# POPULATION GROWTH IN *CLADONIA STELLARIS* (OPIZ.) POUZ. AND VEZDA

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## SUMMARY

Populations of *Cladonia stellaris* in burnt areas of the northern Ontario clay belt were observed photographically from 1968 to 1974. Population growth is logistic with a typical convergent standing crop of 500 g per m², reached about 30 years after establishment. There is considerable oscillation about the convergent standing crops with time, as well as environmentally determined variations between crops at different sites. Rates of growth are strongly correlated with successional maturity, so that time of establishment may influence the subsequent population size. Final carrying capacity is apparently determined by a complex of factors effective through their influence on light and water availability and by direct physical interference of other species. Ericaceous shrubs and *Pleurozium schreberi* seem to be the most influential. *Cladonia stellaris* does not appear until 25 years after fire, but rapidly becomes the most abundant lichen by means of clonal growth. Clones develop by three kinds of budding and subsequently undergo fusion and fission as growth proceeds. Longer range dispersal is by means of small thallus fragments and is evidently highly efficient as newly colonized areas exhibit widespread potential distributions.

## INTRODUCTION

The ecology of *Cladonia stellaris* (Opiz.) Pouz. & Vezda (= *C. alpestris* (L.) Harm.) is better understood than that of most other lichens. Its occurrence in northern forests has been described by Hustitch (1951), Fraser (1956), Ahti (1959, 1964), Ahti and Hepburn (1967), Lambert and Maycock (1968) and Lechowicz and Adams (1974a); all agree that the species is characteristic of dry sandy areas and that its vigour declines with increasing shade. The water relations of *C. stellaris* have been shown to exert a strong influence on the growth and distribution of individual podetia (Kershaw and Rouse, 1971a, b). As in many other lichens, (Harris, 1971; Kershaw and Harris, 1971a, b; Lechowicz and Adams, 1974b) the availability of light and water appear to determine physiological activity. Andreev (1954), Ahti (1959), Scotter (1963) and Karenlampi (1970) have calculated annual growth rates of podetia at various sites, but population growth in *C. stellaris* has not been studied. This paper is concerned with the mode and regulation of population growth in the species.

Birth and death in *C. stellaris* occur in a variety of ways. Thomson (1967) states that most vegetative reproduction in *Cladonia* is by fragmentation of the thallus. This certainly accounts for almost all long range and some short range dispersal and reproduction in *C. stellaris*, but the species also reproduces in three other ways: by dichotomous division at the apex and eventual separation after subsequent growth; by vertical growth from the ends of lateral branches near the base of the podetia; and by vertical growth from the lateral branches of fallen or trampled podetia. These three types of reproduction give rise to more or less contiguous clones. In this paper the clones referred

to are of this type rather than dispersed clones arising from fragments distributed by wind or animals from a parent clone. Scotter (1963) implies that death of individuals may occur from old age after from 30 to well over 100 years. It may also occur from trampling, rupture by frost churning or by the upward growth of ericaceous shoots, removal by grazing or by small mammal activity, increasing shade by shrubs and trees, or from overgrowth by competitors such as *Epigaea repens* L. and *Pleurozium schreberi* (Brid.) Mitt. Changes in population size and composition are the net result of these processes. Harper and White (1974) note the need for distinguishing the roles of 'genets' (clones) and 'ramets' (their components) in population growth. Because of the modes of reproduction in *Cladonia stellaris* this kind of attention is necessary to understand how population growth occurs. This, the form of the overall population growth in mass and in numbers of podetia (ramets), and the nature of regulation of this growth by ecological factors were the initial concerns of this investigation.

