

COMPETITION EFFECTS ON YIELD AND PLANT AND TILLER DENSITY IN MIXTURES OF RYEGRASS CULTIVARS

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SUMMARY: The ryegrass cultivars, Grasslands Manawa and Grasslands Ruanui, were grown in simulated swards in replacement series under systems involving a 2×2 arrangement of height and frequency of cutting.

Estimates of plant survival at two dates indicate greater overall mortality in the Manawa population. In the earlier part of the experiment the death of Manawa, and of Ruanui plants — particularly when mixed with Manawa — was greater under infrequent than frequent cutting. This effect is mainly attributed to competition for light excluding more prostrate individuals. In the later period drought was probably the important factor determining the survival of plants, with Manawa plants of small size and at high densities being most susceptible.

Examination of the frequency distribution of tiller number per plant at three sampling dates showed trends similar to those obtained by Koyama and Kira (1956). The frequency distributions were approximately normal at the earliest sampling date but became progressively more skewed towards L-type distributions later. The skew was more pronounced for Manawa and was emphasised for Ruanui when it was the minority component in mixture with Manawa. Infrequent cutting promoted the development of a skewed distribution.

Changes in the relative reproductive rate of the cultivars with change in the proportion of the cultivars in the mixtures were examined by the use of ratio diagrams. These indicated a general trend of greater relative reproductive rate of Manawa when it was sown at a ratio low in comparison with the intermediate seeding ratio. Thereafter the relative reproductive rate remained constant or increased at higher seeding ratios of Manawa.

INTRODUCTION

In grazed pastures individual ryegrass plants usually lose their identity. When this occurs 'the rooted tiller often becomes the ecological unit' (Mitchell 1954). Because of this, the readily recognisable tiller, rather than the plant, is usually the unit used in determining the density of grass species in pastures. The sampling procedures described by Mitchell and Glenday (1958) in which a circular plug of 20.3 sq. cm. is removed from the sward have been widely applied in New Zealand in recent years. Although earlier evidence suggested that the tiller was a physiologically independent unit the studies of Marshall and Sagar (1965, 1968a, 1968b) have shown that the grass plant is a highly integrated organism, the interdependence of tillers being particularly marked where defoliation occurs. Furthermore the size of a plant may affect its survival under stress. (Hoen 1968).

The stimulated sward technique (e.g. Gardner 1960, Rogers and Lazenby 1966) enables the separation of plants of similar appearance in swards. This technique is particularly useful with ryegrass in swards that are being cut, since the species' tufted habit and low rate of horizontal spread allows the identification of tillers derived

from single seedlings or ramets for a long time after a closed sward or maximum tiller density has been attained. However, the bulk of the data obtained from experiments using this technique have expressed yield and yield components in terms of unit area. Much additional information on the structure of the sward population may be obtained if the yield components are recorded in terms of individual plants. For the understanding of plant competition the importance of individual plant measurements has been stressed by Black (1966) who accepts the definition of competition given by Clements (1904). Black stated that competition involves, (a) the modification of the environment by the presence of a plant, and (b) the effect of these modifications upon surrounding plants. Black concluded that although the results of interaction between individual plants may be expressed at the population and species level the term 'competition' should be restricted to the interaction between individual plants.

EXPERIMENTAL

Data discussed in this paper were obtained from an experiment designed to study competition between the ryegrass cultivars, Grasslands Ruanui perennial ryegrass (*Lolium perenne* L.) and Grasslands Manawa ryegrass (*L. multiflorum*

