path analysis can deal: (i) where there is feedback betwen the variables and (ii) where some of the variables cannot be measured and yet their path coefficients can be inferred from the equations. These will not be discussed.

In conclusion it is as well to emphasise that the results obtained are dependent on both the underlying causal relationships and on the accuracy and appropriateness of the actual data used. Both of these will be influenced by the investigator's knowledge of the probable causal relationships between the various factors and his skill in measuring the aspects of that factor which is appropriate to the particular problem, e.g. the appropriate temperature measurement for relating to plant response. This will require recourse to single-factor experiments in the field, laboratory or growth cabinets. However the utilization of all such data in a causal network offers one method whereby ecological data could be synthesized.

REFERENCES

EZEKIAL, M., and FOX, K. A., 1959. *Methods of correlation and regression analysis.* 3rd edit., J. Wiley & Son, New York.
FERRARI, T. J., 1963. Causal soil-plant relationships and path coefficients. *Plant and Soil* 19: 81–96.
FERRARI, T. J., 1964. Auswertung biologischer Kettenprozesse mit Hilfe von Pfadoeffizienten. *Biomet. Zeit.* 6: 89–102.
TUKEY, J. W., 1954. Causation, regression, and path analysis. In *Statistics and Mathematics in Biology*, O. Kempthorne, T. A. Bancroft, J. W. Gowen, and J. L. Lush (eds.). Iowa State College Press, Ames.
TURNER, M. E., and STEVENS, C. D., 1959. The regression analysis of causal paths. *Biometrics* 15: 236–258.
WRIGHT, S., 1934. The method of path coefficients. *Ann. Math. Statist.* 5: 161–215.

DRY SPELLS IN NEW ZEALAND AS A FACTOR IN PLANT ECOLOGY

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Although most of New Zealand receives a rainfall which is sufficient in total amount to meet the needs of plants, in most places spells of deficient rainfall of varying lengths have significant effects on vegetation. For example, after a few weeks without rain in summer or autumn the growth of pasture is frequently reduced to such an extent that dairy production declines. In the Kaingaroa area, pine trees were adversely affected after four very dry months in the summer of 1945-46 (Rawlings 1961) although they were apparently not harmed in the 1963-64 summer when two periods of approximately five weeks with negligible rain caused severe farm losses. The distribution of indigenous species and of natural plant communities depends in part on the incidence of dry spells—either directly, on account of differences in drought tolerance; or indirectly, through such effects as increased risk of forest fire when summer droughts are frequent. For full understanding, such topics must be examined in terms of water relationships of individual plants or of plant associations in their particular climatic environment. Nevertheless, a broad-scale comparative study of the occurrence of dry spells should provide a useful background for any detailed ecological study.

Precipitation is very irregularly distributed in space and time, and the statistical treatment of the data poses many problems quite apart from that of obtaining representative samplings in mountain areas. A frequency curve of rainfall totals approaches a symmetrical normal distribution as the unit period of observations is increased. In New Zealand, annual rainfall distributions are only slightly skew, monthly rainfalls show a moderate degree of skewness which increases with the degree of variability, whereas daily falls and the interval between rain days have a highly skew or L-shaped distribution. Representative annual rainfall distributions for a number of New Zealand stations demonstrate that in the driest parts of Central Otago annual rainfall is always well below the year's water requirements of vegetation. In low rainfall areas such as Hastings, the rainfall total is deficient in about 50 per cent. of years, but in most of the country the annual totals almost invariably exceed the year's water need.

Statistics of monthly rainfall totals have been widely published and studied. For example Seelye (1946) shows that in areas of highly variable rainfall near the east coast of the North Island, dry months are much more frequent than in western areas with similar average rainfall. Monthly rainfalls characteristically show very wide scatter, for example at Hermitage in February the median rainfall is approximately 10 inches, but extremes of less than one inch and more than 40 inches have been recorded. (Fig. 1). Practically all New Zealand stations experience some months, mostly in the warm half of the year, when rainfall is well below the water needs of plants (about four inches per month in summer).

