SOME ASPECTS OF LEAF DEATH DURING THE REGROWTH OF A PERENNIAL RYEGRASS (Lolium perenne, L.) WHITE CLOVER (Trifolium repens, L.) SWARD

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Introduction

In order to achieve high animal production from grass-legume pastures such as are used in New Zealand, it is necessary to meet three basic requirements.

(a) Large amounts of high quality feed must be grown, the seasonal distribution of which must approximate the seasonal curve of animal requirements. (Conservation practices can be used to rectify minor discrepancies.)

(b) A large proportion of this feed must be harvested by the animal.

(c) Efficiency of conversion within the animal must be at a high level. (McMeekan 1956)

Agronomists are concerned primarily with the first of these factors, but as maximum production for a system is approached, the second factor assumes major importance. These aspects must be studied against the background of a wide range of management techniques that may be employed in defoliating pastures. In the past, the importance of both leaf area grass tiller density and organic reserve materials have been studied as they are influenced by defoliation management, and their role has to some extent been determined. (Milthorpe and Davidson 1965). The emphasis in such investigations has been on the initial stages of regrowth from defoliation and there remains a number of aspects of primary productivity at medium and high Leaf Area Index values (L.A.I. i.e. the area of leaf per unit area of ground) requiring investigation (Brougham 1962, Alberda 1965a, Brown and Blaser 1968). One of these aspects, leaf death, is the subject of the investigation reported below and has been selected because of its significance to both productivity and utilisation.

In order to sustain high growth rates, it is desirable to maintain maximum light interception (high L.A.I.) for as great a proportion of time as possible without incurring dry matter losses or suffering severe reductions in the efficiency of the light intercepting leaves (L.A. Hunt and

Brougham 1967). Information is, therefore, required on the extent to which leaf death results in reductions of green (high quality) herbage, and on rates of leaf death at successive stages of regrowth which may provide an insight into the mechanisms that influence productivity at later stages of growth.

In order to maximise utilisation, it is necessary to channel as much as possible of net primary production through productive domestic animals. Information is also required therefore, on the stages of regrowth and seasons in which dry matter losses via death and decomposition reach significant proportions.

In this study an attempt has been made to provide some of this information through measuring growth and death in a perennial ryegrass-white clover sward.

Chapter 1.

Review of Literature.

1.1. Notes on senescence.

The most comprehensive treatment of the phenomenon of senescence in plants has been made by Leopold (1964). Leopold defines senescence as "the deteriorative processes which naturally terminate the functional life of an organ or organism." Thus senescence is a completely natural process; "unnatural" influences that cause the premature death of leaves being collectively referred to as agents of "ageing". However, as current knowledge of both natural and unnatural factors influencing leaf death in pastures is limited, this distinction has not been attempted with regard to the results discussed below. Consequently, "senescence" will be used to encompass the effects of all processes that lead to leaf death.

Leopold describes four general types of senescence:-

(a) Overall senescence, whereby the entire plant dies by some systemic function (e.g. as with annuals).

(b) Top senescence, involving the death of only the above ground portions so that the root and underground systems remain viable.

(c) Deciduous senescence, as occurs annually with deciduous woody plants whereby all the leaves die but the stem and roots remain viable.

(d) Progressive senescence, involving the least drastic change as there is only a gradual progression of death of leaves from the base upwards as growth of the plant proceeds.

Overall senescence obviously occurs in most pastures due to the inevitable intrusion of annual species such as Poa annua, barley grass, etc. It may also be induced in perennial species due to agents such as disease, pasture insects, treading etc. Top senescence also occurs with a number of pasture weed species. Generally, the perennial pasture species such as perennial ryegrass and white clover exhibit progressive senescence although reproduction development in the ryegrass will eventually result in top senescence, i.e. new shoots arise from the base of the flowering tiller. However, progressive senescence of perennial pasture grass plants eventually includes tillers as well as leaves, for even tillers that fail to flower do not live much longer than a year (Langer 1963). In other words, individual tillers exhibit progressive senescence until such time as top senescence occurs.

Studying a system involving more than one type of senescence obviously may lead to complications. A study of tiller senescence alone would take no account of the progressive senescence of healthy tillers that occurs during their life time of up to a year or more. Individual tillers bear only three to four healthy leaves at any one time (Alberda 1965b, L.A. Hunt and Brougham 1966) but produce a new leaf every 1 to 3 weeks depending upon the environmental conditions (Ryle 1964). A study of leaf death without recognition of tiller death incorporates the risk of over-estimating the rate of leaf death on healthy tillers through including high leaf death rates from senescing tillers. This risk is not considered to be great, however, as the proportion of dying to healthy tillers is likely to be small, being greatest perhaps at times of stress. At such times it is usually recently formed tillers that die first (Langer 1963) and as the leaves of these will weigh little they will not greatly affect death rate per tiller. Also the assumption made above that dying tillers have a higher leaf death rate may not be true in which case varying rates of tiller senescence will have no effect on leaf death rate per tiller.

The general pattern of senescence in individual leaves has been described by Leopold (1964). The leaf reaches its peak of photosynthetic effectiveness about the time it completes its period of most rapid expansion. Thereafter there is a gradual lowering of efficiency until the leaf is shed from the plant. The decline in photosynthesis rates begins soon after the leaf reaches full size and as the assimilative powers deteriorate, so also does the respiratory ability. During the progressive development of yellowing, there is a fall in the protein nitrogen content which is possibly structurally related to the degradation of chlorophyll. The R.N.A. content also declines and there is a general hydrolysis of carbohydrate components and losses of organic acids. The general picture is therefore one of a loss of assimilative powers and a general catabolism of cell components, trends which begin soon after the leaf reaches maturity.

1.2. Senescence and death in pastures.

1.2.1. General discussion

It has been suspected for some time that significant quantities of pasture herbage are lost under situations where leaf death is encouraged. Macfayden (1957) suggests that in grasslands and probably most terrestrial communities, by far the greater amount of net primary production is channelled not through herbivors but through decomposer food webs. Donald (1956) considered that leaf death due to shading was a major factor determining ceiling yields. Brougham (1956) suggested that reduced spelling periods for autumn-sown pastures could help avoid extensive decomposition losses in such situations.

Current opinion appears to favour leaf death as the major cause of reductions in growth rate at high L.A.I. values, so that at yield ceilings the rate of leaf production is offset by the rate of leaf death. (Barnard 1964, Bean 1964, L.A. Hunt 1965, Brougham 1966, McCree and Troughton 1966). It may be however, that other factors are important, such as an increase in respiration relative to photosynthesis or changes in the structure of the leaf canopy. (Alberda 1965b) Even at low L.A.I. values, situations may exist whereby leaf senescence occurs at significant rates. For example Willoughby (1965) reports that even at very high stocking rates, tiller defoliation in a set stocked pasture is not as frequent as is commonly believed. Willoughby suggests that even in such a seemingly highly utilised sward, much pasture (far greater than has hitherto been considered) is enabled by the infrequent defoliation to be lost through death and decay.

1.2.2. Dead matter in pastures.

Dead matter accumulation (leaf fall less leaf decomposition) begins during the regrowth of pastures as soon as leaves senesce and fall. This may occur immediately where defoliation is lenient, but rates of leaf death are generally lowest immediately after defoliation and highest at high L.A.I. values (Huokanui 1960, Bean 1964, Hunt and Brougham 1966, Agyare and Watkin 1967). In the absence of defoliation and complete decomposition, the accumulation of litter can eventually interfere with the development of new shoots to the extent that the plant is choked to death (Luff 1965).

Measurements of the extent of leaf death in pastures and some forage crops have been made in a variety of ways. The simplest technique that has been used is to make periodic measurements of the net yield of dead material (Campbell 1964) and draw general conclusions from the large fluctuations in this amount. Campbell (1964) found the litter yield in pastures to be much greater in the summer than in other seasons, inferring that decomposition rates were retarded under dry conditions and perhaps that leaf death rates were enhanced. The vast reduction in this store of dead material as the season changed from summer to autumn indicated large losses due to decomposition at this time. Increased grazing pressure effectively reduced the absolute amount of dead material but did not have a big effect on the percentage composition.

The obvious disadvantage of this method is that the net yield of dead matter varies both with leaf senescence rates and decomposition rates. It is quite possible to record no changes in the dead matter residue for long periods of time even though rates of senescence and decomposition may be high. However, these measurements do provide indications of the times at which more detailed measurements should be made to obtain the most information.

A more accurate assessment of the relative extent of leaf death has been made through studying the rates of production and senescence on individual plants. Watson and Baptiste (1938) labelled leaves of mangold and sugar beet plants with Indian ink. In this way they were able to determine that the leaf death rate of mangold leaves was nearly twice as great as that of sugar beet. This resulted in one third of the sugar beet and one half of the mangold leaves produced over the growing period being lost mainly through normal senescence but also partly through accidental damage.

Similarly Bean (1964) measured rates of leaf production and senescence on individual cocksfoot tillers. The rate of leaf death was low immediately after defoliation, but subsequently it equalled the rate of leaf production (0.5 - 1.0 leaves per tiller per 2 weeks). Such data emphasises that leaf death can be an important factor during the later stages of pasture regrowth. However, because data is available only on the number of leaves dying, no conclusion about the extent of the dry matter loss can be made. Assuming that the oldest leaves died first, there is likely to be a considerable difference in leaf size between those leaves dying and those being produced (Jewis 1965). Also, the extent of the weight loss undergone by the leaf during senescence through the redistribution of cell constituents (Leopold 1964, Hopkinson 1966) will influence the final dry matter loss. Brougham (1958) found that white clover leaves weighed considerably less when senescent compared with their earlier values at full maturity.

Rates of leaf production and death have been studied by Brougham (1958) and L.A. Hunt and Brougham (1966) at a stage when net changes in the size of the system were small, i.e. near the ceiling yield. In such situations the rate of input in terms of leaf production and the rate of output in terms of leaf senescence are the same, and by measuring the rate of input, an indirect measure of the rate of output is obtained. Thus Brougham (1958) found that in a white clover sward at a ceiling yield in the early summer, the rate of leaf production and death was one L.A.I. unit every 5 days. As the amount of dead material was constant, the rate of decomposition was also one L.A.I. unit every 5 days. In terms of dry matter, this was in excess of 20 lb d.m. per acre per day. Similarly, L.A. Hunt and Brougham

(1966) measured the rate of leaf production and the number of leaves supported on Italian ryegrass tillers at a similar stage of growth. From the data obtained it was estimated that the leaf death rate was in excess of 10 lb d.m. per acre per day. This was approximately one half of the maximum growth rate that can be expected from swards of short rotation ryegrass and white clover at that time of the year (early winter).

Because the above techniques require steady state conditions, they cannot be used to measure death rates at successive stages of growth or to examine changes in death and decomposition rates associated with environmental changes. However, they do provide a starting point, showing the need for data on death rates in various plant communities, during different seasons, and at successive stages of regrowth if factors influencing productivity and energy flow are to be fully appreciated. Together with the work by Bean (1964) and Watson and Baptiste (1938), they emphasise that the nature of the communities studied is one in which an active turnover of leaves results from the well nigh continuous processes of leaf production and senescence. The art of productivity management must include not only maximising the former but also minimising the latter (Brougham 1961).

1.3. Factors affecting leaf death.

There are few reported experiments in which the main object of the investigation has been to study the extent to which variation in leaf longevity exists and what factors may be influential. However, a certain amount of information, incidental to studies on other aspects of plant growth, is available and some tentative conclusions can be made from the more frequently reported observations and opinions.

1.3.1. Intense shading.

Leaves at the base of a plant canopy are shaded to a varying degree depending upon the extent to which they are vertically distributed through the canopy and the light intercepting capacity of leaves above them. Where the shading is not intense the leaves can be expected to make a reduced contribution to overall photosynthesis (Donald 1961) although this aspect is now not considered to be of major importance owing to the reduced photosynthetic capabilities of older leaves (Milthorpe 1963). Intense shading, (complete darkness) however, has been demonstrated by Frank and Kenny (1955) to cause degeneration of chlorophyll and by Vickery et al (1937) to generally accelerate yellowing and browning (senescence) processes in cultured tobacco leaves. Leaf death or accelerated leaf death in the field has been attributed to intense shading by a number of authors. (Mitchell and Calder 1958, Brougham 1962, Lancashire and Keogh 1964, Alberda 1965a, L.A. Hunt 1965, L.A. Hunt and Brougham 1966, Puckeridge and Donald 1967). Direct evidence in support of these opinions has been provided by Hopkinson (1966) who showed that shaded cucumber leaves died well before unshaded ones. Also Brougham (1958) found that the time taken for white clover leaves to senesce was progressively decreased as high L.A.I. values were reached. Both of these experiments involved species that displayed horizontally disposed leaf laminae and intense shading can be assumed to have involved the entire leaf. Shading also has an adverse effect on species with more erect leaves where complete shading of the leaf is ensured. Lucanus et al (1960) found that shading ryegrass tillers to 20 - 25% of full daylight reduced their ability to survive. In this case, however, enhanced senescence is probably confounded with carbohydrate starvation of the tiller as a whole. Puckeridge and Donald (1967) reported large differences in the onset and rate of leaf and tiller senescence in wheat plants associated with density. The date of commencement of leaf senescence ranged from week 10 at the highest density to week 17 at the lowest density. At week 20 the ratios of green, senescent and dead leaf were 1.0: 0.72: 0.33 at the lowest density and 1.0: 0.52: 1.87 at the highest. In discussing reasons for these differences the authors conclude that on the basis of studies made by Wasserman (1964), shading and nitrogen stress are probably important.

It appears, therefore, that intense shading of leaves will cause a marked increase in the rate of leaf senescence. This has only been demonstrated conclusively, however, where shading involves the entire leaf. Where leaves are distributed semivertically through the canopy this condition will probably only apply to very short leaves at high L.A.I. values, if at all.

1.3.2. Wilting

Wilting is a factor which, when severe enough, obviously results in leaf senescence and death as is evidenced by the widespread death that has occured during periods of drought. Leopold (1964) mentions both elevated temperatures and moisture deficit as factors that hasten senescence processes but gives little indication of the extent to which these stresses must develop before they become operative.

Catsky (1962) studied the development of water saturation deficit (W.S.D.) in old and young leaves of wilting cabbage and rape plants. It was found that during the slow wilting of plants, a definite preference in water supply for young leaves was established. This condition was obvious when medium W.S.D. values were reached (i.e. from 8 to 20%). During total lack of water in the plant, the old and mature leaves wilted markedly and died.

Similarly, McWilliam (1968) found the availability of moisture to be important in controlling senescence in Phalaris. Two closely related mediterranean type grasses (Phalaris ruror, Phalaris tuberosa, both from Morocco) were studied in relation to perenniality, one being an annual and the other a perennial. Although senescence usually becomes apparent soon after anthesis with these species, where flowering plants were maintained at field capacity senescence was considerably delayed. When top watering was withheld at the time of flowering, plants senesced quite rapidly even though water was available to the deep roots below 3ft from the surface. The important factor influencing the expression of senescence appeared to be the drying of the surface soil which contained the bulk of the fine root system. This effect may be due not only to restricted water supply but also to the consequent unavailability of plant nutrients that are concentrated at the surface. (Mitchell 1957).

The onset of senescence in response to moisture stress was accelerated by high temperature. Moisture stress also had a greater effect during flowering compared with the vegetative phase. Young vegetative plants of both species recovered from moisture stress with little or no loss in leaf area, whereas when the same stress was applied to flowering plants it caused rapid senescence, and death in the case of the annual. There appears to be certain species differences in the senescence response to flowering. L.A. Hunt and Brougham (1966) found that as Italian ryegrass plants approached flowering there was a marked reduction in both the rate of appearance and senescence of leaves. This contrasts with the enhanced senescence associated with senescence in Phalaris noted by McWilliam (1968). The difference probably reflects adaptation differences between Mediterranean and Temperate grassland species, as senescence and summer dormancy is a survival mechanism with Phalaris (McWilliam 1968).

The magnitude of the moisture stress required to induce senescence in the annual after flowering was quite low which again is probably a reflection of its survival mechanism. For both species studied however McWilliam (1968) concluded that the dominant factor controlling the onset of senescence was the availability of water.

Gates (1955) studied the effect of moderate and severe wilting on the growth of tomato plants. Marked depression of growth rate, net assimilation rate, and lamina weight relative to stem weight occurred with relatively brief periods of water shortage. The treatment effects were interpreted as a tendency towards senescence during wilting and a return to a more juvenile condition upon rewatering.

From the limited information available, it appears that moisture stress and high temperatures can be important factors influencing leaf death rates. The stresses to which response occurs, however, appears to vary with species; medium to high stresses probably being necessary except with those species in which moisture stress is a "signal", triggering the death of annuals or a phase of dormancy in perennials.

1.3.3. Nutrient deficiency

Nutrients apparently differ in their effects on leaf longevity. Watson (1956) reports that nitrogen increases leaf area throughout the growth period. Phosphorus increases leaf area particularly at the early stages of regrowth but later it hastens the senescence of leaves. Potassium on the other hand is most effective at the later stages of growth and tends to delay the senescence of leaves. Nitrogen retards and reduces leaf abscission and conversely nitrogen deficiency increases abscission (Addicot et al 1955). Addicot also notes that deficiencies in Ca, Zn, S and Mg may also result in premature abscission.

Direct evidence of the effect of nitrogen on gramminae is provided by Walkley (1941). Nitrogen applied to the roots of barley plants resulted in mature leaf (not already yellowing) becoming a noticeably darker green. With the controls, however, the greater part of each leaf died, so that it was concluded that the treatment arrested senescence. Similarly, Wasserman (1964) (See Puckeridge and Donald 1967) found that nitrogen deficiency will contribute to the death of wheat leaves. Puckeridge and Donald (1967) considered that nitrogen deficiency and shading were the two most likely factors responsible for the marked differences in senescence they found to be associated with density (see section 1.3.1.).

1.3.4. Mechanical damage.

Apart from the physiological influences of the environment on leaf longevity, a number of factors may cause the death of both young and old leaves due to direct mechanical damage. One of the most common of these is leaf burn due to frost or in some cases, urine. Another common factor is the direct action of animals' feet. For example Lancashire (1961) demonstrated that treading can result in a significant decrease in the ryegrass tiller population.

Frost damage is reported by Watson and Baptiste (1938) to cause a rapid increase in the death rate among old leaves. Wiegert and Evans (1964) attribute the death of old and senescent material in an "old field" to frosts that mark the approach of winter. Similarly Agyare and Watkin (1967) found that frost damage in the winter can result in reduced areas of green leaf. Corbett (1957) when studying winter grazing under rather severe conditions found that there were species differences in susceptability to frost damage. Ryegrass was much less hardy than cocksfoot, apparently due to the much lower crude fibre content. The close growing mass of fine leaves of ryegrass also resulted in a slow drying foggage which was apparently more conducive to decomposition. As a result wastage of ryegrass was estimated at 40% while that from cocksfoot was only 10%.

In some situations the physical effects associated with low temperatures may not be as important as the physiological effects of certain pathogens. Thus Lebeau (1966) has shown that in Canada, winter killing of turf grass and forage crops is seldom due to subzero temperatures alone, but is often caused by dessication or attack by fungi, (e.g. snow mould on turf grass and winter crown rot on forage crops). Apparently the low temperatures enable enzymes secreted by the pathogens to gain access to compounds within the host tissue.

Finally, instances may be found reported in the literature where reductions in leaf area result from abrasions and tearing of leaves by environmental forces. For example Marshall (1967b) reports favourable effects on crop yields through avoiding wind damage to leaves by the use of shelter belts. Similarly, Dungan (1934) describes how reductions in the leaf area of corn crops may occur through injury by hail.

1.3.5. Genetic influences.

Differences in the leaf death rates between species can be expected where differences in leaf longevity exist due to genetic influences. This may be direct, as between clover and grasses, or indirect reflecting species or even varietal resistances to harsh conditions or disease. For example it has been shown by Lancashire and Latch (1966) that ryegrass varietal differences in susceptability to crown rust markedly affect the proportion of green leaf lost through senescence and death. Similarly, differences in tolerance to winter burn between grass species can have a big influence on the proportion of wastage (see section 1.3.4.).

Some estimates of life expectancy of pasture species may be found in the literature. Brougham (1958b) found that white clover leaves, in the summer, had a life expectancy of 5 to 6 weeks. Bean (1964) reports the life expectancy of cocksfoot leaves to be from 8 to 10 weeks. Similarly L.A. Hunt and Brougham (1966) estimate the average life expectancy of Italian ryegrass leaves as approximately 8 weeks. Considering the number of factors reported above that are suspected as having a measurable influence on leaf longevity, and the differing conditions under which the above estimates were made, direct comparisons are difficult to make. It is likely that as yet not all of the important influences on leaf longevity are appreciated. For example, work by Brougham (1962) has shown that marked differences in the life expectancy of clover leaves in an undefoliated stand of white clover occur from season to season. During the winter months clover leaves lived as long as 8 weeks; i.e. as long as Italian ryegrass leaves in an undefoliated stand in the same season. (L.A. Hunt and Brougham 1966).

It appears, therefore, that basic data on the factors affecting leaf death in pastures, and their relative importance have yet to be reported in the literature to the extent that firm conclusions can be made. The indications are however, that leaf longevity is adversely affected by much the same factors that adversely affect growth generally. Ieaves tend to die when deprived of light, moisture, certain nutrients, and when they are physically damaged, but these effects may be more severe with some species than with others.

1.4. Decomposition.

As with leaf death aspects of decomposition in pastures have generally been neglected in terms of research in favour of factors affecting earlier stages of regrowth. This is in contrast with studies on forest communities where the importance of decomposer organisms in recycling nutrients is widely appreciated. Decomposition rates of forest litter are generally very slow compared with pasture litter however, (e.g. 50% dry matter loss in 2 years, see Will and Styles 1967) and so have little utility even as comparisons.

1.4.1. Decomposition rates in pastures.

Estimates of decomposition rates of litter from pasture species have been reported by Brougham (1958) and L.A. Hunt and Brougham (1966). Both these estimates were made when the swards had obtained yield ceilings so that leaf death rates and decomposition rates can be expected to be reasonably high for the conditions prevailing. Brougham (1958) found that in a pure stand of white clover at its ceiling yield in the early summer, dead leaves decomposed at a rate of 1 L.A.I. unit per 5 days, resulting in a release of 3 - 4 lb of nitrogen. From the data it can be calculated that dry matter losses were in excess of 20 lb d.m. per acre per day. L.A. Hunt and Brougham (1966) found the daily loss of dry matter due to decomposition in an undefoliated stand in the winter to be approximately 1.2 gm per m^2 (10.7 lb per acre per day).

Decomposition rates of dead vegetation in an old field in Michigan have been presented by Wiegert and Evans (1964). These authors found that litter disappeared at rates varying from 1.3. to 8.4. mg per g. per day on "uplands" and from 1.8 to 13.6 mg per g. per day in "swales". From the mean dead matter yields on these areas these values correspond to an average of approximately 1 g. per m^2 per day (8.9 lb per acre per day) for the uplands and 3 g. per m^2 (26.8 lb per acre per day) in the swales. In view of the high dead matter yields measured by Wiegert and Evans (mean 197 per m^2 on "uplands", 417 g per m^2 in "swales"), these rates are slow compared with those of Brougham (1958) and L.A. Hunt and Brougham (1966). This is probably a reflection of the build up of a slowly decomposing residue that can occur over the years in the absence of regular defoliation (Luff 1965).

1.4.2. Factors affecting decomposition rates.

Several factors may be suspected of affecting decomposition rates in pastures. For example, species differences in the chemical composition of dead leaves may result in differing decomposition rates. Leaves that have a relatively high nitrogen content will facilitate a rapid build up of the decomposer populations. Leaves that are relatively high in structural components will decompose slowly as such components tend to be most resistant. Environmental factors conducive to the growth and build up of decomposer organisms can be expected to be those that will result in rapid decomposition rates.

A common observation is that decomposition rates tend to be highest where the herbage is kept moist. Brougham (1958) observed that decomposition was rapid under moist and delayed under dry conditions. Corbett (1957) considered decomposition of set foggage to be a factor resulting in higher wastage of ryegrass compared with the drier cocksfoot herbage. Campbell (1964) noted that pasture litter increased to maximum values during the dry summer months and was rapidly reduced by decomposition at the onset of the autumn rains. Other authors that mention moisture as a factor increasing decomposition rates include Wiegert and Evans (1964), Luff (1965), Witkamp (1966) and Will and Styles (1967).

Chapter 2.

EXPERIMENTAL METHODS

2.1. Introduction

An experimental area at the Palmerston North station of Grasslands Division D.S.I.R. (lat 40°30'S) was sown on 10.9.65 with a mixture of N.Z. certified perennial ryegrass (Lolium perenne L. variety "Grasslands Ruanui") and white clover (Trifolium repens L. variety "Grasslands Huia") at 30 and 4 lb of seed per acre respectively. + The pasture was rotationally grazed by sheep until the beginning of the experiments at which stage it consisted of approximately 80% ryegrass and 20% clover.

The soil forms part of a river terrace and was originally mapped as a complex of Manawatu fine sandy loam and Manawatu mottled silt loam. These are recent silty soils from river alluvium and have been flooded and received fresh alluvium during historic times. Natural drainage is good to slightly imperfect. However, since the area was mapped, levelling has been carried out in an endeavour to make the area more uniform, and during this process much of the original structure was destroyed leading to soil compaction and impedance of natural drainage. (J.D. Cowie pers comm). Drainage in the first winter after sowing was poor but there has been a marked improvement subsequently.

Natural fertility is medium, with possible additional requirements for phosphorus, lime and perhaps sulphur. (J.D. Cowie pers comm.) At sowing the area received 10 cwt of lime and 3 cwt of superphosphate per acre. Additional dressings of 2 and 3 cwt per acre of superphosphate were

+ For convenience, perennial ryegrass and white clover will be referred to as "ryegrass" and "clover" respectively, for the remainder of this text.

made in the following autumn and spring respectively, the latter application being at the beginning of the first experiment (2.9.66). It was considered that sufficient fertilizer had been applied to remove any nutrient limitation to growth.

Two experiments were carried out in the spring of 1966 (5.9.66 - 24.11.66) and again in the following autumn (14.2.67 - 26.4.67). For convenience the spring and autumn experiments will be considered simultaneously.

Experiment (1) was designed to measure the rate of pasture regrowth from defoliation. Such measurements are necessary first to enable comparison and integration with measured death rates and secondly to assess stages of regrowth at which possible significant variations in death rate occur.

Experiment (2) was designed to measure aspects of leaf death in pastures. In order to do this objectively, it has been necessary to distinguish between leaf death rates and dead leaf decomposition rates. Leaf death measurements were made frequently enough to avoid decomposition. The extent of the decomposition of the dead leaf was found from the difference between the leaf fall to any given date and the actual dead matter yield at that date. Estimates were also made of the relative decomposition rates of ryegrass and clover leaves.

2.2. Methods.

On September 1st, 1966, the experimental area was mown to approximately $\frac{3}{4}$" above ground level with a rotary mower, and again topped to reduce some of the natural variation in the sward associated with animal excreta. At the end of the spring experiment (25.11.66) the plots were mown and the clippings discarded. From 14.12.66 to 16.12.66 the area was grazed by sheep and on 19.12.66 topped with a rotary mower. The pasture was then mown on 9.1.67 with a Dennis reel type mower and again on 14.2.67, the latter defoliation being associated with the start of the autumn experiment. The above management resulted in considerable growth between defoliations and as a result excessive tillering did not occur, probably due to low light intensity at the base of the sward. (Mitchell and Coles 1955).

Experimental plots were laid out on September 5th, 1966 and 14th February, 1967 as follows:-

2.2.1. Experiment (1)

Pasture growth was measured by adopting the sequential cutting technique first used by Brougham (1955). From previous experience at Grasslands Division it was considered that four replications would be sufficient.

Four replicates, each 36' x 14' were marked out with wooden pegs leaving 2' pathways around and between replicates. Each replicate was then divided in 12 subplots of 14' x 3' which were marked at each end with wire pins. Thus the regrowth from defoliation for each replicate could be measured on 12 succeeding dates by single defoliations.

The first cut was made on 14th September, 1966 in the spring trial and on 22nd February, 1967 in the autumn trial. One subplot in each replicate was chosen at random to be used for the first cut. Later cuts were made on immediately adjacent subplots either progressively to the left or to the right, the direction being chosen at random for each replicate.

2.2.1.1. Dry Matter Yield Measurements.

On each cutting date a 2' wide strip was mown down the centre of each subplot to a height of $\frac{1}{2}$ - $\frac{3}{4}$" above ground level using a Dennis reel-type mower. The length of the mown strip was measured and recorded for each subplot. This left a margin of 1 foot between successive cuts which would prevent any complications through edge effects (Black 1961).

The mown herbage together with grab samples for botanical composition analysis were weighed and the fresh weights for each replicate recorded. The mown herbage was then thoroughly mixed and a sub-sample of over 100 gms of fresh material was then accurately weighed out from each subsample and dried for 24 hours at approximately 180°F.

