A review of reindeer lichen (Cladonia subgenus Cladina) linear growth rates

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Abstract: Cladonia subgenus Cladina (the reindeer lichens) can be a dominant part of terrestrial ecosystems worldwide. They are particularly abundant in arctic-alpine and boreal regions, where they are a primary food source for woodland caribou/reindeer in winter months. Determining the growth rates of reindeer lichen is important for understanding and managing lichen regeneration following disturbances such as timber harvesting, mining, grazing, and wildfire. Regeneration and rehabilitation rates can be calculated with greater accuracy when growth rates are well understood. We provide a summary of 17 studies from 6 countries that determined the linear growth rates of three reindeer lichen groups, Cladonia arbuscula/mitis (mean = 4.7 mm/yr.), C. rangiferina/ C. stygia (mean = 5.1 mm/yr.), and C. stellaris (mean = 4.8 mm/yr.). We use linear growth rates as a proxy for overall growth and biomass. Variables found to influence lichen growth rates are also discussed, which include light, moisture, temperature, air pollution, acid rain, precipitation, snow accumulation, substrate, age of individuals, and type of disturbance. These results can assist land managers in developing more accurate strategies for restoring lichens in disturbed areas.

Key words: Critical caribou habitat; regeneration; rehabilitation; sustainable forest management; transplantation.

Introduction

Cladonia subgenus Cladina (the reindeer lichens) is a group of fruticose lichens that are richly branched and lack an outer cortex (Brodo et al., 2001; Smith et al., 2009). They are typically terricolous and often form large mats that can become the dominant ground cover in boreal forest stands with open canopies (McMullin et al., 2011). Reindeer lichens are the primary winter food source for woodland caribou (Rangifer tarandus caribou; Bergerud & Nolan, 1970; Eriksson et al., 1981; Newmaster et al., 2013; Thompson et al., 2015). They are also an important component of the winter diet of reindeer (Rangifer tarandus) in Russia (Andreev, 1977) and Scandinavia (Skogland, 1984; Kumpula, 2001), where reindeer have an important economic and cultural role as livestock in northern regions (Sandström, 2003;
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sumption models (e.g., Kumpula, 2001) means habitat supply and population dynamics for caribou populations can be better predicted. Moreover, in instances where lichen is harvested for restoration, or other purposes, there is uncertainty about what amount constitutes a sustainable harvest (Duncan, 2015; Rapai et al., 2017). Determining growth rates will provide a better understanding of how long the harvested areas will take to recover, which is an important part in calculating how much can be removed for restoration.

The aim of our study is to review and summarize existing knowledge about the linear growth rates of C. subgenus Cladina, specifically for Cladonia arbuscula, C. mitis, C. rangiferina, C. stellaris, and C. stygia. Our objectives were to locate as many studies as possible that calculate linear growth rates and then explore the reasons for any variation. Knowledge of the growth rates of these species will be valuable to forest managers, herders, and restoration ecologists interested in predicting the rate of lichen regeneration. Given the importance of this subgenus to the imperilled woodland caribou in North America, its declining biomass in northern latitudes globally, and the need for effective habitat restoration strategies, this review of linear growth rates is timely. In fact, our review is a direct response to several inquiries that we have received by land managers seeking a simplified answer for how fast C. subgenus Cladina grows for restoration planning in disturbed caribou habitats.