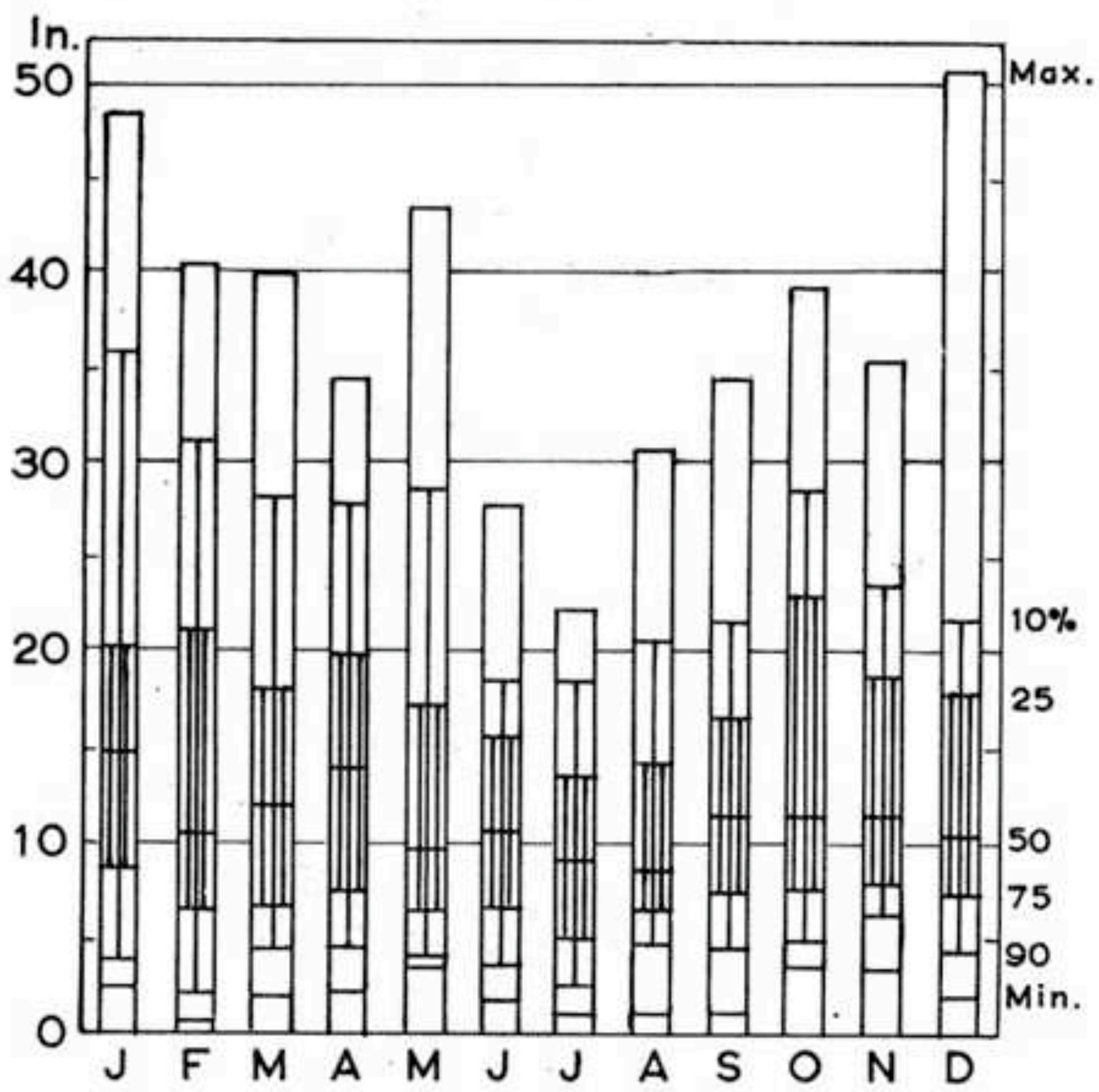


FIGURE 1. *Monthly rainfall totals at Hermitage (Mt. Cook). Rainfall exceeded in 90, 75, 50, 25, and 10 per cent. of years, and highest and lowest recorded fall. (1901–1964).*

Climatologists have used many criteria for drought for agricultural application. For example, "Absolute Drought", is defined as a period of at least 15 days without rain, and "Partial Drought", a period of at least 29 days with rainfall averaging not more than 0.01 inches of rain per day. Their occurrence in New Zealand has been discussed by Bondy (1950).

The frequency of rain-free intervals of different durations and of partial droughts is illustrated for a few contrasting stations in Table 1.