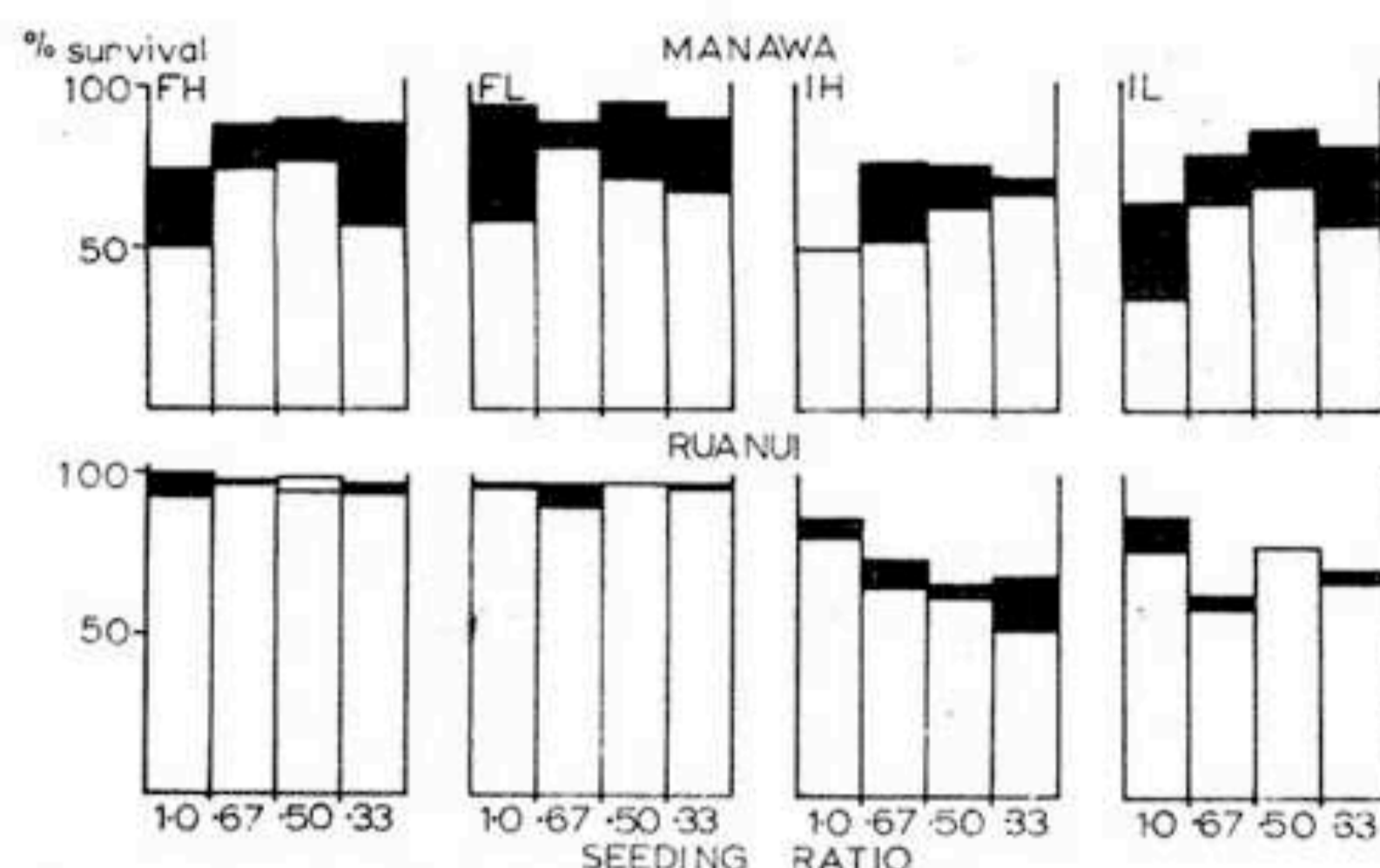


FIGURE 1. Survival of *Manawa* and *Ruanui* plants at four seeding ratios under four cutting systems at two dates. The shaded portion of the bars in the histograms indicate the % reduction of surviving plants between the sampling dates on 7 February and 14 June 1967. FH=frequent hard, FL=frequent lax, IH=infrequent hard and IL=infrequent lax cutting systems.

Lam. x *L. Perenne* L.). Full details of experimental procedure are given in Harris and Thomas (1970). Simulated swards were established at a seedling density of 169/m², and formed a replacement series of *Manawa* to *Ruanui* of 1.0 (M.1.0), 0.67 (M.67 R.33), 0.50 (M.50 R.50), 0.33 (M.33 R.67) and 0 (R.1.0). Cutting treatments were applied as a 2×2 arrangement of height (2 cm. and 8 cm. for the cuts following establishment in early April 1966 until late September 1966, thereafter all plots were cut to 6 cm.) and frequency (frequent plots cut twice as often as infrequent plots). The cutting frequencies were continued until August 1967, after which a common cutting treatment was applied until completion of the experiment in late March 1968.

RESULTS AND DISCUSSION

Plant survival

Counts were made on 7 February and 14 June 1967 of the numbers of surviving plants. Data are plotted in Figure 1 for the percentage surviving for each cultivar as they were sown in the seeding ratios of 1.0, 0.67, 0.50 and 0.33 under each of the four cutting systems. The following effects are indicated:

(1) Overall treatments and seeding ratios there was a smaller survival of *Manawa* plants than *Ruanui*.

(2) Few deaths of *Ruanui* plants occurred under frequent cutting. However, with infrequent

cutting a considerable number of *Ruanui* plants died and this was particularly so when *Ruanui* was growing with *Manawa*. Most of the *Ruanui* deaths occurred before the February sampling.

(3) Infrequent cutting and, to a smaller extent, hard cutting—particularly when combined with infrequent cutting—increased the death of *Manawa* plants in the period up to February. However, treatments with the greatest survival in February showed greater mortality in the interval to June. Consequently, by June there was no difference between cutting heights and the difference between cutting frequencies was smaller.

(4) In June, for all cutting systems, the survival of *Manawa* plants was less in monoculture than in mixture with *Ruanui*. This difference was more apparent for the infrequent than the frequent cutting systems, and was also shown in February for the hard as compared to the lax systems.

(5) There is a contrast between the survival of *Manawa* in mixture with *Ruanui* when the infrequent hard cutting system is compared with the other cutting systems. In the former there is progressively increasing survival of *Manawa* with decreased seeding ratio; whereas in the latter the survival at seeding ratio 0.33 was less than at the 0.50 and 0.67 ratios. This difference was established in the interval between February and June, during which there was a progressive change towards the dominance of *Ruanui*, particularly in the frequent cutting systems and the infrequent lax system.

Considering the climate of the experimental site and the seasonal development of the cultivars, it is possible to distinguish two sets of factors which caused the death of plants:—

(a) Competition for light resulted in the death of more prostrate individuals. Growth rates were high for both cultivars up to the February count. During the spring–early summer period increased yields were obtained, particularly for *Manawa*, with infrequent cutting (Harris and Thomas 1970). As infrequent cutting accentuated the height difference between *Manawa* and *Ruanui*, prolonged shading of *Ruanui* plants mixed with *Manawa* resulted in the weakening and sometimes the death of these plants. This was not restricted to an inter-cultivar effect, as intra-cultivar exclusion of more prostrate individuals is shown by the lower survival of plants in the monocultures of both *Ruanui* and *Manawa* under infrequent, as opposed to frequent, cutting. The greater effect for