2.2.1.2. Botanical Composition Analysis.

Immediately before mowing, grab samples (5 in the spring, 20 in the autumn), were taken at random down the length of each subplot for botanical composition analyses. Each grab sample consisted of a handful of herbage from approximately 2 - 3 square inches cut to mowing height with a pair of hand shears. By taking samples in this manner instead of subsampling the shorter mown herbage, the herbage dissection was made correspondingly easier. The samples were taken indoors, thoroughly mixed and a subsample of 15 - 20 gm dissected into ryegrass, clover, other species and dead matter fractions. Each fraction was dried at approximately 180°F for 24 hours and weighed.

From the results of the dry matter determinations and the botanical composition analysis, the yields of ryegrass, clover, other species, and dead matter were calculated for each cutting date.

2.2.1.3. Leaf Area Index Measurements.

In the spring experiment leaf area measurements were made. Two ½ square foot quadrats were placed at random in each subplot immediately before mowing and the herbage cut to ground level. (1 square foot was subtracted from total area harvested during dry matter yield calculations). Each sample was taken indoors, carefully mixed and a subsample of about 20 gms fresh weight taken for dissection. The remainder of the sample was dried for 24 hours at 180°F and weighed. The subsample was dissected into ryegrass leaf, ryegrass stem, dead ryegrass, clover leaf, clover stem, dead clover, and other species. Thirty ryegrass leaves were then selected at random and measured once for length and twice for width, the latter measurements being made $\frac{1}{3}$ and $\frac{2}{3}$ of the way down the length of the leaf. Thirty core samples were taken from thirty clover leaflets selected at random giving a total area of cores of 8.48 sq. in. All the above fractions were dried and weighed along with the remainder of the original sample. The weight of ryegrass and clover leaf per quadrat was then calculated from the percentage of ryegrass and clover leaf and the total weight per quadrat. The area of the thirty measured leaves and the weight of those leaves was then used to calculate the leaf area: weight ratio for ryegrass and clover. The area of leaf per quadrat and eventually the leaf area index was then derived from the leaf area: weight ratio and the weight of leaf per quadrat.

2.2.1.4. Plant Density Measurements

Plant density measurements were made on each subplot immediately after each mowing and, in the autumn experiment, at the initial defoliation. This was done by taking at random 25 (spring) or 30 (autumn) tiller plugs from each subplot, each plug being 2" in diameter. The number of ryegrass tillers and clover 'plants' were counted from each plug. From the mean value of ryegrass and clover 'plants' per plug an estimate of the ryegrass and clover plants per square foot was obtained.

2.2.2. Experiment (2)

2.2.2.1. Leaf Death Rate

The leaf death rate in the pasture was measured by collecting dead leaves from a number of tagged plants along line transects frequently enough to avoid any weight loss from the leaves due to decomposition. In the spring the collections were made every two days but on the basis of the spring results, the collection interval in the autumn experiment was extended to four days.

The experimental plots each 4 ft wide by 36 ft long and containing 2 line transects, were marked out with wooden pegs as soon as the pasture was defoliated. The line transects were located $1\frac{1}{2}$ ft in from the 2 ft wide pathways, and during tagging, were marked by stretching a thin cord between wooden pegs at each end of the transect. Shortly after defoliation 70 plants were tagged systematically along each line transect. The large number of plants per transect was considered desirable to ensure measurable quantities and minimum variation at each collection date. By systematically tagging plants, personal bias for either ryegrass or clover was avoided and each line transect contained ryegrass and clover plants in proportions representative of the pasture population.

Tillers were tagged with lengths of button cotton (spring) or white wool (autumn) to aid in rapid relocation at each collection date (see Fig. 1). However as the pasture canopy obstructed any view of the tag after a few weeks it was necessary to devise some method of quickly arriving at the approximate position of each plant. This was achieved by pushing into the ground 2 ft wire pins 6 inches behind each plant as viewed from the pathway. In this way the plants in both line transects in any one plot could be marked by a single row of pins halfway between the two transects. (See Fig. 2). The marker pins were numbered from one end, every 10th pin being marked with a twist of wire, the number of twists corresponding to the number of tens that had been counted, i.e. number 30 had 3 twists and number 40 had 4, etc. Thus any tagged plant could immediately be referred to by noting the line transect that it was in and its number in that transect.

The plants were tagged with the aid of a metal frame in which six pointers were rigidly held six inches apart, and the supports at each end three inches away from the nearest pointer. The frame was pushed into the ground at one end of the line transect so that the first pointer was approximately six inches in from the end of the plot. The closest ryegrass

Fig 1a

1b Clover 1c Ryegrass

Fig 1 Examples of Tagged 'Plants'

Fig 2 The Frame and Line Transect

or clover plant to the tip of each pointer was tagged and the frame removed. By moving the frame along the line transect and placing the rear support in the hole made earlier by the front support, the next plant to be tagged was located six inches away from the last. In this way the frame was moved progressively along the line transect systematically locating plants at six inch intervals.

At each collection date all tagged plants in appropriate transects were inspected and any dead leaves removed with a pair of forceps. Six replicate transects were used in the spring experiment and four in the autumn. A dead leaf was defined as any leaf in which greater than 50% of its area was brown or yellow. (Langer 1956) Clover leaves were easily distinguished as either dead or alive as the colour change is rapid, but ryegrass leaves tended to change colour progressively from the top downwards. Thus occasionally some ryegrass leaves were harvested that still displayed some green pigmentation.

Dead leaves from any one transect were placed in a closed plastic container bearing a letter identifying the transect as they were harvested. Any dead plants were noted and the date at which their death was observed recorded. The tag from the dead plant was then tied to the wire pin either by its middle or one end, depending on which transect it belonged to. At the next inspection date time would thus not be wasted by looking for plants that had died.

After all replicate transects were inspected the containers were taken indoors and the ryegrass and clover leaves separated for each transect. The number of leaves and the dry weights (after drying for 24 hours at 180°F) were recorded for ryegrass and clover separately.

2.2.2.2. Disturbance of the Canopy.

Regular inspection of the tagged plants resulted in a certain amount of sward disturbance. This was barely noticeable at early stages of regrowth but was more obvious when the pasture grew longer. The use of wire locating pins removed the need to search for tagged plants however, and by carefully dividing the canopy for inspection, the disturbance was minimized. However, in the spring and especially after inspections had been made on rainy days, evidence that the canopy had been disturbed remained as much as 48 hours later. Therefore in the autumn experiment light interception measurements were made in order to assess whether or not the disturbance was great enough to influence the light regime at the base of the sward.

The percentage of daylight that penetrated into the sward was measured by using a small (1.8 x 1.1 cm) barrier layer selenium photo cell connected to a sensitive galvanometer (Barrowman 1956). Measurements were made in bright sunlight around local noon when light fluctuation is minimal (Brougham 1958a). Readings were taken at six sites roughly equally spaced along the length of each line transect for the transects involved in death rate measurements and also for identical transects involved in estimating relative decomposition rates which were not inspected as frequently (i.e. every 8, 16 or 24 days). At each measurement site, a reading was first taken in bright sunlight and then a second reading was made with the recording head carefully pushed into the base of the sward so as to approximately coincide with the line transect.

2.2.2.3. Relative Decomposition Rate Measurements.

Decomposition rates for total dead matter can be estimated from measurements of leaf death rate and the dead matter yield at the various cutting dates. To provide information on the relative decomposition rates of ryegrass and clover a further 12 line transects in the spring and 8 in the autumn were tagged in an identical manner to those described above. The transects involved in measuring death rate were harvested frequently enough to avoid losses by decomposition. The transects involved in the relative decomposition rate measurements were harvested at longer intervals so that decomposition of the first dead leaves occurred. These harvest intervals were 4 days, 8 days and 24 days in the spring and 8 days and 16 days in the autumn.

The amount and number of ryegrass and clover leaves to die over an interval of say 24 days can be estimated by integration of the death rate measurements over that period (i.e. the summation of the 2 or 4 day samplings). The difference between this amount and the quantity of ryegrass and clover leaves actually harvested in 24 days provides an estimate of the degree to which leaves that died in that period have decomposed. Thus the decomposition rates of ryegrass and clover leaves that died in that period can be compared. Any absolute decomposition rate so obtained underestimates the actual decomposition in the field to the extent that decomposition of any leaves that may die before the measurements were made continues. A summary of the dates at which experiments began and measurements were made is given in appendix 1.

2.2.3. Statistical Procedure.

Analyses of Variance and Regression, and Standard errors of the mean were calculated according to methods described by Snedecor (1956). Mathematical equations were fitted to both the growth rate and death rate data in order to provide the best estimate of growth rate and death rate at any time for further computation. Logistic equations (with 3 parameters) were fitted using the iterative procedure of Deming (1934) (see appendix 2).

The logistic, fitted with 3 parameters (A, B and C) was as follows:-

$$W = \frac{A}{1 + Be^{-ct}} \qquad (1)$$

where W = yield in lb dry matter per acre and t = time measured in days from initial defoliation. This equation is the solution of the differential equation

$$\frac{dW}{dt} = \frac{C}{A} W(A-W)$$

expressing the idea that growth rate, $\frac{dW}{dt}$, is a dynamic function of both growth present at any instant and the amount of growth yet to be added before ceiling yield is reached.

From equation (1) several important parameters of growth can be determined:-

(a) The maximum growth possible is given by (A)

(b) The maximum rate of growth is given by $(\frac{CA}{4})$

(c) The maximum rate of growth occurs at a time given by $t = \frac{\text{Log}_e B}{C}$

Mathematical calculations were simplified by use of an I.B.M. 1620 computor program designed by Miss W. Humphries of the Applied Mathematics Division, D.S.I.R.

The method of orthoganal polynomials (Snedecor 1956) was used to fit polynomials of successively higher order to the death rate data and to test for significance at each stage. The equations were fitted to the cumulative death curves as these showed least variability and greater conformity to polynomial form. The appropriate curves representing death rate were then obtained by differentiation of the fitted curves. The highest significant order of fitted polynomial was the quartic. In the interest of conformity, quartics were fitted to nearly all cumulative curves, even though in some, significance was not quite obtained. The only exception was with the cumulative curve of ryegrass death per unit area in the autumn, where a particularly good fit was obtained with the cubic, and a poor fit with the quartic.

Chapter 3

RESULTS

3.1. Experiment (1)

3.1.1. Dry Matter Yield Measurements.

The measurements of pasture growth are shown in Fig. 3 as lbs dry matter per acre plotted against time in days. Logistic equations, shown to adequately describe pasture growth at Palmerston North by Brougham (1956) have been fitted to the data for total herbage, ryegrass and clover.

The parameters from the fitted curves are shown in Table 1.

Table 1

Parameters of logistic curves fitted to growth data

Data Described		Parameters A	B	C	S.E. of Estimate
Spring	Total Herbage	6948.8	13.350	0.0671	± 99.009
	Ryegrass	5632.8	20.438	0.0599	± 656.379
	Clover	1928.4	39.515	0.1486	± 605.866
Autumn	Total Herbage	2070.4	21.893	0.0959	± 79.092
	Ryegrass	355.7	9.634	0.0877	± 47.632
	Clover	1704.7	28.596	0.1009	± 56.505

Two important parameters of growth derived from the logistic equation are given in Table 2.

Table 2

Growth parameters derived from fitted equations

Data Described		Growth Parameters Maximum rate of growth lb/acre/day	Time to maximum growth rate (days)
Spring	Total herbage	116.583	38.6
	Ryegrass	84.355	50.4
	Clover	71.640	24.9
Autumn	Total Herbage	49.639	32.2
	Ryegrass	7.779	25.8
	Clover	43.022	33.2

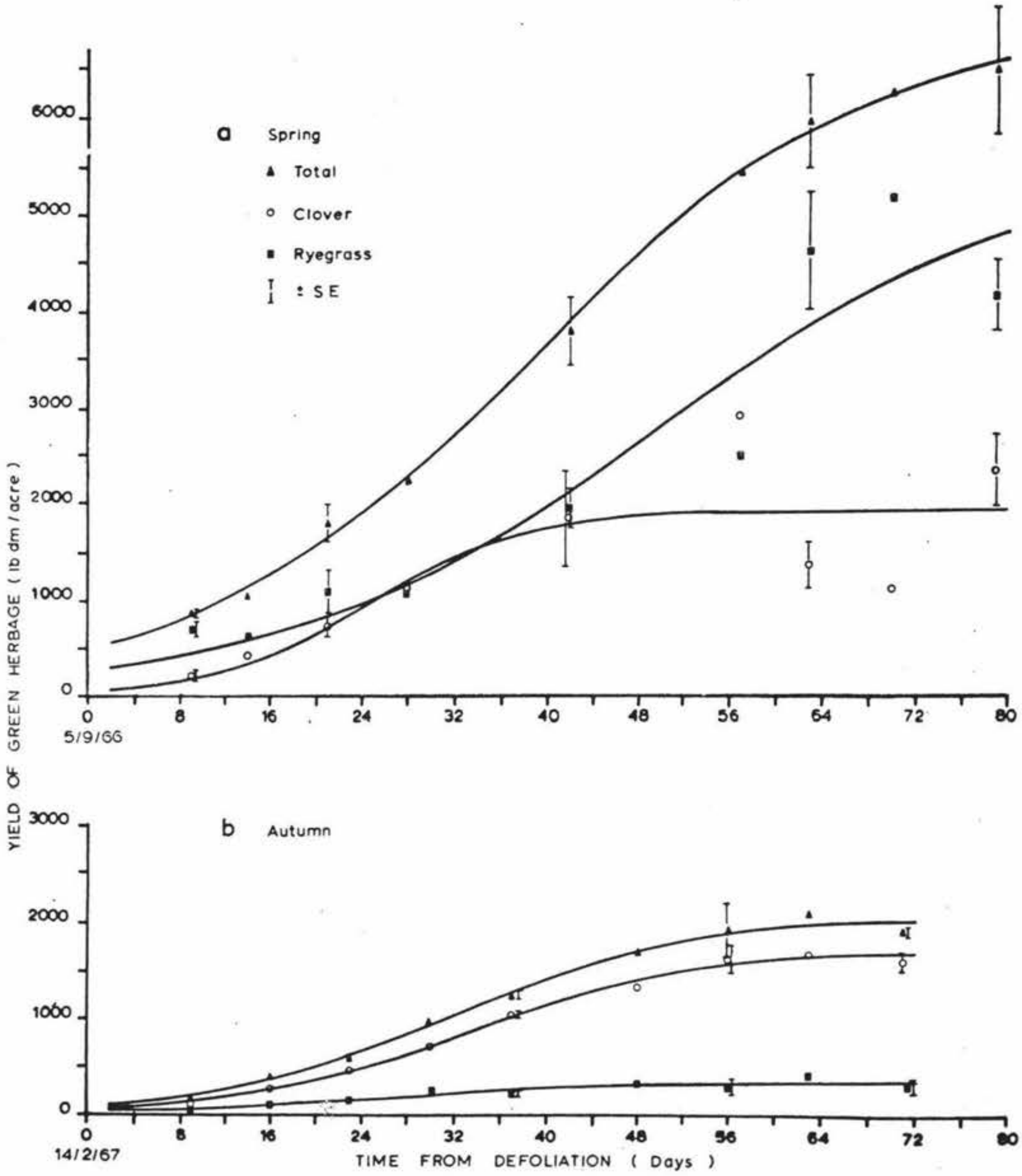

Fig 3 Logistics Fitted to Regrowth Data

The experimental data to which the logistic equations were fitted may be found in appendix 3.

3.1.2. Plant Populations

Measurements of ryegrass and clover plant unit densities are shown in Fig 4 plotted as the number of plant units per square foot against time from defoliation in days. Smoothing processes were employed in order to obtain the best estimate of plant densities at any particular date i.e. where the data presented varied little from obvious trends (e.g. data for ryegrass populations in spring) adequate smoothing was obtained by plotting the mean values of successive pairs of measurement points. Linear regressions were fitted to the data for clover populations in the spring as it was more variable, and to the data for both ryegrass and clover populations in the autumn. No reduction in the sums of squares of deviations from regression could be obtained through fitting curvilinear regressions to the autumn data. The equations of the regression lines fitted are presented in Table 3 and a summary of the data and analyses of regression is given in appendix 4. A regression equation for the spring ryegrass data is presented for comparative purposes.

Table 3

Regression equations fitted to plant population data

Data	Regression Equation	S.E. of Regression
Spring	$y = a + b_{yx}x$	$S_{b_{yx}}$
Ryegrass	$y = 961.1 - 10.813x$	± 1.484
Clover	$y = 295.3 - 0.923x$	± 1.472
Autumn		
Ryegrass	$y = 269.7 - 2.655x$	± 0.625
Clover	$y = 107.9 + 2.793x$	± 0.923

Significance was obtained in all regressions with the exception of the

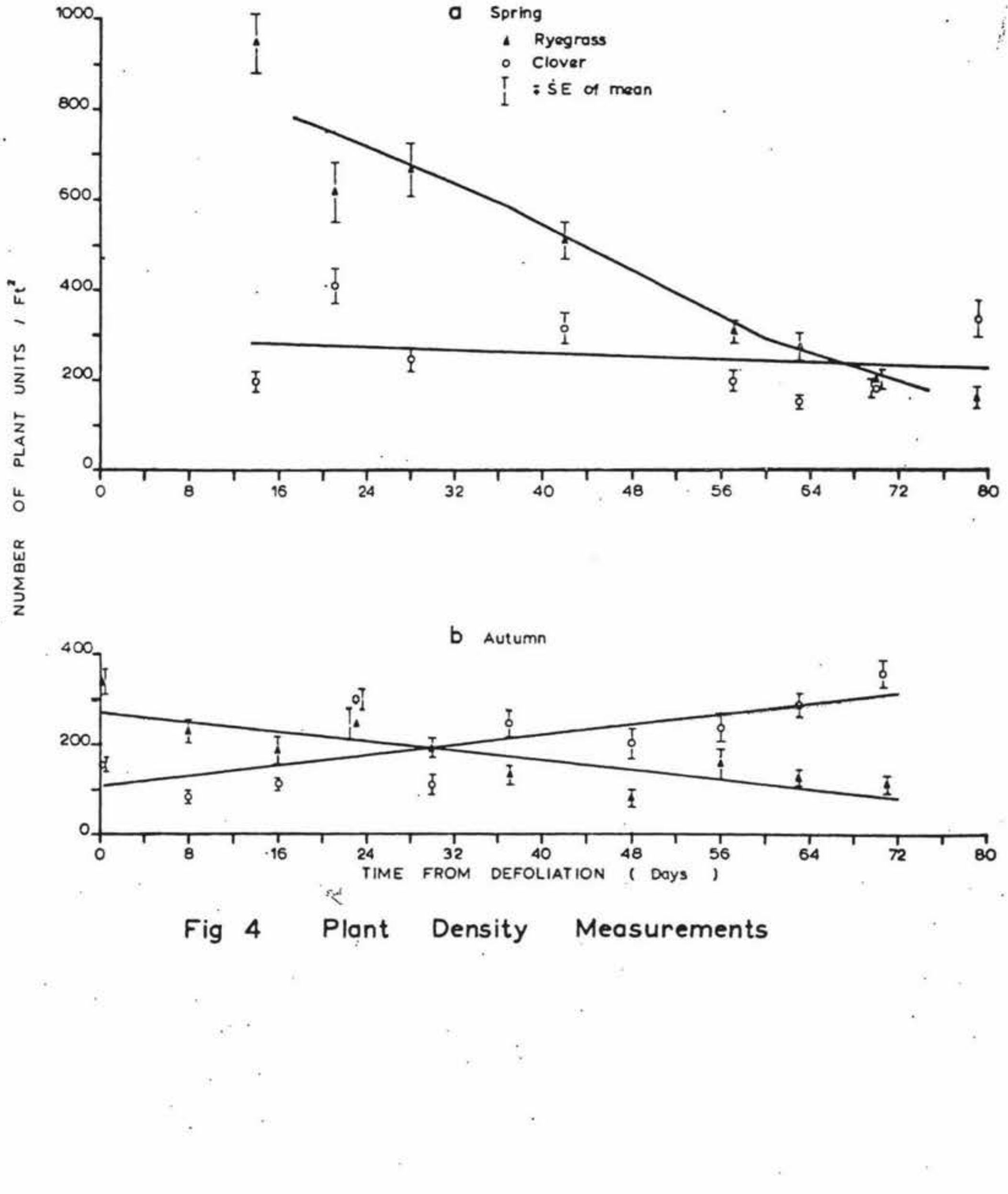

Fig 4 Plant Density Measurements

spring clover data. However, the regression line obtained is still regarded as the best estimate of clover plant populations at any date within the experimental period.

At the beginning of the spring experiment, the ryegrass density was high. Allowing undisturbed growth for the duration of the spring experiment severely reduced the ryegrass plant numbers per square foot from over 800 to 150. The spring clover plant density measurements, although more variable than ryegrass, showed little evidence of any major change with time.

Ryegrass density measurements decreased also during the autumn experiment (270/Ft^2 to 80/Ft^2) but clover measurements showed a definite increase (140/Ft^2 to 330/Ft^2).

3.1.3. Leaf Area Index Measurements

Measurements of total, ryegrass, and clover leaf area indices for the spring experiment are plotted in Fig. 5 against time from defoliation in days. Clover leaf area increased rapidly to an index value of 2.5 - 3.0 after which further increases were substantially slower. The rate of increase in ryegrass leaf area was slower than that of clover in the initial phase and after a maximum index value of 6.0 was reached the leaf area declined. As a result the total leaf area shows an almost linear increase to a maximum index value of 9.00 (after 6 weeks) followed by a gradual decline.

3.2. Experiment (2)

3.2.1. Death rate per Transect

3.2.1.1. Dry Weight of Dead Matter per Transect per Day

Death rate measurements per transect per day are expressed in terms of gms of dry matter per transect and are calculated as a mean

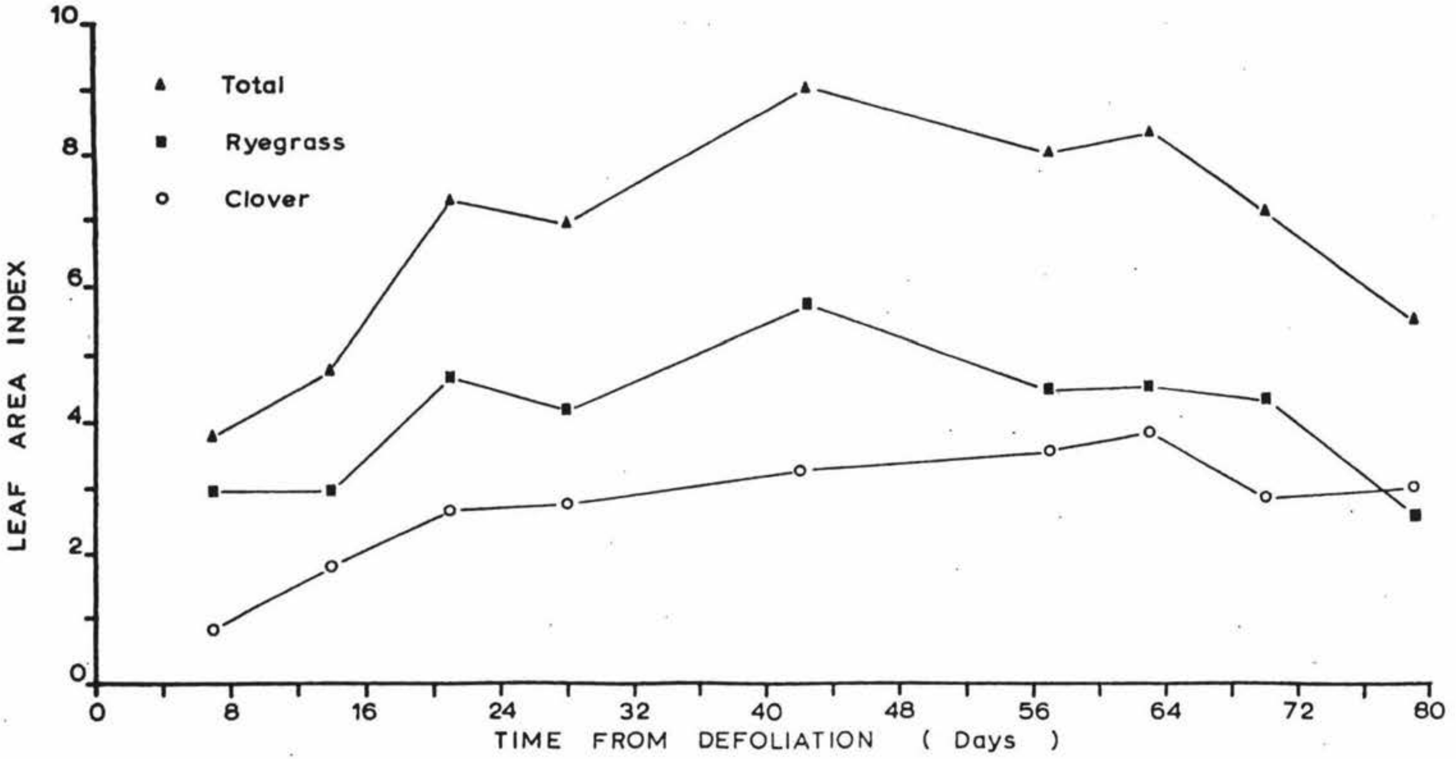

Fig 5 Leaf Area Index Developement (spring)

from 4 or 6 transects. A summary of the data is presented in appendix 5.

The cumulative death curve, derived by integration of the death rate data, is a much smoother curve than that of death rate and the form of the curve more definite. From observation it appeared that the form of the cumulative death curve could be adequately represented by a polynomial, perhaps a cubic or quartic. In order to obtain the best estimate of death rate at any particular day from defoliation, Orthoganal Polynomials were fitted to the cumulative death rate data. The highest significant order of the curves fitted was the quartic. (See section 2.2.3.) The curve of death rate, derived by differentiation of the fitted curve was, therefore, the cubic.

Figs. 6 and 7 show the experimental data and fitted polynomials for the cumulative death data and the death rate data respectively. The formulae of the fitted equations and the standard error of the estimate are given in Table 4.

Table 4

Polynomials fitted to dry weight measurements of leaf death.