TABLE 1. *Average number of days per year falling within (a) a rain-free period of at least n days (n = 1, 5, 10, 15, 20) (b) a "partial drought".*

	a					b
	1	5	10	15	20	
Lake Rotoiti (Nelson) (1958-1965)	200	110	40	10	0	0
Milford Sound (1955-1964)	160	80	20	0	0	0
Hermitage (Mt. Cook) (1955-1964)	210	125	50	20	5	0
Wellington (1863-1913)	200	100	30	5	2	20
Nelson (1862-1880, 1907-1947)	240	—	—	35	—	35
Christchurch (1864-1880, 1904-1947)	235	—	—	25	—	60

(— not available)

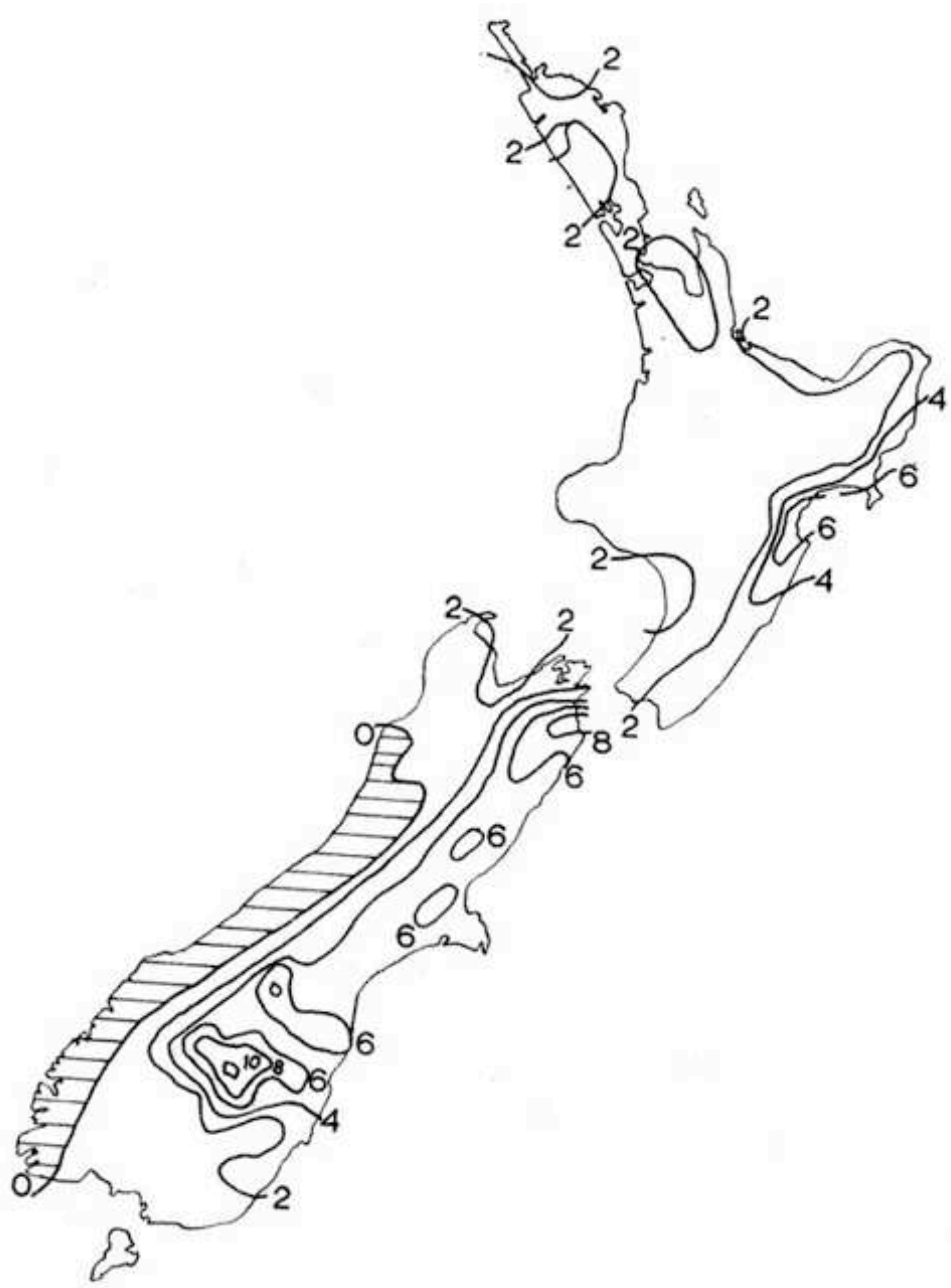
Partial drought is a useful index for agricultural application in New Zealand but the value of parameters of this kind is limited in that they do not take account of the current water needs of plants (which may be four times as great in summer as in winter) or initial conditions of the soil and vegetation resulting from past weather.

