

## SHORT COMMUNICATIONS

### AN UNUSUAL GROWTH FORM OF *CLADONIA FURCATA*: THE TRAMPLING-RESISTANT PRIMARY THALLUS COLONIZING A PAVED PATHWAY

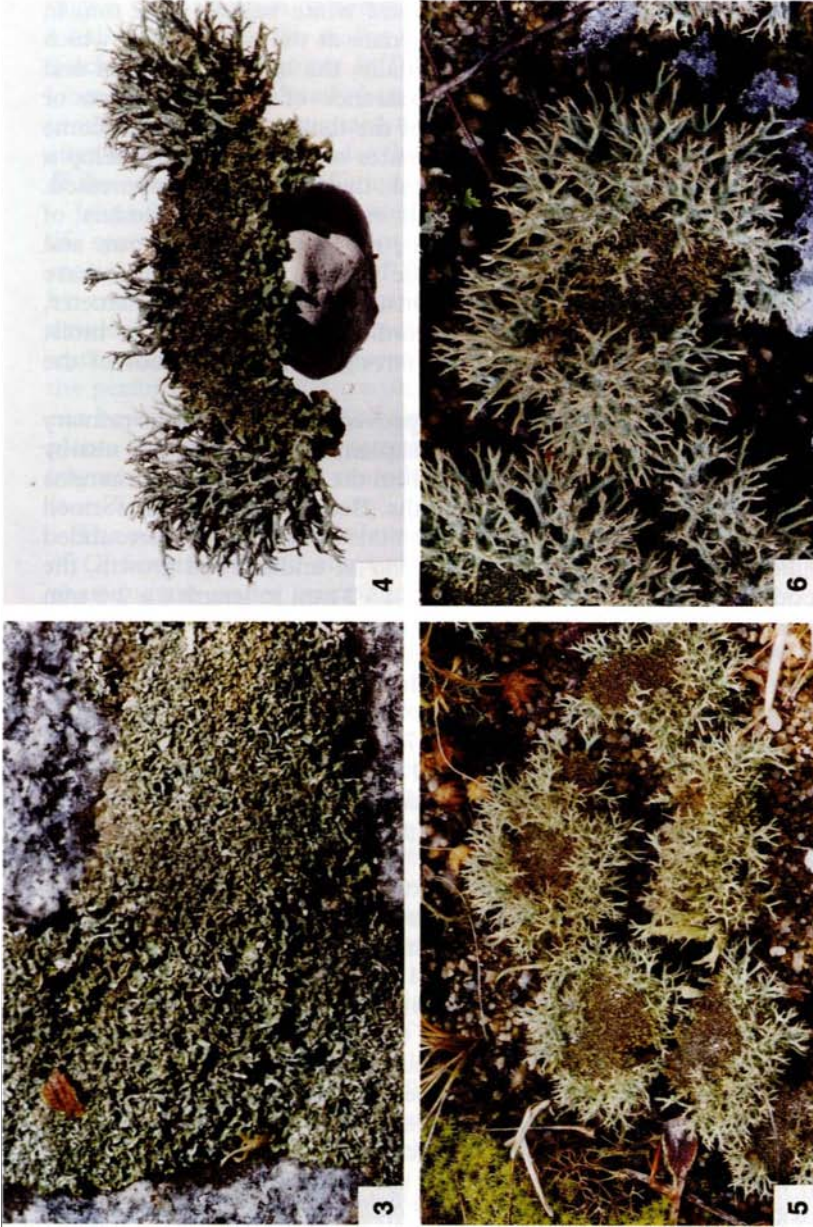
Lichens are well known to be susceptible to damage by trampling (Parkesit *et al.* 1995; Pegau 1970; Willard & Marr 1979). Fruticose species, with their highly branched structure, are particularly sensitive and Bayfield *et al.* (1981) described substantial damage to *Cladonia uncialis*, *C. arbuscula*, *C. rangiferina*, and *C. impexa* on paths in lichen-rich heath communities in north-east Scotland. Less visible communities, biotic soil crusts in arid and semi-arid areas with their cover of crustose lichens, are also easily disturbed by walking, car driving, or grazing (see West 1990) and recovery can take decades (Cole 1990; Belnap 1995).