Source of Data	Formula of fitted polynomial	S.E. of Estimate
<u>Spring</u>		
Total:	$y = 574.533 + 25.759t + 0.1828qt^2 - 0.00433t^3 - 0.00003qt^4$	$^{+}{-}$ 14.02
Ryegrass:	$y = 226.177 + 10.184t + 0.0940t^2 - 0.001898t^3 - 0.000036t^4$	± 7.808
Clover:	$y = 345.539 + 15.840t + 0.1582t^2 - 0.002525t^3 - 0.000067t^4$	± 6.708
<u>Autumn</u>		
Total:	$y = 575.549 + 76.185t + 0.0340t^2 - 0.03165t^3 + 0.01388t^4$	± 19.71
Ryegrass:	$y = 149.427 + 24.4125t + 0.540t^2 - 0.06408t^3 - 0.00101t^4$	± 5.831
Clover:	$y = 430.414 + 51.862t - 0.9518t^2 + 0.03069t^3 + 0.020268t^4$	± 18.09

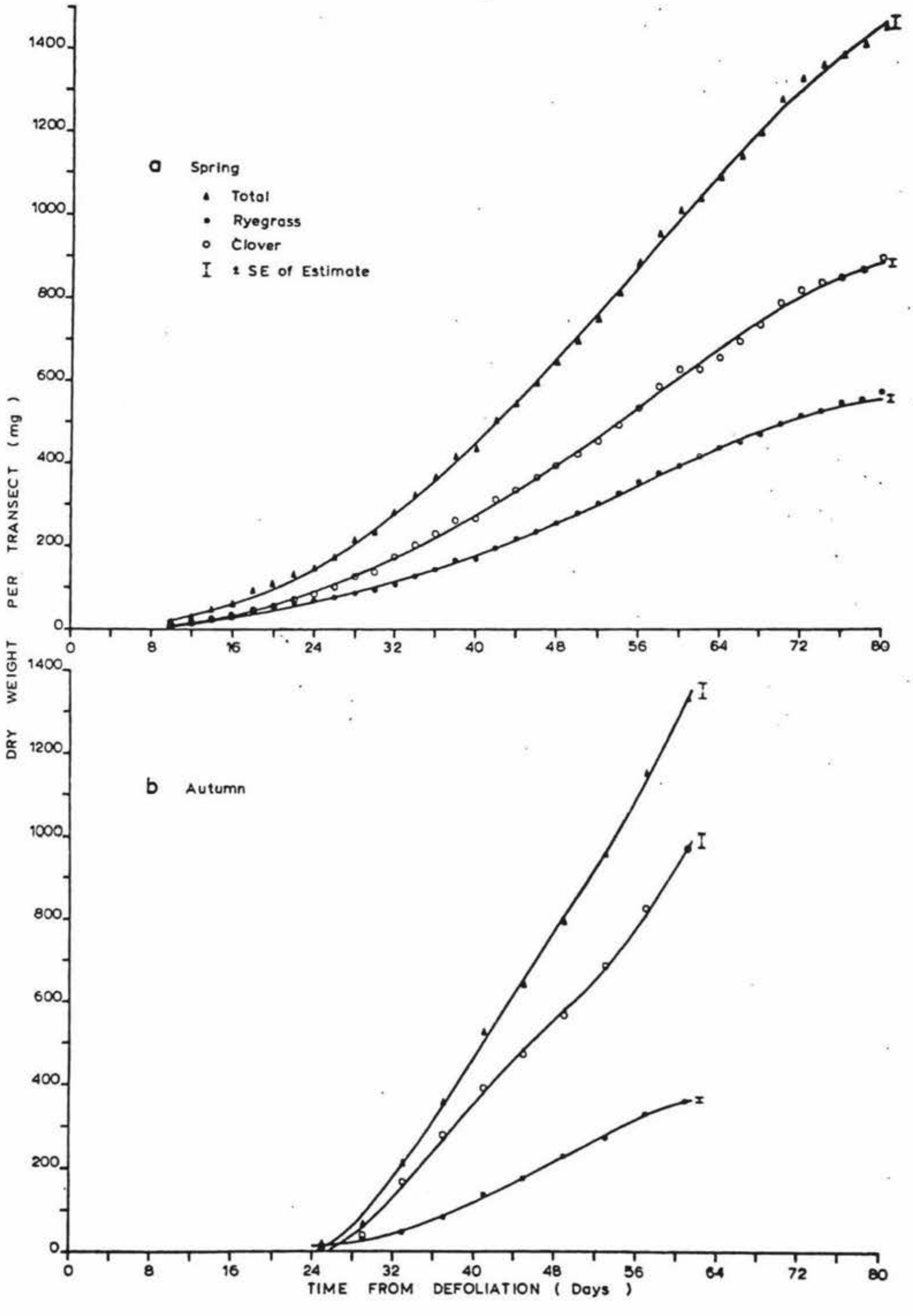

Fig 6 Cumulative Curves of Leaf Death per Transect

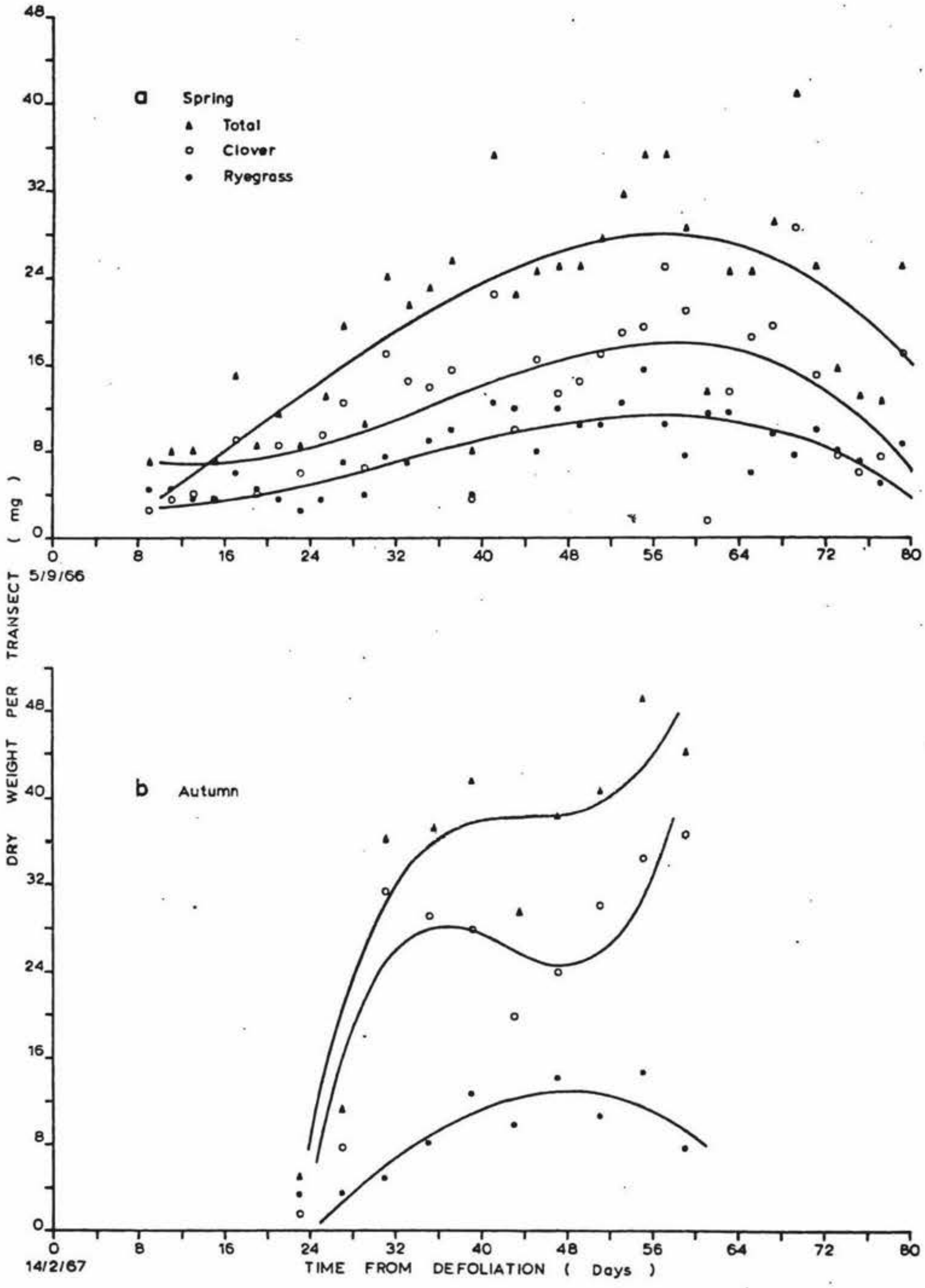

Fig 7 Leaf Death Rate per Transect per Day
(THE CURVES ARE THE DIFFERENTIALS OF THOSE PRESENTED IN Fig 6)

All curves show an increase in death rate with time from defoliation until a maximum is reached. In the spring both ryegrass and clover exhibit a decline in death rate after the maximum is reached. In the autumn, however, while the curve of ryegrass death rate follows a similar pattern to that of the spring, the clover death rate was maintained once the maximum had been reached for the duration of the experiment. The curve of total death rate in the autumn follows a similar pattern to that of clover.

3.2.1.2. The Number of Leaves that Died per Transect per Day.

The data of the number of leaves that died per day was also calculated as the mean of 6 or 4 transects. The data are shown plotted against time from defoliation in days in Fig. 8, and a summary of the data may be found in appendix 6.

Fig. 8a shows that once leaf death began, the number of ryegrass leaves that died per transect was high and remained relatively constant until 40 days after defoliation, after which it steadily declined. With clover, the number of leaves that died per transect increased to a peak approximately 32 days after defoliation, after which it declined in a manner similar to that of ryegrass. During the autumn however, the curves for both ryegrass and clover show an increase from low initial values but no definite decline was apparent at the end of the experiment. This was undoubtedly a reflection of the lack of any substantial decline in plant numbers per transect in the autumn, such as occurred in the spring (Fig. 9). The increase in the number of ryegrass leaves that died per transect in the autumn began about 33 days after defoliation. The clover values were exceptionally high by this time, however, compared with the values for the remainder of the experiment. It is possible that some short term environmental influence resulted in the premature death of a number of clover leaves that were approaching or in various stages of senescence. Their subsequent abscence may thus be responsible for the relatively low number of clover leaves that died per transect 45 days

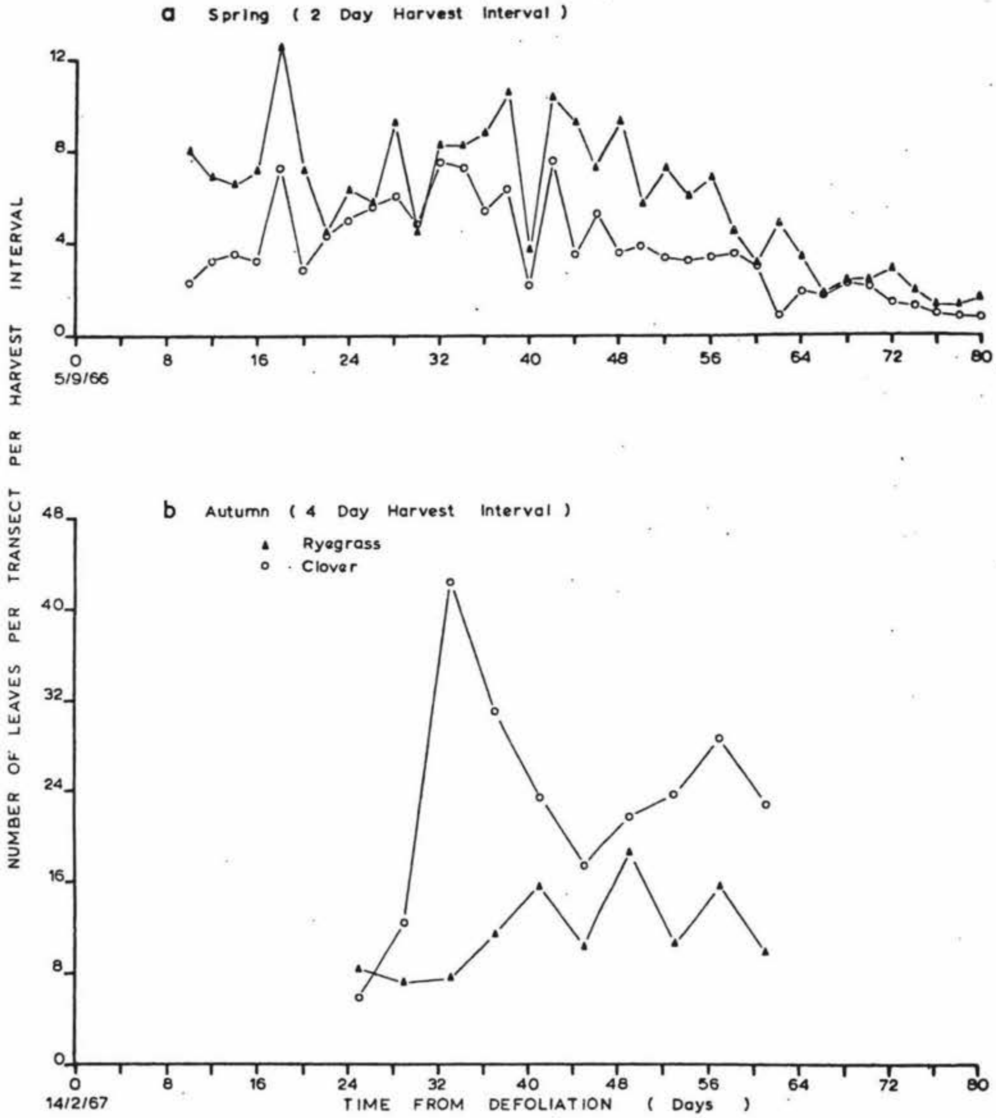

Fig 8 The Number of Dc.g Leaves that were Harvested per Transect

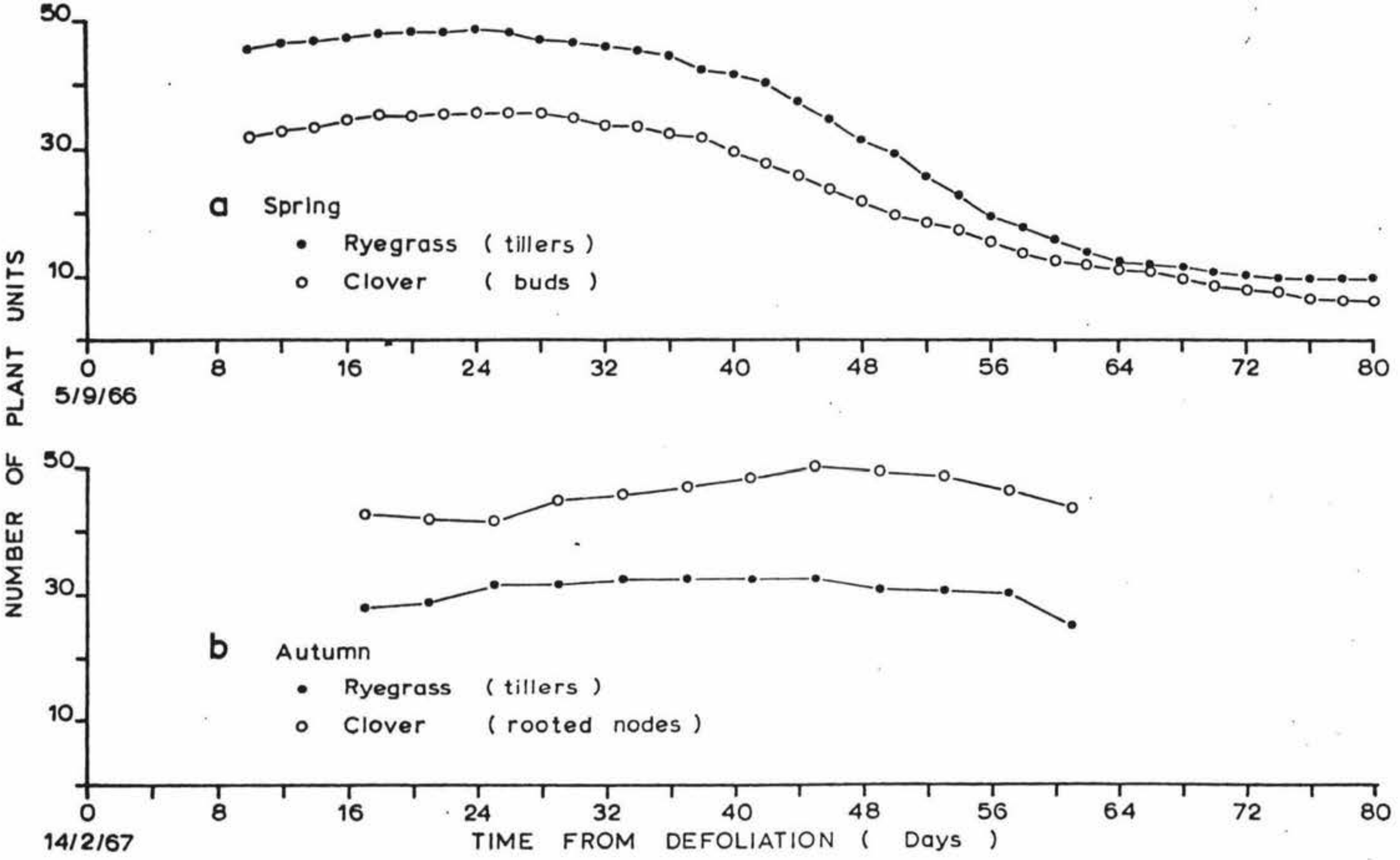

Fig 9 The Number of Plant Units per Transect

after defoliation.

3.2.2. The Number of 'Plants' per Transect

Deviation in the number of 'plants' per transect from the original 70 marked may occur due to -

(1) the death of 'plants'

(2) vegetative propogation of marked 'plants'.

i.e. tillering of marked ryegrass tillers and nodal rooting of marked clover stolons. Because the 'plants' were marked at random, the proportional increase or decrease in the transect 'plant' numbers was representative of the proportional trends in the pasture population as a whole.

The number of 'plants' per transect are presented in Fig. 9 as the proportion of the original 70 marked plotted against time from defoliation in days. Substantial reductions in the transect 'plant' populations occurred during the spring resulting in a 77% decrease by the end of the experiment. Relatively little variation occurred during the autumn experiment, however, clover transect 'plant' populations eventually increasing by 5%, and ryegrass decreasing by 14%.

3.2.3. Relative Decomposition Rate

3.2.3.1. Dry Weight Accumulation of Dead Matter

The curves showing the cumulative death of ryegrass and clover leaves for a range of collection intervals are plotted in Figs 10 and 11 as gms of dry matter per transect against time from defoliation in days.

In the spring experiment the cumulative dry weight curves measured at four day collection intervals were essentially the same as those measured at two day intervals for both ryegrass and clover. Substantial losses were associated with harvesting clover at eight day intervals during the first half of the experiment but no loss was apparent during the second

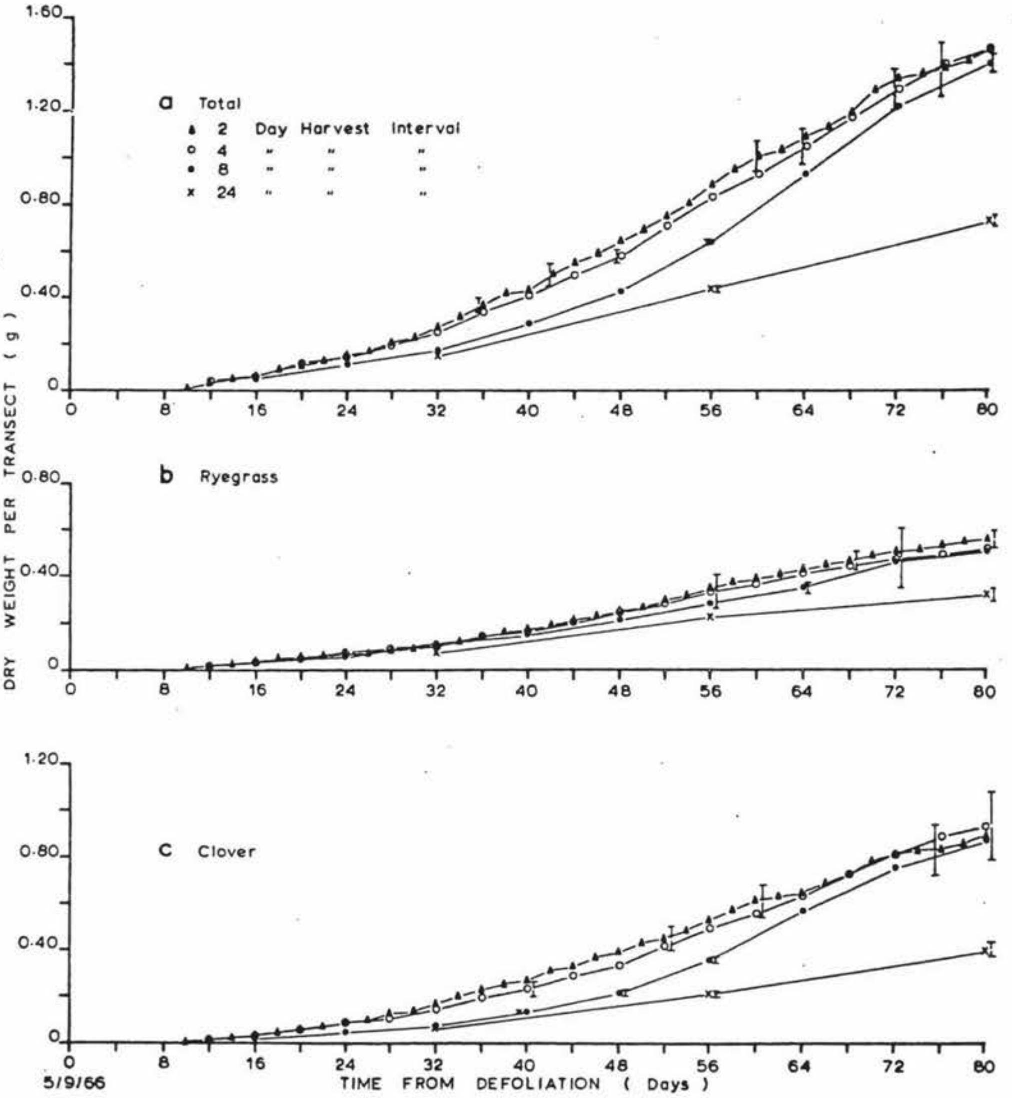

Fig 10 Cumulative Dry Weight of Dead Leaf per Transect : Spring

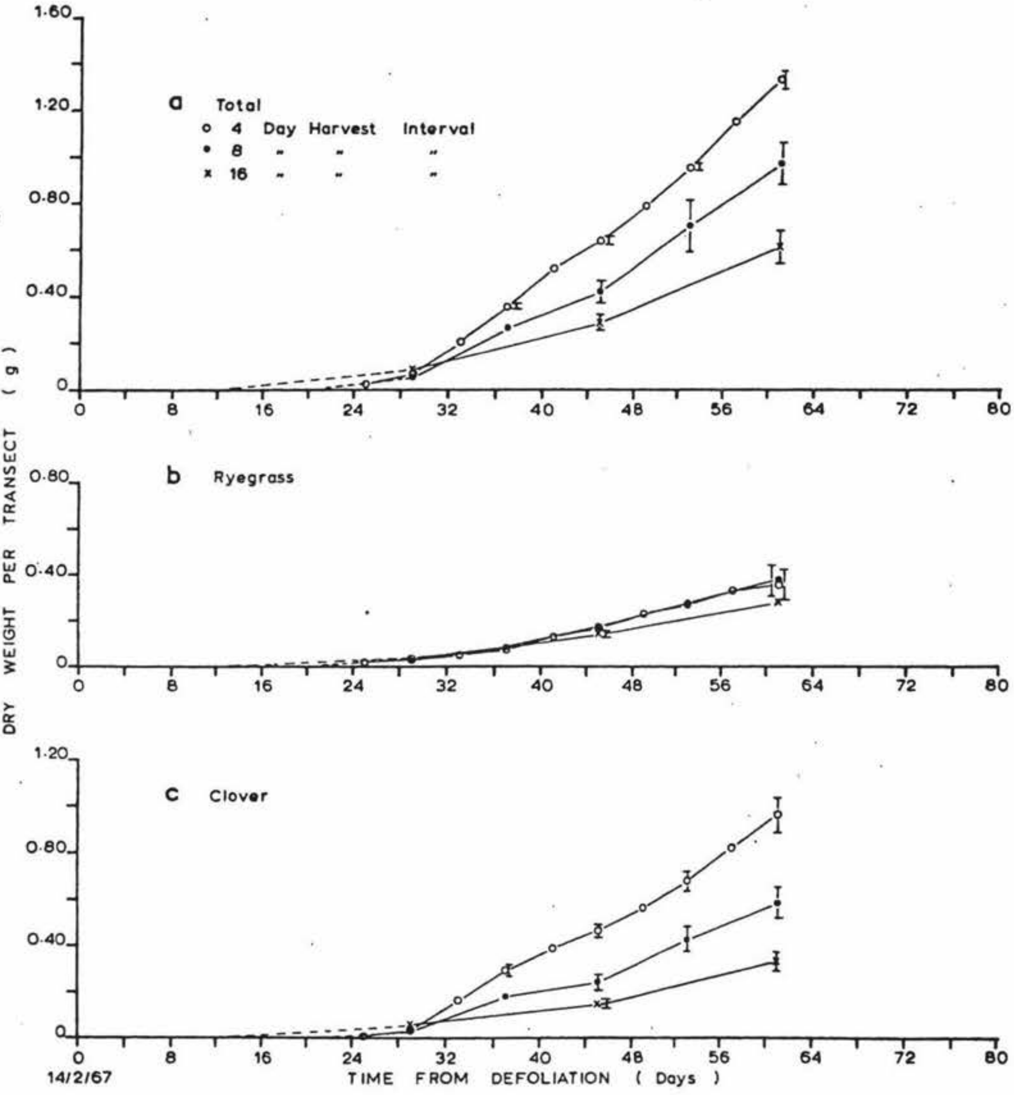

Fig 11 Cumulative Dry Weight of Dead Leaf per Transect : Autumn

half. With ryegrass, there was an indication of some weight loss associated with the eight day collection interval during the second half of the experiment but it was not detectable statistically. Substantial weight losses were associated with harvesting at 24 day intervals with both ryegrass and clover. By the end of the experimental period (80 days) the accumulation of dead ryegrass leaves had been reduced by 43% and that of clover leaves by 55%.

During the autumn experiment, harvesting at eight day intervals indicated substantial reductions in the accumulation of clover leaves compared to four day intervals, but there was no comparable reduction in the accumulation of ryegrass leaves. Harvesting at 16 day intervals indicated a reduction in the accumulation of dead leaves of both species although the reduction of ryegrass leaves was small. By the end of the experimental period (61 days), the reduction in the accumulation of dead leaves associated with harvesting at 16 day intervals was 22% for ryegrass and 64% for clover.

3.2.3.2. The Cumulative Total of Dead Leaves

The curves of the number of ryegrass and clover leaves accumulating when harvested at a range of intervals are plotted in Fig. 12 against time from defoliation in days.

Decomposition of leaves to the extent whereby they cannot be harvested is indicated by significant reductions in the number of leaves that have accumulated. Ryegrass leaves in the spring showed no sign of complete decomposition when harvested at 4 day intervals but did show significant reductions in the number of accumulating leaves when harvested at both 8 day and 24 day intervals. In the autumn however, harvesting at 8 day intervals revealed no reduction in the number of leaves harvested. Complete decomposition of approximately 25% of the leaves occurred however, where

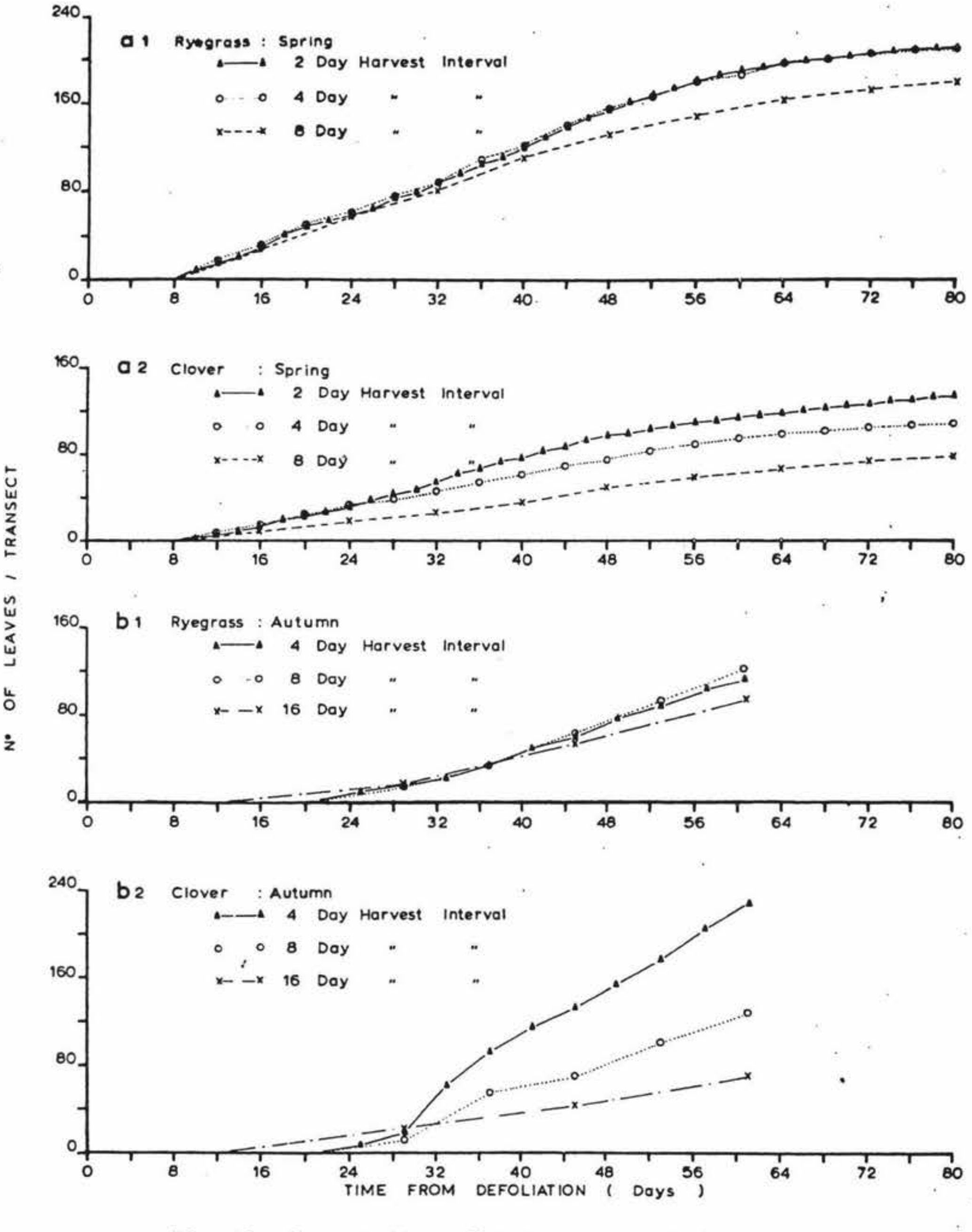

Fig 12 Cumulative Total of Dead Leaves per Transect

where leaves were harvested at 16 day intervals.

The number of clover leaves accumulated from harvesting at 4 day intervals in the spring was not significantly less than those from 2 day intervals although the two curves show some divergence between day 24 and day 44. Significant reductions in accumulating leaf numbers did occur however, where leaves were harvested at 8 day and 24 day intervals. Similar reductions in the number of accumulating clover leaves occurred in the autumn experiment for 8 day and 16 day collection intervals, compared with 4 day collection interval.

3.2.4. Light Penetration Measurements.

Analyses of variance were carried out on light penetration measurements made during the autumn experiment, comparing light penetration along transects disturbed regularly with those disturbed infrequently. There was no significant difference in the light penetration in the swards disturbed at 4 day, 8 day, and 16 day intervals on any of the days at which measurements were made. A summary of the analyses of variance may be found in appendix 7.

The amount of light intercepted at 1 cm above ground level on the measurement days is presented in Table 5.

Table 5.