## STUDY AREA

The northern Ontario clay belt provides an excellent opportunity for the study of *Cladonia stellaris*, which is a successful plant in the area; it appears approximately 25 years after fire and increases rapidly to become the most abundant lichen in jack pine (*Pinus banksiana* Lamb.) stands 45 years of age or older. It typifies the 'late stage' of succession described by Shafi and Yarranton (1973b). If it is assumed that similar sites burned at different times fall into a successional sequence, information about the population dynamics of *Cladonia stellaris* about the successional process and about the relations between the two can be obtained simultaneously. An added advantage of the area is that Beasleigh and Yarranton (1974) and Yarranton and Yarranton (1974) have examined the population dynamics of *Equisetum sylvaticum* L. and *Pinus banksiana* there providing a basis for comparison with *Cladonia stellaris*.

The sampled sites lie from 20 to 60 m (30 to 100 km) east of Cochrane in the northern clay belt section of the boreal forest (Rowe, 1959). Most of the area is covered by glacial surface deposits, about 90% of which are clay which was laid down in postglacial lake Barlow-Ojibway; the remaining 10% are sand and there are a few granite outcrops. The sites examined are all located on overdrained sand deposits (Table 1) but the two

Table 1. *Experimental areas*

| Township | Location | Year burned | Dominant tree | Approximate living and dead tree density per acre |
|---|---|---|---|---|
| Dempsay | 49°09′N 80°38′W | 1941 | *Pinus banksiana* | 2000–3000 |
| Hepburn | 49°02′N 79°41′W | 1934 | *P. banksiana* | 2000–3000 |
| Dempsay | 49°04′N 80°36′W | 1927 | *P. banksiana* | 2000–3000 |
| Freele | 49°05′N 80°25′W | 1915 | *P. banksiana* | 6000 |
| Abbotsford | 49°06′N 79°44′W | 1912 | *P. banksiana* | 4500 |
| Potter | 49°23′N 80°45′W | ? | *Picea mariana* | 600 (clumped) |

Dempsay sites are less elevated compared to their immediate surroundings, and presumably less severely overdrained than the others. Nearby lakes also indicate a water table closer to the surface at these sites. Soils are nutrient poor with a thin (2 cm) humus layer above several cm of leached sand.

Long cold winters and short warm summers characterize the climate of the area

(Chapman, 1953). Summer drought appears to be an important factor at sandy sites (Yarranton and Yarranton, 1974). According to MacLean and Bedell (1955) all parts of the clay belt have been burnt within the last 140 years and periods of extreme fire risk recur every 30 years or so. The fire risk is highest at dry sites.

The vegetation of the clay belt has been described by MacLean and Bedell (1955), Baldwin (1958) and Shafi and Yarranton (1973a, b). Sandy sites are dominated by jack pine with some black spruce (*Picea mariana* (Mill.) BSP in places. Such sites support a layer of ericaceous shrubs including *Vaccinium angustifolium* Ait., *V. myrtilloides* Michx., *Kalmia angustifolia* L. and *Ledum groenlandicum* Oeder. Common on the ground are *Epigaea repens, Pleurozium schreberi* and many *Cladonia* species of which *C. stellaris* is the most conspicuous. Potter is the only one of the sampled sites where black spruce is dominant; at the other sites less than 5% of the trees are black spruces. Vegetation of the lower layers is very similar from site to site with the exception of the abundance of *Ledum groenlandicum*. This species is abundant at Abbotsford and common at Freele, but less frequent at the other sites.

## METHODS

In May 1968 ten 1 × 1 m quadrats were marked out in each of the burnt areas listed in Table 1. The quadrats contained various quantities of *Cladonia stellaris* representing the entire range of local frequencies present at that time. All sixty plots were photographed at intervals between 23 May and 7 Sept. as follows: in 1968 five times; in 1969 three times; in 1970 five times; in 1971 three times; in 1972 three times; in 1973 and 1974 once each. At least one set of photographs was taken at the end of May each year, before the spring outburst of leaf growth in the shrub layer. At this time the podetia are most easily seen. On each occasion coloured slides were taken from vertically above the plots by means of a specially designed stand and wide angle lens; sometimes oblique photographs were also taken. Projection of the slides enabled counting of individuals in the plots and measurement of their diameters. Attempts were also made to trace individuals from year to year.