Water used by plants is derived from soil moisture accessible to roots and in general is supplied by rain. Some rain water is lost as run-off or drainage in wet weather. The remainder may be termed "effective rainfall". If plants are never to undergo a restriction of moisture supply the effective rainfall must be sufficient to balance potential evapotranspiration, i.e. the moisture which would be lost by evaporation and transpiration from a well-watered vegetation cover.

Since these losses are determined primarily by meteorological conditions, it is possible to calculate from measurements of precipitation and other meteorological elements the day-to-day changes in soil moisture and so determine more precisely periods of effective drought, irrigation requirements and so on. This method has been developed by many agricultural climatologists and others in recent years (Thornthwaite and Mather 1955, Gabites 1956). Parameters for drought derived in this way have potential uses in ecology as well as in agriculture. "Meteorological Drought", defined as "a prolonged and abnormal moisture deficiency", was used in studies of droughts in Kansas and Idaho where severe droughts have sometimes persisted for several years (Palmer 1965). "Agricultural Drought" was used by Rickard (1960) in assessing irrigation needs of pasture at Ashburton where dry periods commonly last for several weeks or months but seldom persist throughout winter. It was defined as "a period when (calculated) soil moisture in the root zone was at or below wilting percentage, ending when rain fell in excess of daily evapotranspiration". For the pasture-soil combination studied by Rickard the available soil moisture capacity was approximately two inches.

A broad survey of drought incidence and irrigation need (or water deficiency) in New Zealand has been made on the basis of a simplified water balance using monthly rainfall totals, arbitrarily-chosen soil moisture capacity constants (S), and average potential evapotranspiration or water need values (PE) estimated by Thornthwaite's method. Punch-card data from about 200 rainfall stations have been analysed and maps drawn showing the approximate distribution of several derived parameters. Only approximate results suitable for making broad comparisons may be obtained in this way because of the unrealistic assumptions involved, and because dry spells of short duration may not be reflected in monthly data.

Figure 2 shows the average annual moisture deficit or irrigation need for S = 2 inches. This is obtained by summing the individual monthly deficits in "years" taken from July to June.



