

NICHE SEPARATION AND OVERLAP IN THE FOLIOSE LICHENS *LOBARIA PULMONARIA* (L.) HOFFM. AND *L. VIRENS* (WITH.) LAUNDON IN THE KILLARNEY OAK WOODS, IRELAND

Allan Pentecost and C. Barry Richardson

This paper is dedicated to the memory of Barry Richardson, who died suddenly during the course of this study.

ABSTRACT

An investigation of the lichens *Lobaria pulmonaria* and *L. virens* on the trunks of mature oak (*Quercus* spp) revealed differences in their ecological preferences. These species were found to occupy significantly different niches, with *L. pulmonaria* occurring in the more exposed sites. The niche widths were similar with respect to exposure and there was a high degree of overlap between the species, although they did not differ significantly in aspect preference. The chlorophyll content and biomass per unit area was similar for both species, but they showed strong morphological differences that could influence light capture. Fertility, measured as apothecium abundance, was greater in *L. virens*, but *L. pulmonaria* reproduced both asexually and asexually in this region. A recent decline in the abundance of *Lobaria scrobiculata* and the potential effects of deer grazing on the lichen flora are discussed.

INTRODUCTION

It has long been recognised that organisms tend to attain maximum development under a particular range of conditions (ter Braak 1996), and, as a consequence, each organism can be described in terms of its niche. This is defined formally as the requirements the environment has to meet to allow the persistence of a species (Hutchinson 1957). Considerable effort has been made to identify the factors responsible for the optimal development of species and their range of tolerance. The quantification of these requirements for both individual species and communities is also an important ecological goal that has received much attention (Krebs 1989). While there is a growing literature on this topic for vascular plants, less work has been undertaken on the cryptogamic plants, many of which are particularly sensitive to environmental change, making them important indicators of such relevant factors as climate change and pollution (Nimis *et al.* 2002). In this study we focus upon two species of *Lobaria*, corticolous macrolichens that are both highly sensitive to environmental change (Ellis and Coppins 2007) and make a significant contribution to the total cryptogamic biomass in ancient deciduous woodland.

The genus *Lobaria* contains some of the largest known lichens. *L. pulmonaria* has been aptly described as a 'spectacular' lichen (Gilbert 1977), particularly where it clothes trees with thalli that may reach over 50cm in diameter. Four species of *Lobaria* occur widely in the oceanic montane regions of Europe, and they are notable for their sensitivity to acidic atmospheric pollutants. This is one reason why they are now rare or absent in many parts of Europe (Walser *et al.* 2002). The two most common species in the British Isles are *L. pulmonaria* and *L. virens*, and in parts of western Scotland and Ireland they are may be sufficiently abundant to account for the bulk of the cryptogamic biomass of the trees of these areas. The co-occurrence of these two species has often been noted in the lichenological literature (e.g. Rose 1976) and although they are structurally different, they are often found growing together in the older deciduous forests of the British Isles. In this paper we investigate the ecological relationships of these magnificent lichens in the Killarney oak woods, where they are particularly well developed. We also provide some information on their reproductive capacity (as apothecium production) and note temporal changes in their abundance in the Killarney oak woods.

Allan Pentecost
(email: Allan.
Pentecost@kcl.
ac.uk), Division of
Health and Life
Sciences, King's
College London, UK.
Current address: The
Freshwater Biological
Association, The
Ferry Landing, Far
Sawrey, Cumbria
LA22 0LP, UK.

Cite as follows:
Pentecost, Allan
and Richardson,
Barry C. 2011
Niche separation
and overlap in
the foliose lichens
Lobaria pulmonaria
(L.) Hoffm. and
L. virens (With.)
Laundon in the
Killarney oak woods,
Ireland. *Biology
and Environment:
Proceedings of the
Royal Irish Academy*
111B. DOI: 10.3318/
BIOE.2011.05.

Received 3
November 2009.
Accepted 31 May
2010. Published 20
April 2011.