In 1972 at least 100 podetia were collected from each site and their dry weights, diameters and heights determined. Entire clones were collected to ensure representative sampling. In 1974 the diameters of, and numbers of individuals in, at least 100 clones were determined in the field at each of the following sites: Potter, Dempsay 1941 and 1927, and Freele 1915. The Hepburn 1934 and Abbotsford 1912 sites were inaccessible in 1974. The 100 or more clones sampled at each site constituted entire populations within areas centred on fixed points.

## RESULTS

The podetia are subject to disturbance during the summer by the growth of higher plants and by animal activity; in one photograph evidence of the crushing of a podetium by a moose foot is quite clear. However, summer disturbance is insignificant compared to that occurring between September and May, when whole clones are churned. This churning presumably occurs in early spring when freezing and thawing alternate. It prevents the tracing of many individual podetia from year to year by photography.

Some small clones or parts of clones, in sparsely populated plots could be followed closely from 1968 to 1973. Outline traces of podetia taken directly from the projected

slides are seen in Figs. 1–3. Fig. 1 covers the period from 27 to 32 years after fire when population growth is most rapid; it shows the production of six individuals from a single large podetium. Fig. 2 from Dempsay 1927 (41–46 years after fire) shows the considerable annual fluctuation frequently encountered; in this clone a good deal of budding takes place, but three of the new individuals are lost after 1970; churning is evident. These processes are even more pronounced in Fig. 3 from Abbotsford 1912. It appears from the figures that the chance of a vegetative bud surviving increases with size.
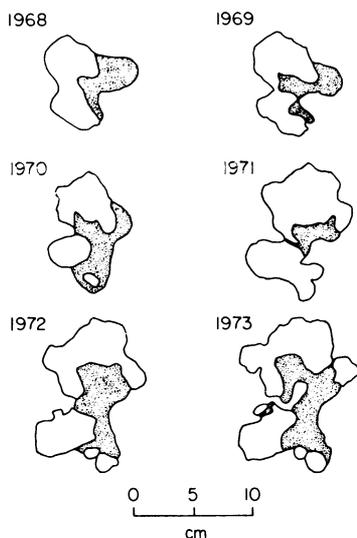


Fig. 1. Growth of *Cladonia stellaria* from May 1968 to May 1973 in Dempsay township, Ontario; site burned in 1941. In this and Figs. 2 and 3 the shaded portions represent de-corticate tissue; individual podetia are outlined.
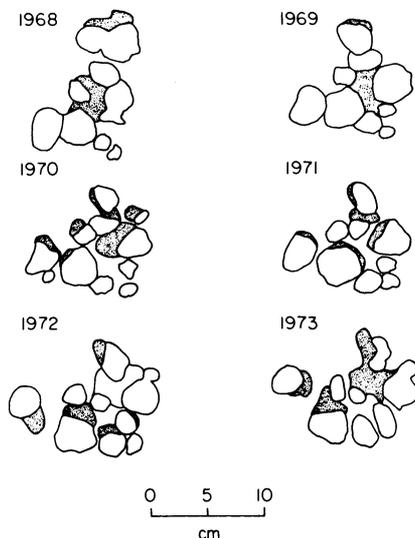


Fig. 2. Growth of *Cladonia stellaris* from May 1968 to May 1973 in Dempsay township, Ontario; site burned in 1927.