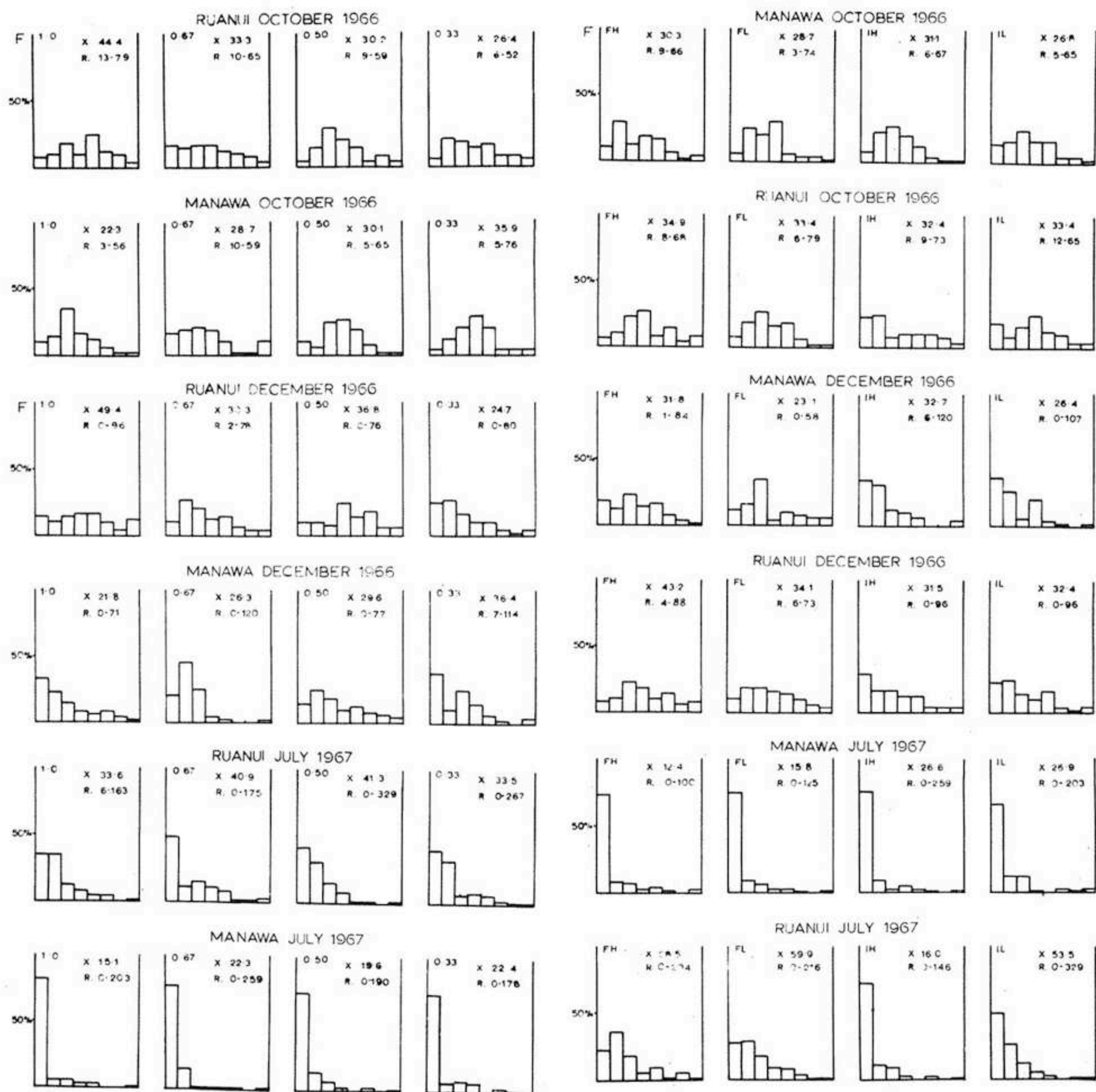


FIGURE 2. Frequency distributions of tiller numbers per plant, shown separately for the cultivars *Manawa* and *Ruanui* as these were sown in four ratios in replacement series. Samples were obtained on three dates. \times = mean tiller number per plant, R = range of per plant tiller number in each population.