We report here an interesting situation where a lichen is apparently being maintained and even spread in a habitat because trampling prevents it from completing its monocarpic life cycle. The lichen, *Cladonia furcata*, grows as slightly rounded or flat cushions composed entirely of the primary thallus in the gaps between stone cobbles of a footpath in the Würzburg Botanical Garden (Germany, Northern Bavaria) (Figs 1 and 2). The gaps are 1–2 cm wide and were originally filled with sand. Competition is mainly from mosses (predominantly *Barbula* species), trampling-resistant, small and appressed forbs (such as *Herniaria glabra*, *Taraxacum erythrospermum*, *Plantago intermedia*, *Sagina procumbens*, *Polygonum aviculare*, *Euphorbia humifusa*) and grasses (such as *Poa annua* and *Eragrostis poaeoides*). *Collema crispum* and *Lempholemma chalazanum* are the only other lichens present but are rare and transient. Depending on the season, cyanobacteria, especially *Nostoc cf. commune*, can occur but mainly in the shaded parts. The pathway is the main throughfare of the Botanical Garden and is used frequently, not only by local personnel and students but also by about 30 000 visitors per year. In addition there is limited car traffic by maintenance vehicles of the Botanical Garden.

The species was first documented 17 years ago, in 1981, when it was already common. Four years earlier, it was apparently absent or at least very inconspicuous because it was not mentioned in the first inventory of the lichens of the Würzburg Botanic Garden (Eva Baumann, Die Flechten des Botanischen Gartens der Universität Würzburg, unpublished Zulassungsarbeit für das Lehramt an Gymnasien, Würzburg 1978). Thus, successful establishment took place sometime between 1977 and 1981, possibly because of the ending of herbicide treatment previously used to keep the pathways free of 'weeds'. In autumn 1997 we counted several hundred individual thalli on the path, which is 150 m long and 6.5 m wide. Although there are no exact records, we have gained the impression over the years that new areas have been colonized and that there have been density changes at



Figs 1 and 2. (*legend opposite*)



Figs 3–6.

FIGS 1–6. *Cladonia furcata* var. *furcata* in the Würzburg Botanical Garden. FIGS 1 & 2. *Thallus primarius* in the gaps between stone cobbles of a footpath. Size of cobbles c. 8–10 cm times 10–12 cm. FIG. 3. Basal squamules of the *thallus primarius*. Length of the thallus c. 4 cm. FIG. 4. Growth of podetia at the margins of a *thallus primarius* cushion after 12 months of undisturbed growth. Length of the thallus c. 5–8 cm. FIG. 5. Several *thallus primarius* cushions after 17 months of undisturbed growth. Note interspersed podetia of *C. fimbriata* and *C. coniocraea*. FIG. 6. Thalli after 20 months of undisturbed growth.

existing sites. Dispersal by thallus fragments was demonstrated for *Cladonia furcata* by Fink (1917) and this is certainly the process occurring here with pedestrians both producing and distributing the particles.

The lichen has small lobes, green above and white below, <1–2 mm in diameter, rounded and usually irregularly crenate at the whitish rim, which are fixed to the ground by thin rhizinae. Initially, the lobes are upright and so densely crowded that they give the appearance of a small cushion or carpet (Fig. 3). Following trampling, many of the thallus squamules become broken with deformed upper tips and the centre of the cushions develop a more or less closed surface as the warty and scale-like lobes become appressed. At protected sites between the stones and especially at the borders of the cushions, small, branched podetia occur, no longer than 1–3 mm and most of them broken and deformed. Mature podetia with apothecia have never been found in this habitat. The cushions, initially 1–3 cm in diameter, spread along the gaps and often become confluent (Fig. 2). Under moist conditions, the bright green thalli contrast strongly with the colour of the pavement.

A clear determination of the lichen species proved difficult from the primary thallus. However, when some thalli were transplanted to a protected, nearby sand-bed, the first podetia started to emerge from the upper surface or margins of the primary squamules within three months. Because the podetia formed predominantly on the outer parts of the cushions (Fig. 4) they surrounded the centre like a wreath (Fig. 5). After one year of undisturbed growth, the 30 largest podetia on three cushions averaged 13.3 mm in length ( $\pm 2.8$  mm SD), the longest being 18.3 mm, and had up to six (average three) bifurcations. After an additional 8 months, irregularly branched 20 to 30 mm high tufts of podetia had formed (Fig. 6), with abundant dark brown pycnidia at their tips and, most probably, resembling 'stage 3' in the development of fruiting bodies as defined by Jahns *et al.* (1978). By then the primary thallus also began to change, having larger (4–5 mm) looser lobes with some standing upright. Unequivocally the species is *Cladonia furcata* (Huds.) Schrader (subsp. *furcata*). A very small number of podetia of *C. fimbriata* and *C. coniocraea* were also interspersed (see Fig. 5). These species are more frequent on a moist and protected section of the walkway.