% Light interception at 1 cm above ground level

Days from Defoliation	% light interception
21	50.5± 8.54
27	75.1± 8.38
32	90.5± 4.20
41	95.7± 3.11

Light interception increased rapidly up to day 32 at which time over 90% of daylight was intercepted at 1 cm above ground level.

Chapter 4

DISCUSSION

4.1. Experimental Techniques.

In succeeding sections of Chapter 4 the results presented in Chapter 3 are used to describe the growth and death of the pasture during undisturbed regrowth from defoliation. This section of chapter 4 will be devoted to the discussion of assumptions involved and problems encountered in obtaining data representative of the growth and death in one particular pasture.

4.1.1. Integration of Data

Measurements of pasture growth and pasture death were made on adjacent experimental areas. Both measurements could not be made simultaneously on one plot as one type of measurement was destructive whereas the other was not. Integration of the growth rate and death rate data therefore, involves the assumption that both types of measurement are representative of the same pasture. This assumption is not unrealistic as the areas are adjacent to each other and therefore subject to the same soil environment, and have at since sowing received identical management and fertilizer treatment.

4.1.2. Sward Disturbance

Sward disturbance during plant inspection in experiment (2) was unavoidable and it is assumed that this disturbance did not measurably affect death rate measurements. The use of easily recognisable tags and locating pins greatly reduced the degree of disturbance necessary to observe the plants to that comparable with natural disturbance occurring on a windy day. However as the disturbance was occurring in the same place at 2 or 4 day intervals an effort was made to assess its significance to pasture death rate.

Sward disturbance could conceivably alter the leaf arrangement and so change the amount of light that penetrates to the lower layers of the sward. As it is possible that the degree of shade that a leaf receives will affect its longevity (Hopkinson 1966), an increase or decrease in the light penetrating to ground level could result in a change in death rate. However, light penetration measurements made in the autumn on swards disturbed frequently and infrequently did not reveal any difference in the degree to which light penetrated the sward. These measurements were made up to and at the stage of approximately 95% light interception when any difference in light penetration would be most readily detected at ground level. The first and the last measurements were made on the days at which disturbance actually occurred. The two intermediary measurements were made between harvesting dates. On the basis of the above results, therefore, it is considered that the assumption that disturbance did not measurably affect leaf death rate, is valid.

4.1.3. The Problem of Defining Individual Plants.

Experiment (2) is essentially an experiment in which information is sought about the pasture as a whole from studying a small sample of the individuals that make up the pasture. Any study involving individuals in plant communities must resolve problems in defining exactly what is to be regarded as an individual. The difficulty arises out of two interlinked properties of higher plants: plasticity and vegetative propogation. (Harper 1967). For example, if sections of clover stolon were to be defined as plant units, a single clover bud protruding from the soil surface would have the same numerical value as a stolon of several inches in length with perhaps several buds and a number of adventitious root systems. Such a definition will therefore result in a wide range in the biological significance of individual units. Also, vegetatively produced tillers and ramets remain attached to and partially dependent on parent tillers sometimes for considerable periods. (Marshall 1967a). Thus as Harper (1967) points out, arbitrary distinctions must be made if plant units are to be counted.

The interweaving nature of tillers and ramets during pasture growth precludes attempts to count all material derived from a common seed as a plant in an established pasture. Mitchell and Glenday (1958) suggest for intensively grazed pastures in temperate zones, the primary growth unit is the individual tiller. According to their definition, "tiller" is used to describe all types of living shoots in a pasture.

In experiment (2) a plant unit is required that will facilitate the accurate computation of death rate per Ft^2 from the mean death rate per plant, and the number of plants per Ft^2. Such a plant unit must be distinguishable as an individual producer of dead leaves and relatively unaffected by minor environmental fluctuations. The tiller, defined as "any type of living shoot" provides a convenient plant unit for ryegrass as far as mature tillers are concerned. Young tillers however, are not distinguishable as independant units for some time. Definitions of graminaceous plants cited by Brown (1954) specify that where the turf can be dissected, to constitute an individual plant unit a tiller must have at least 3 rootlets. However such a definition is impracticable where plants are not to be uprooted and for the purposes of experiment (2) all visible tillers were included in the definition of a 'plant unit'.

Clover plant units are more difficult to define owing to the creeping stoloniferous growth habit and associated adventitious nodal rooting, and the plasticity in bud formation. Clover plant units have been defined as 'any length of runner up to 3 inches long bearing functional rootlets' but this is not universally accepted as being practical (Brown 1954). Another method of numerating clover populations, presumably used by Mitchell and Glenday (1958) is to count the number of clover buds ('living shoots') per unit area regardless of the number of buds dependent on one stolon or root system. The latter method was developed in the spring experiment, a plant unit being defined as any 'living shoot' or bud. While this system provided the information required it was not entirely satisfactory as bud numbers appear subject to considerable short term variability. In the absence of competition, especially for light, bud development on the stolons is encouraged, while the effect of competitive stress is to inhibit the development and bring about the death of all but a few buds. The result is that relatively short term changes in environment can result in large fluctuations in bud numbers although the quantity of stolon and clover herbage has changed little. In the spring experiment the number of clover 'shoots' per unit area displayed a much greater variability than the number of ryegrass shoots. This variability is reflected in the correlation coefficients; r for clover = -0.25 whereas r for ryegrass = -0.95.

An attempt was made in the autumn experiment to arrive at a definition of a plant unit for clover that would not be as subject to short term variation as that used in the spring. The 'plant unit' used was defined as any section of stolon that exhibits both leaves and a root system. Plants are numerated therefore, according to the abundance of root systems rather than shoot systems. In containing both leaves and roots, each 'plant unit' represents a physiologically complete system presumably able to survive and flourish if dissected from other such units or the parent plant. The number of buds on the stolon is not critical, fluctuations in bud numbers thus having no influence on 'plant' numbers but merely reflecting plasticity in 'plant' size in response to competitive influences. (Donald 1963). Changes in the number of root systems per stolon do affect plant numbers however. Thus, adventitious rooting of an elongated stolon results in the formation of a new 'plant unit'. Although differences in clover population variability due to the definition of a 'plant unit', were confounded with differences associated with season, the reduction in clover variability relative to ryegrass variability in the autumn compared to that in the spring was marked enough to suggest that the autumn clover plant unit was inherently more stable. The correlation coefficients showed much closer agreement in the autumn, being -0.83 for ryegrass and 0.73 for clover.

Obtaining a 'plant unit' that displays minimal variability is desirable as more definite conclusions can be made owing to the greater accuracy or narrower confidence interval. However the calculation of death rate per Ft^2 is valid whatever the definition of 'plant unit' as long as the same definition applies to the measurement of both leaf death per 'plant unit' and the 'plant unit' density. Thus although the autumn and spring measurements of clover density and clover leaf death per 'plant unit' are not directly comparable, the autumn and spring calculations of death rate per Ft^2 are comparable.

4.1.4. The Line Transect

Individual line transects consisted of a number of tagged 'plant units' (originally 70). In making calculations and drawing conclusions about the population as a whole, it is assumed that each transect contains a representative sample of the parent population. This assumption is statistically valid provided that the plant units constituting the transect are chosen at random.

Random selection implies that every individual 'plant unit' in the population has a known probability of appearing in the sample. (Snedecor 1956). One method commonly used to attain randomness, where mixing is impossible, is to limit the choice of the sample to some mechanical device that cannot be influenced by the controller. Efficient coverage of an area to be sampled is often achieved using a scheme known as "Stratified Random Sampling". Bias due to too many samples being taken from a restricted area is avoided by dividing the area into a number of obvious sub areas and the number of random samples taken from each is made proportional to its area. (Snedecor 1956). In its ultimate form the field is divided into as many equal sized areas as there are samples to be taken, one sample being randomly located within each area. Theoretically, there is no objection to equally spaced samples provided the spacing is made sufficient to ensure independence between sites (Mitchell and Glenday 1958).

The above principles were employed in obtaining a random sample of pasture 'Plant units'. A mechanical device was used to systematically locate equally spaced 'plants'. The spacing between plants (6 inches) was considered ample to ensure independence between sites, i.e. the spacing was sufficiently large compared with the growth habit of the pasture species 'plant units' to ensure that the location of one 'plant' as say ryegrass, did not affect the probability of the next 'plant' being ryegrass.

In effect a randomly located strip of pasture 6 inches wide has been subdivided into sub areas 6 inches square. One plant unit has been selected at random in each sub area. It is statistically valid therefore, to make inferences about the parent population from the measurements made on line transect samples.

4.2. Pasture Growth.

4.2.1. Fitting Growth Curves

The growth curves in Experiment (1) have been smoothed by the fitting of Logistic regressions. The technique of fitting a regression curve to raw growth data results in a smoothed growth curve, the form of which may or may not have biological significance but which provides the best estimate of the major trends in growth associated with the prevailing environmental and internal plant conditions. Short term fluctuations of less significance due to experimental errors or short term changes in the environment are for the most part averaged out. Work by Brougham and Glenday (Brougham 1959), has shown that weekly fluctuations in growth rate attributable to weather fluctuations can be as large as ± 50% of the weekly growth rate. When growth is measured on a daily basis, such fluctuations can be as great as ± 100% (Brougham _pers comm_). These figures serve as a reminder that such fluctuations can be of great importance and should not be forgotten.

The success of using mathematical curves for describing data depends greatly on the data lending itself to a particular form in the first place. Generally, the more complex the growth process becomes and the longer the period over which growth is considered, the more difficult it becomes to approximate the process with a mathematical formula. Thus although a simple compound interest formula can describe well the early growth of an annual plant (Blackman 1919), no single formula, even though a potential series of curves, will satisfactorily describe growth over the life cycle of animals, particularly man (Brody 1945). Where growth is measured over a restricted period it may be difficult to distinguish features of formulae found to satisfactorily fit growth over longer intervals. (e.g. Brougham and Glenday, 1967; c.f. Anslow and Back, 1967).

The most characteristic feature of growth curves generally is the sigmoid or S-shape that can be seen in all curves covering the major stages of growth. (Gregory 1921, 1928, Brody 1945, Thompson 1948, Brougham 1955, Milthorpe 1963). Various empirical formulae have been used to smooth such data but these have limited general application. (Brody 1945, Thompson 1948). Probably the most successful is the Verhulst-Pearl curve. Both Verhulst, who derived his logistic in 1838, and Pearl who arrived independantly at the same conclusions in 1920 were concerned with the growth of human populations. This curve has considerable biological significance to studies such as the growth of fruit-fly populations in a restricted space as factors controlling changes in population are few, easily distinguished and can be validly described by mathematical functions incorporated into the equation. Variations of the logistic used in other biological fields have been made plastic in some cases by the incorporation of up to four parameters (e.g. Milthorpe 1963). This has been found necessary owing to the greater number of factors that may influence growth although a certain amount of biological significance is retained where dominant processes can be related to the mathematics of the equation, (e.g. the exponential increase of yield due to the relationship between light interception and yield immediately after defoliation of pastures).

The three parameter logistic fitted to the data of Experiment (1) was considered to adequately describe the data over the entire measurement period but arbitrary distinctions had to be made between the various "growth phases". This is necessary because although it can be argued biologically that pasture regrowth may be linear for a period after a limiting factor becomes operative, there is no linear section in a logistic curve. However, where the data indicate that such a factor was operating, changes in the slope of the logistic are very small and with the use of a straight edge, the duration of the various growth phases can be determined fairly accurately.

4.2.2. The Cumulative Growth Curves.

The logistic equations representing cumulative growth curves of total herbage fit the experimental data well, both for spring and autumn. In both cases, the three characteristic growth phases may be distinguished:-

i.e. Phase I, indicated by a logarithmic increase in herbage yield in accordance with the Exponential Law;

Phase II, during which growth rate is relatively constant and the cumulative growth curve is approximately linear;

and Phase III, in which growth rate decreases proportionately as the ceiling yield is approached in accordance with the Mitscherlich Law.

(Brougham 1956).

Logistic Equations also satisfactorily describe the data of ryegrass and clover growth although undue variability appeared over the last four measurement dates in the spring. This variability is probably unreal and due to errors in botanical composition sampling. The standard error of the estimate for total herbage for the autumn is similar to that of the spring. (See Table 1). However the values for ryegrass and clover for the autumn are 7.3% and 9.4% of the spring values respectively.

Phase I of the total herbage growth curves lasted four weeks in the spring and slightly less than four weeks in the autumn. The nature of growth during this phase can be explained in terms of increased light interception and thus photosynthetic production with successive increases in leaf area (Brougham 1955). The duration of this phase depends on the intensity of defoliation, the relative rate of increase in leaf area, and the extent to which increased growth rate is uninhibited. Different factors appear to be involved in determining maximum growth rate in the spring and autumn.

In the spring experiment, the phase of approximately linear growth began 28 days after defoliation. This date coincides with the attainment of a leaf area index of 7.00 (see Fig. 5) which approximates the Critical L.A.I. for ryegrass (7.10) reached by Brougham (1958a) at Palmerston North at a similar time of the year. Although the sward was ryegrass dominant (80% ryegrass initially) the Critical L.A.I. of the mixed pasture would be less than 7.00 due to the higher light intercepting capacity of the clover present. (Brougham 1958a). It is reasonable to assume therefore, that despite the extrapolation of the critical L.A.I. from one year to another, the maximum growth rate was reached in this experiment when complete light interception occurred. The intensity and manner of distribution of light over the photosynthetic surface were probably, therefore, the main factors preventing higher growth rates in the spring (Brougham 1960).

In the autumn experiment however, the end of the exponential growth phase was reached 26 days after defoliation, at which stage only 71% of the incident light was intercepted at 1 cm above ground level. (See Table 5). The growth rate at that stage (near maximum as the phase of approximately linear growth was commencing) was 46.6 lb per acre per day, which is substantially lower than the growth rate at the equivalent stage in the spring (102.9 lb per acre per day). Comparisons of clover growth are more revealing in indicating factors limiting growth rate as the marked seasonal influence of ryegrass growth is removed. From table 2 it is evident that the maximum clover growth rate (43.02 lb per acre per day), reached 33 days after defoliation in the autumn, was only 60% of the maximum clover growth rate in the spring (71.6 lb per acre per day) reached 24 days after defoliation.

Growth in the autumn experiment was predominantly from white clover (see Fig. 3) whereas in the spring the pasture was ryegrass dominant. Restrictions to clover growth due to competition with ryegrass would therefore have been least in the autumn. The light environment from September to November at Palmerston North is essentially the same as that from February to April (see Fig. 13) although it is increasing in intensity in the spring and decreasing in the autumn. This results in similar patterns of leaf development and maximum dimensions obtained in undefoliated stands of white clover. (Brougham 1962). It is unlikely therefore, that the seasonal difference in clover growth rate could be explained in terms of intensity or duration of daylight. Similarly, the diurnal range in temperature during the first growth phase in the autumn (55 - 73°F, see Fig 14) was more conducive to white clover growth which has an optimum growing temperature of 75°F (Mitchell 1956), than the temperature range during the equivalent phase in the spring. (45 - 63°F)

The lower growth rate in the autumn under environmental conditions that were otherwise more conducive to clover growth than those in the spring, may be attributed to the relatively dry conditions that prevailed. Rainfall

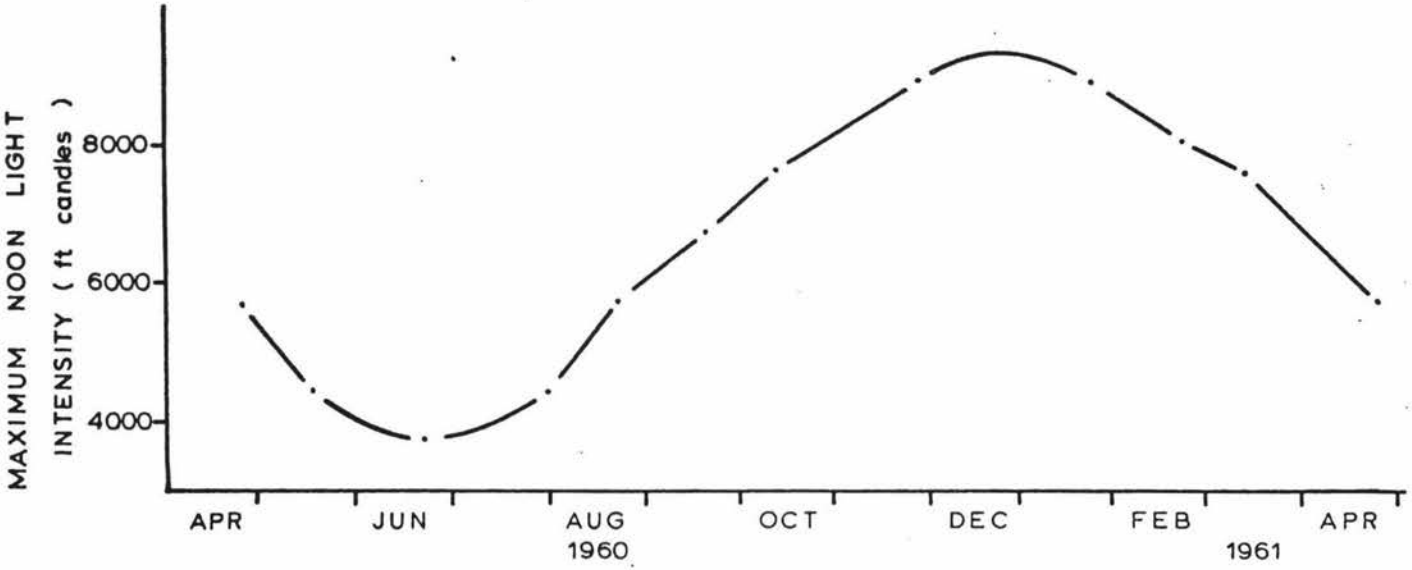

Fig 13 Estimates of Noon Light Intensities
(After Brougham 1962)

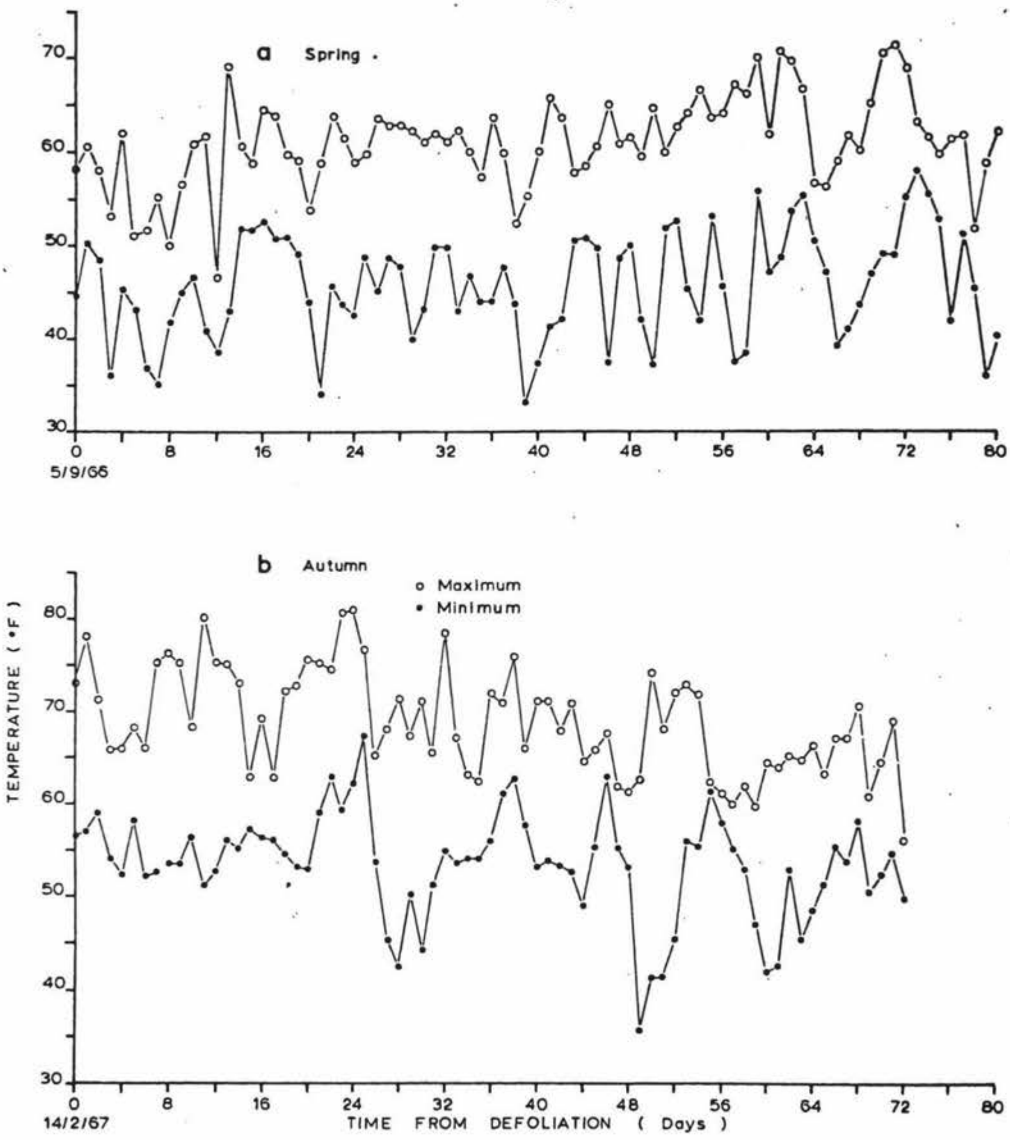

Fig 14 Maximum and Minimum Temperatures Recorded during the Experiments

from defoliation until the maximum growth rate was reached, totalled 0.88 inches (in 32 days) in the autumn compared with 2.90 inches (in 38 days) in the spring (see Fig 15). It is probable therefore, that for the first four weeks following defoliation in the autumn, the limited supply of moisture, and therefore possibly also of nutrients (Mitchell 1957), from the relatively dry soil surface layers was insufficient for utilization of more than approximately 70% of the incident light at local noon. The reduced availability of some nutrients may also have been agravated by the discarding of the clippings (representing about 7000 lb of dry matter per acre) at the end of the spring experiment. As a consequence of this moisture and/or nutrient stress, the observed maximum growth rate was lower than might otherwise have been expected and was reached after a shorter interval from defoliation.

The linear growth phase may be distinguished in all growth curves with the exception of the curve of clover growth in the spring. Factors influencing the duration of the linear growth phase and the attainment of the ceiling yield are discussed in section 4.3.4.

4.2.3. Plant Populations

4.2.3.1. Perennial Ryegrass Tillers

The estimates of ryegrass tiller densities made at the beginning of the spring experiment were similar to that of the ryegrass component of "Sheep pasture (2) " (851 / Ft^2) as measured by Mitchell and Glenday (1958). By the end of the experiment, however, they were lower than that of "Old Dairy pasture" (400 / Ft^2).

The changes observed may be explained in terms of seasonal response to the microclimate, and modification of this response by management effects on the microclimate.

The seasonal pattern of tillering in perennial temperate grass species

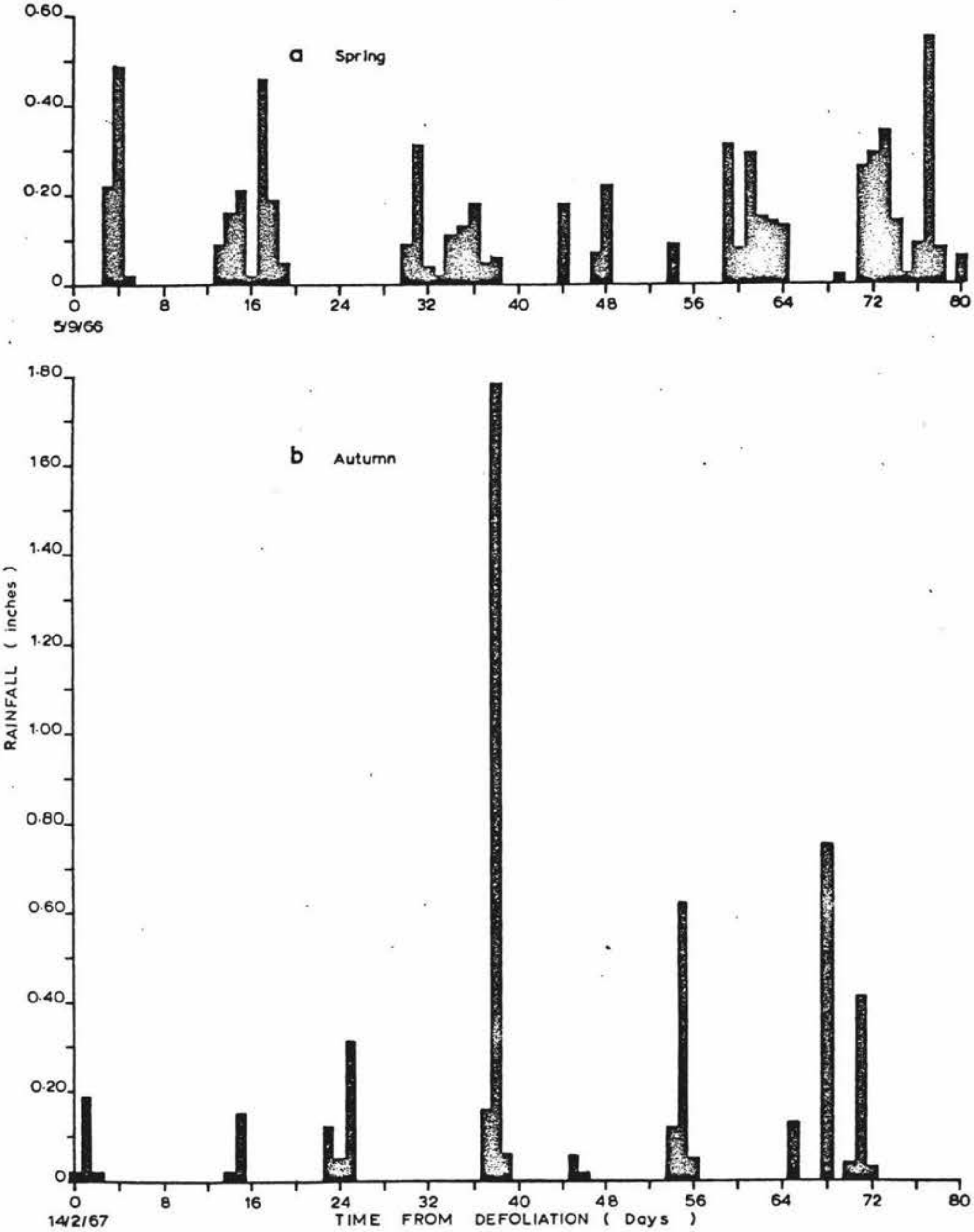

Fig 15 Rainfall Recorded during the Experiments

has been described by Evans et al (1964). Active tillering occurs during the winter, increasing in tempo into the spring. In early spring, an acceleration in leaf growth and stem elongation following the initiation of flowering is associated with a decline in tillering. After flowering in the summer, some renewal of tillering occurs followed by a marked increase in tillering and root growth in the autumn.