Where individual growth and clone formation can be directly observed in the photographs it is clear the reproduction occurs by the varieties of budding described in the introduction. There is evidence for the establishment of a few individuals from small fragments not visible in the photographs, but only at the youngest site. This type of
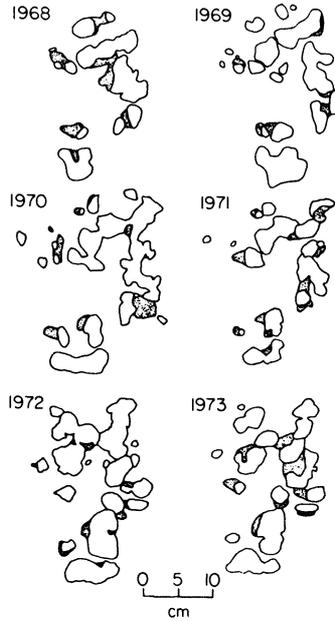


Fig. 3. Growth of *Cladonia stellaris* from May 1968 to May 1973 in Abbotsford township, Ontario; site burned in 1912.
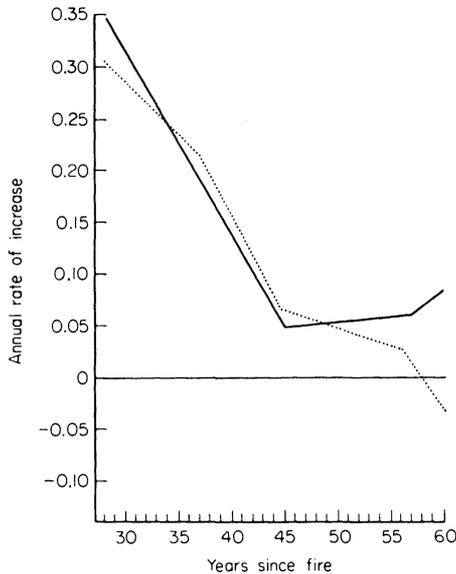


Fig. 4. Annual rates of increase in numbers (———) and biomass (··········) of *Cladonia stellaris* on burned areas near Cochrane, Ontario.

reproduction evidently accounts for the initial establishment of the populations by long range dispersal, but plays little part in subsequent clonal growth. Photographs of the older sites, especially Dempsay 1927, revealed the disappearance of some podetia beneath rapidly growing mats of the moss *Pleurozium schreberi.*

The local density of podetia is variable at all sites, but the mean density increases with age; at the older sites there are progressively larger areas covered by very dense fused clones. At Potter one continuous patch 5 × 10 m in extent was estimated to contain 35 000 podetia. Site to site differences in mean densities of podetia do not represent
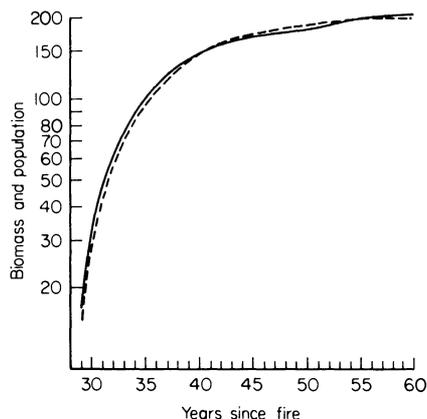


Fig. 5. Population growth in numbers (————) and biomass (– – – – – – –) of *Cladonia stellaris* on burned areas near Cochrane, Ontario.
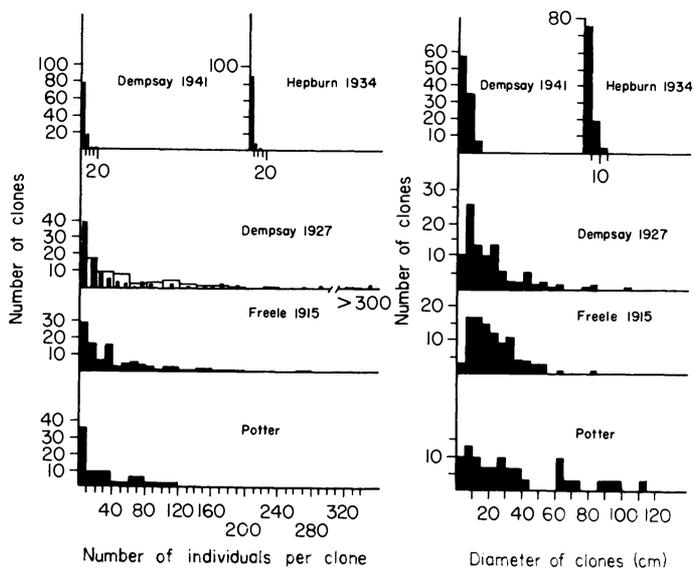