*Cladonia furcata* is an extremely variable species and many infraspecific taxa have been described to accommodate the different morphotypes; Sandstede (1931) listed not less than five varieties and 14 forms for *C. furcata* (exclusively subsp. *subrangiformis*), and Grummann (1963) mentioned two varieties and eight lower categories for Germany. Most of these forms are almost certainly not genetically fixed taxa but, instead, phenological modifications (see Ahti 1977). However, we cannot find any described morphotype with a persistent primary thallus. The taxonomic literature (see Wainio 1887; Sandstede 1931; Purvis *et al.* 1992) suggests that evanescence of the *thallus horizontalis* (or *t. primarius*) is a characteristic feature of this species. Jahns & Ott (1997), on the life strategy of *C. furcata*, stated that 'The *thallus horizontalis* of this species is evanescent while the podetium is pluriennial'. They found that this lichen is monocarpic and dies after sporulation: 'There is no vegetative continuum'. Within any individual population, induction and development of fruit bodies

are synchronized (Jahns *et al.* 1978). Fink (1917) observed a time span of 6 years for growth of *C. furcata* from thallus fragments to completely developed, fruiting thalli and Jahns *et al.* (1978) estimated a maximal total longevity for a thallus of 8–10 years. It seems that, normally, the transition from the initial basal squamules of the *thallus horizontalis* to development of podetia is rather quick. Stocker-Wörgötter & Türk (1993) depict field-grown juvenile thallus lobes of *C. furcata* already bearing small, branched podetia. In their cultures produced from homogenized thalli, the first primordia were already present after 4–5 months and, under those optimal growth conditions, a high number of the squamules had differentiated podetia after 6 months.

Jahns & Ott (1997) suggested that sterile specimens may have an extended life span and our observations seem to confirm this assumption. Under the special habitat conditions of frequent and continuous mechanical impact by trampling, *C. furcata* suspends the time sequence of its ontogenetic development and remains perennial in its 'vegetative' phase, the basal squamules of its *thallus horizontalis*. To a certain extent this feature resembles the performance of monocarpic phanerogams, the vegetative phase of which can be extended by artificially preventing flowering. Death for a monocarpic plant, it seems, is not a question of the age *per se* but occurs through an interaction between the reproductive organs and the remainder of the plant (see Ziegler 1991).

The persistent, compact layers of the predominantly sterile, primary thallus of *C. furcata* are well adapted for successful competition with mosses and phanerogams under trampling conditions. However, the ability to develop upright podetia with organs for sexual reproduction was still present and only temporarily suppressed as long as damage continued. As soon as trampling ceased, normal podetia were developed in a short time and grew rapidly. This ability is possibly enhanced by the fact that, in *C. furcata* and in contrast to other *Cladonia* species, no sexual organs were formed at the level of the primary thallus ('ontogenetic type II/IV' in Jahns & Beltman 1973; see also Jahns 1970). The primordium forms a tall, sterile podetium and ascogones and trichogynes are only differentiated during growth or at the top of the adult podetium, where the apothecia are formed. Thus no sexual processes can be interrupted or disturbed when emergence of young podetia is prevented by mechanical impact. A stable population is, however, possible in the primary thallus stage and propagation can also occur by thallus fragments.

The ability to develop a persistent *thallus horizontalis* that, in contrast to the highly susceptible usual tufts of podetia, is resistant against trampling, has for *C. furcata* opened an ecological niche involving the colonizing of an unusual anthropogenic habitat. We will continue to record changes in these populations of sterile *C. furcata* and we would be interested to learn whether similar observations have been made elsewhere on this or other *Cladonia* species.

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*Note added in proof.* One of us (R.T.) has discovered, at an autobahn parking lot between Regensburg and Passau (Bavaria), another site where the *thallus primarius* of a *Cladonia* species grows abundantly in the gaps of a pavement. Material has been transplanted in order to study its development. This observation shows that the special life form of *Cladonia* described here is not a unique occurrence.