At the start of the spring experiment therefore, the high perennial ryegrass tiller density (over 800 tillers / Ft^2) reflected the tillering activity during the previous winter and autumn. As the pasture had been regularly grazed with sheep, it is unlikely that tillering would have been severely inhibited through shading. (Mitchell and Coles 1955). Regular grazing also prevents individual tillers from gaining maximum dimensions and thus restricts their competitive influence. During the spring experimental period, intertiller competition would have been intense as individuals from a dense population were able, in the absence of defoliation, to reach large dimensions resulting in high individual demands for the essentials of growth. The death of ryegrass tillers is probably a direct result of such intertiller competition. The pattern of tiller death as measured in the line transects is shown in Fig. 16 as the number of 'plants' dying per day plotted against time from defoliation in days. Consideration of the relative death rate per tiller (see Fig. 17) gives a clearer picture of the pattern of tiller death with respect to intertiller competition. The relative death rates per tiller were calculated as

$$\frac{\text{Log}_e n_1 - \text{Log}_e n_2}{d_2 - d_1}$$

where n_1 and n_2 are the numbers of tillers at days d_1 and d_2 from defoliation respectively (Langer 1956). n_1 includes all tillers produced up to d_1 but n_2 does not include tillers produced during $d_2 - d_1$. This is to avoid any underestimate of relative

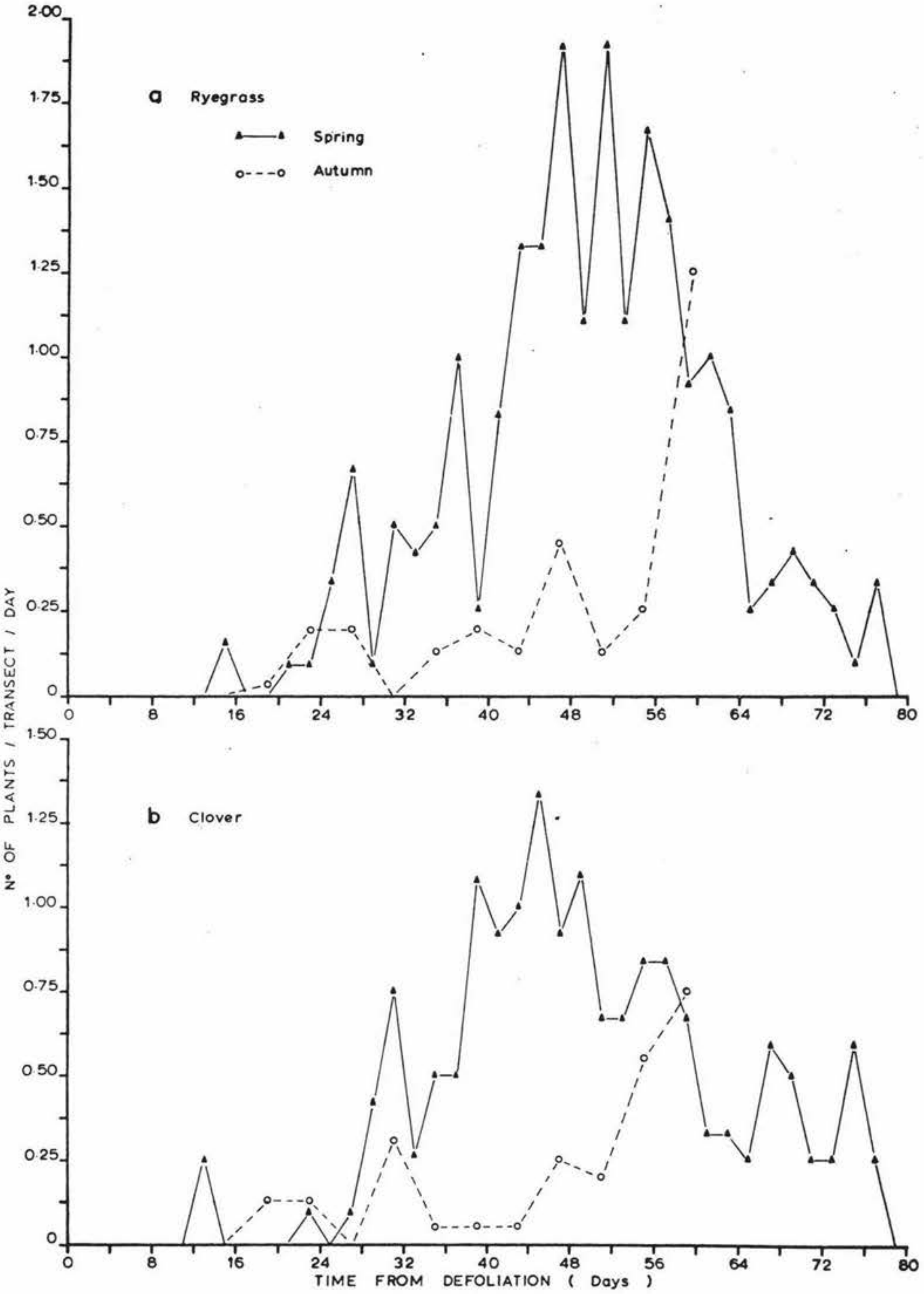

Fig 16 Number of Plant units Dying per Transect per Day

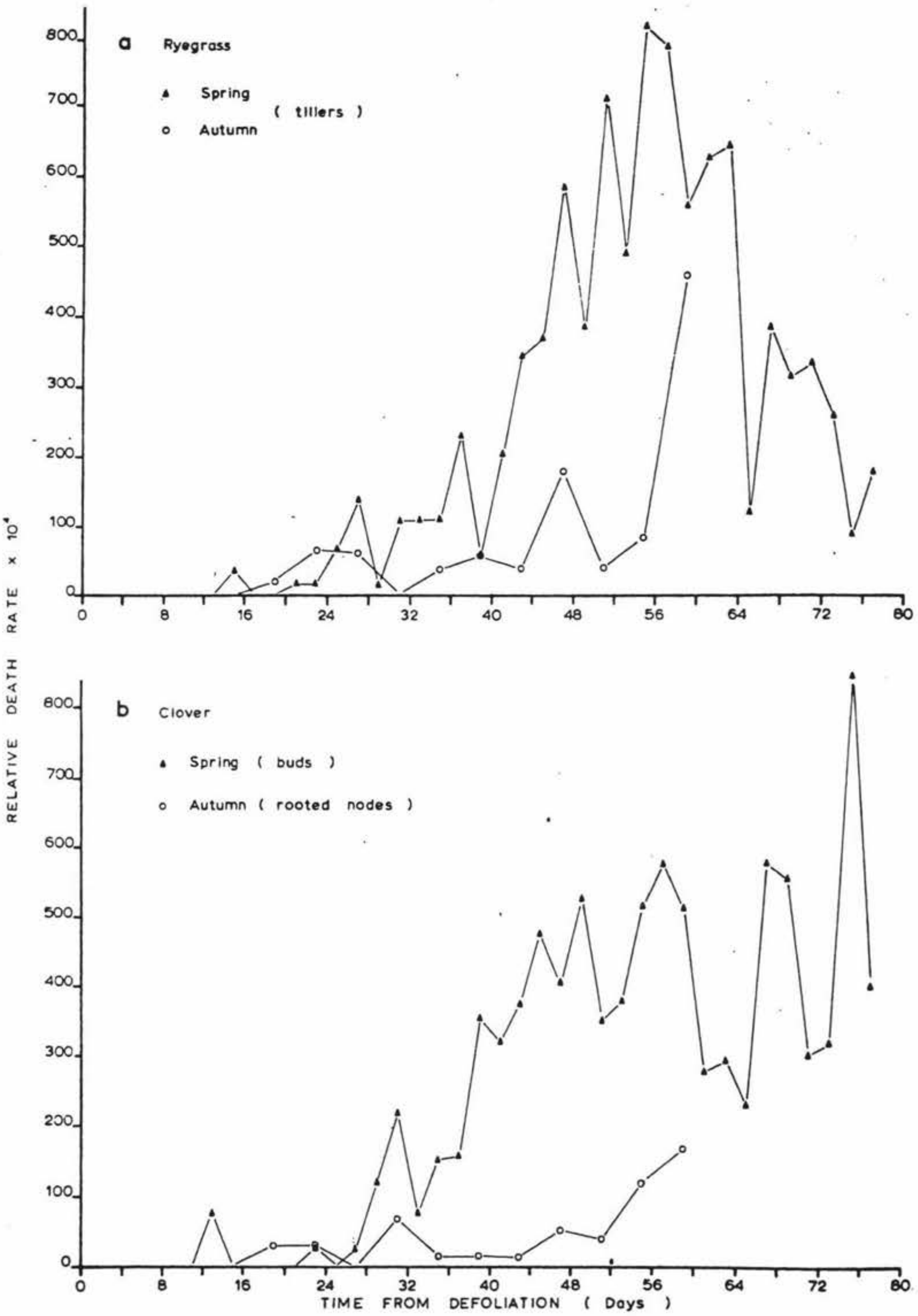

Fig 17 The Relative Death Rate of Plant Units

death rate through the replacement of dead tillers by new ones giving an inflated value of n_2.

Comparison of Fig. 17 with Fig. 3 shows that the phase of rapid increase in the relative tiller death rate (from 40 to a peak at 56 days after defoliation) coincides with the latter half of the phase of linear growth during which it is considered that growth rate is limited by the manner of light interception. (see section 4.2.2.). This indicates that competition for light was probably an important factor in determining the pattern of tiller death during this experiment.

The pattern of tiller death as measured in the line transects is not reflected distinctly in the 'plant' density data, which indicates essentially a linear relationship between plant density and time. The pattern of tiller death described in Fig. 16 would suggest that tiller density was initially relatively constant (or increasing in density if tillering was occurring) before passing through a phase of rapid reduction in tiller number, and then another phase of slower tiller death rate. The initial phase of no tiller death is not present in the 'plant' density data as no measurements were made until 14 days after defoliation at which time tiller death had begun. However the reduction in 'plant' density from day 14 to day 28 is substantial although the tiller death rate as measured on the line transects was not great. This discrepancy may be due to differences in tiller differentiation associated with the method of measurement. Random selection of tillers that were included in the line transects was made from those tillers that were of sufficient size to be tagged. Smaller tillers than these, however, at varying stages of emergence could have been counted in the tiller plugs. If such tillers were the first to die under the influence of intertiller competition (as occurred with "establishing" Italian ryegrass; L.A. Hunt and Brougham 1966), substantial reductions in 'plant' density as measured by the tiller plugs would occur with little indication of tiller death from the line transects.

The phase of 'rapid' and 'slower' tiller death rate indicated in Fig. 16 can be distinguished in Fig. 4 although the change is not marked. This lack of definition of trends in the plant density data compared with the line transect data could probably have been largely avoided had the number of measurement dates for the tiller plug data been increased. The data are not incompatible especially when the variation associated with the estimates of tiller density at each measurement date and between measurement dates is taken into account. The standard errors shown in Fig. 4 include variation between plots, between tiller plugs, within subplots, and 'error' variation within tiller plugs. However, because different subplots were sampled within plots on successive sampling dates, comparison of tiller densities at different dates involves an additional source of variation; namely, between subplots.

Ryegrass tiller densities changed much less during the autumn experiment. Initial densities were not high (up to 300/Ft^2), reflecting the situation at the end of the spring experiment but also indicating that some tillering had occurred during the intervening period. The suppression of tillering that normally is to be expected in the autumn (Evans et al 1964) and the decline in tiller density during the experiment may be attributed to the combined effects of dry weather, strong competition from white clover, and the shading of tiller sheaths in the absence of defoliation (Mitchell and Coles 1955). The pattern of tiller death as measured in the line transects (Fig 16) indicates that the tiller death rate was low but relatively constant with a tendency to increase at the end of the experiment. This constancy was reflected in the plant density data (Fig. 4) but the final increase was not apparent.

The relative death rate of tillers per tiller per day (Fig 17) in the autumn is also relatively constant with a tendency to increase after 44 days from defoliation. This increase occurs during the third phase in the regrowth curve (cf. Fig. 3) and thus at a later stage of regrowth compared with the spring. However, it also occurs shortly after the stage at which complete light interception occurred (95.7% on day 41, see table 5), suggesting that competition for light may have influenced tiller death in the autumn experiment also. Comparison of the relative death rates per tiller per day for spring and autumn using the date at which the critical L.A.I. was reached as a common reference point (Fig 18) shows a remarkable similarity between the curves considering the extent to which the conditions of growth differed. The reference date for the spring was taken as the date at which the phase of approximately linear growth began and that for the autumn as the day at which 95% of the incident light was intercepted at local noon.

The data strongly suggest therefore, that competition for light was the major factor influencing the tiller death rate, for although ryegrass growth was slow in the autumn and competition for moisture and nutrients by clover over most of the growth period likely to be high, the rapid increase in the relative tiller death rate did not occur until after the stage of complete light interception had been reached. Rapid increases in tiller death rates have been demonstrated prior to heading in barley (Laude et al 1967) under conditions in which shading was avoided. Although such an effect, associated with reproduction, may have been present in the spring, the close agreement between the relative death rate curves in Fig. 18 for the period over which measurements were made in the autumn (when growth was vegetative) suggests that its influence was small or else delayed. High rates of tiller death have been attributed to shading by Langer et al (1964) and L.A. Hunt and Brougham (1966), and this view is supported with direct evidence by Lucanus et al (1960). However, these latter authors also showed that tiller survival was adversely affected by soil moisture stress and high temperatures, and that susceptability to these factors was increased where soil nitrogen levels were also high. Although conditions of soil moisture stress certainly existed up to 36 days from defoliation in the autumn experiment (See section 4.2.2.) a substantial amount of rain fell between 36 and 40 days from defoliation:- about 4 days before the increase in relative tiller death rate (See Fig. 15). Also the considerable herbage cover about 44 days after defoliation (over 1500 lb dm per acre) together with the fact that the temperatures experienced were not excessively high (54°F - 70°F see Fig. 14) makes it unlikely that high temperatures influenced tiller death rate. The temperature treatment used by Lucanus et al (1964) averaged 80°F whereas the controls were at 65°F.

It is probable therefore that moisture stress and high temperatures were not factors influencing tiller death rate, even though due to the strong growth of the clover, soil nitrogen levels may have been relatively high.

4.2.3.2. White Clover 'plant' units.

White clover bud densities in the spring (Fig. 4) changed little during the experiment and again the variation between subplots was such that in the absence of additional sampling dates, trends indicated in the line transect data (Fig. 16) were obscured. Little is known of how the pattern of clover bud density may change with season. However, it is reasonable to suppose that densities at the beginning of the experiment were not at a peak owing to slow clover growth and thus bud development during the early spring. Suppression of any increase in clover bud number that may have been imminent as the seasonal conditions became more favourable to clover growth and the gradual decline in bud number may be attributed to the increased competitive stress between plants in the absence of defoliation discussed above.

In the autumn the plant unit used was defined in relation to the root system rather than the shoot system in an attempt to reduce short term

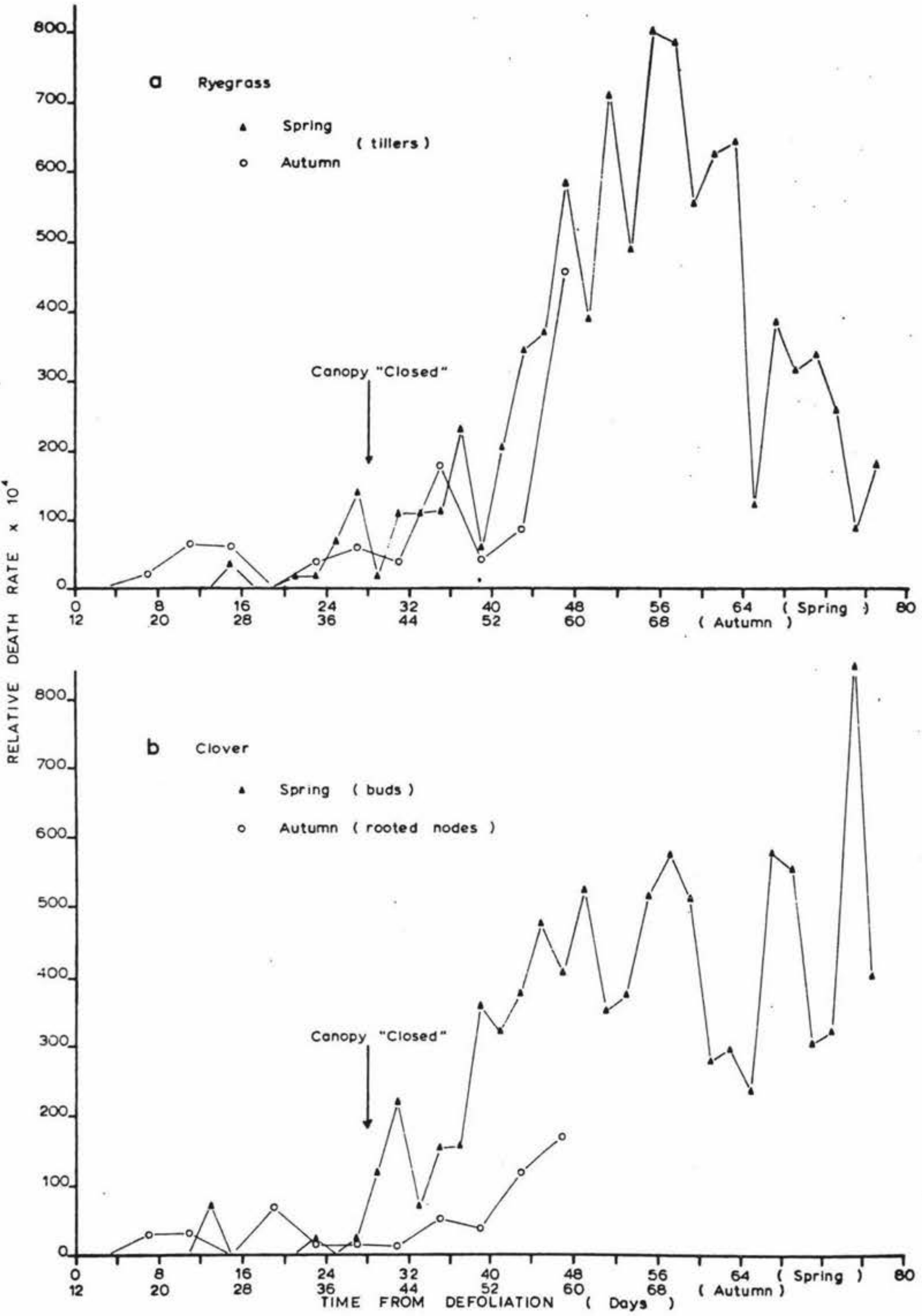

Fig 18 Relative Death Rate of Plant Units with reference to the stage of Complete Light Interception

fluctuations in 'plant' density (see section 4.1.). The gradual increase in the autumn clover plant units reflected the superior ability of clover to grow in the autumn compared with ryegrass, and the strong clover dominance of the sward that developed during the experiment (see Fig. 3). Increased yields from red and white clover have been reported during the summer and early autumn at Palmerston North by Brougham (1957), who attributed this seasonal ability of clover to compete well with ryegrass to a better tolerance to high temperatures and low water supplies.

Spring and autumn plant densities are not directly comparable owing to the different plant units used which may even affect the patterns of 'plant' death rate. Seasonal differences in the pattern of plant death are confounded with differences associated with plant definition such as the death of buds indicating a reduction in plant size rather than plant number in the autumn but vice versa in the spring. On the other hand the pattern of 'plant' death may be altered little by the unit used where the only buds to die are those associated with unsuccessful 'plant' competitors.

Examination of the relative plant death rate (Fig. 17) even with reference to the stage at which complete light interception occurred (Fig. 18) failed to show the agreement between spring and autumn data that was apparent with ryegrass tiller death rate. This may be due to differences in the plant unit used but as the clover density was gradually increasing it is more likely that competition for light (and other factors) between autumn clover plant units was not severe enough to affect their survival greatly. The relative death rate of clover buds in the spring increased rapidly after complete light interception occurred but unlike the relative death rate of the ryegrass tillers there was no subsequent decline (Fig. 18). It would appear that after the peak of tiller death the surviving ryegrass tillers (the strongest competitors) were increasingly large enough and sufficiently well established to withstand the effects of competition. The continued relative death rate at a maximum however, suggests that no such selection occurred with clover buds. This may be due to steadily increased competition by ryegrass eventually forcing the death of even the most persistent clover buds, or it may suggest a fundamental difference in the pattern of growth of ryegrass and clover under such conditions. Whereas tillering and death of tillers tends to a minimum with ryegrass, the growth of clover may depend upon the continued replacement of dying buds with new ones. The dynamic equilibrium observed in undefoliated stands of white clover by Brougham (1958b) in terms of the continued replacement of old leaves by new may thus also apply with clover buds. The survival of clover in a mixed sward would, in these terms, only be threatened when the microenvironment is such that the establishment of new clover buds is inhibited as may occur, for example, under conditions of intense competition for light by ryegrass in the spring.

4.2.4. The Leaf Area Index.

The phase of rapid increase in the total L.A.I. for the mixed sward (Fig. 5) coincides with the phase of exponential growth in the total herbage growth curve. (Fig. 3). During the phase of approximately linear growth the total herbage yield which increased at a maximum must have contained a decreasing proportion of leaf as the rate of increase in total leaf area slowed to zero. This and the decline in total L.A.I. during the third growth phase was undoubtedly due to the increase in stem and seed head as the ryegrass came into flower. Comparison of the clover leaf area index with the curve of clover growth shows a marked similarity in the pattern of the two curves indicating that clover herbage was predominantly leaf at all stages. With ryegrass however, growth rate was at a maximum when the ceiling L.A.I. was reached and when growth rate slackened the ryegrass L.A.I. decreased. Thus as the pattern of both ryegrass and clover leaf production and death was such that no increase in leaf yield occurred after 42 days from defoliation, all increases in ryegrass and total yield during the latter half of the experiment consisted mainly of increased ryegrass stem and seed head. The decrease in, particularly, the ryegrass leaf area during the final growth phase is closely associated with the onset of lodging observed 72 days after defoliation. L.A. Hunt and Brougham (1966) found that the rate of leaf production and senescence of Italian ryegrass was reduced as many tillers flowered. A similar decline in the number of leaves dying per ryegrass plant occurred after flowering in this experiment (see Fig 21a). It would appear however, that after lodging occurred the decline in the rate of leaf production was faster than that of the rate of leaf senescence, the latter being enhanced perhaps by poorer light penetration into the collapsed canopy.

The fall in the number of leaves that died per tiller occurred during the third growth phase, i.e. after the period of most rapid growth. Consequently, the suggestion made by L.A. Hunt and Brougham (1966) that the rapid increase in yield as the sward approached flowering may partly have been due to a fall in the rate of loss by decomposition finds no support in this data.

4.3. The Pattern of Leaf Death.

4.3.1. Death Rate per Transect.

The results of the death rate measurements made on the line transect have been presented in section 3.3.1. both as the weight of dead leaf dying per day and the number of leaves dying per day, at successive stages of regrowth from defoliation. As the measurements were made over short intervals, particularly in the spring, the data show short term variation which was often averaged out when measurement was made over longer intervals even though the latter provide an under estimate of leaf death rate to the extent that the leaf tissue decomposes before harvesting. Added confidence in the results may thus be gained through confirming the pattern observed from frequent measurements by comparison with measurements made over longer intervals. The comparison has been made graphically in Figure 19 where the weight of dead leaf per transect was plotted against time from defoliation in days for a range of collection intervals. Although the scale of the vertical axis must necessarily vary with the collection interval the pattern of the death rate curve was quite consistent. In the spring the death rate per transect for both ryegrass and clover steadily increased to a peak after which a short decline occurred whether the harvest interval was two days, four days or eight days. The autumn data for both a four day and eight day harvest interval, showed a rapid increase in clover death rate to a near maximum which apart from a marked drop 45 days was maintained over the remainder of the measurement period. The pattern of ryegrass death rate in the autumn was similar to that found in the spring.

4.3.2. Death Rate per Plant.

A better understanding of the factors responsible for the observed patterns is possible through analysis into measureable components. The death rate per transect per day (Fig. 7) and the number of leaves dying per transect per day (Fig. 8) can both be analysed in terms of the death rate per plant (Fig. 20) and the number of leaves dying per plant (Fig. 21) respectively, and the number of plants per transect (Fig. 9). A common pattern emerges from this analysis in terms of death rate per plant. In both seasons and under differing conditions of competition and environmental stress the death rate per plant was initially low, increased rapidly for a period which generally coincided with the latter half of the linear growth phase and then with the exception of ryegrass in the spring (Fig. 20a) was maintained at a maximum for the remainder of the measurement period. The decline in death rate per ryegrass plant in the spring was not marked and undoubtedly reflected the decline in the number of leaves dying per ryegrass plant that occurred at that time. (See below).

The pattern of leaf death per transect results therefore from

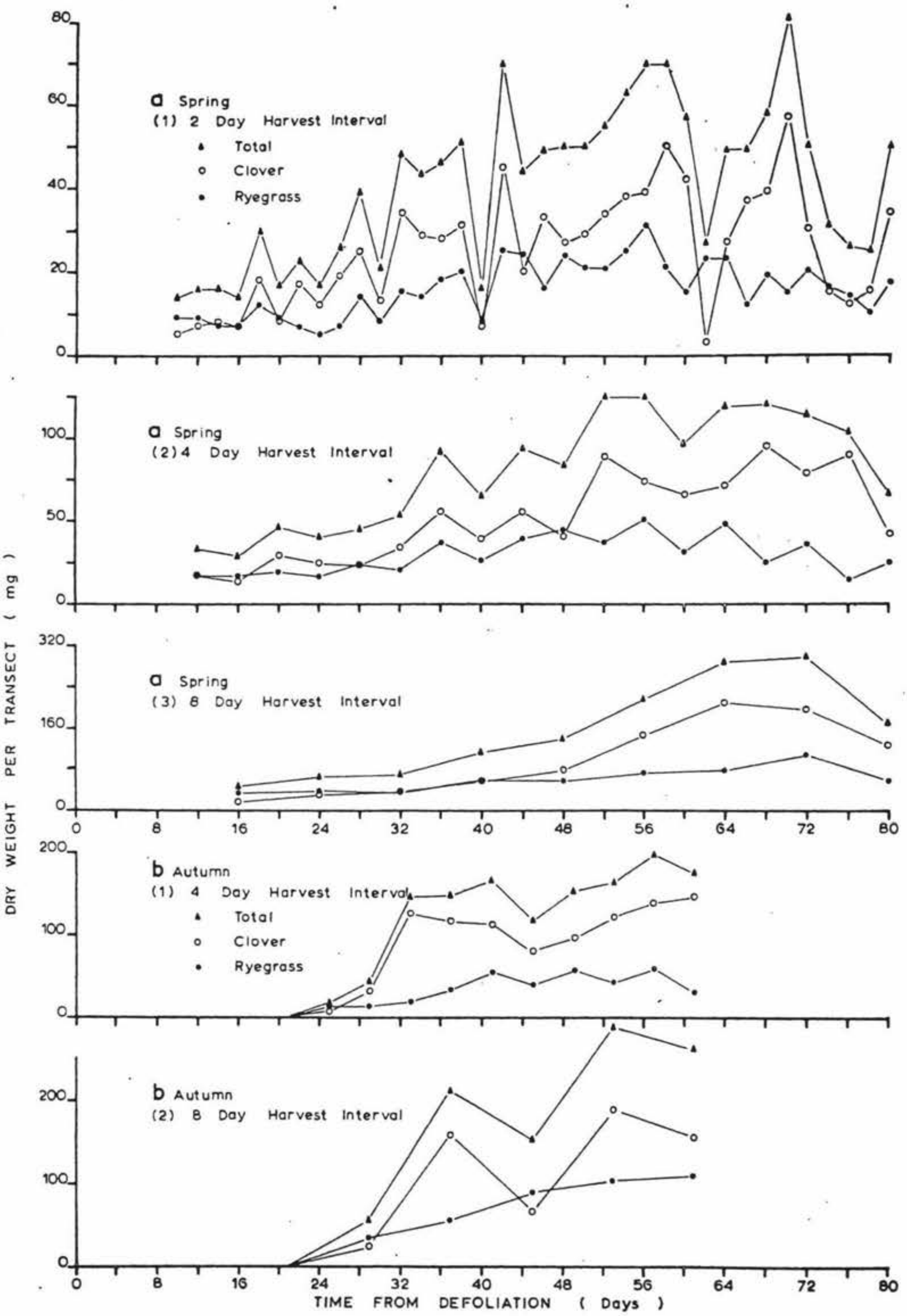

Fig 19 Death Rate per Transect for a number of Harvest Intervals

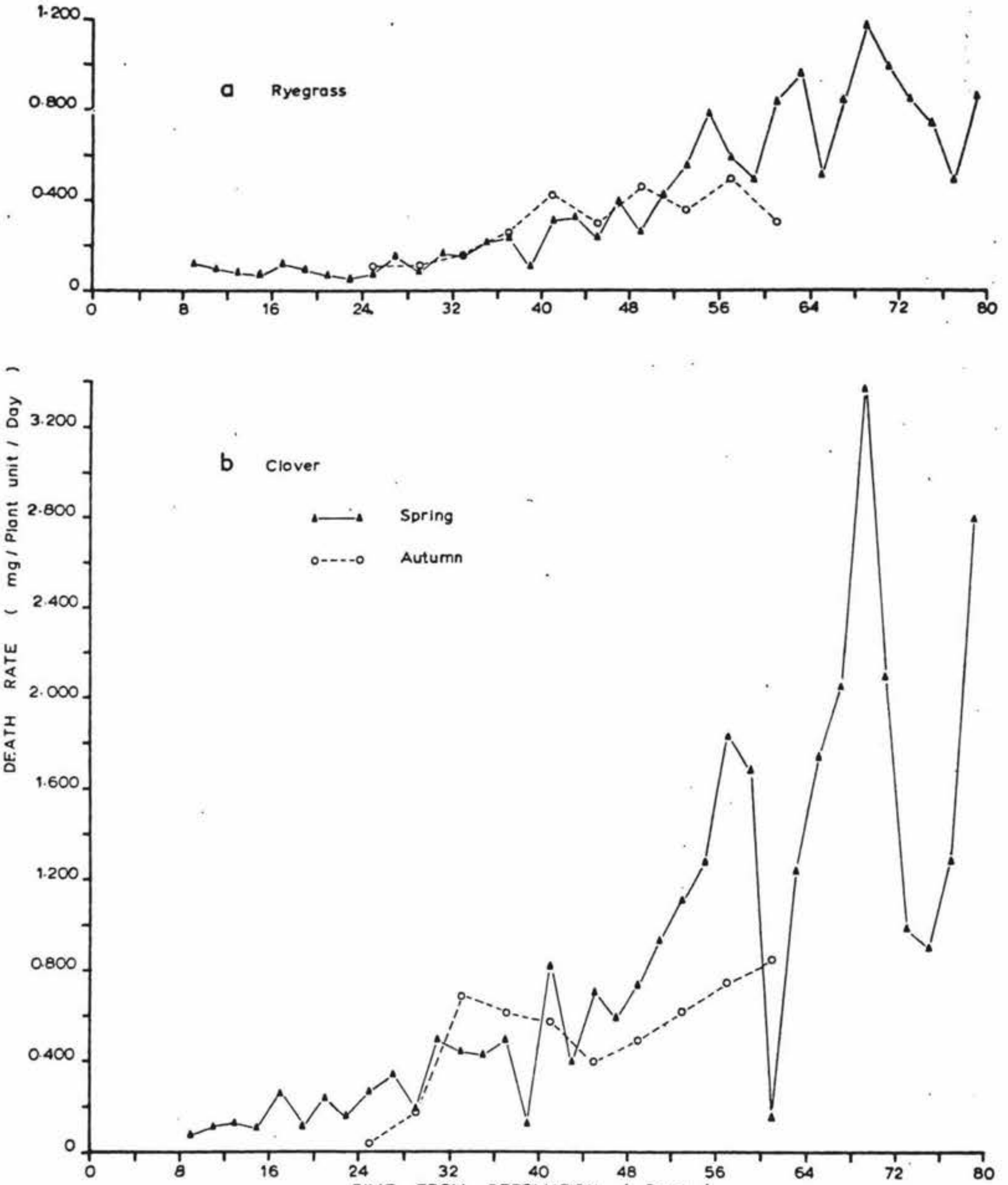

Fig 20 Death Rate per Plant (Dry wt / Plant unit / Day)