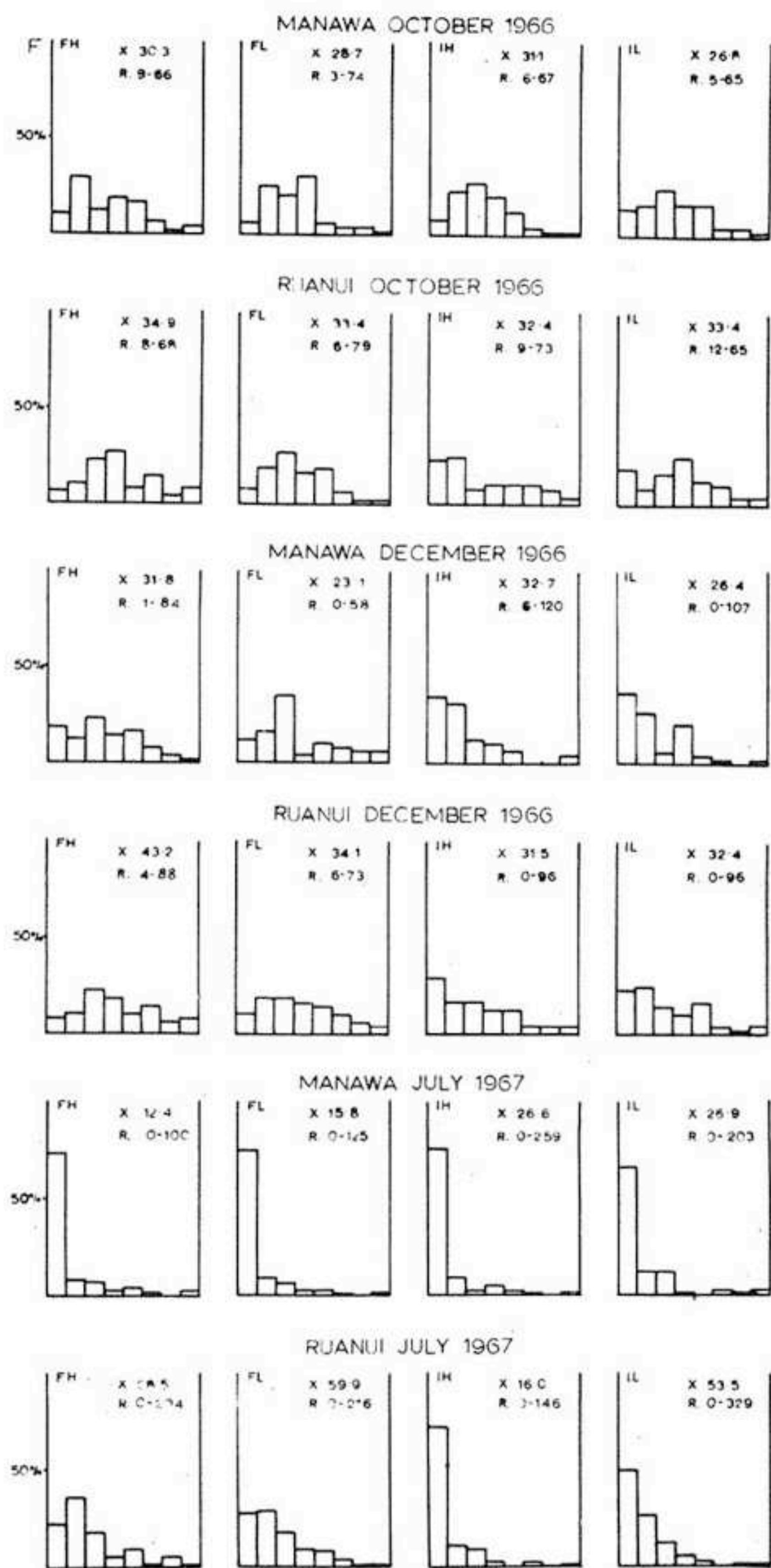


FIGURE 3. Frequency distributions of tiller numbers per plant, shown separately for the cultivars *Manawa* and *Ruanui* as these were grown under four systems of cutting. Cutting systems are: FH = frequent hard, FL = frequent lax, IH = infrequent hard, IL = infrequent lax, \times = mean tiller number per plant, R = range of per plant tiller number in each population.

Manawa may be attributed to the greater range of habits in this cultivar which derive from its hybrid origin, whereas Ruanui is mono-specific.

(b) Following the February count, growth rates were markedly reduced, especially for Manawa, until the onset of the 'autumn flush growth' beginning in April. During this period the critical factor determining plant survival was probably the availability of water and the effect of this was accentuated by heat stress. It has been demonstrated that Manawa is more susceptible to these stresses than Ruanui (Lucanus *et al.* 1960). The data imply that when surviving Manawa density was high at the beginning of the 'drought period', then the individual plant susceptibility to drought or heat was greater (compare cuttings FH, FL and IL with IH). This can be related to the general conclusion that as the water deficit increases, the plant density at which water stress occurs decreases (Donald 1963). However, the effects of plant size *per se*, could have been equally important in determining plant survival during the 'drought period' (Hoen 1968). This is indicated by the relatively better survival of Manawa plants in mixture with Ruanui than in monoculture. This relationship is complicated by the depressed survival of Manawa at seeding ratio 0.33 in the cutting systems; in these Ruanui clearly became dominant during the summer. It is likely, under these systems, that when the content of Ruanui was high at the seeding ratio R.67 M.33, growth of Ruanui and consequent demand on the supply of water subjected Manawa plants to more water stress than when the content of Ruanui was low either at high seeding ratios of Manawa, or when the cutting system (IH) had markedly reduced the content of Ruanui at all seed ratios.

Frequency distribution of tiller numbers per plant

Tiller numbers per plant were counted at intervals during the first 15 months. Three of these samples were examined in a way proposed by Koyama and Kira (1956). The frequency distributions drawn are based on eight classes with the class interval given by

$$\frac{1}{n} [(W_{\max.} + \alpha) - (W_{\min.} - \alpha)]$$

where n is the number of classes, $W_{\max.}$ and $W_{\min.}$ are the maximum and minimum plant tiller number and α is a small number (0.5) which prevents the observed values from falling on the border between classes.

Frequency distributions are shown separately for the varieties Manawa and Ruanui and comparisons are drawn between, (1) the seeding ratios combined for all cutting systems (Fig. 2), and (2) the four cutting systems over all seeding ratios (Fig. 3). The frequency distributions were constructed from data obtained from 48 planting positions for the October and December samples and 72 planting positions for the July sample.

The results of these observations are very similar to those obtained by Koyama and Kira (1956):—

(1) The frequency distribution of individual plant size (tiller number) is approximately normal in the early stages following sward establishment, but becomes progressively more skewed with time until the mode is the class of smallest plant size. Thus the change is from a normal to an L-shaped or log normal distribution (Koyama and Kira 1956).