METHODS

The Killarney oak woods in County Kerry, Ireland, which cover an area of 12km², are dominated by *Quercus petraea*, often accompanied by an understorey of *Ilex aquifolium*. *Q. robur* and the hybrid *Q. petraea* × *Q. robur* are probably also present, but we did not distinguish between them. We confined our study to mature oak trunks over a 0–2.4m height range on the trunks to facilitate recording and reduce any potential selectivity of *Lobaria* on other tree species. Ten areas of woodland were chosen where oaks predominated and invasive *Rhododendron ponticum* was absent (Fig. 1; Table 1). Only mature trees were sampled: the great majority of those sampled had a diameter at breast height (DBH) ranging from 50cm to 110cm. Trees were selected by starting at a randomly chosen individual and then proceeding to the nearest neighbouring mature tree, and the process continued until more than seven trees had been examined. On each trunk, presence or absence of the species was noted and if one or both species of *Lobaria* was present the number of thalli was recorded. In cases where more than one plant of either *L. pulmonaria* or *L. virens* occurred on a tree, an individual was chosen using the random number generator of a calculator, the tree being divided into an imaginary grid in which each square contained a single plant. In this manner, sampling bias was minimised.

Once a lichen thallus had been chosen five measurements were made.

- The aspect was determined using a compass placed against the tree where the lichen was growing.
- The forest density was determined using a relascope (Holgate 1967), a well-established method. A relascope consists of a measuring rod of known length fixed with two sights at one end. The sights are lined up with tree boles with the observer viewing at the far end, and all boles whose widths equal or exceed the intersight distance are scored within a 360° sweep. With the relascope used here (1m length and sights of 25mm), a value of zero represents open country with few if any trees surrounding the selected tree, while a value of around 19 represents an extremely dense forest (Holgate 1967).
- The extent of understorey *Ilex aquifolium* was assessed by determining the percentage of the 180° sweep in front of the lichen thallus that was not occupied by evergreen foliage to a distance of up to 50m from the sampled tree.
- The percentage of unobstructed sky was estimated to the horizon to provide a TOPEX value of exposure (Pyatt *et al.* 1969). The TOPEX value was modified using the aspect weighting method of Pentecost and Zhang (2006) so that south-facing plants received a higher weighting than north-facing plants by a factor of 1.75. The weightings were determined from standard meteorological measurements (Walsh 1961).
- The diameter of each selected *Lobaria* thallus, its height above ground level and its fertility as indicated by presence/absence of apothecia were measured. A small number of lichen samples were also removed from Site 4 (Table 1) for chlorophyll and biomass determination.

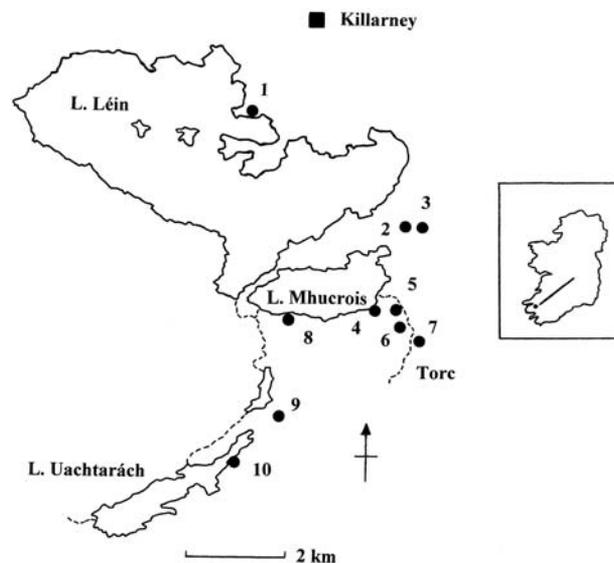


Fig. 1—Map of the Killarney oakwoods surrounding the three Killarney lakes (Léin, Mhucrois and Uachtarách) showing the ten sampling areas (filled circles).

Table 1—Sampling locations and summary data for lichen diameters and trees.

Site no. (see Fig. 1)	Nat. Grid ref.	Location	No. of trees sampled	<i>L. pulmonaria</i>			<i>L. virens</i>		
				Mean (cm)	s.d. (cm)	No. of thalli	Mean (cm)	s.d. (cm)	No. of thalli
1	V 9481 8845	Ross Island	8	22	—	1	2	10	3
2	V 9686 8606	Muckcross Estate Farm	22	10.9	5.61	7	20.3	17.6	11
3	V 9725 8594	Muckcross Estate drive	29	13.0	0.0	2	11.3	7.6	11
4	V 9601 8473	Mhucrois Lakeside, SE	14	8.7	2.14	7	—	—	—
5	V 9645 8461	Torce Falls area	58	7.3	3.53	17	15.2	10.8	37
6	V 9645 8430	Torce Falls upper	63	8.4	3.65	14	16.1	12.6	29
7	V 9664 8388	Cloghereen Upper	22	15.7	7.0	14	*	*	*
8	V 9430 8505	Dinish	50	13.9	4.78	17	*	*	*
9	V 9308 8250	Gortdenaree	18	11.0	6.57	10	*	*	*
10	V 9236 8240	Lough Uachtarách, SE shore	18	20.7	19.0	6	17.5	10.1	12

* Not sampled.