Methods
We performed a literature review of studies that have calculated the linear growth rates of Cladonia arbuscula, C. mitis (Fig. 1B), C. rangiferina (Fig. 1A), C. stellaris (Fig. 1C), and C. stygia (Fig. 1D), which are members of the subgenus Cladina. These species were selected because they are the most abundant and widespread species available as winter forage for wood-
land caribou in North America (McMullin et al., 2011; Newmaster et al., 2013; Thompson et al., 2015) and reindeer in Scandinavia and Russia (Andreev, 1977; Eriksson et al., 1981; Sandström, 2003; Roturier, 2009). *Cladonia rangiferina* and *C. stygia* were grouped together because they were conspecific in the past (Ahti & Hyvönen, 1985) and they are similar in size (McMullin et al., 2011; Brodo et al., 2001). We also grouped *C. arbuscula* and *C. mitis* for the same reasons. Taxonomically, they are difficult to separate (Piercy-Normore et al., 2010) and they are similar in size (Pagau, 1968; Prince, 1974; Brodo et al., 2001). Our search was initiated on several databases (i.e., Recent Literature on Lichens, Scopus, Google Scholar, Web of Science, JSTOR, and BioOne). Our search terms were “Lichen growth” and “Cladonia growth”. Once relevant articles were located, we used the references they cited to locate additional articles. All articles that included a new calculation for annual linear growth rate for any of the species in *C. subgenus Cladina* mentioned above were included in our summary. All but one of the studies we included (presented in Table 1) calculated linear growth following the method developed by Andreev (1954): length of living podetium divided by the number of nodes. Holt and Bench (2008) tested this method by comparing it to another and found it to be reliable. The study that used a different method cut the top 1/3 or 2/3 of the podetia off using scissors to simulate grazing affects, but they used the same method otherwise to calculate linear growth (Barashkova, 1968).

Figure 1. Common reindeer lichen. A) *Cladonia rangiferina*, scale = 0.4 cm. B) *Cladonia stellaris*, scale = 1 cm. C) *Cladonia mitis*, scale = 1.2 cm. D) *Cladonia stygia*, scale = 0.6 cm.
Results
The measurements we recorded are the annual average linear growth-rates calculated in previous studies (Table 1). We then averaged linear growth rates for each of the three species groups, *C. arbuscula/mitis* (mean = 4.7 mm/yr.), *C. rangiferina/C. stygia* (mean = 5.1 mm/yr.), and *C. stellaris* (mean = 4.8 mm/yr.). The lowest mean annual growth rates were *C. arbuscula/mitis* (mean = 3.3 mm/yr.), *C. rangiferina/C. stygia* (mean = 3.9 mm/yr.), and *C. stellaris* (mean = 3.3 mm/yr.). The highest mean annual growth rates were *C. arbuscula/mitis* (mean = 6.0 mm/yr.), *C. rangiferina/C. stygia* (mean = 6.5 mm/yr.), and *C. stellaris* (mean = 6.5 mm/yr.). The combined annual average linear growth rate for all the species groups from all previous studies is 4.9 mm/yr.

Discussion
The mean annual linear growth-rate determined for the 17 studies reviewed were similar (4.7 to 5.1 mm/yr.). However, since the linear growth rate range is 3.3-6.5 mm/yr., more precise estimates may be preferred. An understanding of the variables that limit and promote lichen growth is then required.

Table 1. Mean annual growth rates (mm/yr) of *Cladonia arbuscula/mitis*, *C. rangiferina/stygia*, and *C. stellaris* from a wide variety of global localities

| Cladonia arbuscula/mitis | Cladonia rangiferina/stygia | Cladonia stellaris | Location | Reference |
|--------------------------|----------------------------|--------------------|----------|----------|
| -                        | 5.5                        | 5                  | Russia - Open Forest | Andreev, 1954 |
| -                        | 3.9                        | 3.3                | Russia - Tundra | Andreev, 1954 |
| -                        | 4.8                        | 6.5                | Newfoundland | Ahti, 1957 |
| -                        | 5.0                        | -                  | Russia | Barashkova, 1961 |
| 3.6                      | 4.1                        | 3.4                | Northwest Territories | Scotter, 1963 |
| -                        | 4.9                        | 4.1                | Northern Saskatchewan | Scotter, 1964 |
| -                        | 5.1                        | -                  | Russia | Barashkova, 1968 |
| -                        | 5.9                        | -                  | Russia | Barashkova, 1968 |
| 5.8                      | 5.6                        | 5.5                | Alaska - *Picea* Forest | Pegau, 1968 |
| 4.6                      | 5.1                        | 5.3                | Alaska - Tundra | Pegau, 1968 |
| 5.2                      | -                          | -                  | Wisconsin – *Picea* Barrens | Lechowicz & Adams, 1973 |
| 4.6                      | -                          | -                  | Scotland | Prince, 1974 |
| -                        | 5.3                        | -                  | Antarctic Region (South Georgia) | Lindsay, 1975 |
| 6.0                      | 5.9                        | -                  | Finland – southern | Vasander, 1981 |
| 3.3                      | 4.1                        | -                  | Finland - northeast | Helle *et al.*, 1983 |
| -                        | -                          | 5.6                | Northern Québec and Labrador | Boudreau & Payette, 2004 |
| -                        | 6.5                        | -                  | Alaska | Holt & Bench, 2008 |

