transpiration rates are at their maximum. To identify these periods from the climatological record details of the daily observations would have to be examined.

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THE QUANTITATIVE DESCRIPTION OF NEW ZEALAND BRYOPHYTE COMMUNITIES

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INTRODUCTION

A surprising feature of New Zealand ecological work is the scarcity of information on bryophytes. Their role in the vegetation is seldom even described (except by Allison 1931, Cockayne 1909, Martin 1946, 1949, 1950, 1950a, 1960, Murray 1963, Zotov *et al.* 1938) and the only quantitative study is that of Robbins (1952). This lack of data reflects a shortage of bryologists not bryophytes, for there can be scarcely another country where bryophytes are so numerous, so luxuriant and so important a part of the vegetation.

A field technique has recently been used at Otago which permits the quantitative description of bryophyte-dominated communities, even by ecologists with no bryological expertise; it is designed to provide a reasonably complete and objective description in the few days normally available on field trips to remoter areas.

The two strata which, in New Zealand forests at least, tend to consist largely of bryophytes are the ground layer and the epiphytes; each of these requires a different method of sampling.

GROUND VEGETATION

Of the four commonest measures of species performance available for a description, one, *dry-matter production*, is usually impracticable except within reach of a laboratory; *density* is frequently impossible to determine since the limits of an individual bryophyte may be indeterminate; *cover*, although the most satisfactory feature for interpretation, is very laborious to measure with any reasonable accuracy. That leaves *frequency* as the easiest characteristic to estimate although the most difficult to interpret. Difficulties in interpretation can be lessened by using the same sampling unit in all studies; we have standardised on a decimetre square quadrat, and normally use a grid of 25 of these in the form of a subdivided frame 0.5 m. square. This is a convenient and workable implement in all but the densest scrub.

The location of these grids on the ground presents something of a problem since the figures obtained for different areas or for different species may be compared statistically only when they are based on randomly-located quadrats (Greig-Smith 1957); but the truly random location of quadrats is quite impracticably time-consuming. A quick approximation to restricted random sampling is obtained by staggering the grid of quadrats alternately to right and left along a series of short transect lines through the middle of the stand being surveyed. Of the order of 200 grids (5,000 quadrats) may be necessary to smooth out the variability in composition of forest floor communities. In a rich area this represents about 3 full days' work for two people, one observing and the other recording.

As well as recording frequency for each species an estimate of the total ground cover may be conveniently and readily obtained by using the 36 points marked by the intersections of the grid.

In rain forest such as in Fiordland or Westland the number of species may easily exceed 100 in the ground flora and 150 in the epiphytes. It is clearly impracticable for most, or perhaps all, ecologists to identify even the majority of these in the field. All that is required is to *recognise* the species as consistently as possible, give them provisional names and take voucher specimens for later identification. This is a simple and rapid process, much more so than with flowering plants, and there is no reason why the results should be inaccurate if plenty of specimens are taken. The only precaution needed is the allotting to the species of provisional names which have some relevance to the appearance of the plants. Names such as "A34" or "Species B" are much more difficult to associate with a particular plant than provisional but descriptive names of the form *Nigrihypnum longifolium* or *Megafrullania rubra*. With increasing skill in recognising taxa the number of voucher specimens can be much reduced.

The same procedure of giving provisional names is also used in the recording of epiphytes where, however, the problems of sampling are much more formidable.

EPIPHYTIC VEGETATION

The recording of epiphytic vegetation places the ecologist in his customary dilemma of choosing between many samples of low accuracy and few samples of greater accuracy. This common problem is abnormally acute in dealing with epiphytes because the variation to be encompassed is virtually the square of that found in the ground layer. The normal variation with position on the substratum is multiplied by the variation in the type of substratum, that is, in the species on which the epiphytes occur, their inclination, exposure and other features. At present, techniques for handling variation of this complexity are not readily available and obtaining data to reveal it may be impracticably arduous, so a drastic simplification must be imposed during sampling.

There are two parts to the sampling of epiphytes: the choice of trees to be sampled and the sampling of the epiphytes on them. A variety of methods is available for each.

To select trees for sampling as rapidly as possible but without personal bias, we choose all those encountered either along transects or within sample areas. This non-random but objective method is much more rapid than the completely random selection used by Culberson (1955) and Hale (1955), but does not suffer from the disadvantages, for quantitative work, of completely subjective selection as practised by many phytosociologists (e.g. Barkman 1958). It is customary to consider as trees only those specimens which exceed a minimum diameter (usually 10 cm. d.b.h.) and which satisfy various conditions of erectness, healthiness, etc. Following established practice the term *phorophyte* will be used to signify those trees on which epiphytes are borne.

The number of trees sampled is purely a matter of the time available. We have used a limit of 10 for each of the principal tree species and as many as are encountered of the other species, but this seldom gives an adequate number even when the data from all trees are classed together regardless of species. When the epiphytes on different species of phorophyte are to be treated separately, 50 or more trees of each species would be a suitable number to aim at if time permitted.

Given a number of trees, by whatever method selected, the sampling of epiphytes on them may be carried out in many different ways as regards both the location of the samples and the estimation of species performance. Phytosociologists and others, concerned more with the recording of all plant groupings than assessing their relative abundance, have used quadrats deliberately placed to enclose particular assemblages of plants, either of a standard size (e.g. Iwatsuki 1960) or varying according to the size of the community (e.g. Proctor 1962). This method, being non-quantitative, is the most rapid of all and the most efficient where time is very limited, but has all the attendant disadvantages of subjectivity. The alternatives are to place the samples randomly (e.g. Kershaw 1964) or systematically at predetermined positions.