(2) Koyama and Kira observed that usually the appearance of the L-type frequency distribution is earlier the higher the plant density. As increased plant density results in an increase in the rate and extent of interference between plants (Kira *et al.* 1953), when the magnitude of interference, per plant, of a species or cultivar is greater than that of another, then the development of a skewed size distribution at equivalent density should be more rapid when the first species is the predominant component of a community. In the period up to the December count Manawa was clearly the more competitive of the two cultivars; and the well-defined skewed distribution which had developed in the Manawa monoculture (as compared to the mixtures with Ruanui) is a consequence (Fig. 2). Furthermore, the most skewed distribution of Ruanui tiller plant number in December, as affected by seeding ratio, occurred when Ruanui (0.33) was sown with the highest proportion of Manawa (0.67).

The July frequency distributions for Manawa imply the same effects, in that the occurrence of individual tiller numbers in the left-hand class decreases with decreasing seeding ratio of Manawa. The earlier effect of Manawa dominance results in the more skewed distribution of Ruanui when it is mixed with Manawa than when it is in monoculture. However, in the mixtures there is a trend of increasing skewness of Ruanui from seeding ratio 0.33 to 0.67. As Ruanui became dominant between December and July, interference from Ruanui plants would have been

greater than that from Manawa plants. Consequently, a readjustment of the frequency distribution of Ruanui towards a greater skewness as the proportion of Ruanui in the swards increased could be expected.

Infrequent cutting promoted the degree of inter-plant interference in Manawa itself and between Manawa and Ruanui (Harris and Thomas 1970), so that by December skewed frequency distributions had developed with this type of cutting. However, although there was a clear distinction between frequent and infrequent cutting for the frequency distributions of Ruanui in July, it was not distinct for Manawa in which the least skewed distribution occurred for infrequent lax cutting. This arose from drought-induced mortality in the Manawa populations which, as shown previously, was related to density and size of plant prior to the period of water stress.

(3) The results confirm the conclusions of Koyama and Kira (1956) that the early appearance of a L-type frequency distribution is associated with a high mortality of plants caused by self-thinning.

Cutting effects on the relative reproductive rate

The reproductive rate (or replacement rate) of a species is the number of seeds (tillers, yield) harvested (O) at the end of a growing period (ideally a year), divided by the number of seeds sown or tillers or yield (Z) at the beginning of the growing period. The relative reproductive rate (or relative replacement rate) of Species 1 (S_1) with respect to Species 2 (S_2) is equal to the ratio of the reproductive rates of S_1 and S_2 , i.e.

$$RRR = \frac{O_1/Z_1}{O_2/Z_2}$$

The use of the ratio diagram devised by de Wit (1960), in which the ratio $\frac{Z_1}{Z_2}$ of the sown mixture

is plotted against the harvested mixture O_1/O_2 on a log-log scale, allows one to distinguish several competitive situations related to the constancy of the relative reproductive rate to the botanical composition of the mixture. For the purpose of the present discussion three of the situations are briefly distinguished here:

(1) The relative reproductive rate is constant regardless of the botanical composition of the mix-

ture. In this case the plots of $\log \frac{O_1}{O_2}$ against $\log \frac{Z_1}{Z_2}$ lie on a line with a slope of 45° .

(2) The relative reproductive rate changes with the botanical composition of the mixture in such a way that it is high when the species occurs in a small proportion in the mixture and is low when the species forms a large proportion. Because of this the botanical composition of the mixture moves towards an equilibrium. The plotted line has a slope $< 45^\circ$.

(3) The relative reproductive rate changes with the botanical composition of the mixture so that it is relatively low when the species forms a small