Fig. 6. Frequency distributions of the numbers of podetia in clones and of clone diameters of *Cladonia stellaris* at various burned areas. Expected number of podetia in clones in the Dempsay site burned in 1927 (open columns) were calculated by applying growth rates for appropriate years in the succession to the sample of clones from the Dempsay site burned in 1941.

population growth because of variations in local density and environmental differences between sites. Observed changes in densities in the plots from 1968 to 1973 are much more informative; computation from these of annual rates of increase (Fig. 4) indicate that the rate of growth in numbers declines linearly from 28 to 45 years after fire and then levels off. Integration of this curve yields the numerical population growth shown in Fig. 5.

What does the increase in numbers represent in terms of clonal growth? Distributions of mean diameters and numbers of individuals in apparent clones at sites accessible in
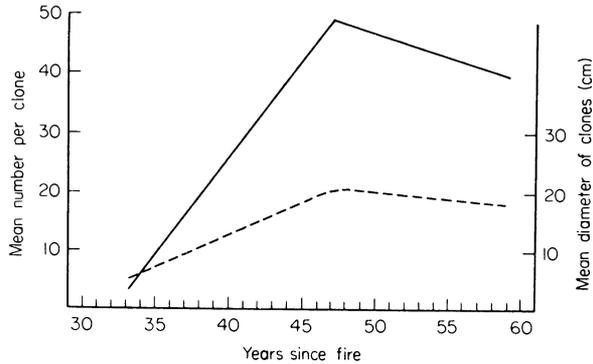
Fig. 7. Mean number of podetia per clone (———) and mean clone diameter (– – – – – –) of *Cladonia stellaris* at sites of various post fire ages.
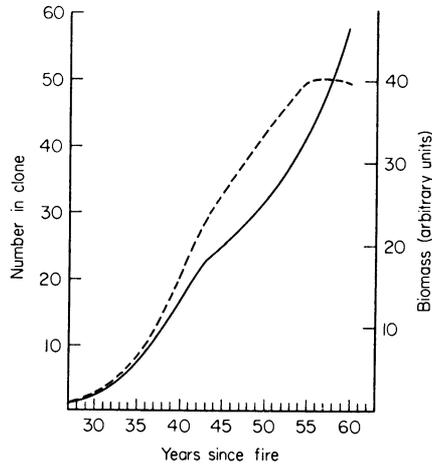
Fig. 8. Projected growth in numbers (———) and biomass (– – – – – –) of a clone of *Cladonia stellaris* starting from a single podetium of unit weight 27 years after fire.

1974 and at Hepburn 1934 (1972 data) are presented in Fig. 6, and increases in mean diameter and number of individuals per clone are given in Fig. 7. How do these compare with increases projected by the population growth rates calculated earlier? Assuming growth in numbers at these rates from a single individual established 27 years after fire a typical clone would increase as in Fig. 8. The upper part of this curve suggests that very large clones must arise from clonal fusion; given a random or contagious distribution of initial establishment this is inevitable. Small clones at the older sites arise from clonal fragmentation; there is no evidence for establishment of new clones.

As the two Dempsay sites are environmentally very similar they afford an opportunity for testing the reliability of the assumption that the older sites have passed through stages represented at present by the younger ones. Growth of the clones found in 1974 at the site burned in 1941 was simulated using the growth rates calculated for 33–47 years after fire. This brought the population to a simulated age equal to that of the 1974 population at the site burned in 1927. The simulated clone distribution is shown in Fig. 6. It compares reasonably closely with the observed population but there are a greater number of extremely large and extremely small clones in the actual distribution. This indicates the occurrence of clonal fusion and fission.