Mean = 4.7 5.1 4.8
Environmental conditions influence lichen growth rates: those in more favourable habitats grow faster than those in less favourable ones. Lichen growth rates have been shown to be positively correlated with moisture and light, specifically the amount of light received while wet (Harris & Kershaw, 1971; Palmqvist & Sundberg, 2000; Sulyma & Coxson, 2001; Jonsson Čabrajič et al., 2010). This is because lichen metabolism is regulated by water availability, both from precipitation and relative humidity (Armstrong, 1974; Lange et al., 1986; Rundel, 1988; Green et al., 1994). Growth rates are negatively correlated with air pollution (Henderson, 2000; McMullin et al., 2016; Nash & Gries, 1995), acid rain (Lechowicz, 1982, 1987; Scott & Hutchinson, 1987), and the accumulation of snow (Bidussi et al., 2016). Species specific lichen growth is also influenced by elevation (Lindsay, 1975; Berryman & McCune, 2006), substrate (Brodo, 1973; Esseen, 1981; Tolpysheva & Timofeeva, 2008), and temperature (Gaio-Oliveira et al., 2004).

Lichen growth rates also vary within individuals, which suggests that fine scale growth rate measurements should be calculated using the average of several lobes or branches (Hale, 1970; Armstrong, 1993). Reindeer lichen growth is also influenced by mat thickness, over-all growth rate is greater in younger mats, and the basal area begins to decay when they reach their maximum size (Andreev, 1954; Kärenlampi, 1970; Richardson, 1975; Sveinbjörnsson, 1987; Boudreau & Payette, 2004). The type and amount of disturbance also influences growth rates. For example, Barashkova (1968) simulated the effects of grazing and measured growth-rates when 1/3 of the length of the podetia of C. rangiferina were removed and the mean growth was greater (5.9 mm/yr.) than when 2/3 of the length of the podetia were removed (5.1 mm/yr.). Their result is likely because the photobiont in reindeer lichens is concentrated near the tips, so productivity is greater in that region (Gaio-Oliveira et al., 2006). Consequently, lightly browsed lichens grow faster than those that are heavily browsed (Gaio-Oliveira et al., 2006). The substrate is also important for the growth of reindeer lichens (Rapai et al., 2018). Tolpysheva and Timofeeva (2008) show that C. mitis and C. rangiferina have greater growth on soil than on wood. In addition, Kershaw and Rouse (1971) found that the length and the diameter of C. rangiferina and C. stellaris podetia are positively correlated with the humidity of the soil.

In summary, the over-all growth-rates of reindeer lichen are dependent on a wide variety of variables. In general, growth is positively correlated with light, moisture (i.e., precipitation and relative humidity, both in the soil and the atmosphere), younger individuals, and soil as a substrate. These results are consistent with a modelling study in northern Scandinavia that found the overall growth of C. stellaris (measured in dry weight) is positively correlated with light, humidity, and precipitation (Jonsson Čabrajič et al., 2010). Another modelling study in Sweden showed that the biomass of C. subgenus Cladina is positively correlated with summer precipitation and negatively correlated with the amount of canopy cover (Uboni et al., 2019). All of these conclusions showed that the variables affecting lichen growth are similar. As a result, precise estimates of lichen growth need to be calculated for individual sites, since annual growth rates can differ depending on variation in habitat conditions.

In North America, woodland caribou populations are declining (Bergerud, 1974; Festa-Bianchet et al., 2011; COSEWIC, 2014a,b), and reindeer lichens are an important part of their critical winter diet (Newmaster et al., 2013; Thompson et al., 2015). Although the precise causes of woodland caribou decline vary among populations (Vors et al., 2007; Festa-Bianchet et al., 2011), a reliable winter food source is essential for these animals. In Russia and Scandi-
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*Manuscript recieved 3 February 2019
revision accepted 27 July 2020
manuscript published 12 August 2020*