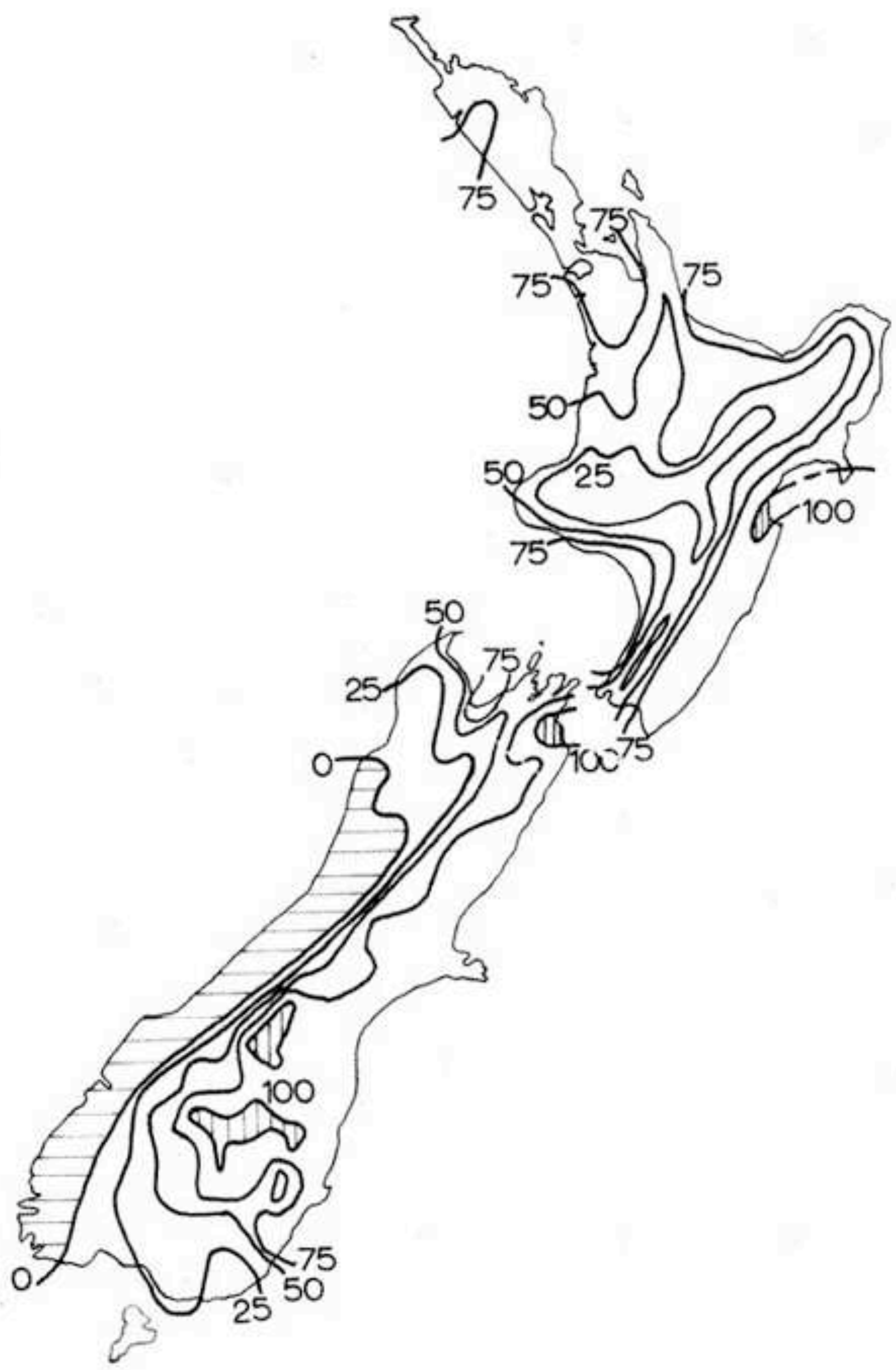


FIGURE 2. *Average annual water deficit in inches. (S = 2").*

FIGURE 3. *Percentage of years with water deficits in at least one month. (S = 2").*