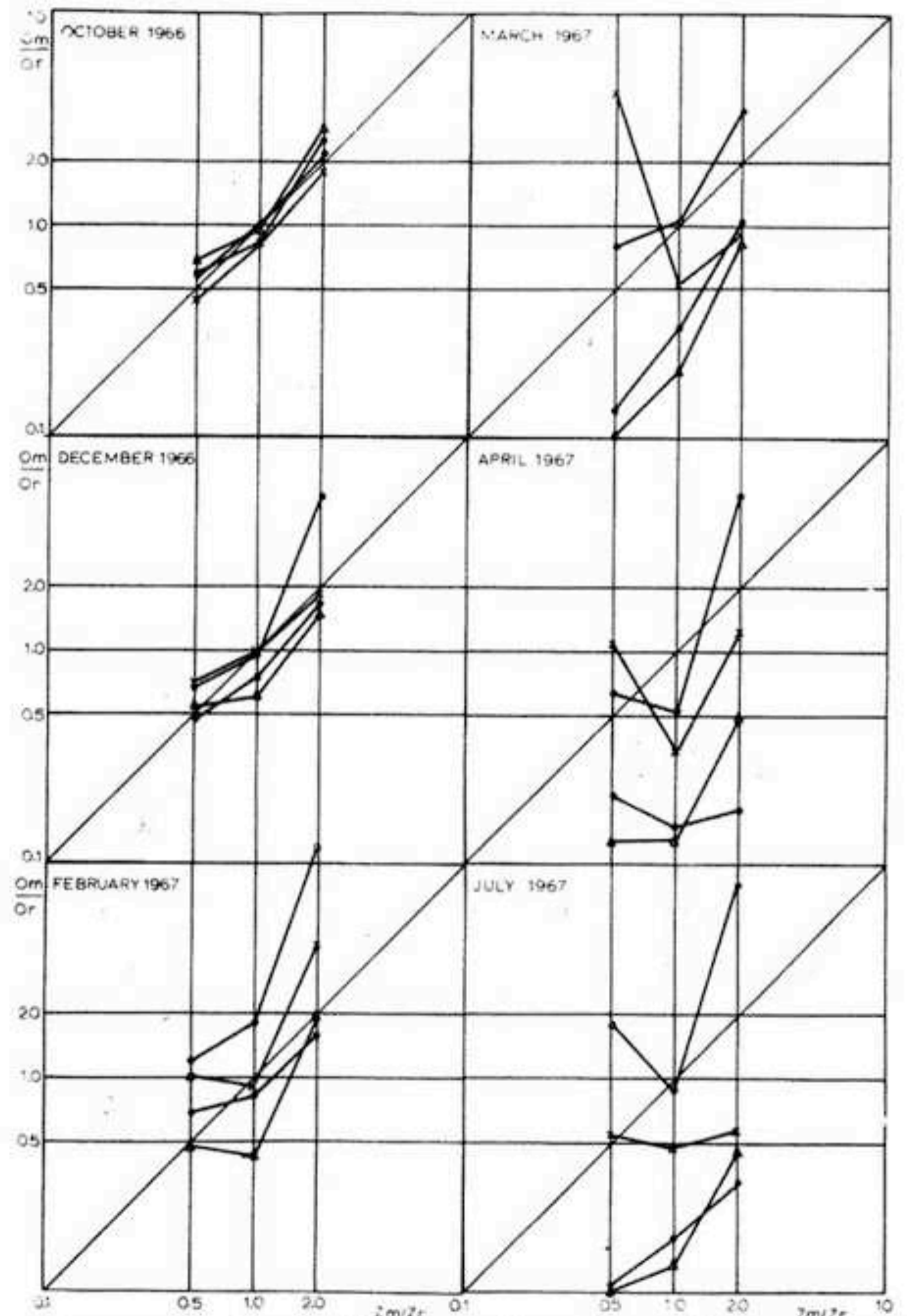


FIGURE 4. Ratio diagrams based on tiller numbers of Manawa and Ruanui at six sampling dates as affected by four cutting systems: Δ frequent hard cutting; \bullet frequent lax cutting; \circ infrequent hard cutting; \times infrequent lax cutting.

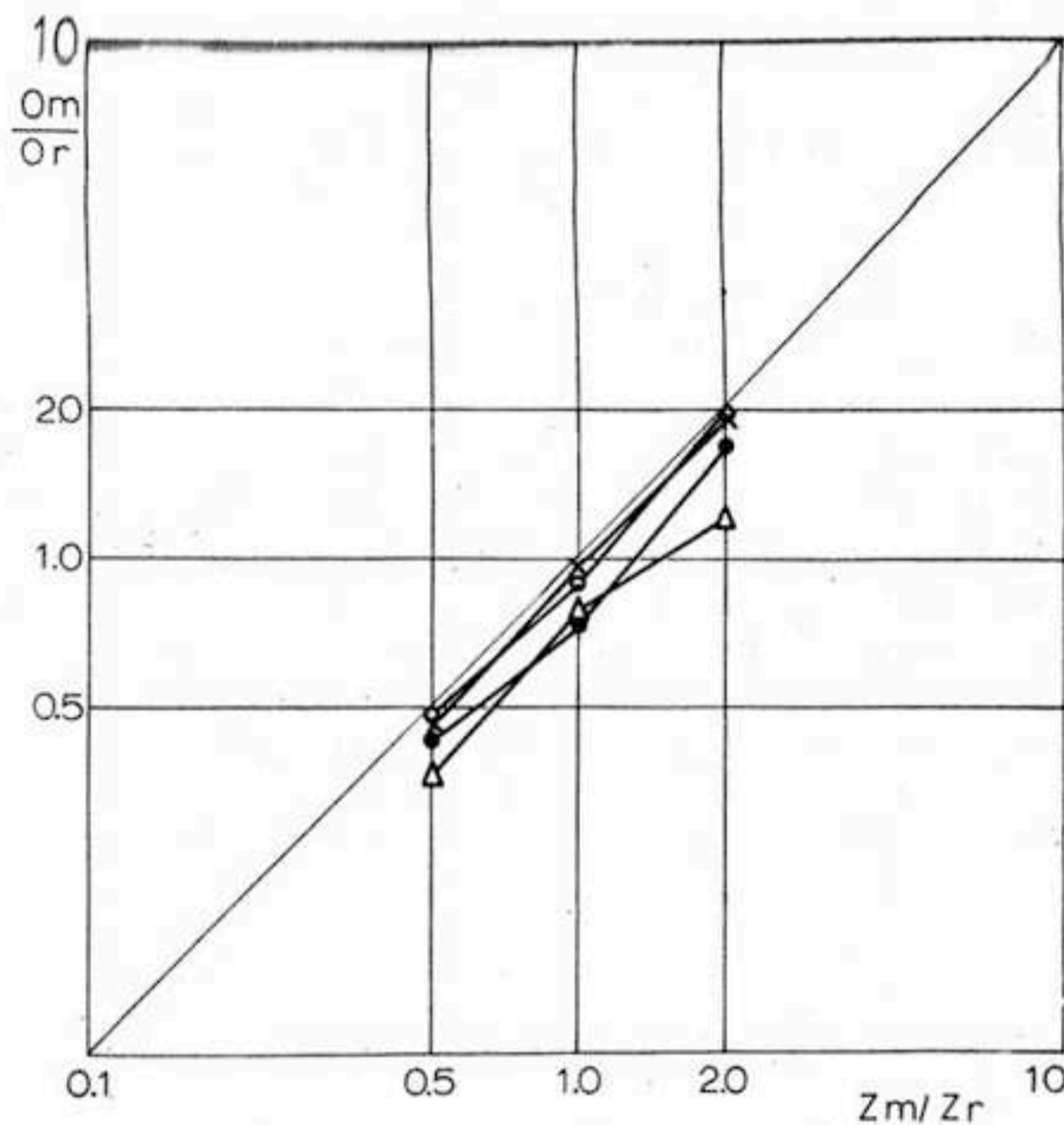


FIGURE 5. Ratio diagram based on plant numbers of Manawa and Ruanui in June 1967 as affected by four cutting systems: Δ frequent hard cutting; \bullet frequent lax cutting; \circ infrequent hard cutting; \times infrequent lax cutting.