The three estimates—relascope value, evergreen-free sweep and unobstructed sky (TOPEX)—were combined to provide an index of light exposure. In order to provide an index of light exposure, the relascope value obtained was determined as a fraction of 19, converted to a percentage and the inverse taken so that low percentages represented low light levels. This inverse relascope percentage was defined as R.

TOPEX values (T) were expressed as a fraction of 90 since this represents the maximum angle of open sky from zenith to horizon. Again low values represent low light intensities. These two were then added to the complement of evergreen percentage cover (E) to provide a total score of 290 from which the final measurement (R+T+E) of exposure was obtained. For example, suppose a relascope value of 12 was obtained. This gives an R value of $100 - [(12/19) \times 100]$ or 37%. The evergreen sweep complement (E) was determined as 90%, meaning that evergreens were present to the extent of 10% as viewed in front of the lichen, with finally the TOPEX value determined as 75%. This gives a total of $37 + 90 + 75 = 202$. Since the maximum score is 290, the exposure index, measured as a percentage is $202/290 = 70\%$, indicating a moderately exposed site.

Chlorophyll content was obtained from circular discs of area 1cm^2 cut from the lichens with a cork-borer. These were ground in a pestle and mortar with a few millilitres of 90% methanol, extracted at 90°C for 15 minutes, centrifuged and then measured according to the method of Talling and Driver (1963).

RESULTS

LICHEN SIZE, ASPECT AND ASSOCIATION

Thalli of *L. pulmonaria* were smaller than *L. virens*, and the difference in the means was significant (*t*-test; $p < 0.001$) but they had a similar size range (Table 2). Aspect on the trunks is illustrated in Fig. 2 as frequency of occurrence in the cardinal octants. North-easterly aspects are avoided by both species, but otherwise their distribution does not appear to be strongly affected by this factor.

A G-test of independence (Sokal and Rohlf 1995) demonstrated a strong association between the two species on the oak trunks ($p = 0.01$). Twenty per cent of the trees examined had both species on their trunks, while 39% had *L. virens* only and 7% had *L. pulmonaria* only.

Table 2—Lichen position and size on oak trunks.

Taxon	Mean diameter range (cm)	Diameter range (cm)	Mean height above ground (m)	Height range (m)	Number of samples
<i>L. pulmonaria</i>	11.9	2–55	1.32	0.25–2.4	95
<i>L. virens</i>	15.7	1–52	1.47	0.2–2.4	102

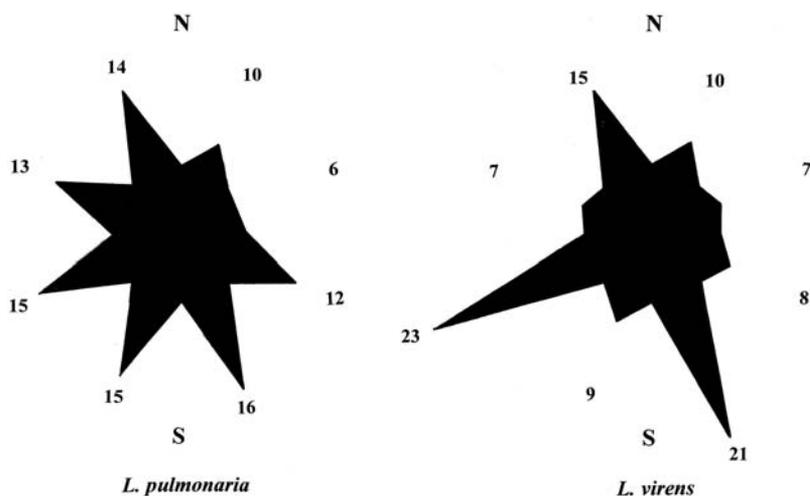


Fig. 2—Frequency of occurrence for *Lobaria pulmonaria* (left) and *L. virens* (right) within the cardinal octants in the Killarney oakwoods.