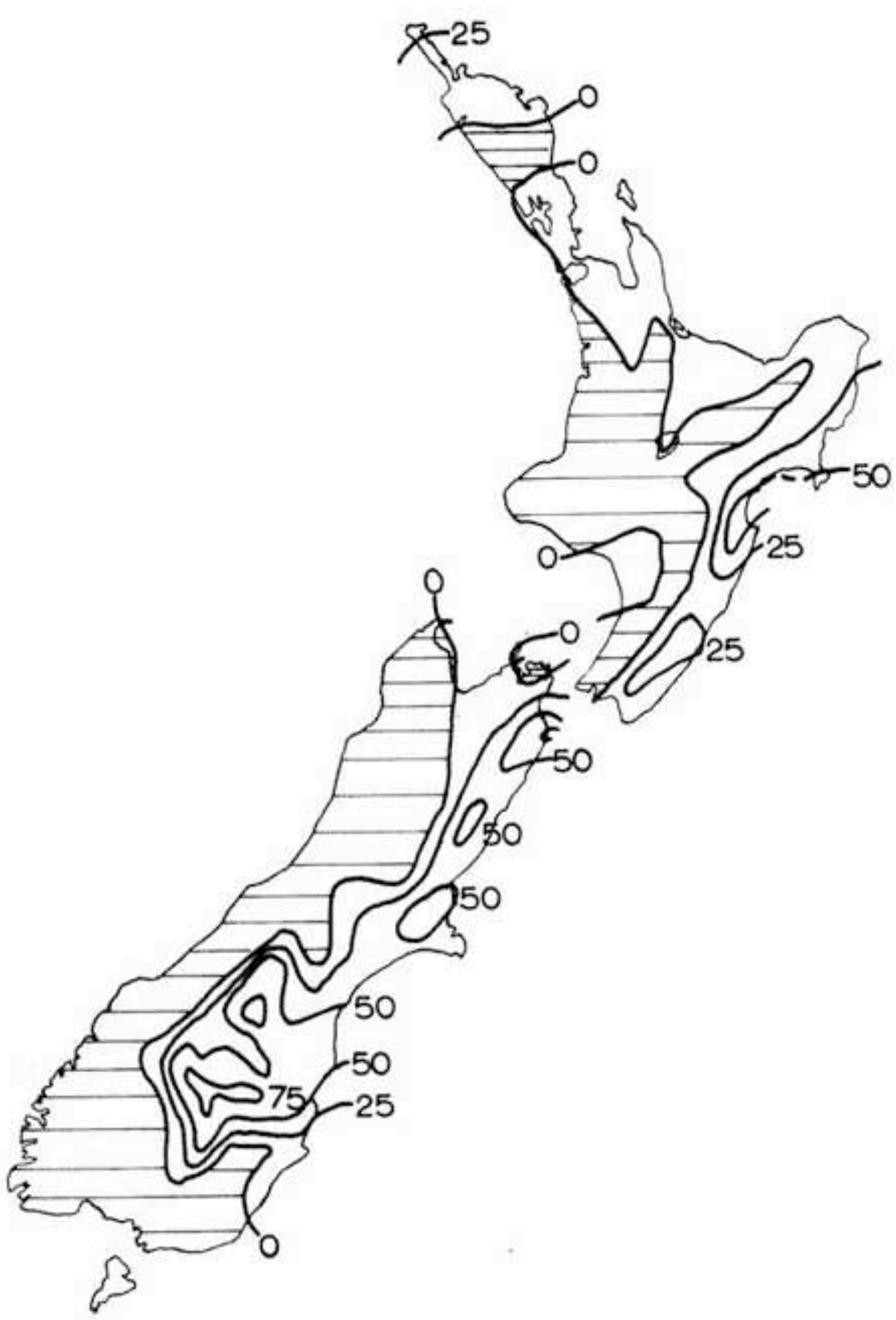


FIGURE 4. *Percentage of years with annual water deficit of 6 inches or more.* ($S = 2''$).

Deficits are found throughout New Zealand except Westland and some other mountain areas. They average more than 10 inches per year in parts of Central Otago and exceed six inches in small areas of Hawke's Bay, Marlborough and Canterbury. Figure 3 shows the percentage frequency of years with a deficit in at least one month. This is high (more than 80 per cent) in eastern districts from Otago to Gisborne and in parts of Nelson, Manawatu, Waikato and Northland. Prolonged dry periods are most frequent in North and Central Otago, Canterbury, Marlborough and near the East Coast of the North Island. In these areas deficits persist for three consecutive months or longer in at least 50 per cent. of years. Such long periods of deficient moisture supply are not common in the west and south of the South Island or in most of the North Island. Figure 4 shows the percentage frequency of large deficits (six inches or more). A noteworthy feature of the maps is the rapid transition between Southland and Otago. Moisture deficits tend to be greatest and most frequent in January, and in most places are seldom found in winter or early spring. (Fig. 5.)