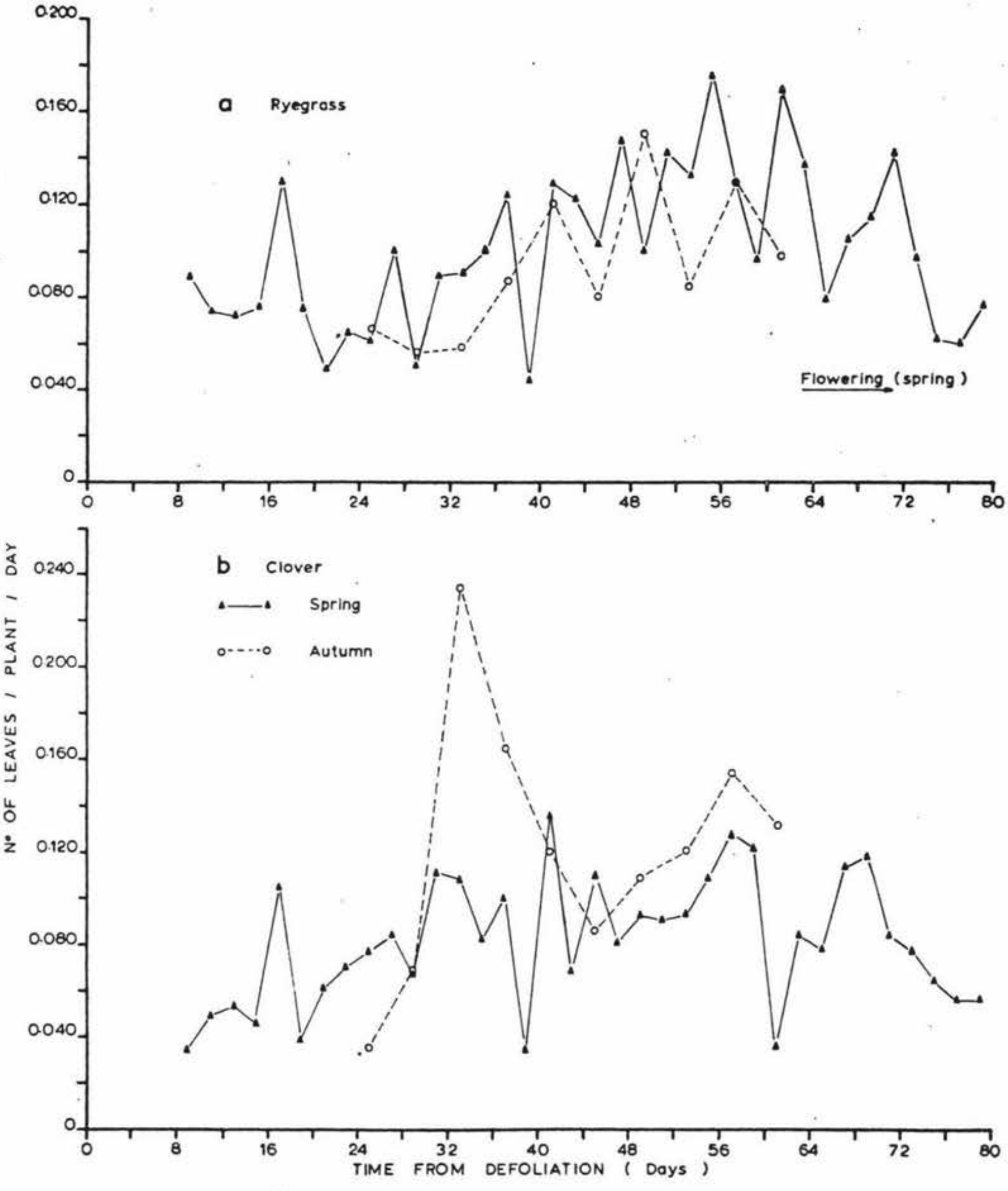

Fig 21 Number of Leaves Dying per Plant unit per Day

modification of the general pattern of leaf death per plant according to changes in the number of plants per transect and apparently, in the case of ryegrass in the spring, to the physiological effect of flowering. Thus because changes in the number of plants per transect in the autumn were minimal, there is a marked similarity between the pattern of death rate per transect and per plant. In the spring, however, the increase in death rate per transect is due to increased death rate per plant in spite of a decreasing number of plants per transect. When the death rate per plant reached a maximum or, as with ryegrass, tended to decline, the continued (but slower) decrease in plant numbers per transect effectively reduced the death rate per transect.

A similar situation existed with respect to the number of leaves that died per transect. Generally, when leaves began to die, there was a phase of increase in the number of leaves that died per plant to a maximum which was maintained for the rest of the measurement period. In both seasons, this phase of increase in the leaf number death rate was over by the time that the third growth phase of total herbage began. The curve of the number of ryegrass leaves that died per plant in the spring (Fig. 21a) showed two important deviations from the pattern outlined above however. There was a relatively high leaf number death rate per plant shortly after defoliation. This may represent stimulated leaf death due to defoliation whereby early senescence was induced in a number of partially defoliated leaves through injury (injury is one cause of abscission in higher plants: Carns 1966), or it may be that as defoliation was not severe in the spring, enough partially defoliated leaves of varying ages were present to maintain a relatively high rate of the number of leaves that died. Alternatively Fig. 8a shows that during the early stages of the spring experiment the number of ryegrass leaves that died per transect was relatively constant. The drop in the number of leaves that died per plant 21 days after defoliation (Fig. 21a) may be due to the production of young tillers at this stage increasing the number of plants per transect but making no contribution to the number of leaves that died per transect. In the autumn experiment there was no high leaf number death rate initially (Sampling began 7 days after defoliation) as defoliation was severe, removing all the leaf blade of most leaves.

Secondly the ryegrass leaf number death rate in the spring was not maintained after the maximum was reached, as generally occurred, but declined sharply from day 64 to day 80. This decline coincided with the bulk of ryegrass flower emergence, flowers first appearing in the leaf area index samples 63 days after defoliation. A similar reduction in the rate of leaf senescence was observed by L.A. Hunt and Brougham (1966) as many tillers developed towards flowering in an undefoliated stand of Italian ryegrass. The absence of any decline in the number of ryegrass leaves that died per plant in the autumn (Fig. 21a) is probably due to most of the tillers remaining vegetative.

The data of the number of clover leaves dying per plant (Fig. 21b) has a particularly high point marking the beginning of the phase of "constant" leaf number death rate, but it is considered that this point alone is not sufficient to contradict the general pattern described above. It is more likely that at that date some short term environmental factor had temporarily increased the leaf number death rate. Attempts to correlate short term fluctuations in death rate with weather parameters were, however, unsuccessful.

To complete the analysis of the pattern of leaf death mention must be made of the influence of leaf size, as the death rate per plant varies not only with the number of leaves dying per plant but also with changes in the size of the dying leaves. Fig. 22 shows the mean weight of dead leaves plotted against time from defoliation in days. All curves show a similar pattern

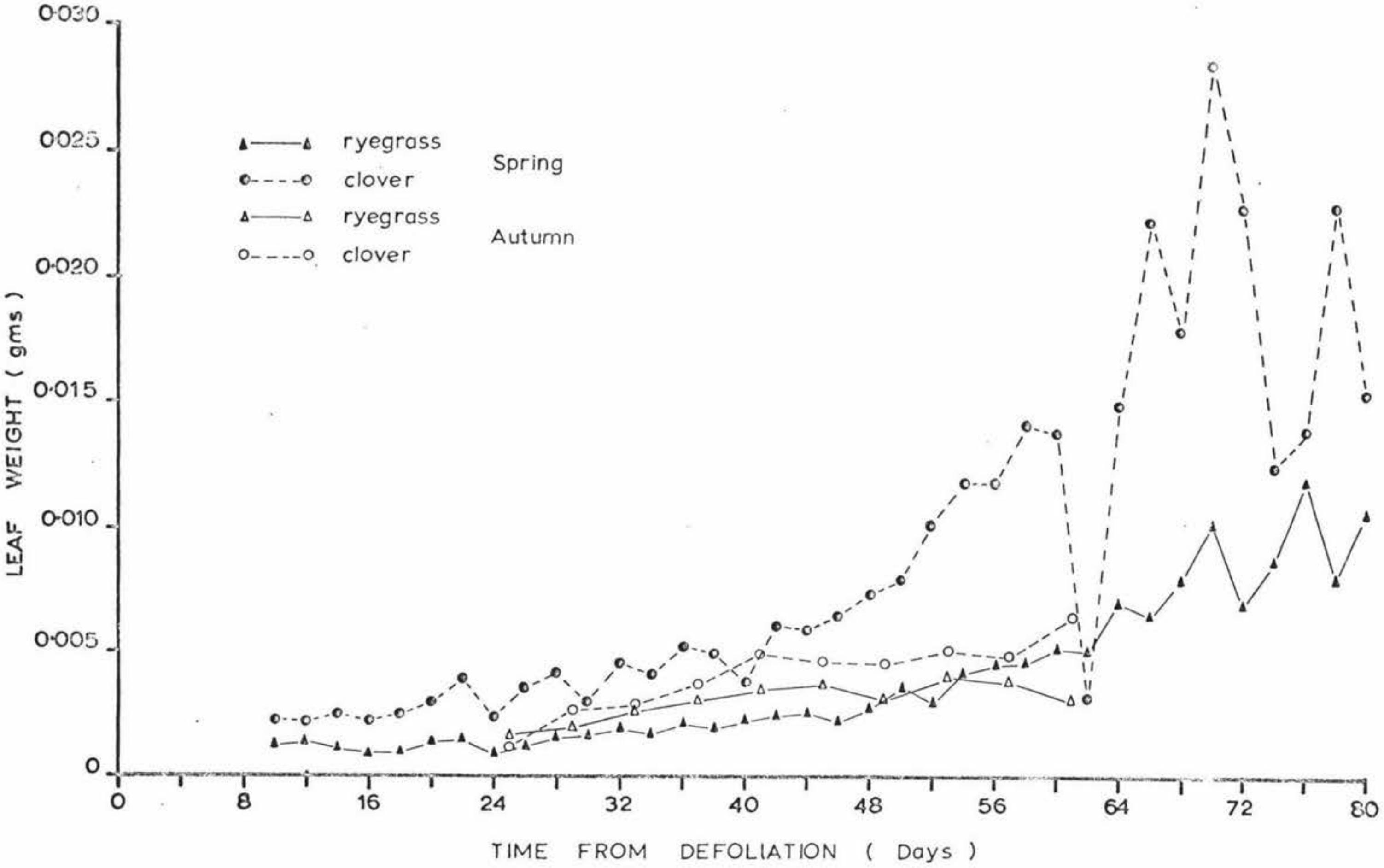

Fig 22 Mean Weight of Dead Leaves

in that there was an increase in leaf weight to a maximum. In the autumn the maximum dimensions were attained at the beginning of the third growth phase while in the spring the maximum dimensions were much greater and were attained in the latter half of the third growth phase.

A comprehensive description of the pattern of leaf death at successive stages of regrowth is now possible. Death rate per plant increased, from relatively low values associated with the first growth phase, through the second growth phase until a maximum was reached just after the beginning of the third growth phase. Although the death rate per clover plant in the autumn reached a maximum approximately halfway through the linear growth phase (Figs. 3 and 20b), this was due to the exceptionally high number of leaves that died per plant 29 to 33 days after defoliation (Fig. 21b) mentioned above.

During the spring experiment, there was no increase in ryegrass death rate per plant (Fig. 20) over the first 24 days from defoliation, as no increase occurred either in the weight of dead leaves (Fig. 22) or the number dying per plant (Fig. 21). From day 24 to about 48 death rate per plant rose mainly due to an increase in the number of leaves that died per plant although some increase in the size of leaves is evident. From day 48 on, the substantial increases in death rate per plant can be attributed wholly to increased leaf size as the number of leaves that died per plant was either constant or declining during this period. A similar pattern of death rate per clover plant developed, with initial increases being due largely to an increase in the number of leaves dying per plant and major increases in leaf size occurring towards the end of the experiment.

In the autumn however, the increase in both ryegrass and clover death rate per plant was due to a simultaneous increase in both the size of leaves and the number of leaves that died per plant, and these components appeared to be of equal importance.

It is interesting to note that in the spring the mean weight of dead clover leaves was twice that of ryegrass throughout the experiment and over a wide range in leaf size, whereas in the autumn the clover leaves were only slightly heavier than ryegrass. Also large fluctuations in the mean weight of clover leaves (62 and 74 - 76 days after defoliation) have resulted in similar fluctuations in the clover death rate per plant. This may be the result of rapid decomposition (i.e. within 2 days from dying) or leaching, as these periods coincided with periods of persistent rain (Fig. 15).

During the third growth phase, the number of leaves that died per plant was maintained at a maximum except for ryegrass in the spring where a decline occurred after flowering commenced. This "maximum" also does not appear particularly stable with clover which shows irregular fluctuations in both seasons. Where the maximum dimensions of dead leaves were attained by the end of the linear growth phase as in the autumn, death rate per plant was maintained at a maximum throughout the third growth phase. As the maximum size of dying leaves was not reached until the middle of the third growth phase in the spring, the attainment of the maximum death rate per plant was correspondingly delayed.

Examination of absolute values in Figs. 20, 21 and 22 give an indication of the effect of season on death rate, especially with ryegrass where the same plant unit was used. Most striking is the similarity in the curves of the number of ryegrass leaves that died per tiller per day (Fig. 21a) which differ mostly in that the maximum spring values were slightly higher than the autumn and were reached at a later date.

The only abvious seasonal difference in the pattern of leaf death is associated with leaf size. During the autumn experiment the dead leaves, although comparable with those in the spring over the first half of the experiment, reached ceiling values about day 40 that were at best only half of the maximum eventually obtained in the spring (Fig. 22). The smaller leaves in the autumn have consequently resulted in a much lower maximum death rate per plant, and in an earlier attainment of the maximum, even though differences in the number of leaves that died per plant were small.

4.3.3. Death Rate per Unit Area.

From a practical point of view, death rate is better expressed per unit area. From the estimates of death rate per plant for individual transects and the plant density (Fig. 4), death rate per unit area per day was calculate for each measurement date. The mean values over six transects in the spring and four in the autumn are shown as lb of dry matter per acre plotted against time from defoliation in days in Fig. 24. As with the data of death rate per transect orthoganal polynomials were fitted to the cumulative data in order to provide the best estimate of death rate of any particular date (see Fig. 23). The equations of the fitted polynomials together with the appropriate analyses of variance may be found in appendix 8.

From Fig. 24 it is evident that in both seasons clover death figured prominently. This was the result of a higher death rate per plant (Fig. 20) and a proportional increase in the clover plant density in both seasons (Fig. 4). The seasonal differences in death discussed above are again evident. In the autumn, the death rate reached a maximum much sooner after defoliation than in the spring with both species, and the start of the increase was about 24 days after defoliation in all curves. Seasonal differences in the maximum death rate per plant, associated with the substantial differences in maximum leaf size, have resulted in similar differences in the maximum death rate per unit area.

Fig. 24 shows that in both seasons losses of green herbage via leaf

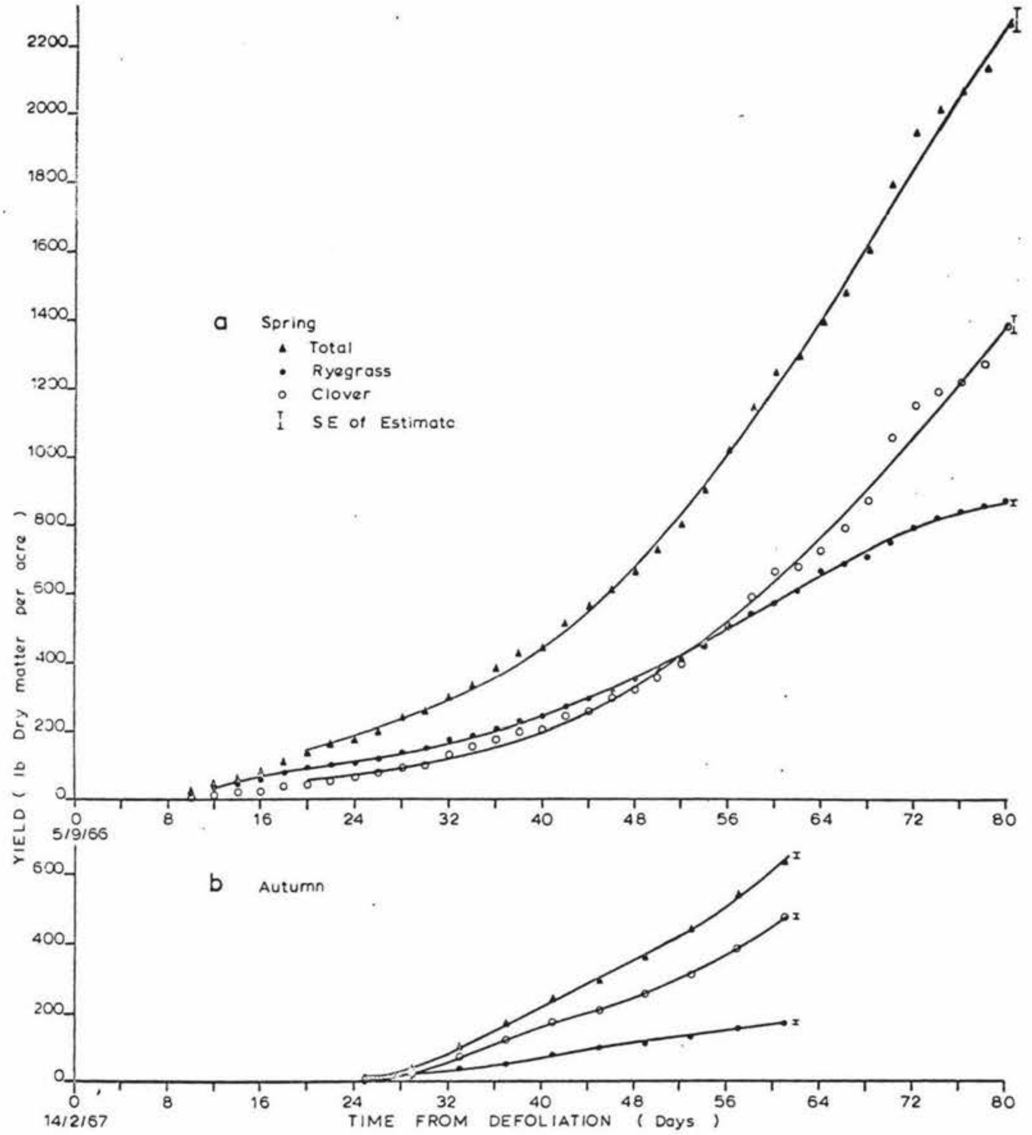

Fig 23 Cumulative Yield of Dead Leaf per Unit Area

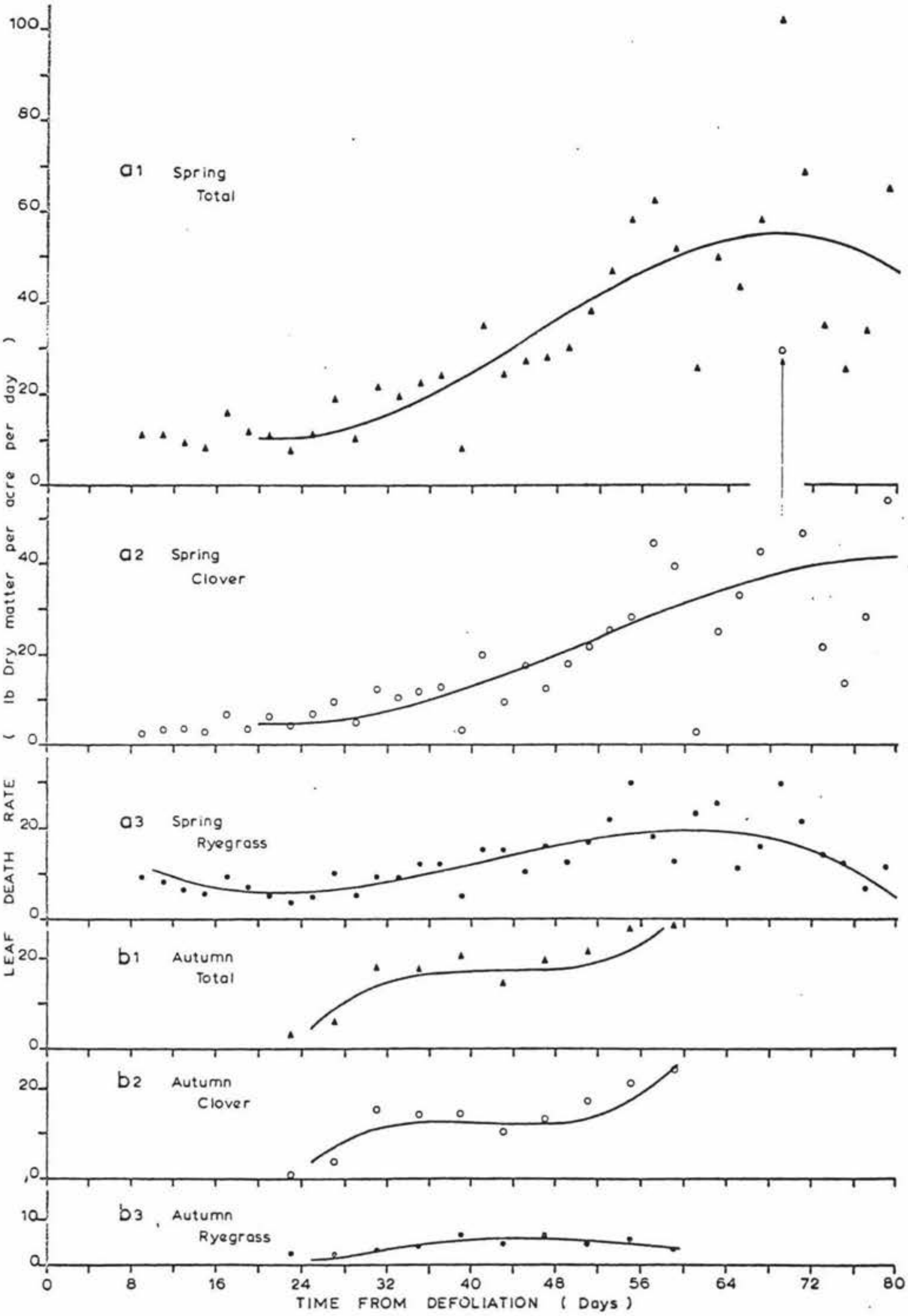

Fig 24 Leaf Death Rate per Unit Area per Day
(THE CURVES ARE THE FIRST DIFFERENTIAL OF THOSE PRESENTED IN FIG 23)

death can reach significant proportions in undefoliated pastures. The maximum calculated values of total leaf death rate were 56 lb dm per acre per day in the spring, and 27 lb dm per acre per day in the autumn. These rates were reached 68 and 59 days after defoliation respectively.

Milking Jersey cows have a daily dry matter intake requirement of approximately 28 lb of pasture of a 70 - 80 % digestibility, i.e. about 20 lb of D.O.M. (digestible organic matter) per day (Hutton 1962). The digestibility of dead leaf in these experiments can be expected to be lower than that of fresh pasture but perhaps not as low as Eadie's figure of 40% quoted by Edmond (1967). Eadie's work refers to dead matter that had accumulated in a winter saved pasture under harsh conditions in Scotland (J.A. Lancashire pers comm.) and which would thus be subject to weathering. The above data were obtained by harvesting leaves frequently enough to prevent weathering. Also, Eadie's material probably included considerable amounts of sheath and stem whereas the above data refer only to leaf tissue.

If it is assumed that the digestibility of dead leaf was 50%, then the maximum rates of green herbage loss via leaf death would be equivalent to the feed requirements of 1.4 milking Jersey cows per acre in the spring, and 0.7 milking Jersey cows per acre in the autumn. In these terms, the stage at which losses in the spring reached the equivalent of the feed requirements of one milking Jersey cow per acre occurred 50 days after defoliation.

4.3.4. The Influence of Leaf Death on Growth.

4.3.4.1. "Gross" Growth Curves.

The estimate of death rate per unit area at successive stages of regrowth obtained above makes possible the quantative examination of the influence of leaf senescence on the pattern of pasture growth. In a defoliated pasture the yield of total dry matter will increase with time so long as the incremental synthesis of above ground tissue (i.e. true photosynthesis less respiration) exceeds incremental reductions via principally leaf tissue decomposition but also including consumption by the soil fauna. In the above experiments changes in the yield of green herbage have been studied. The yield of green herbage will increase so long as the incremental synthesis of above ground tissue exceeds the incremental reduction from tissue (leaf) senescence and consumption of green herbage by the soil fauna. The importance of the soil fauna in this respect is unknown but it is assumed to be small if not negligible in this experiment so that for practical purposes losses of green herbage are attributed to leaf senescence.

The regrowth curves of green herbage in experiment (1) have been presented in Fig. 3. The initial growth phase exhibited by the curves has been explained in terms of increased light interception and the influence of factors which limit further increases in growth rate (see section 4.2.2.). The second growth phase of approximately linear increases in yield indicates that the growth processes operated at a maximum for the conditions prevailing and that losses of green herbage due to leaf senescence had a minor influence on net growth. Fig. 24 shows that this period coincides approximately with the period during which leaf death rates rose from low values to those approaching the maximum.

During the third growth phase a decline in net growth rate is evident in the regrowth curve which then approaches a ceiling yield. This decline may be due in part to a reduction in the rates of net photosynthesis for the whole canopy, e.g. an increase in the rate of respiration relative to true photosynthesis (Davidson and Donald 1958), or due wholly to losses of green herbage through senescence and eventually decomposition (Brougham 1959, Brougham and Glenday 1967). Indications of whether or not changes in rates of synthesis of above ground herbage occurred can be derived from the integration of net growth and death. For example, if the productive processes continued unaltered, the sum of the death rate and the net growth rate should be constant and equal to the maximum "net" growth rate at any stage after the maximum "net" growth rate was reached. Provided that leaf senescence is the only major factor causing losses of green herbage and has not been underestimated, lower values for the sum of growth and death rates must indicate a lowered "gross" growth rate. In terms of cumulative growth, the situation in which net photosynthetic processes continued at a maximum would be represented by the addition of cumulative death to the regrowth curve resulting in a continued phase of linear "gross" growth.