LIGHT EXPOSURE INDEX

Individual values of the light exposure index are plotted in histogram form in Fig. 3. While the spread of the measurements is similar, they do not coincide, and the medians (79.0% and 58.3%, respectively) were found to be significantly different ($p < 0.001$) using the non-parametric Mann–Whitney test. It can be concluded that while there is a good degree of overlap between the two taxa, *L. pulmonaria* has a significantly higher light exposure requirement than *L. virens*. It is also clear that low light levels are avoided by both species.

FERTILITY, CHLOROPHYLL AND BIOMASS

Large differences were noted in the fertility of species determined as presence/absence of apothecia. In *L. pulmonaria* fertility was low, with only 8% of the thalli fertile, which compared with 69% for *L. virens*. In both cases, fertility was significantly related to thallus size (t -test, $p < 0.01$), with small thalli more often sterile than large thalli.

Biomass, measured as grammes dry weight m^{-2} was similar for both species (*L. pulmonaria*, mean $177g m^{-2}$, s.d. $5.26g m^{-2}$; *L. virens*, mean $165g m^{-2}$ s.d. = 24.4 , $t = 0.54$, n.s.). Likewise, the difference in mean chlorophyll-*a* content between the two species was not statistically significant (*L. pulmonaria* mean $205mg m^{-2}$, s.d. $46.9mg m^{-2}$; *L. virens* $197mg m^{-2}$, s.d. $55.2mg m^{-2}$).

DISCUSSION

The requirements defining an ecological niche take two forms (Hurlbert 1978; Krebs 1989): 1) ranges

of conditions such as irradiance, water availability and pH; and 2) ranges of depletable resources such as nutrients and energy-providing molecules such as carbohydrates. Irradiance occupies a special place, since according to circumstances, it can be regarded either as a condition or a resource. In our study, we recognise irradiance as a resource that is measured semi-quantitatively by the exposure index described above. As such, the frequency of two species can be measured against this resource (Fig. 3) to provide a measure of both niche width and niche overlap. We found a significant difference in the niches occupied by the two species as measured by this index, but there is considerable overlap, amounting to about 80%. Both species also appear to have a similar tolerance range to the index, so in this respect their niche widths are similar. Although light is obviously an important ecological factor for all photosynthetic organisms, it is almost certain that other resources and conditions are involved in defining the niches of these lichens. Likely candidates include the moisture regime and water ionic composition (e.g. pH, $pHCO_3^-$, pCa). Differences in water availability are likely to be responsible for reduced colonisation of both taxa on north-eastern aspects (Fig. 2). However, the two taxa did not differ significantly with respect to their aspect preferences. This factor reflected the moisture regime more than light. With the prevailing wind direction from the west, these lichens avoided the driest north-easterly aspects.

Studies with transplants of *L. pulmonaria* suggest it is moderately light-demanding in forest canopies, with a preference for forest openings (Gauslaa *et al.* 2006; Coxson and Stevenson 2007). These observations also apply to the Killarney population, although

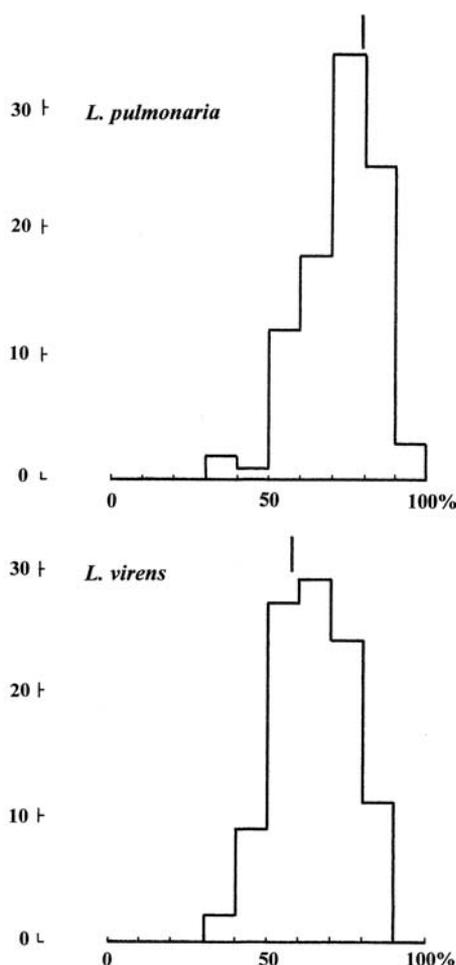


Fig. 3—Frequency distributions showing the response of *Lobaria pulmonaria* (above) and *L. virens* (below) to irradiance as measured by the exposure index. Exposure is considered as an exploitable resource by these lichens. Vertical lines show positions of the medians.

