density on lichen ranges and the condition of the lichen ranges (Fig. 3) suggests that to keep lichen ranges in the Finnish herding system at such a condition level, the number of reindeer on lichen ranges in winter should not exceed 5–7 reindeer/km^2.

This means that, in this kind of grazing system, 16–20 ha of lichen pasture per reindeer (winter stock) are needed. However, Skuncke (1969) has concluded that with a good pasture rotation system, 8–10 ha lichen pasture per animal would suffice for reindeer winter nutrition. Earlier estimates in Finland (Anon., 1914; Alaruikka, 1964) had indicated that with a reasonable pasture rotation system, 10–15 ha of moderate-condition lichen pasture per animal would satisfy the winter nutritional needs of reindeer while preserving the lichen pastures in an unchanged condition.

The shape of the correlation that we found between reindeer density on a lichen range and the condition of the lichen range was quite similar to that reported by Helle et al. (1990). It seems that when reindeer density on lichen ranges increases from very few to 5–7 animals per km^2, the condition of lichen ranges deteriorates rapidly. After that, an increasing animal density has little effect on the condition of lichen ranges because scanty lichen ranges are difficult to graze, and reindeer (or herders) must compensate for the lack of lichens with other food items. Thus, the first step toward improving the condition of lichen ranges in those Finnish reindeer management districts where such ranges are still very important winter pasture resources should be to reduce the density of reindeer (winter stock) to less than 10 animals/km^2. In addition, the whole pasture rotation system should be developed to protect lichen ranges more effectively from reindeer grazing and trampling from early spring to late fall. And finally, lichen ranges should be protected effectively from other land uses.

Various methods have been used to determine the growth rate of reindeer lichens. One of the oldest ways is to measure the height increase of lichens by dividing the height of the podetium by the number of joints on the podetium (Igoshina, 1939; Andreyev, 1954; Scotter, 1963). Using this method, researchers have estimated the growth rate of individual lichens as 2.0–4.0 mm/yr (Igoshina, 1939), 2.5–6.0 mm/yr (Scotter, 1963), and 2.8–5.1 mm/yr (Skuncke, 1969). This method has been criticized (Kärenlampi, 1970) because it is not useful in an overgrazed area, and it does not allow separate measurements of growth rate for lichens of different ages. Our results show that the maximum annual thickness increase in the living part of the whole lichen stand is only 1.5–1.6 mm. Clearly the height increase in the living part of the whole lichen stand does not correspond to the height increase measured on individual thalli.

The amount of lichen in a climax-stage stand and the annual yields of lichen stands at various succession levels, are difficult to quantify because of the wide variety of methods used to estimate the biomass of lichen stands. In the Finnish literature, it has been estimated that the highest annual yield of lichens (120–160 kg d.m./ha) is achieved from lichen stands that contain lichen biomass of 600–1200 kg d.m./ha (Kärenlampi, 1972; see Helle et al., 1990). According to Kärenlampi (1972), a climax-stage lichen stand weighs just over 3000 kg d.m./ha. However, Norwegian researchers have estimated the weight of a climax-stage lichen stand 5–6 cm high that contains some higher plants at more than 11 000 kg d.m./ha (Gaare and Skogland, 1980). Väre et al. (1996) studied the vegetation and soil communities in protected ungrazed and grazed sites in dry and very dry soils in the Finnish reindeer management area. They measured, on average, nearly 8000 kg d.m./ha of lichen (total amount) at ungrazed sites. Arseneault et al. (1997) compared the lichen biomass of various-aged forest fire sites in the caribou areas of Quebec, Canada. They found that on stands over 90 years old, lichen (total amount) averages over 8000 kg d.m./ha.

On the whole, the succession rate of a lichen stand we found was very similar to that presented by Ahti (1957), Morneau and Payette (1989), and Thomas et al. (1996).

Our model gives a good overview of the development and productivity of lichen stands in various development stages. Development and productivity in a grazed lichen stand after (or during) grazing may differ from development and productivity in ungrazed lichen stands after a forest fire. This is because the growth of lichens occurs on the top zone, which is most easily available to reindeer grazing. However, a comparison of predictions from our model to real measurements of lichen growth indicated that our results could be applied quite reliably to the recovery rate of grazed woodland lichen stands after grazing. Kärenlampi and Kytöviita (1988) studied the recovery rate of lichens after heavy grazing in fenced sites built in 1968 in a subarctic mountain birch forest zone of Finland. They measured average lichen biomass inside these fences twice, in 1972 and in 1987. When we substituted their initial lichen biomass in Equations (2) and (3), our model predicted that 12.5 years would be needed to achieve their final lichen biomass. The actual time was roughly 15 years.

Although the recovery of lichen ranges to maximum productivity seems very difficult, and may not even be feasible within the main part of the Finnish semidomesticated reindeer management area, keeping the most important lichen ranges in adequate condition is essential for ecologically and economically stable reindeer husbandry in the future. If this desired condition level is 1000 kg d.m. lichen/ha, then recovery time would be much shorter than that required for recovery to optimum productivity level.

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