The cumulative yields of dead leaf produced during the experimental periods have been presented in Fig. 23. Estimates of "gross" growth i.e. the increase with time of the absolute amount of net photosynthetic production from defoliation, have been obtained from the addition of the fitted cumulative death curves to the curves of green herbage yield (i.e. "net growth"). These estimates are presented in Fig. 25 for the periods over which the cumulative death curves accurately fit the leaf death data. They show that the linear phase for the production of total herbage is about 50% longer than in the "net" growth curve, lasting for at least 24 days in the spring and 16 days in the autumn. The depression of net growth rate marking the start of the third growth phase can therefore be attributed directly to losses in leaf death reaching significant proportions. However neither of the "gross" growth curves of total herbage have the linear phase continued indefinitely. This implies that although losses via leaf death had an increasing influence

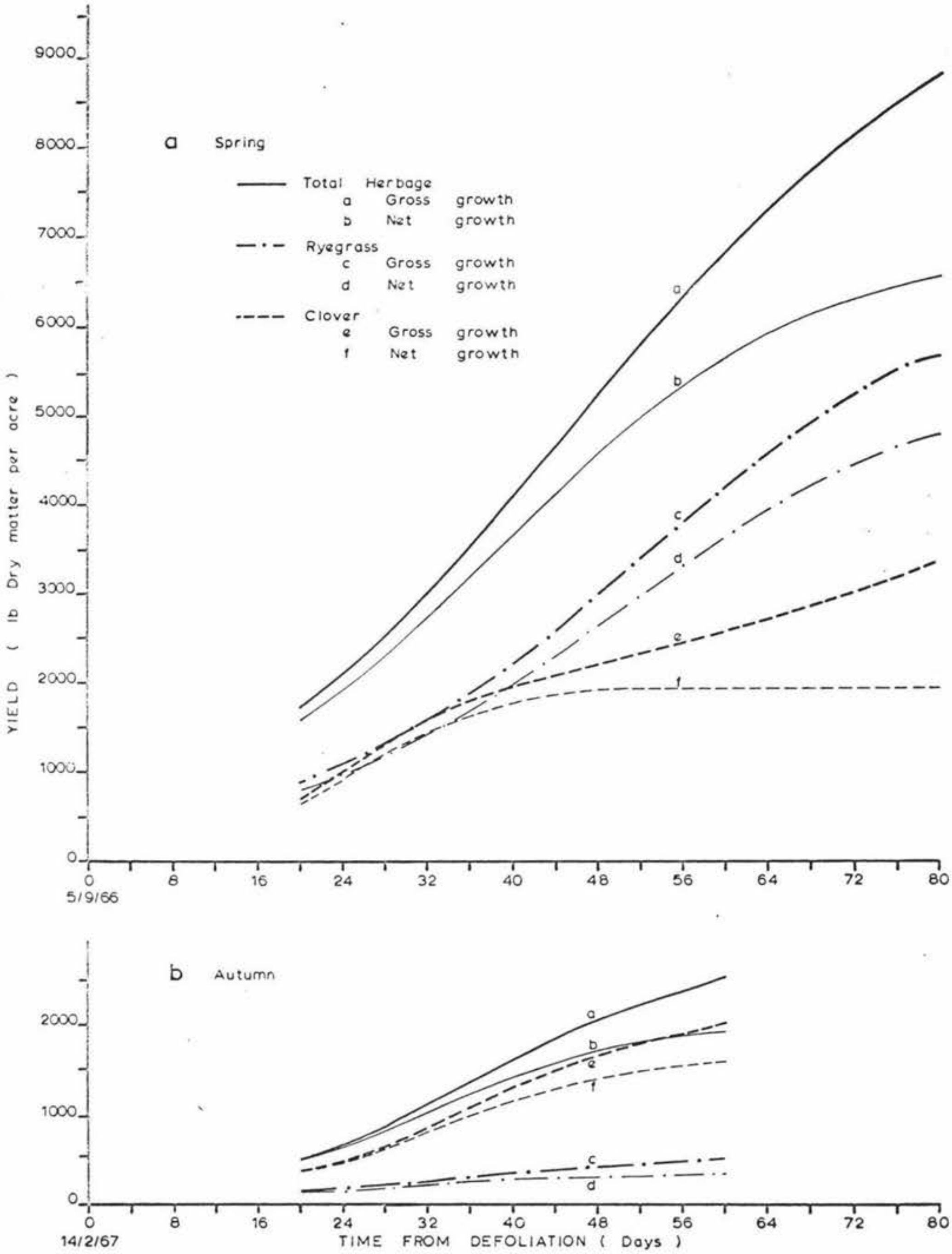

Fig 25 An Estimate of Gross Growth

on the pattern of "net" growth during the latter part of the third growth phase, reductions in the rate of net photosynthesis, at least of above ground parts, reached significant proportions also. The departure from linearity is less obvious in the spring total "gross" growth curve and owing to the smoothing of data that has been employed, its significance may be questioned. However, Fig. 24 shows that over this period a definite decline in ryegrass (and thus total) leaf death rate occurred; this decline being associated with reproductive development (see Section 4.3.1.). A fall in the rate at which dead leaf is accumulating will have a depressing effect on "gross" growth and as no compensatory increase occurred in the rate at which total green herbage was accumulating (Fig. 3) the indications are that the depression of total "gross" growth rate towards the end of the spring experiment was a real one.

Examination of the species "gross" growth curves reveals some interesting contrasts. For example, in the spring, the ryegrass gross growth rate is maintained at a maximum (once it is reached) for a considerable period, declining only over the last week or so of the experiment. With clover however, the "gross" growth rate is reduced soon after the maximum is attained but remains constant thereafter for the remainder of the experiment. In the autumn experiment the ryegrass growth was poor, but remarkably, the "gross" growth curve is almost linear throughout, i.e. the "gross" growth rate, although low, changed little throughout the experiment and remain constant particularly over the stages of high L.A.I. The clover gross growth curve followed essentially the same pattern as that in the spring with "gross" growth rate dropping to a lower but constant value, in this case about two weeks after the maximum was first attained.

Due to the marked species differences in the "gross" growth curves any attempt to examine the factors influencing "gross" and "net" growth over the later stages of regrowth must begin with individual species. Because the species react differently at comparable stages of regrowth, the total "gross" growth curve does not lend itself to easy interpretation. It serves best as a statement of the integrated effects of the two species components.

4.3.4.2. Factors Affecting the Pattern of Clover Growth.

It has been argued that clover growth in both seasons increases exponentially after regrowth until the limiting supply of some factor essential to growth presents a barrier to further increases in growth rate. It was postulated that in the spring the maximum growth rate was determined by the amount of light received and the manner in which this light was distributed over the leaf surface, whereas in the autumn conditions of moisture stress and possibly nutrient supply limited the growth rate until the stage of near complete light interception was reached. The subsequent pattern of clover "gross" growth can be explained in terms of the effect of canopy development on the rate of respiration relative to photosynthesis after the attainment of the critical L.A.I.

It has been demonstrated by Davidson and Donald (1958) that the growth rate of a subterranean clover sward can be significantly reduced when the L.A.I. exceeds the "optimum" (the optimum L.A.I. refers to the L.A.I. at which growth rate is at a maximum, and where light utilization is the major determinant of growth, it approximates the "critical" L.A.I. at which near complete light interception occurs). These authors suggest that when the L.A.I. is at the optimum the lowest leaves are in a state of equilibrium between photosynthetic gains and respiratory losses and that the intense shading of these leaves that results from further increases in L.A.I. destroys this equilibrium resulting in a net respiratory loss in such leaves. As the amount of leaf actively photosynthesizing would remain unchanged by increases in L.A.I. above the optimum (assuming that canopy structure is unaltered) but the amount of leaf respiring have increased, the rate of respiration relative to photosynthesis ($\frac{R}{P}$) for the canopy as a whole would have increased. The authors suggest that as a direct result shaded leaves become "parasitic" and the growth rate is lowered. They support this argument by showing that when $\frac{1}{3}$ of the subterranean clover canopy was intensely shaded, the growth rate was depressed by about 30%.

Certain aspects of this argument are open to criticism. For example, the depression of growth rate is attributed wholly to increased $\frac{R}{P}$ whereas Fig. 25 shows that losses of herbage via leaf death is a major factor in depressing growth rate at high L.A.I. values. Secondly, the concept that the lower leaves become "parasitic" has been criticised (Ludwig et al 1965) as movement of carbohydrate material in significant amounts into ageing leaves seems not to occur. Autoradiograph studies with radioactive carbon have shown that although a considerable degree of movement of labelled compounds may exist between tillers of Italian ryegrass, it is concentrated towards young expanding leaves; mature leaves showing only traces of activity. (Marshall 1967a). Respiratory weight losses due to leaves being below their compensation point are thus probably confined to the utilization of respiratory substrate within individual leaves. Thirdly the optimum L.A.I. concept as presented by Davidson and Donald assumes that the respiration rate of the canopy as a whole is directly proportional to the amount of leaf present. Contrary evidence has been presented by Ludwig et al (1965) and McCree and Troughton (1966) which suggests that respiration rates depend to a larger extent on the immediate substrate supply and so are related to current rates of photosynthesis.

The situation envisaged by Davidson and Donald (1958) in which shaded leaves in high L.A.I. canopies respire for considerable periods at high rates is thus an oversimplification. In fact, respiration rates appear to drop rapidly after available substrates have been utilised and if the leaves are still below the then lowered compensation point, they die. (Ludwig et al. 1965). Dead leaves do not affect $\frac{R}{P}$ and if all leaves died immediately they were shaded $\frac{R}{P}$ would not differ from that at the optimum L.A.I. It appears therefore that for $\frac{R}{P}$ to increase significantly enough to affect growth rate, a situation must exist whereby a considerable quantity of living leaves with relatively high contents of respiratory substrate are subjected to intense shading. Such a situation can exist in clover swards, and thus the arguments of Davidson and Donald (1958) are not completely invalidated, when it is appreciated that at high L.A.I. values, clover canopies are in a state of dynamic equilibrium whereby new leaves are rapidly being produced to replace older senescent ones. (Brougham 1958b). The rate of leaf turnover in swards of white clover at Palmerston North was shown by Brougham to be as high as one L.A.I. unit every five days. Thus although individual leaves that become shaded may rapidly respire away available substrate and die, because of the rapid turnover of leaves their place is immediately taken by leaves that have just been actively photosynthesizing. Although aged leaves have been shown to be capable of only low rates of photosynthesis (Brown et al. 1966, Milthorpe 1963, Sing and Lal 1935) this factor may be of less significance to clover canopies owing to the relatively short leaf life expectancy, so that when leaves become shaded, the level of respiratory substrate will probably not be exhausted due to depressed rates of photosynthesis. Although such aspects of this argument need confirming, the basic concept that utilisation of substrate for respiration in leaves shaded below their compensation point results in a loss that will have a depressing effect on "gross" growth at high L.A.I. values, still stands. Where a large number of leaves suffer this loss, even though the loss may be rapid for individual leaves, it is reasonable to expect that this loss will reach significant proportions and have a depressing effect on growth rate. That no depression of growth rate at high L.A.I. due to increased $\frac{R}{P}$ was detected by McCree and Troughton (1966) is not surprising as in their experiment the condition that a quantity of living leaves with relatively high amount of respiratory substrate be subject to intense shading was not fulfilled. The artificial sward was held in shape by a wire frame which must have allowed lateral illumination. In one case, lateral illumination was provided artificially so that the lower leaves were never subject to intense shade. The individual leaves probably therefore never fell below their compensation point during their entire life cycle so that $\frac{R}{P}$ would not increase.

In the experiments reported here one of the factors responsible for depressed growth rates at high L.A.I. values (losses via leaf death) has been estimated. It is possible therefore to assess the extent to which other factors such as increased $\frac{R}{P}$ are also influential. The "gross" growth curves presented in Fig. 25 indicate that $\frac{R}{P}$ for the clover component increased significantly enough at high L.A.I. to affect growth in both seasons. This interpretation is based on the fact that in both seasons the reduction in the clover "gross" growth rate mentioned above occurred shortly after the critical L.A.I. was reached (i.e. approximately 28 days after defoliation in the spring (see Section 4.2.2.) and about 40 days after defoliation in the autumn (table 5)). Also, in both seasons, the reduced clover "gross" growth rate remained approximately constant for the remainder of the experiment as might be expected from such a canopy in a state of dynamic equilibrium. Although there were major seasonal differences in the maximum clover growth rates (table 2) the final slopes of the clover "gross" growth curves in Fig. 25 are almost identical, both increasing by 30 lb. dm per acre per day between 50 and 60 days after defoliation. This is a large reduction in the growth of the spring clover component compared with its maximum (table 2). As the ryegrass maximum growth rate did not occur until much later than the clover, it is possible that some of this depression in clover growth rate is due to increased competition by ryegrass.

It has been argued (see section 4.2.2.) that during the first 36 days after defoliation in the autumn, conditions of moisture and possibly nutrient stress presented a barrier to increased growth rate. This situation was to some extent alleviated during the latter part of the experiment, however, as between days 36 and 40 a considerable amount of rain fell (2.02 inches, see Fig. 15). As the critical L.A.I. was attained about this time also (table 5) and the temperature range in the autumn was at least as favourable as that in the spring (Fig. 14) it is possible that at the later stages of growth, clover "gross" growth was largely limited by similar mechanisms as in the spring such as the manner of distribution of available light energy over the leaf surface. If this is so, then there is good reason to expect that clover "gross" growth in the spring at high L.A.I. values would be greater than that in the autumn. This is because although the range of maximum noon light intensities were comparable for the two experimental periods, light intensity in the spring was increasing, whereas in the autumn it was decreasing (Fig. 13), so that by the end of the experiments (24.11.66 and 16.4.67) a difference in the maximum noon light intensity of about 2000-2500 f.c. would be expected. This advantage was apparently offset in terms of clover growth however by the large seasonal difference in ryegrass growth. In terms of yield, ryegrass dominated the association in the spring but made very little growth in the autumn. Competition from ryegrass to clover growth in terms of light interception particularly, would be a major factor in the spring but have little significance in the autumn.

It can be concluded therefore that during the regrowth from defoliation of clover in both seasons, the rate of accumulation of green herbage (the net growth rate) was initially governed by the amount of leaf available to intercept light. This situation existed until the net growth rate was limited by the supply of moisture or nutrients, or until near complete light interception occurred. When the critical L.A.I. was reached, growth rate was limited by the manner of distribution of light over the leaf surface, i.e. the efficiency in light utilization of the canopy structure. About this time two additional factors had a significant influence on growth. Shortly after the critical L.A.I. was reached, owing to competition for light by ryegrass in the spring, the overtopping of clover leaves by younger ones in both seasons and the rapid rate of clover leaf turnover as a whole, a continual situation was created in which a considerable amount of leaf was subject to intense shading. This situation resulted in an increase in the rate of respiration relative to photosynthesis so that for the clover component as a whole net photosynthesis was depressed to a lower but constant rate thereafter.

Secondly due to larger and a greater number of leaves that died per plant unit, losses via leaf death reached significant proportions either before (autumn) or after (spring) the critical L.A.I. was reached, and also had a depressing effect on net growth rate. As a result the yield of green herbage tended to a ceiling whereby "gross" growth of about 30-40 lb. dm per acre per day was offset by losses via leaf death (Fig. 24 a2). This ceiling was not reached in the autumn experiment but losses via leaf death were approaching 30 lb dm per acre per day (Fig. 24 b2) at the end of the experiment.

4.3.4.3. Factors Affecting the Pattern of Ryegrass Growth.

The most striking feature of the ryegrass "gross" growth curves in Fig. 25 is that, unlike clover, there is no depression of growth rate associated with complete light interception. In the spring no depression in "gross" growth rate occurred until during the last week of the experiment and in the autumn no discernable depression occurred for the entire measurement period. Obviously therefore, in terms of the argument applied to the pattern of clover growth, the ryegrass growth was not influenced by an increase in $\frac{R}{P}$. This implies that with ryegrass the situation in which considerable amounts of living leaves with relatively high substrate levels were subject to intense shade did not exist. This may be attributed to species differences in growth habit. Ryegrass swards characteristically allow light to penetrate deeper into the sward at comparable L.A.I. values than clover (Brougham 1958a, 1966; Mitchell and Calder 1958). Grassy patches in the sward would thus not be subject to as intense shade as clovery patches. Secondly, the surface of individual ryegrass leaves is distributed semi-vertically throughout the canopy whereas with clover the leaf surface is near horizontal. Consequently overtopping by younger leaves that can completely shade clover leaves at the bottom of the canopy would only shade part of lower ryegrass leaves. In fact it would take very high L.A.I. values to cause complete shading of reasonably large ryegrass leaves, the tops of which may be receiving sufficient light to photosynthesize enough substrate to meet their respiratory needs. (Alberda 1965b). Because factors such as these enable ryegrass leaves to complete their life cycle or a substantial part of it without being intensely shaded the situation required for $\frac{R}{P}$ to increase is rarely created. Furthermore, because shading is a more gradual process with ryegrass there is a greater opportunity for the export of substrate from the leaf to more favourably illuminated sites (Hopkinson 1966). Respiration rates of such leaves when and if they finally become completely shaded would be insignificant due to the very low substrate levels.

It has been demonstrated, however, that at least in artificial grass swards, the situation in which $\frac{R}{P}$ increases with higher L.A.I. can exist (Alberda 1965a) and this may be one explanation for the depressed ryegrass "gross" growth rate during the last week of the spring experiment. Lodging was evident 68 days after defoliation and widespread lodging occurred 72 days after defoliation after heavy rain. The poorer light penetration into the collapsed canopy, (Mitchell and Calder 1958), would have in creased dramatically the area of shaded leaf. On the other hand the decline in gross growth after lodging may be due simply to lowered total photosynthesis resulting from less efficient light distribution over the leaf surface. (Alberda 1965a, 1965b).

Probably the most important factor influencing ryegrass gross growth at high L.A.I. values in the spring and one that frequently deserves more attention than it gets, is the effect on both the rate of increase in yield and leaf area development of flowering. Fig. 5 shows that ryegrass reached a ceiling L.A.I. 42 days after defoliation and thereafter, if anything, leaf area declined. However, from Fig. 3 it is evident that in terms of yield at 42 days after defoliation ryegrass was growing at a maximum. Therefore, any increment in yield after day 42 was due to tissue other than leaf, i.e. stem and seed head. This situation is emphasized in Fig. 26 which shows that up to day 42 there was a close relationship between L.A.I. and yield, an increase of 417 ± 48 lb dm per acre in yield. This is in close agreement with the figure obtained by Brougham (1956) of 468 ± 28 lb dm per acre and that obtained by Brougham and Glenday (1967) using Anslow's (1965) data of 415 ± 12 lb dm per acre. However, after day 42 the relationship did not exist.

Flowering can affect the gross growth curve in a number of ways; The reduction in leaf production and senescence associated with flowering (L.A. Hunt and Brougham 1966) will cause a shift in the balance of young and mature leaf in favour of the latter. As old leaves do not have the photosynthetic capabilities of young ones (Brown et al. 1966, Milthorpe 1963, Sing and Lal 1935), overall photosynthesis may be reduced. Secondly, if rates of senescence are not reduced to the same extent as rates of leaf production, photosynthesis may be reduced through reductions in leaf area. This may be important between days 72 and 80 in the spring experiment where, due possibly to lodging, rates of leaf senescence appear not to have been reduced to the same extent as rates of leaf production as leaf area declined (Fig. 5). Thirdly the preflowering period in Graminae, when a high proportion of

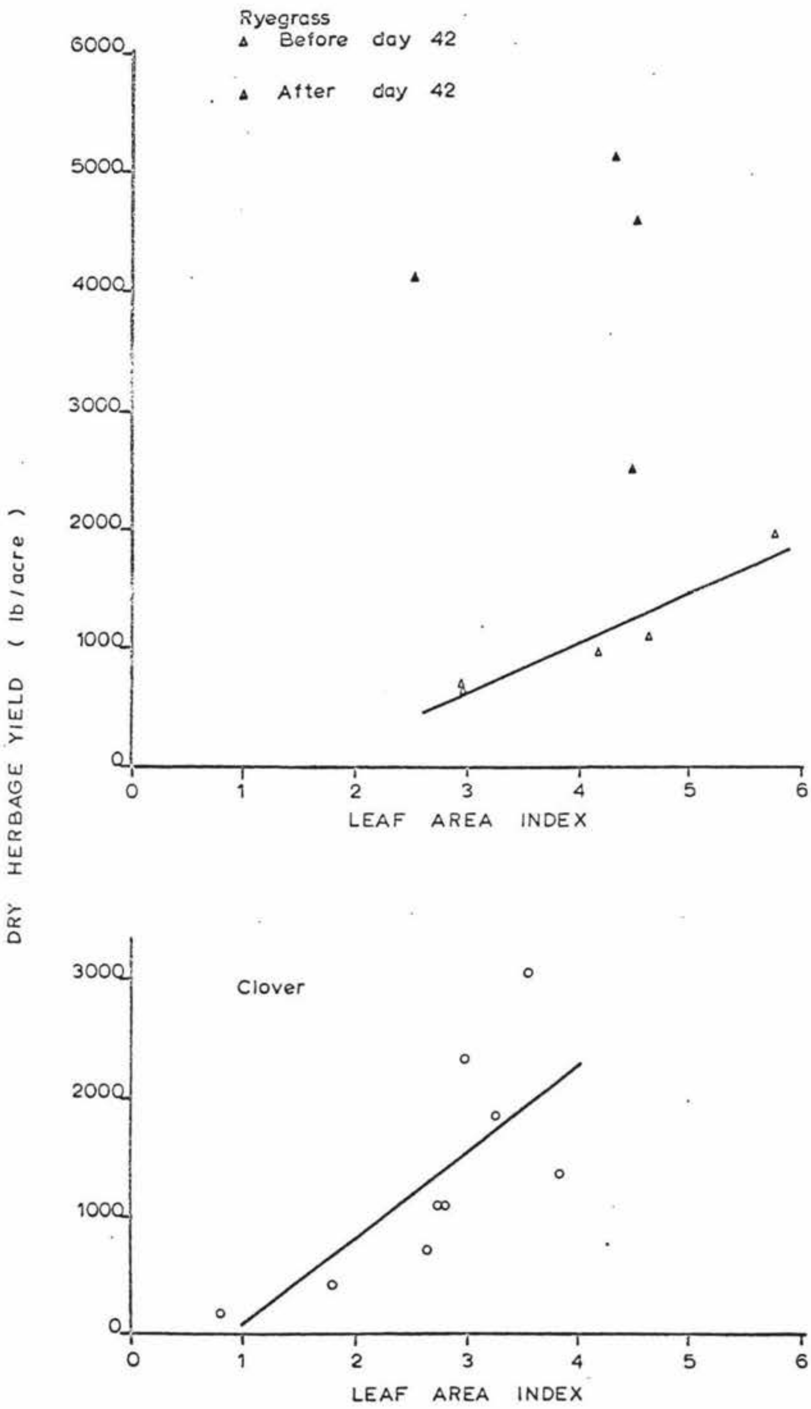

Fig 26 The Relationship between Leaf Area and Herbage Yield

tillers are rapidly elongating, is recognised as the period of most rapid growth, Milthorpe and Davidson (1965). This period has also been noted as one in which minimum concentrations in reserves can occur. (Weinmann 1952). The possibility of reserve utilization during stem development resulting in inflated growth rates of above ground material due to the development of "sinks" (for soluble carbohydrate) such as intercalary meristems in elongating stems cannot be discounted. The reduction in ryegrass gross growth observed at the end of the spring experiment may thus represent a depletion of reserves or a reduction in intensity of the "sinks".

The reduction in intensity of the "sinks" associated with reproductive development is probably the major factor depressing "gross" growth of ryegrass over the last week or so in the spring experiment. This is because yield increments at this time were due entirely to reproductive tissue (stem and seed head) and thus as the seeds matured and stem elongation ceased a marked reduction in the yield increment could be expected. As the shade at the base of the sward would inhibit the utilization of consequent surpluses of substrate in vegetative tillering (Mitchell and Coles 1955) such surplus would probably be used in re-establishing reserves in the roots and stubble.

The slow growth of ryegrass in the autumn is probably due mainly to successful competition by clover, initially for moisture and later for light. A reduction in autumn ryegrass growth compared with spring would have been accentuated, however, through the reduction in ryegrass density (Fig. 4) due to shading (See section 4.2.3.1.). Fig. 4 shows a proportional increase in the spring and an absolute increase in the autumn of clover numbers as the ryegrass tiller population dropped. However the lack of any depression in the autumn ryegrass "gross" growth curve when the critical L.A.I. was reached indicates that shading of the lower leaves in the sward was of significance to ryegrass growth only in that losses via leaf death increased in importance.

In conclusion it appears that while the growth of ryegrass at low L.A.I. values is governed by the same factors as clover, at high L.A.I. values depressions in net growth rate can generally be attributed to losses via leaf death. However, the development of a large proportion of the tillers towards flowering complicates the situation and may facilitate the introduction of a number of additional factors such as changes in the proportion of young and mature leaf, in the rates of leaf production relative to rates in senescence, and the pattern of utilization and distribution of reserves and photosynthate. Further changes in light penetration and distribution can occur from lodging.

The curves of total "gross" growth are dominated by the pattern of ryegrass "gross" growth in the spring and clover in the autumn although losses via clover leaf death in the spring play an important part in depressing total net growth below the estimate of total gross growth.

4.4. Factors Influencing Leaf Death in Pastures.

4.4.1. Species, Season and Management.

Although the experiments reported in this thesis were designed primarily to measure rates of leaf death in pastures, some information about factors influencing leaf death can be derived. Because of the confounding of many of these factors, species, season and management are considered simultaneously.

From Fig. 25 it is evident that considerable species differences exist in terms of the extent to which yield increments of green herbage are depressed by leaf death. These differences are more critically examined in Fig. 27 in which the Relative Death Loss (R.D.L.) for ryegrass and clover in both seasons is plotted against time from defoliation in days. The R.D.L. is defined as the proportion of gross production of green herbage from defoliation that has been lost through leaf senescence and death, and has been derived from:

$$\frac{\text{Cumulative yield of dead leaf from defoliation to day d.}}{\text{"Gross" growth from defoliation to day d.}}$$

The most striking species difference occurred in the spring. A substantial increase in the clover R.D.L. of from 7 to 42% occurred between days 32 and 80 whereas the ryegrass R.D.L. increase was only from 10 to 15% over the same period. There is an even more marked difference between the spring and autumn trends in the ryegrass R.D.L. With clover however, the R.D.L. development was almost identical after day 32.

Differences in these curves may be explained in terms of patterns and interactions of management and seasonal growth. In the spring the pastures were defoliated more leniently than in the autumn. This was the result of both a lower cutting height in the autumn, and the short tight nature of the pasture in the spring induced by a previous management of regular grazing by sheep. Consequently the spring defoliation did not completely remove mature and senescing leaves which then made immediate contributions to death rate measurements (See section 4.3.2.). In the autumn, the previous spring and summer management of long intervals between defoliations resulted in growth whereby leaves grew from an elevated stubble. Defoliation succeeded in removing most of the mature leaves completely so that for three weeks after defoliation leaf death was negligible. This seasonal difference in management and consequently initial leaf death rates has resulted in a seasonal difference in the initial R.D.L., the spring values, particularly of clover, being substantially above those of the autumn. As soon as leaf death began in the autumn, however, the R.D.L. increased rapidly and soon equalled or surpassed (as with ryegrass) spring values at similar times from defoliation.

Reproductive development had a strong influence on the R.D.L. In the spring the R.D.L. reached a maximum of only 15% because after day 42 at

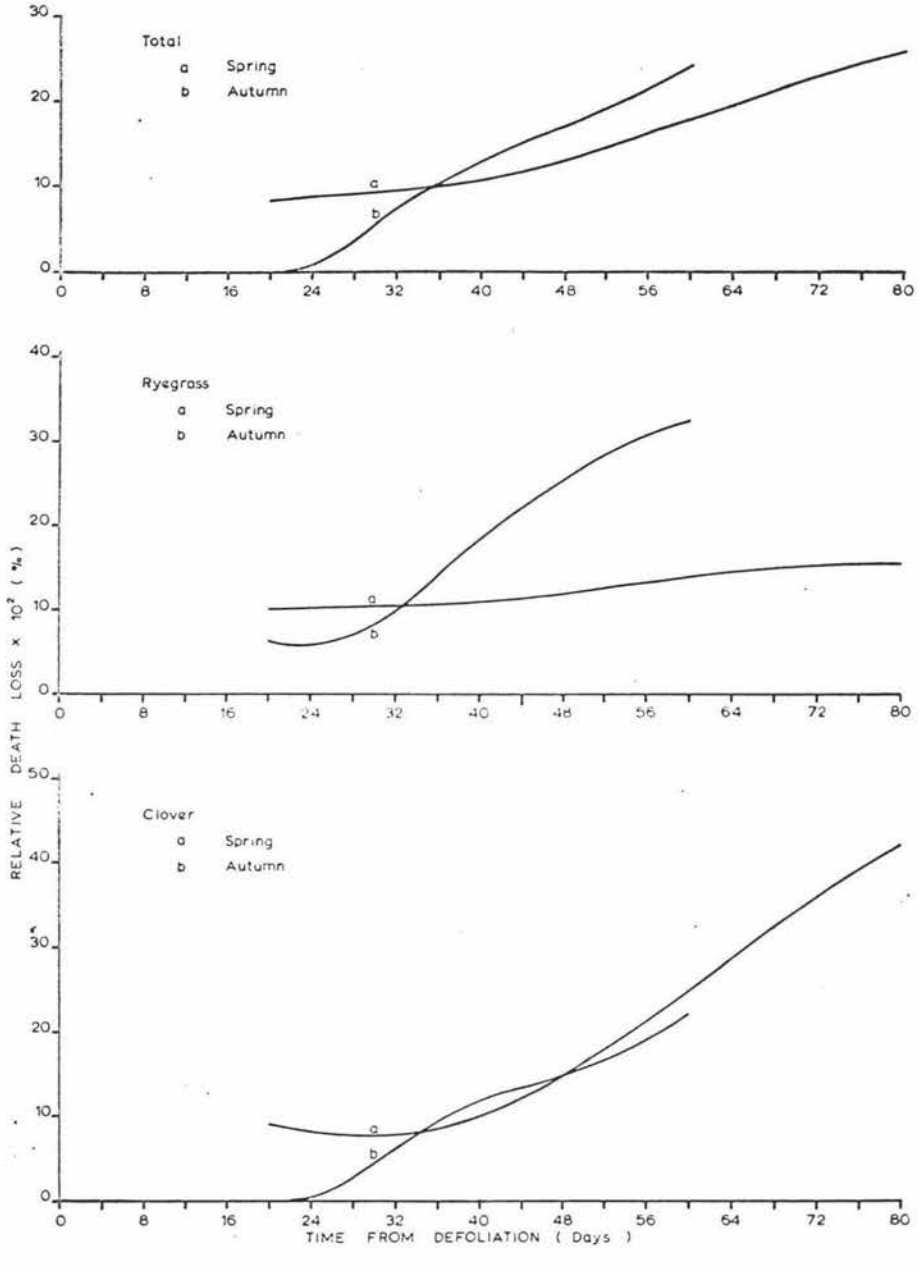

Fig 27 The Relative Death Loss
(i.e. THE PROPORTION OF NET PHOTOSYNTHESIS LOST VIA LEAF SENESCENCE AND DEATH)

least stem and seed head became an increasingly important component of the net yield (See section 4.3.4.3.). Because such tissue did not senesce during the experiment, and because a decline in the number of leaves that died per tiller (associated with flowering) and thus the ryegrass leaf death rate occurred towards the end of the experiment, (see section 4.3.4.3.) the R.D.L. remained at a relatively low level.