proportion of the mixture and is high when the species forms a large proportion. Here, the observations on the ratio diagram are on a line with a slope $>45^\circ$ so that, depending on the proportional occurrence of the species in the mixture, the mixture changes in direction opposite to an intermediate botanical composition.

Data obtained from the present experiment for tiller numbers, plant numbers and yields have been plotted in ratio diagrams. No attempt has been made to adjust for the size difference of tillers and plants between Ruanui and Manawa (generally larger plants with large loosely arranged tillers), as both undoubtedly varied with cutting treatment and, possibly, with the seeding ratio. Thus the degree of dominance of Manawa is underestimated on the ratio diagrams derived from tiller (Fig. 4) and plant number (Fig. 5) data, but this is not so for the yields (Fig. 6).

Although the accuracy of the information derived from the ratio diagram is limited both by the range and number of seeding ratios, the consistent trend in the slope of the plotted lines probably indicates a competitive situation not previously elucidated by de Wit. The trend, which

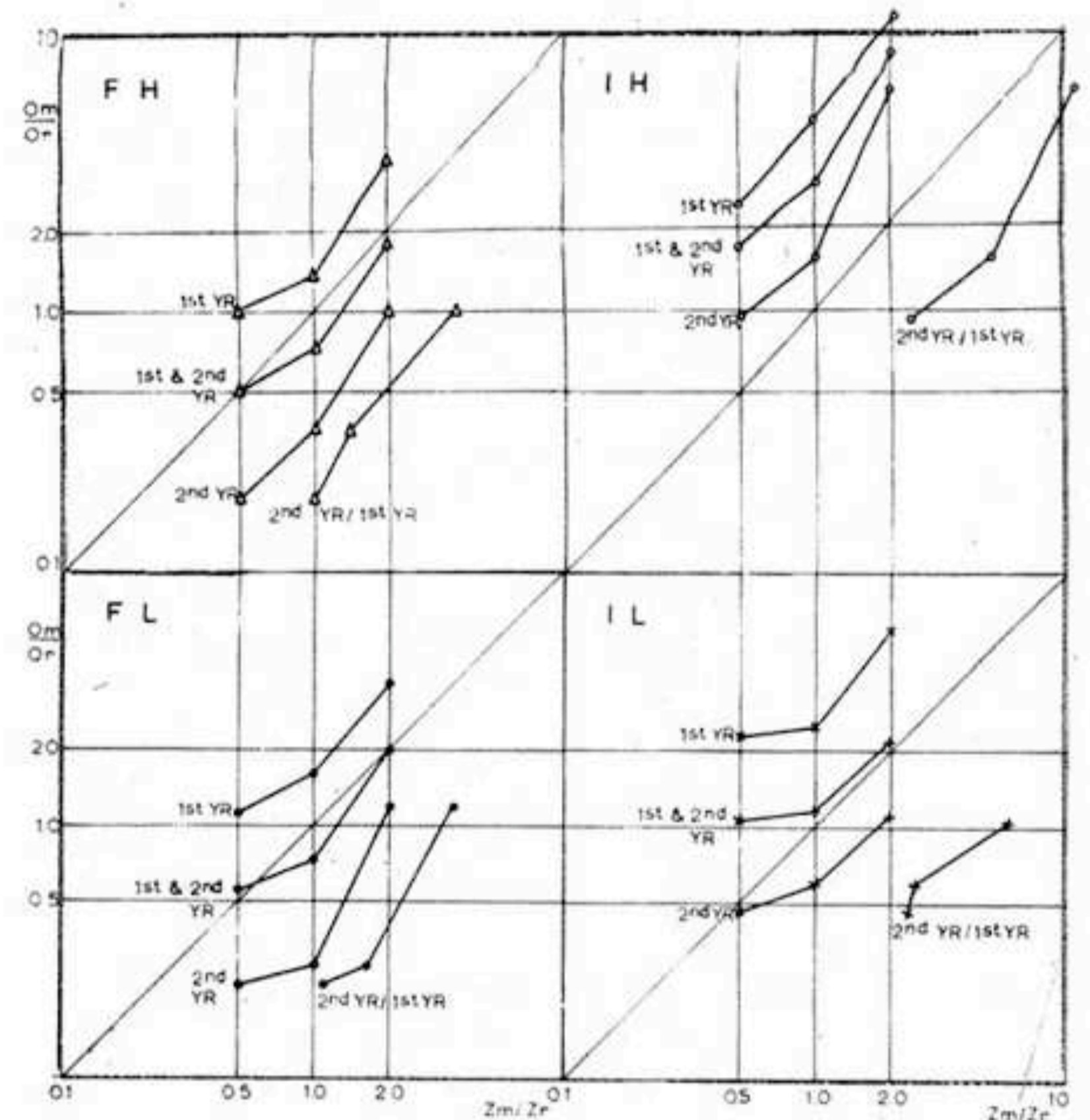


FIGURE 6. Ratio diagrams based on yields of Manawa in the first year, second year and for two years. The yields of the second year are also plotted against the yields of the first year.

is not shown for the more inflexible yield component of plant numbers, is as follows:

(1) The relative reproductive rate of Manawa relative to Ruanui is higher at the seeding ratio of M.33 R.67 than at the M.50 R.50 ratio. Hence the line joining the two ratios is $<45^\circ$, which indicates a decreasing rate of increase of Manawa relative to Ruanui with change of the cultivar composition towards a 50/50 mixture.