Studies of the sizes of individual podetia using photographs are hampered by variations in size with the degree of saturation of the thallus. One hundred and twenty-nine podetia were collected and their dry and saturated diameters found to differ by an average of 28%. As the late May slides in 1970 and 1973 were taken under very dry conditions these photographs were used for measures of podetial diameter. Twenty individuals nearest the centre of each plot were sampled, making 200 in all from each site. Most podetia are elliptical and the two major axes were measured and averaged. Actual diameters (Fig. 9) provide information about the composition of the standing populations, but changes in diameter from 1970–3 are the resultant of growth, death and vegetative reproduction.
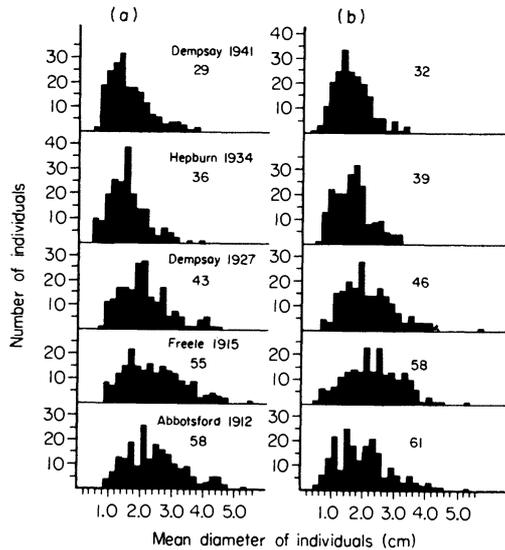


Fig. 9. Frequency distributions of the mean diameters of podetia of *Cladonia stellaris* at burned areas sampled in 1970 (a) and 1973 (b). Years in which burning occurred are indicated after the township names and years between burning and sampling beneath them.

Regressions of dry weight on the squares of the mean diameters of the podetia collected in 1972 accounted for more than 75% of the variance at all but one site (Abbotsford, 1922) where 64% was accounted for. Using the regression equations so obtained, the dry weights of individuals in the 1970 and 1973 records were estimated. Their distributions are similar to those of the diameters (Fig. 9). Annual growth rates in individual
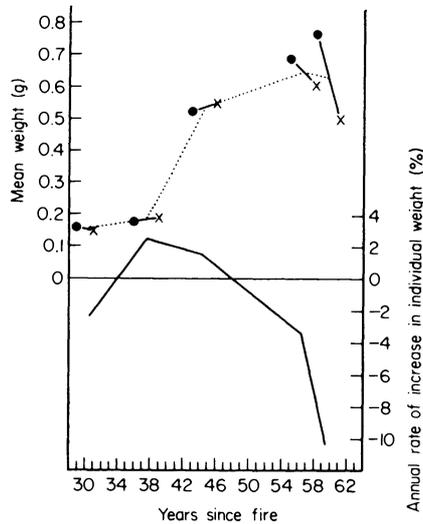
Fig. 10. Above: Mean estimated weights of podetia of *Cladonia stellaris* at burned areas near Cochrane, Ontario in 1970 (●) and 1973 (×). Below: annual rates of increase of individual podetia computed from the above.

weight were also calculated (Fig. 10); the mean weight of an individual shows an early decrease as cloning begins and a late decrease as crowding becomes severe. In the intervening period there is a slight increase in individual weight.

Combination of the annual rates of increase in numbers and weights of individuals permits computation of annual rates of increase in biomass or gross production (Fig. 4). Populations growth obtained by integrating this curve is indicated in Fig. 5. As the standing crop varies from plot to plot the mass is given in arbitrary units. The biomass curve in Fig. 8, corresponding to the simulated clonal growth, was obtained by correcting the rates of growth in numbers for the rates of change in weights of individuals (Fig. 10). It assumes an initial population of 1 individual of unit mass 27 years after fire; successive weights are multiples of the initial unit mass.