For example, Patterson (1940) used a single 100 $cm.^2$ quadrat at a height of 5-7 ft. (but subjectively placed) and Culberson (1955) used girdle quadrats 35 cm. wide encircling the trunk at the base and at 1.4 m. This type of sampling is extensive rather than intensive and allows a large number of trees to be sampled, revealing the manner in which, on a regional scale, the variation in epiphytic communities is related to the variation in phorophytes. It is not designed to give information on the actual quantitative composition of epiphytic communities nor on the effects of local habitat factors rather than regional ones.

More intensive sampling has been used by Hale (1952), working with girdle quadrats at 4.5 m. intervals right up the trunk to provide a record of the vertical zonation of epiphytes. Still more thorough sampling of individual trees may be obtained by dividing up the entire tree into sample regions (e.g. Iwatsuki and Hattori 1957) and ultimately by treating as one quadrat the entire tree or as much of it as is accessible. In practice, on large trees this means only the basal 2 m. of trunk (Cain and Sharp 1938, Szczawinsky 1953). Studies of complete trees including the crowns are scarce and necessarily limited to very few specimens, since such a study is only possible on felled or fallen trees (Hale 1952, Iwatsuki 1960).

Treating the entire phorophyte as a single quadrat in this way, rather than using small quadrats, gives a more accurate measure of the abundance of epiphytic species in a single forest stand, which is what is required for a record of the vegetation, but quite ignores the smaller scale variations on different parts of the phorophyte.

The procedures which have been used for estimating plant performance within the samples are similarly varied and depend partly on the measure of performance chosen. *Frequency* (presence or absence data) is by far the simplest to estimate and has been used mainly in the sampling of large numbers of trees (e.g. by Culberson 1955, Hale 1955). A more informative measure is *cover* of which an accurate estimate may be obtained by using a large number of point quadrats. However, it is most commonly estimated visually according to the Domin or Domin and Krajina 10-point scale (e.g. Proctor 1962, Szczawinsky 1953) or the Braun-Blanquet 5-point scale (e.g. Patterson 1940). The measurement of cover using point quadrats, either in frames of 10 as advocated by Kershaw (1964) or by point intercepts along a line wound round the tree, is satisfactory only in the easiest communities. In the evergreen rain forests of Fiordland the light may be too poor to use points with any accuracy and because of the luxuriant many-layered growth of epiphytes, the use of points will usually require the identification of species from quite unrecognisable portions. Moreover, even estimating the point intercepts as rapidly as possible with no attempt at precision, we have found that the method takes at least two and a half times as long as visual estimation and leaves many of the rarer species unrecorded. On the other hand the effectiveness of the visual method is impaired by the difficulty of estimating cover in accordance with an arbitrary scale of values.

It seems a more satisfactory procedure to make use of the classes of cover values most easily recognised by the individual observer. Our technique is to make a visual estimate of abundance for every species of epiphyte on all the accessible parts of the trunk (i.e. below 2 m.) using the familiar 5-point scale of rare, occasional, frequent, abundant, dominant, to which we add a sixth, "present", for species which are found only in laboratory examination of voucher specimens. These visual estimates vary widely, of course, from person to person but are reasonably constant for one worker. Since the visual estimation of abundance of bryophytes (and lichens) depends largely on their cover, we then convert these abundance estimates to cover percentages using personal conversion factors which have been established at another time. These factors are obtained by visually estimating the abundance of epiphytic species on a series of trees and then estimating their cover using several hundred point quadrats regularly arranged round the trunk; the conversion factor for each visual abundance class is then taken as being its mean cover value. We have found the conversion factors to be fairly stable, showing a significant difference (at 1% level) in only one category when re-calibrated a year later by the same worker with a different assistant each time (Table 1).

TABLE 1. *Personal factors for conversion of visual estimates to cover values, established in 1964 and re-calibrated independently a year later. P. is the probability of the two values not being significantly different.*

	1964		1965		P
	Mean	95% C.I.	Mean	95% C.I.	
d.	80	—	84.2	—	
a.	47.17	± 11.92	30.39	± 30.39	0.20–0.21
f.	15.23	± 4.46	14.04	± 13.98	0.08
o.	6.54	± 1.49	3.06	± 1.79	< 0.001
r.	1.22	± 0.42	0.64	± 0.21	0.01–0.02

Frequent re-calibration is clearly a necessity both to increase the accuracy of the conversion factors and to expose any changes in personal standards. This conversion to cover values probably leads to a further inaccuracy in the final data but has the great advantages (i) that the results for any species of phorophyte can be averaged over all those sampled, which would otherwise have to be presented separately in the data (as in Proctor 1962, Iwatsuki 1960, Barkman 1958 suppl., etc.), and (ii) that it allows comparison of figures obtained by different workers. The rapidity of this method allows 20-30 trees to be sampled each day in forests which are very rich in epiphytes. By using provisional names and taking voucher specimens the time taken in sampling and later laboratory work is much less than in the common procedure of removing bark from the entire quadrat and taking it back to the laboratory (e.g. Iwatsuki 1960).

Other measures of performance have been used, such as *sociability* and *vigour* (e.g. Szczawinsky 1953), but have little to offer except in the description of individual patches of epiphytic vegetation.

SUMMARY

The technique used at Otago for the quantitative description of bryophyte-dominated communities, mainly in forests is: (a) to estimate the frequency of ground species in $dm.^2$ quadrats arranged in grids of 25, laid out semi-systematically on the ground, total cover of all plants in the ground layer being estimated at the same time; (b) to estimate the cover of epiphytes on the bottom 2 m. of trees in an objectively drawn sample, using visual estimates of abundance and later converting these to cover values using personal conversion factors. All species are given provisional names and voucher specimens taken for later identification.

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