(2) Between the seeding ratios M.50 R.50 and M.33 R.67 the reproductive rate of Manawa relative to Ruanui either approximates a constant value or increases; i.e., the line is either close to 45° or is $>45^\circ$.

The causes of these results may have been as follows:

(1) When the seed ratio of Manawa was low (M.33 R.67), the taller Manawa plants would have been subjected to considerable lateral illumination because of the spacing between double rows of prostrate Ruanui plants. This would lead to greater photosynthesis of the entire Manawa plant. More growth and a greater demand on the mineral nutrient and, possibly, water supply by Manawa would impose stress on Ruanui plants for these factors.

(2) With increasing content of Manawa in the swards, mutual shading would reduce the amount of lateral illumination of Manawa plants. Furthermore, leaf in the lower layers of the canopy would be increasingly shaded and the situation could arise in which more prostrate plants (i.e. Ruanui in particular) would be below the compensation point. At this point these heavily shaded plants might have shown either a threshold response of rapid yield and tiller number reduction through an increased susceptibility to fungal attack (Grime 1965) or the attainment of a biomass for individual tillers below which normal physiological processes were not possible. Under these circumstances the unshaded plants (Manawa) would show an apparent increase in reproductive rate relative to the shaded plants (Ruanui) because of a marked reduction in yield and tiller number in the latter.

(3) The previously-implied greater survival of large plants under drought stress may have contributed to the greater reproductive rate of Manawa at the low—as opposed to the medium-seeding ratio.

(4) Although not demonstrated experimentally, a $>45^\circ$ slope has been invariably attributed to a toxic effect of one species on another (de Wit 1960). However, it is unlikely that the secretion of a toxin affected the course of competition between the cultivars in the present study.

The yield data plotted in the ratio diagrams of Figure 6 demonstrate that the reproductive rates of Manawa compared to Ruanui decreased in the second year so that, under all cutting systems except infrequent-hard, Ruanui was dominant when second year yields were plotted against the initial seeding ratios. This change to dominance of Ruanui in the second year is emphasised if the yields of the second year are plotted against those of the first year. Although this is not an entirely satisfactory procedure, for reasons stated by de Wit and van den Bergh (1965), it gives an indication of the inconstancy of the relative reproductive rates in a perennial sward from year to year. The changes of the reproductive rates between the years can be attributed to:—

(1) The application of a common cutting treatment to all swards for most of the second year. This was closer to the frequent than the infrequent cutting system of the first year and was more conducive to the dominance of Ruanui than Manawa.

(2) The dominance of Manawa in the first year was largely a function of the greater rate of seedling establishment and seedling growth of Manawa relative to Ruanui. This effect was absent in the second year.

(3) The abundance of a species relative to another at the end of an annual cycle may have little relationship to the total yields of the species during the preceding year. In the present experiment, although Manawa dominated the yields of the mixtures, its abundance at the end of the year was reduced in relation to Ruanui both by its comparative intolerance of drought and by a greater input of biomass into reproductive rather than vegetative growth. This effect is, in part, the basis of the objection by de Wit and van den Bergh (1965) to the use of yields of dry matter to compare reproductive rates in stands of perennial herbage.

CONCLUSION

One of the problems of lax-rotationally grazed pastures is the general reduction of tiller numbers, particularly as this is accentuated by the clumping of the surviving tillers (Mitchell and Glenday 1958; Harris and Brougham 1968). Consequently, the interception of light after defoliation is low and much of the incident light penetrates to the soil surface. A more even distribution of tillers at this stage would presumably increase the efficiency of the interception of light per unit of tissue by a reduction of the mutual shading which would occur within tiller clumps. Possibly this could be achieved with a genetically-homogeneous population. However, data presented suggest that a grass population consisting of a high density of small plants may be particularly susceptible to stress.

Results also suggest that tall, tufted plants may grow more efficiently when they occur in a low proportion mixed with more prostrate species. This is because of greater lateral illumination of the herbage. It is commonly observed in older pastures that Manawa ryegrass occurs as isolated plants which stand above the rest. Can the ability of Manawa to survive at these low densities, even when the defoliation system is generally unfavourable to the growth of the cultivar (Harris and Brougham 1970), be related to its selection from plants primarily assessed when growing widely-spaced? Alteration in the order of performance of genotypes grown as spaced plants and in simulated swards has been demonstrated by Lazenby

and Rogers (1965a, b), and these studies have indicated the large differences in plant size between the different spacings. The present study also demonstrates the very great size range of ryegrass plants in swards.

There is little doubt that the integration of tillers as plants is an important factor in the distribution and density of tillers in swards. Thus, the clumping of tillers in laxly and infrequently grazed pastures arises from the death of competitively suppressed plants which leave gaps between the competitively successful plants or clumps of tillers. If the tiller were a truly independent organ it is difficult to envisage how this clumping would become so apparent. Thus, for the various reasons cited, the concept of the grass tiller as an independent unit must be considered as being something of a physiological and ecological convenience. Accordingly, development of techniques which recognise the integration of tillers in grass plants must provide us with greater insights into processes operating within grass swards.

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