it is apparent that they are scarce in the most exposed situations. High irradiance, combined with wind can lead to rapid desiccation and there is some evidence that *L. pulmonaria* is sensitive to this (Gauslaa *et al.* 2006). The peculiar and complex morphology of this taxon may be an aid against photoinhibition and desiccation. Bartak *et al.* (2006) noted that the thalli of this species curled inwards when drying, protecting the algal layer from high insolation. This process may also help retain some moisture. On re-wetting, thalli expand outwards, although they still stand proud of the trunk, a feature that may trap more radiation lower in the canopy. There have been no comparable studies on *L. virens* and less is known of its ecology. This taxon changes little on drying and remains closely adhered to tree bark.

It was hypothesised that the chlorophyll-*a* content of this lichen would be higher than that of *L. pulmonaria* to provide some compensation for the lower light intensities experienced, but this could not be demonstrated as no significant difference was found. There were no comparable data for the chlorophyll content of *L. virens*, but the total carotenoid content at least appears to be less in this taxon compared with *L. pulmonaria* (Czeczuga and Richardson 1989). Levels of chlorophyll have been reported in *L. pulmonaria* by Schofield *et al.* (2003) and are comparable to those found in our study.

The chlorophyll:biomass ratios of the two taxa are similar, and the apparent lack of cephalodia in *L. pulmonaria* indicates an absence of nitrogen-fixing cyanophytes in the sample and would benefit from further investigation. Schofield *et al.* (2003) also reported their absence, although they are described as being abundant in some collections (Rikkinen *et al.* 2002; Smith *et al.* 2009).

Sexual reproduction in the *L. pulmonaria* sample was much lower than in *L. virens* but the former also reproduced by the formation of specialised propagules termed isidioid soredia (Esslinger 1977) or by simple fragmentation. Low levels of fertility have also been observed in North American populations (Denison 2003). *L. virens* does not possess such propagules and this may be one reason why it is more abundantly fertile. Fertility of these lichens is clearly related to age, a phenomenon that has been recognised in other lichen genera.

The Killarney oak woods are internationally recognised for the range and diversity of their cryptogams. This diversity is the result of a varied but high-humidity environment that is little impacted by air pollution and deforestation. However, the authors observed some worrying changes since their first studies here in the 1960s. For example, in our recent survey, *L. scrobiculata* seemed far less abundant than formerly. In 1967 it was growing well on oak close to Lough Uachtarách (Site 7), but we did not re-find it here, and it occurred on only two of the *c.* 200 trees examined in our study. *L. pulmonaria* was also less abundant around this lough than formerly. *L. pulmonaria* is of particular interest as it has been recognised as a good indicator of high lichen diversity (Campbell and Fredeen 2004). The reasons for these changes are not clear, since the areas studied here were not heavily impacted by *Rhododendron* growth, although it is possible that *Ilex* had increased recently. Increase in the growth of these two evergreens will have a deleterious effect on the

cryptogamic flora, since deciduous tree boles support a wealth of species, several of which, such as *L. virens*, are less well adapted to growth in the upper canopy owing to the increased exposure. Grazing of undergrowth by sika deer is a recognised problem in Killarney National Park, where regeneration of oak appears to be inhibited (Perrin *et al.* 2006). Combined with vigorous *Rhododendron* invasions, the nature of these woods could change dramatically unless remedial action is taken.

ACKNOWLEDGEMENTS

We are grateful to the staff of Killarney National Park Authority and Muckcross Estate for their helpful advice and permission to undertake this study within the boundaries of the National Park. We also thank Mrs Lorna Richardson for her support throughout the investigation.

DEDICATION

This paper is dedicated to the memory of Barry Richardson, who died suddenly during the course of this study.