## DISCUSSION

The biomass growth curve (Figs. 5 and 8) is logistic until 55 years after fire. The slight decrease in mass at Abbotsford suggests oscillation about the converging value after this time, i.e. about 30 years after establishment. Even at high densities the number of individuals continues to increase (Fig. 5) although their mean weight decreases; the range of diameter and mass also increase. Fig. 3 illustrates the process in actual specimens.

The logistic curve implies that population growth is limited by some density-related factor such as space. In the most crowded plots the podetia are literally jammed together, but such crowding is a local phenomenon. The maximum standing crop observed was at Potter with 1507 individuals per m² having an estimated dry weight of 980 g, but the next largest, at Freele, was 913 per m², weighing 560 g. 500 g/m² is a typical converging value about which oscillations occur, but this 'carrying capacity' varies with environmental conditions. Light intensity and soil moisture probably influence the carrying

capacity (Kershaw and Rouse, 1971a), but the time at which *Cladonia stellaris* first enters the succession at the site concerned may also be important.

A feature of the growth curves (Figs. 5 and 8) that is of particular interest is how well the results for Dempsay 1941, Hepburn 1934 and Dempsay 1927 fit together. The Dempsay sites are environmentally similar, but the Hepburn site is drier. Judging by observed clone sizes (Fig. 6) Hepburn was also colonized later in the postfire successional sequence than the other two sites. However, the growth rates of *C. stellaris* fall into place on a linear sequence with respect to the time elapsed since fire occurred. This sequence reflects the overall successional status of the stand, not the time elapsed since colonization by *C. alpestris*. If population growth were entirely determined by density or its correlates this would not be anticipated. Given that Hepburn was colonized at a later successional stage than the Dempsay sites, why does the rate of population growth in *C. stellaris* describe the same curve there with no apparent lag? If annual growth rates are determined by successional maturity then the final convergent density at a site will be limited by the time of colonization.

Why are growth rates, at least for the first 20 years of growth, correlated with successional maturity? The composition of the tree and shrub layer in jack pine stands changes little after the appearance of *C. stellaris* except for local invasion by black spruce. Environmental factors likely to change after this time are light penetration of the canopy as the trees grow and soil moisture capacity as humus accumulates and the moss carpet thickens. Direct competition with *C. stellaris* by the mosses in this carpet may also increase.

Kershaw and Rouse's (1971a, b) evidence for the impact of soil moisture on podetial size and Yarranton and Yarranton's (1974) evidence for the incidence of drought and of competition for water between the jack pines at the Freele site suggest that soil moisture may be a significant factor. If soil moisture alone is the crucial factor differences in growth rates and maximum standing crops between the sites will depend on how its availability is determined. If it depends on humus accumulation and the development of the moss carpet apparent successional control of the growth of *C. stellaris* is confirmed; if it depends, at least in part, on absolute differences between sites, such as drainage, then clear site to site differences should be evident. Present results suggest that growth rates for at least 30 years after establishment (25–55 years after fire) are correlated with successional maturity; it seems unlikely that environmental differences between Hepburn and the Dempsay sites would be exactly those required to enable them to fit perfectly in the successional sequence (Fig. 5).

What determines the convergent values of standing crop and podetial density? Kershaw and Rouse (1971a, b) have demonstrated the influence of soil moisture and of the presence of *Ledum groenlandicum* on lichen distribution. The vigour of *Pleurozium schreberi* is another significant competitive factor. *Epigaea repens* and other *Cladonia* species are direct competitors, and ericaceous shrubs other than *Ledum groenlandicum* also reduce the light intensity beneath them and physically disrupt the podetia. Carrying capacity is apparently determined by a complex of factors effective through their influence on light and water availability, and by interference involving direct contact by other species. These factors give rise to considerable small scale heterogeneity in carrying capacity.