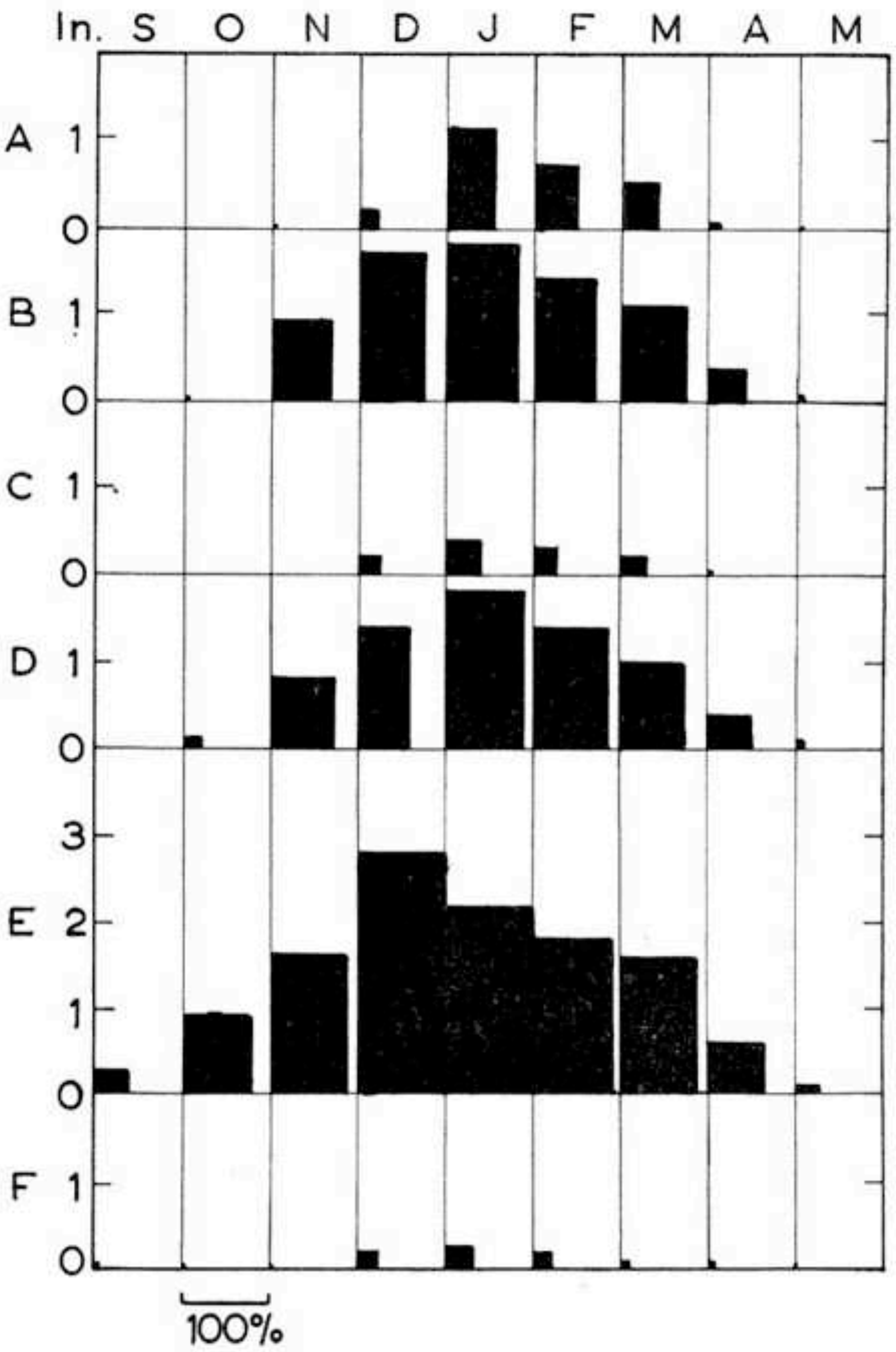


FIGURE 5. *Monthly water deficits.* ($S = 2''$). *A Auckland; B Hastings; C Wellington; D Christchurch; E Alexandra; F East Gore. (The height of a column represents the average deficit amount, its width is proportional to the percentage frequency of occurrence of deficits.)*

In very humid climates, such short dry periods as occur are of little importance to most plants because sufficient soil moisture is usually available. For such plants as cannot draw on stored moisture to any extent, however, even the Westland climate provides some periods of moisture stress in summer when transpiration rates are at their maximum. To identify these periods from the climatological record details of the daily observations would have to be examined.

REFERENCES

BONDY, F., 1950. Droughts in New Zealand, *N.Z.J. Sci. Tech.*, 32B: 1–10.

GABITES, J. F., 1956. Estimation of natural evaporation and water need. Proc. Conf. on Soil Moisture Sept. 1954. *N.Z. D.S.I.R. Inf. Ser.* No. 2: 128–130.

PALMER, W. C., 1965. Meteorological drought. *U.S. Weather Bureau Res. Paper* No. 45.

RAWLINGS, G. B., 1961. Entomological and other factors in the ecology of a *Pinus radiata* plantation. *Proc. N.Z. Ecol. Soc.* 8: 47–51.

RICKARD, D. S., 1960. The occurrence of agricultural drought at Ashburton, New Zealand. *N.Z.J. Agric. Res.*, 3: 432–41.

SEELYE, C. J., 1946. Variations of monthly rainfall in New Zealand. *N.Z.J. Sci. Tech.*, 27B: 397–405.

THORNTHWAITE, C. W., and MATHER, J. R., 1955. The water balance. *Publ. Climatol. Drexel Inst. of Tech., Lab. of Climatology*, 8 (1).

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.