REFERENCES

- Bartak, M., Solhaug, K.A., Vrablikova, H. and Gauslaa, Y. 2006 Curling during desiccation protects the foliose lichen *Lobaria pulmonaria* against photo-inhibition. *Oecologia* **149**, 553–60.
- Campbell, J. and Fredeen, A.L. 2004 *Lobaria pulmonaria* abundance as an indicator of diversity in interior cedar–hemlock forests of east-central British Columbia. *Canadian Journal of Botany* **82**, 970–82.
- Coxson, D.S. and Stevenson, S.K. 2007 Growth rate responses of *Lobaria pulmonaria* to canopy structure in even-aged and old-growth cedar–hemlock forests of central interior British Columbia, Canada. *Forest Ecology and Management* **242**, 5–16.
- Czczuga, B. and Richardson, D.H.S. 1989 Carotenoids in some lichen species from Ireland. *Lichenologist* **21**, 363–7.
- Denison, W.C. 2003 Apothecia and ascospores of *Lobaria oregana* and *Lobaria pulmonaria* investigated. *Mycotaxon* **95**, 513–6.
- Ellis, C.R. and Coppins, B.J. 2007 Changing climate and historic woodland structure interact to control species diversity of the ‘Lobarion’ epiphyte community in Scotland. *Journal of Vegetation Science* **18**, 725–34.
- Esslinger, T.L. 1977 A chemosystematic revision of the brown Parmeliae. *Journal of the Hattori Botanical Laboratory* **42**, 1–211.
- Gauslaa, Y., Lie, M., Solhaug, K. A. and Ohlson, M. 2006 Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. *Oecologia* **147**, 406–16.
- Gilbert, O.L. 1977 Lichen conservation in Britain. In M.R.D. Seaward (ed.), *Lichen ecology*, 415–36. London. Academic Press.
- Holgate, P. 1967 The angle-count method. *Biometrika* **54**, 615–23.
- Hurlbert, S.H. 1978 The measurement of niche overlap and some relatives. *Ecology* **59**, 67–77.
- Hutchinson, G.E. 1957 Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* **22**, 415–27.
- Krebs, C.J. 1989 *Ecological methodology*. New York. Harper & Row.
- Nimis, P.L., Scheidegger, C. and Wolseley, P. 2002 *Monitoring with lichens—monitoring lichens*. NATO Science Series. Dordrecht. Kluwer Academic Publishers.
- Pentecost, A. and Zhang, Z. 2006 Response of bryophytes to exposure and water availability on some European travertines. *Journal of Bryology* **28**, 21–6.
- Perrin, P.M., Kelly, D.L. and Mitchell, F.J.G. 2006 Long-term deer exclusion in yew-wood and oak-wood habitats in southwest Ireland. *Forest Ecology and Management* **236**, 356–67.
- Pyatt, D.G., Harrison, D. and Ford, A.S. 1969 Guide to the site types in forests of north and mid Wales. *Forest Record* **69**, 1–24.
- Rikkinen, J., Oksanen, I. and Lohtander, K. 2002 Lichen guilds share related cyanobacterial symbionts. *Science* **297**, 357.
- Rose, F. 1976 Lichenological indicators of age and environmental continuity in woodlands. In D.H. Brown, D.L. Hawksworth and R.H. Bailey (eds), *Lichenology: progress and problems*, 279–307. London. Academic Press.
- Schofield, S.C., Campbell, D.A., Funk, C. and McKenzie, T.D.B. 2003 Changes in macromolecular allocation in nondividing algal symbionts allow for photosynthetic acclimation in the lichen *Lobaria pulmonaria*. *New Phytologist* **159**, 709–18.
- Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. and Wolseley, P.A. 2009 *The lichen flora of Great Britain and Ireland*. Slough, UK. Richmond Publishing Company.
- Sokal, R.R. and Rohlf, F.J. 1995 *Biometry*. 3rd edn. New York, W.H. Freeman.
- Talling, J.F. and Driver, D. 1963 Some problems with the estimation of chlorophyll-*a* in

LOBARIA ECOLOGY

- phytoplankton. *Proceedings of the Conference of Primary Productivity Measurement, Marine and Freshwater, Hawaii, 1961*, TID-7633, 142–6. Washington, DC. US Atomic Energy Commission.
- ter Braak, C.J.F. 1996 *Unimodal models to relate species to environment*. Wageningen. DLO-Agricultural Mathematics Group.
- Walser, J.-C., Zoller, S., Büchler, U. and Sheidegger, C. 2002 Species-specific detection of *Lobaria pulmonaria* (lichenized ascomycete) diaspores in litter samples trapped in snow. *Molecular Ecology* **10**, 2129–38.
- Walsh, J.W.T. 1961 *The science of daylight*. London. McDonald.