Height increments of about 5 mm were observed in most podetia. This fits the geographical distribution of growth increments described by Scotter (1963). The largest single podetium found was at Dempsay 1927. It had a mean diameter of 5.7 cm and an

estimated dry weight of 3.1 g. This is considerably smaller than the maximum size of podetia found further north.

Why does *Cladonia stellaris* not appear until 25 years after fire? It seems unlikely that poor dispersal is the reason because individuals are widely distributed in the very early stages of colonization. It is possible that this is a secondary effect; a few pioneer clones may be established earlier and a secondary distribution of new clones may arise from them. If this is the case poor dispersal may limit the first stage of colonization. There are a few clones apparently 5 years or so older than the remainder in one small patch of the Dempsay 1942 site, but they could be the result of locally dense colonization and rapid fusion. At Hepburn 1934 there are no equivalents. Mapping of the spatial distribution of clones and their sizes at Dempsay 1927 and examination for nonrandomness proved fruitless because of the masking effect of clonal fission and fusion. Two-stage coloniza- tion may occur but it is not universal; therefore it is unlikely that poor dispersal prevents establishment of the species earlier in the succession. The work of Smith (1966) and Shafi (1973) suggest that at least 14 years is required for soil chemical conditions to return to their pre-fire state. The surface conditions and humus layer take at least as long. *C. stellaris* is probably unable to establish until these processes are complete.

Given the frequency of fires, *C. stellaris* appears rather late in the succession yet it is conspicuously successful in dry sites in the boreal forest. Its tolerance of drought and of nutrient poor conditions are clearly telling; what of its allocation of resources? Exact estimation of this proved impossible, but it is evident that throughout life a major portion of production is devoted to vegetative propagation by various forms of budding. These large, energetically expensive propagules have a very high probability of survival in the early stages of population growth and enable relatively rapid dominance of the sites to be achieved independently of other forms of reproduction. Production of small fragments and their longer range dispersal seems to be very efficient. The proportion of production that is devoted to these fragments is small except where they arise from trampling. An investigation of the production, viability, persistence of potency and conditions for establishment of such fragments would be informative. Fink's (1917) work on other lichens provides a foundation for such studies.

How does the ecological strategy of *C. stellaris* compare with those of other boreal forest plants? Most mosses are also destroyed by fire, re-establish by means of fragments of the gametophyte or spores, and reproduce rapidly by vegetative means. Among the higher plants *Epilobium angustifolium* L. is similar in producing many light seeds (equivalent to thallus fragments) and propagating vegetatively by means of ramets. However, its vegetative propagation is less vigorous, proportionally more effort is devoted to seed production, and the species does not persist beyond closing of the forest canopy (Shafi and Yarranton, 1974b). Other species which appear ephemerally after fire, such as *Taraxacum officinale* Weber and *Achillea millefolium* L. devote even less effort to vegetative reproduction.

*Equisetum sylvaticum, Rubus strigosus* Michx., *Alnus rugosa* (DuRoi) Spreng., many ericads and other boreal species show very similar strategy to *Cladonia stellaris* in long range dispersal and vegetative propagation but they survive fire by means of underground structures (Beasleigh and Yarranton 1974). Disposition of energy or dry weight in these species is hard to compare with *C. stellaris* because of the dual purpose of their under- ground organs. *Epigaea repens* is the flowering plant most similar in strategy to *Cladonia stellaris*, but its vegetative reproduction and long range dispersal are apparently less efficient; it occurs consistently but much less abundantly in the same stands. The

strategy of *Picea mariana* in dry sites is somewhat similar; it appears late in the succession and reproduces by layering, but it is primarily a species of wet sites and its dispersal range is short.

## ACKNOWLEDGMENTS

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