It is difficult to comment upon whether or not the spring R.D.L. for ryegrass in the absence of flowering would have reached values similar to those of the autumn owing to the variety of mechanisms that may influence the ratio. For example the ratio may be increased not only by factors that increase death rate but not growth rate, but also by those that decrease growth rate but not death rate. Some information can be gained from the seasonal comparison of the ryegrass R.D.L. curves between days 32 and 42, however, as the linear relationship between yield and leaf area up to day 42 (Fig. 26) indicates that over that period ryegrass growth in the spring was predominantly vegetative. At 40 days after defoliation the ryegrass R.D.L. had reached 18.5% in the autumn and 11.0% in the spring. This difference cannot be attributed to a higher leaf death rate per tiller in the autumn as this has been shown to be almost identical (over this period, Fig. 20). The higher R.D.L. in the autumn must therefore have been due to a depression of growth rate per tiller (but not death rate) compared with that in the spring. If such was the case, it can be expected that the mean tiller weight in the autumn would be substantially less than that in the spring. This is verified in table 6 in which the mean tiller weights from days 32 and 40 have been derived from the plant population and ryegrass yield data, and thus lends support to the above interpretation.

Table 6

The mean dry weight of vegetative ryegrass tillers

	Dry weight (g)	
	Day 32	Day 60
Spring	0.023	0.037
Autumn	0.014	0.018

The factors to which the depressed growth rate in the autumn have been attributed are moisture and possibly nutrient stress (see section 4.2.2.), aggravated by competition from clover. It is interesting to note that these factors were apparently severe enough to affect growth but not affect leaf death rates.

The seasonal curves of clover R.D.L. are much more consistent than ryegrass as might be expected as the seasonal pattern of clover growth was more consistent. However, where only one phase of rapid increase in R.D.L. was present in the spring (after days 36 to 40) there were two in the autumn, i.e. up to days 36 to 40 and after days 48 to 52. As clover growth in the autumn was limited by moisture stress (See Section 4.2.2.) and there were only minor differences in clover death rate per plant between days 28 and 40 (Fig. 20) the rapid increase in the autumn clover R.D.L. up to days 36 to 40 was probably due in part to a depressed growth rate but not death rate. The slightly higher death rate per plant in the autumn at this time (Fig. 20) was due to some extent to seasonal differences in clover plant units, a rooted node in the autumn sometimes having more than one clover bud. Between days 32 and 48 the autumn clover leaf death rate remained constant (Fig. 24) so that although gross growth was depressed the R.D.L. increased at a slower rate. The more rapid increase in R.D.L. after 48-52 days from defoliation was due to an increase in clover death rate (Fig. 24).

The curves of total R.D.L. are best regarded as a statement of the integrated effect of the two components and thus are weighted in favour of the dominant species. In the spring the R.D.L. of clover reached a maximum of 40% but because of the ryegrass dominance in terms of yield the total R.D.L. never exceeded 26%. Similarly, in the autumn, the high R.D.L. of ryegrass had little influence on the total R.D.L. which closely followed that of clover, owing to the minor contributions to total yield by the ryegrass.

It appears therefore, that during dry seasons a greater proportion of the herbage grown is lost through senescence and death. This is the result of depressed growth rates relative to wet seasons but not death rates, resulting in a lower mean weight per plant. Curves of clover R.D.L. varied much less than those for ryegrass because clover was less susceptible to seasonal variation in moisture and nutrient stress (being the better competitor, see section 4.2.3.2.) and because reproductive development in ryegrass had a large effect on the proportion of sward that senescent ryegrass represented. Severity of defoliation can affect initial R.D.L. values but these differences soon become insignificant.

4.2.2. Shade.

The influence of intense shade on the rates of senescence of the lower leaves can be examined between seasons as the critical L.A.I. was reached after different intervals from defoliation, i.e. 28 and 41 days after defoliation in the spring and autumn respectively (See section 4.2.2., Table 5).

Fig. 21 shows that the number of ryegrass and clover leaves that died per plant unit increased after day 28 in the spring. This cannot be attributed to shading with ryegrass however, as a similar increase in the number of leaves that died per ryegrass plant occurred in the autumn after day 28 when light was penetrating to the bottom of the sward (Table 5). Also, no increase in the number of ryegrass leaves that died per tiller occurred in the autumn after 40 days from defoliation. The argument presented in (See section 4.3.4.3.) that ryegrass leaves, due to their semi-vertical distribution through the canopy, are not subject to complete shading therefore finds support in these data. At first sight this may appear to conflict with the data in Fig. 18 and the conclusions in Section 4.2.3.1. where the rate of tiller death in both seasons was considered to be related to the incidence of shading. It is proposed, however, that shading influenced tiller death through inhibiting the production of new leaves in small semi-shaded tillers rather than increasing the senescence rate in older ones. Consequently, the leaves on such tillers, although receiving sufficient light in their upper regions to meet their individual needs, were not photosynthesizing at sufficiently high rates to meet the demands for cell division and elongation in young leaves which had to reach a relatively large size before they could become self supporting. Because new leaf production was inhibited but senescence rates in old leaves apparently unaltered, the tillers were eventually reduced to one leaf and then died.

Interpretation of the effect of shading on the number of clover leaves that died per plant (Fig. 21b) is difficult owing to fluctuations in the data but increasing trends are evident after day 28 in the spring and day 40 in the autumn. These trends are more distinct in the data of death rate per plant (Fig. 20b) and death rate per unit area (Fig. 24 a2 and b2). These trends appear to be influential in bringing about the above mentioned rapid increases in R.D.L. (Fig. 27) which began about 36 to 40 and 48 to 52 days after defoliation in the spring and autumn respectively, i.e. in both cases about 8 to 12 days after the critical L.A.I. was reached. There is an indication therefore that shading may have been influential in measurably affecting the rate of clover leaf death. Shading is more likely to be influential with clover leaves owing to their higher light interception capacity and horizontal distribution of individual laminae (See section 4.3.4.2.). It has been shown to increase rates of senescence in white clover by Brougham (1958b).

4.5. Dead Leaf Decomposition.

The actual senescence of leaves is not necessarily to be regarded as an avenue of dry matter loss as much may be recovered by close cutting or grazing (L.A. Hunt 1965). It does, however, result in the loss of considerable quantities of green herbage as has been demonstrated above. Lancashire and Keogh (1968) have demonstrated that with sheep grazing normally on pasture, dead herbage may constitute up to 34% of their total intake. By forcing the sheep to graze close to the ground much of the dead matter could probably be utilized. Failure to utilize the dead matter by grazing results in decomposition of the tissue. The advent of decomposition (at significant rates) is crucial to productivity management for it determines whether solar energy captured via photosynthesis is to be utilized in the formation of agricultural products or whether it is to be channelled into a decomposer food web and respired away by non-productive organisms. An estimate is therefore made in this section of absolute rates of decomposition that occurred during the experimental periods, and species differences in decomposition rates are examined.

4.5.1. Absolute Decomposition Rates.

An estimate of the quantity of leaf fall during the experiment that was lost due to decomposition has been presented in Fig. 28. Dead matter residues were present at the beginning of the experiments in both seasons and unless they were accounted for, decomposition, as estimated by the difference between the cumulative dead matter yield and the measured net dead matter yield, would be underestimated. The net dead matter yield measurements were therefore corrected for the yield of dead matter at the beginning of the experiment so that positive increments in the net dead matter yield in

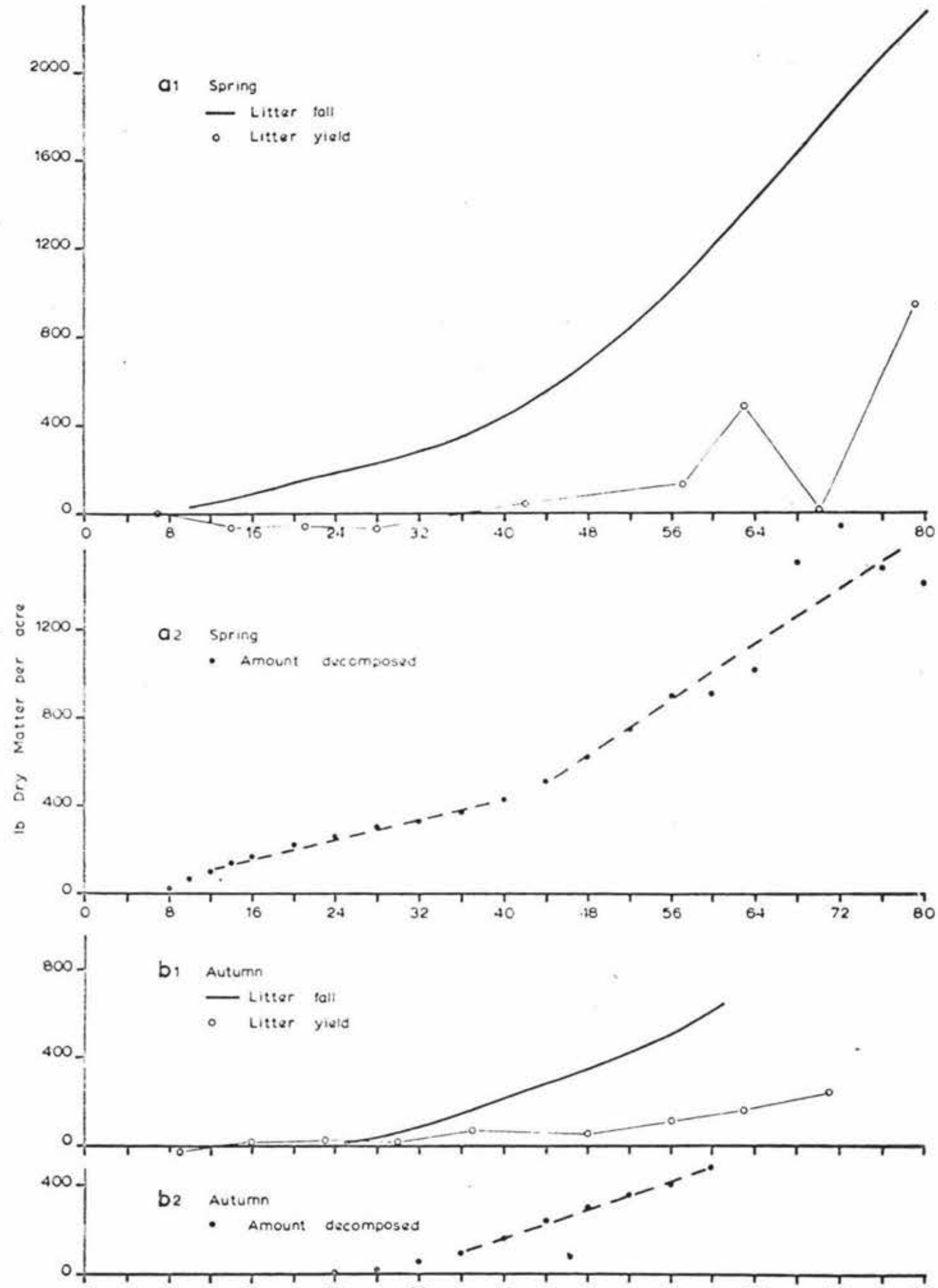

Fig 28 An Estimate of Litter Decomposition

Fig. 28 are due to the accumulation of undecomposed dead matter that has fallen during the experimental period. The decomposition rate of the residue is likely to be slow by the time that leaf death reached significant proportions as the rapidly decomposable fraction would have disappeared. Also, because of its small size proportionately compared with the potential of cumulative dead leaf it will have a negligible effect on estimates of decomposition rate over the latter periods particularly. Even so, the decomposition rate estimate over the first month or so in the spring may be slightly inflated due to residue decomposition. Dead matter yield measurements were obtained from the herbage yield measurements in the autumn, and the L.A.I. data measurements in the spring. In both cases measurements were made infrequently so that short term fluctuations in decomposition rate have evened out and only reasonably long term trends can be described.

Fig. 28 shows that decomposition of dead material in pastures can be very rapid. For example in the autumn, the rate of death of senescent leaf tissue was up to 20 lb dm per acre per day by day 36 - 40 (Fig. 24). From Fig. 28, it can be shown that the mean decomposition rate of this dead leaf from day 36 to 60 was about 16.8 lb of dm per acre per day. At a 50% digestibility, this is equivalent to the feed requirements of 0.30 cows per acre per day.

Two phases in decomposition associated with stage of growth can be seen in the spring (Fig. 28). Decomposition was relatively slow up to about 40 days from defoliation, but increased markedly for the latter half of the experiment. This is logical, for absolute decomposition rates per unit area are determined to a certain extent by the amount of leaf litter present per unit area. Because death rate increased rapidly after day 30 in the spring (Fig. 24) the potential for higher decomposition rates increased also.

The mean decomposition rate up to day 40 in the spring was 10.8 lb dm per acre per day (the equivalent of the feed requirements of .20 cows per acre per day). Between day 48 and 80, the mean decomposition rate was 31.2 lb. dm per acre per day (the equivalent of the feed requirements of .56 cows per acre per day). In the relative terms however, decomposition per amount of dead matter produced was slightly faster in the early part of the experiment. The depression of net dead matter yield due to decomposition (i.e. the proportion of cumulative dead matter yield that has decomposed) was 80 to 90% in the spring (varying due to decomposition of the residue) at day 40, but had dropped to 70% by day 80.

No marked seasonal differences in decomposition rate are obvious. This is not surprising considering that differences in climatic conditions between the two seasons concerned were slight. Most of the leaf death occurred after day 36 in the autumn when the moisture stress conditions had been alleviated, and differences in the temperature conditions were not marked. Thus while the proportion of litter that decomposed ranged from 70% to 90% in the spring, the proportion was about 77% in the autumn also. Very probably, decomposition is only severely reduced in dry periods as Campbell (1964) found that high yields of dead matter per acre only occurred over the dry summer months. However, Campbell considered that the autumn was a period of particularly rapid decomposition which is probably true on a per unit area basis but not necessarily per unit of dead material.

4.5.2. Relative Decomposition Rates.

An indication of possible species differences in decomposition rates is possible by comparing the degree to which the delayed harvesting of leaves from tagged plants depresses the cumulative yield of dead matter per transect, (i.e. the proportion of dead leaf produced over the interval involved that decomposes due to infrequent harvesting). From Figs. 10, 11 and 12, it is evident that generally, a greater proportion of clover leaves decomposed with delayed harvesting than with ryegrass. These differences are more critically examined in table 7 where the depression in the cumulative yields of dead leaf per transect over several harvest intervals is compared at two different stages of growth. Significant differences between the means for the various harvest intervals at the end of each period considered are shown in parenthesis.

Table 7.

Percentage decomposition of dead leaf due to delayed harvesting.

Period under consideration	% decomposition					
	Ryegrass			Clover		
	Harvest Interval			Harvest Interval		
Spring	4	8	24	4	8	24
day 8 - 32	1.8 (NS)	7.3 (NS)	22.9 (NS)	18.7 (NS)	55.0(≠≠)	59.6(≠≠)
day 32 - 56	5.3 (NS)	25.7 (NS)	42.4 (≠≠)	1.4 (NS)	22.1(NS)	59.4 (≠)
	Harvest Interval			Harvest Interval		
Autumn	8	16		8	16	
day 29 - 45	1.4 (NS)	22.2 (NS)		48.6 (≠≠)	79.6 (≠≠)	
day 45 - 61	-11.8 (NS)	21.9 (NS)		31.7 (NS)	63. (≠≠)	

NS = not significant
≠ = P 0.05
≠≠ = P 0.025

Dead clover leaves decompose faster than dead ryegrass. The percentage decomposition of clover due to harvesting at 24 day intervals in the spring was about 1.5. to 3 times that of ryegrass, depending upon the stage of growth. In the autumn the percentage decomposition of clover when harvested at 16 day intervals was 3 to 4 times that of ryegrass. It is also evident from Fig. 12 that complete decomposition of clover leaves (to the extent that the number of harvested leaves is depressed by infrequent harvesting) can occur in a much shorter period than with ryegrass. For example, in the spring complete decomposition of clover leaves (but not ryegrass) was associated with harvesting at four day intervals. This had only a small effect on the yield of dead matter per transect (Fig. 10c), and was confined to the early stage of growth (Table 7), and so was probably due to the small leaves close to the ground which can more easily be missed at harvesting after decomposition has begun. From Figs $12a_1$ and $12a_2$, it can be shown that harvesting at 8 day intervals was associated with a reduction in the number of leaves harvested. By the end of the experiment, this reduction was 16% for ryegrass and 41% for clover. During the autumn (Figs. $12b_1$ and $12b_2$), the reduction was 46% for clover but zero for ryegrass.

Differences in species' decomposition rates are likely to be associated with differences in the chemical composition of the dead leaf. For example, leaves with higher nitrogen contents will be liable to a more rapid breakdown as they facilitate the rapid increase of microbial populations. Leaves with a high content of structural material will take longer to decompose as decomposition of such tissue is slow. (Garret 1963). However, as no detailed information on the differences in chemical composition of dead ryegrass and clover leaves is available, and because decomposition is likely to be a complex process involving successions of decomposers specific for certain fractions of organic tissue, (Garrett 1963) no analysis of the various possible causes of species differences in decomposition rates will be attempted here. It is possible however, that as fresh clover leaves have a higher nitrogen and a lower cellulose content than ryegrass on a dry weight basis (Baily 1964), these factors may be among those that affect differences in species' decomposition rates.

Seasonal comparisons of the percentage decomposition cannot be made directly from Table 7 as the comparisons were made over 24 day intervals in the spring experiment and 16 day intervals in the autumn. However, because the curves in Fig. 10 and 11 are reasonably linear over these periods, the mean daily percentage decomposition can be calculated. The mean daily percentage decomposition data are presented in table 8.

Table 8.

The mean percentage decomposition per day.

Period under consideration.	% Decomposition.					
	Ryegrass			Clover		
	Harvest Interval			Harvest Interval		
Spring	4	8	24	4	8	24
Day 8-32	0.075	0.304	0.954	0.779	2.29	2.48
Day 32-56	0.221	1.070	1.770	0.058	0.920	2.04
	Harvest Interval			Harvest Interval		
Autumn	8	16		8	16	
Day 29-45	0.875	1.39		3.04	4.98	
Day 45-61	0.0	1.37		1.98	3.99	

The main features of table 8 are that over the longest harvest intervals, decomposition of ryegrass dead leaf varied little between the seasons, the larger species difference in the autumn being due to a faster percentage decomposition of clover in the autumn.

Another feature of interest in tables 7 and 8 is the decomposition rates associated with stage of growth. For example, the percentage decomposition of clover due to 8 day harvest intervals in both seasons is slower at the latter stages of growth by 20 to 30%. This is probably due to changes in the size of the leaves and in the height of the canopy. At early stages of growth the dead leaves are relatively small and the canopy close to the ground. The dead leaves therefore are likely to make contact with the ground quickly, to be rapidly colonized by decomposer organisms and to remain in a moist condition. At later stages of growth the leaves are larger and the canopy higher so that due to mechanical support by other dead and living leaves, contact with the soil is not so rapid. Immediate colonization by decomposer organisms is thus less certain and the leaves would dry out to a greater extent resulting in a delay of the onset of decomposition. These initial differences had disappeared where the harvest interval was 24 days in the spring, however.

There appears to be little or no influence of stage of growth on the decomposition of ryegrass leaves. During the spring experiment some decomposition occurred where leaves were harvested at 8 day intervals between 32 and 56 days from defoliation to the extent that fewer leaves were harvested compared with harvesting at more frequent intervals, (Fig. 12a). Decomposition is also indicated at this time in table 7 although it was not detectable statistically. The indication is that in the spring decomposition of ryegrass was slower at the earlier stage of growth; an opposite trend to that observed with clover and one for which no explanation is offered.

It may be concluded that in the spring experiment there was generally little or no tissue lost through harvesting at 4 day intervals compared with 2 day intervals. In the autumn there was no loss of ryegrass leaf from harvesting at 8 day intervals. Decomposition can occur with longer harvest intervals than these and with 8 day harvest intervals for clover in the autumn. The extent to which decomposition of clover has occurred by 8 days appears to vary with stage of growth but such differences are reasonably short term, having disappeared with 24 day interval harvesting in the spring. Dead clover leaves decomposed by 1.5 to nearly 4 times as fast as ryegrass depending on season and stage of growth. In terms of total dead matter however, (Fig. 28) there was little seasonal difference in the proportion of litter that disappeared. As relatively few dead clover leaves were observed in the net dead matter yield measurements, it is probable that clover leaves rapidly decompose completely. The above data have shown that during the first three weeks after death at least, decomposition of clover is much faster than ryegrass. As a result the residue build-up would consist mainly of partially decomposed ryegrass leaves. The seasonal differences in the proportional contribution of ryegrass and clover to the leaf litter (about 25 to 33% see Fig. 23) were apparently not great enough to result in marked differences in the proportion of the leaf fall that remained as a residue.

Summary and Conclusions

An experiment is described whereby rates of leaf death in a perennial ryegrass - white clover sward were determined at successive stages of regrowth by measuring both the rate of leaf death per plant, and the plant density. Measurements were also made of the regrowth yield and of certain aspects associated with pasture regrowth. By integration of growth and death data, an estimate was obtained of absolute levels of productivity throughout the successive stages of regrowth, and particularly at the high L.A.I. values. The results are discussed in relation to possible and probable factors involved in determining rates of increase in green herbage at high L.A.I. values.

The main points arising out of the discussion are as follows:-

(1) Regrowth from defoliation increased in an exponential manner until limiting factors became operative. These factors were considered to be the manner of light interception and distribution over the leaf surface in the spring, and the supply of moisture and possibly nutrients to the plants in the autumn.

(2) The relative tiller death rate of ryegrass tillers increased rapidly as shading of the lower canopy became intense. As no increase in ryegrass leaf death rate was found to be associated with the onset of shading, this effect was attributed to carbohydrate starvation rather than accelerated senescence.

(3) During the linear phase of pasture regrowth, leaf death rates increased due to increases in the number of leaves that died per plant unit and the size of the dead leaves. These factors may be influential at slightly different stages (as in the spring) or simultaneously (as in the autumn), and have a similar effect during the earlier stages of growth. In terms of

determining maximum leaf death rates, however, leaf size assumes major importance during the third growth phase and may vary considerably with season.

(4) Considerable quantities of green herbage were lost via death and decomposition in both seasons. The maximum leaf death rates obtained were 56 lb dm per acre per day (on day 68) and 27 lb dm per acre per day (on day 59) for the spring and autumn respectively. This dead material decomposed at approximately 30 lb dm per acre per day in the spring (during the latter growth stages) and 16 lb dm per acre per day in the autumn.

(5) Dead white clover leaves decomposed 1.5 to nearly 4 times as fast as dead ryegrass leaves, depending on season and stage of growth.

(6) Initial reductions in the rate of accumulation of green herbage that mark the beginning of the third growth phase in the spring can be accounted for by leaf death. In the autumn, however, when clover was the dominant component, there was an apparent reduction in the rate of overall synthesis as well. This reduction occurred with clover shortly after complete light interception was attained in both seasons. The lack of any similar effect with ryegrass until lodging occurred is attributed to species differences in growth habit and the subsequent effects of intense shading of the lower canopy. Lowered rates of accumulation of green ryegrass at high L.A.I. values can generally be attributed to leaf death. However, a number of additional factors may be introduced with flowering in the spring.

(7) Factors that inhibit growth processes but not leaf death, such as moisture stress, result in a greater proportionate loss of herbage. Also, the development of a large number of tillers towards flowering in the spring effectively reduces the proportionate loss of herbage owing to the large non-leaf and (in the short term) non-senescent fraction, and to a reduction in the rate of leaf senescence.

(8) Although shading of the lower canopy appeared to enhance the senescence of clover leaves, there was no evidence that it had a similar effect on ryegrass leaves.

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APPENDIX 1

Summary of Measurement dates.

Measurement:

(a) Dead leaf harvest

Spring: 2 Day Interval		4 Day Interval		8 Day Interval		24 Day Interval	
Date	Days	Date	Days	Date	Days	Date	Days
15.9.66	10						
17.9.66	12	17.9.66	12				
19.9.66	14						
21.9.66	16	21.9.66	16	21.9.66	16		
23.9.66	18						
25.9.66	20	25.9.66	20				
27.9.66	22						
29.9.66	24	29.9.66	24	29.9.66	24		
1.10.66	26						
3.10.66	28	3.10.66	28				
5.10.66	30						
7.10.66	32	7.10.66	32	7.10.66	32	7.10.66	32
9.10.66	34						
11.10.66	36	11.10.66	36				
13.10.66	38						
15.10.66	40	15.10.66	40	15.10.66	40		
17.10.66	42						
19.10.66	44	19.10.66	44				
21.10.66	46						
23.10.66	48	23.10.66	48	23.10.66	48		
25.10.66	50						
27.10.66	52	27.10.66	52				
29.10.66	54						
31.10.66	56	31.10.66	56	31.10.66	56	31.10.66	56
2.11.66	58						
4.11.66	60	4.11.66	60				
6.11.66	62						
8.11.66	64	8.11.66	64	8.11.66	64		
10.11.66	66						
12.11.66	68	12.11.66	68				
14.11.66	70						
16.11.66	72	16.11.66	72	16.11.66	72		
18.11.66	74						
20.11.66	74	20.11.66	76				
22.11.66	78						
24.11.66	80	24.11.66	80	24.11.66	80	24.11.66	80

Autumn:

4 day Interval		8 day Interval		16 day Interval	
Date	Days	Date	Days	Date	Days
3.3.67	17				
7.3.67	21	7.3.67	21		
11.3.67	25				
15.3.67	29	15.3.67	29	15.3.67	29
19.3.67	33				
23.3.67	37	23.3.67	37		
27.3.67	41				
31.3.67	45	31.3.67	45	31.3.67	45
4.4.67	49				
8.4.67	53	8.4.67	53		
12.4.67	57				
16.4.67	61	16.4.67	61	16.4.67	61

(b) Herbage yield

Spring		Autumn	
Date	Days	Date	Days
14.9.66	9	22.2.67	8
19.9.66	14	2.3.67	16
26.9.66	21	9.3.67	23
3.10.66	28	16.3.67	30
17.10.66	42	23.3.67	37
1.11.66	57	3.4.67	48
7.11.66	63	11.4.67	56
14.11.66	70	18.4.67	63
23.11.66	79	26.4.67	71

(c) Tiller density

Spring		Autumn	
Date	Days	Date	Days
19.9.66	14	14.2.67	0
26.9.66	21	22.2.67	8
3.10.66	28	2.3.67	23
12.10.66	42	9.3.67	23
1.11.66	57	16.3.67	30
7.11.66	63	23.3.67	37
14.11.66	70	3.4.67	48
23.11.66	79	11.4.67	56
		18.4.67	63
		26.4.67	71

APPENDIX 2

Fitting of Growth Functions

The logistic

$$y = \frac{A}{1 + Be^{-ct}}$$

was fitted by Demings iterative method. For this it was required to find the values of (A), (B) and (C) that minimise the expression

$$E = \Sigma \left\{ y - \frac{A}{1 + Be^{-ct}} \right\}^2$$

Firstly approximations (A_o), (B_o) and (C_o) were found by fitting a curve roughly by eye to the data. These estimates were then fed into the computor program.

The program calculated

$$F_A = \frac{F}{A} = \frac{-1}{1 + Be^{-ct}}$$

$$F_B = \frac{F}{B} = \frac{Ae^{-ct}}{(1 + Be^{-ct})^2}$$

$$F_C = \frac{F}{C} = \frac{tABe^{-ct}}{(1 + Be^{-ct})^2}$$

$$\text{and} \qquad F = y - \frac{A}{1 + Be^{-ct}}$$

at each observed point (t,y) for (A_o), (B_o) and (C_o).

The normal equations were formed:

$$\Sigma F_A^2 (a) + \Sigma F_A F_B (b) + \Sigma F_A F_C (c) = \Sigma F_A F$$

$$\Sigma F_B F_A (a) + \Sigma F_B^2 (b) + \Sigma F_B F_C (c) = \Sigma F_B F$$

$$\Sigma F_C F_A (a) + \Sigma F_C F_B (b) + \Sigma F_C^2 (c) = \Sigma F_C F$$

and solved for (a), (b) and (c).

Second approximations to (A), (B) and (C) were then given by

$$A_1 = A_0 - a$$

$$B_1 = B_0 - b$$

$$C_1 = C_0 - c$$

The process converges to the required parameters of the fitted curve and ΣF^2 converges to a stable value of sum of squares of deviations.

APPENDIX 3

Summary of growth data.

(a) Spring.

Day	Herbage yield (dry weight gms/Ft^2)			S.E.		
	Ryegrass	Clover	Total	Ryegrass	Clover	Total
9	7.28	1.71	8.93	0.88	0.50	0.36
14	6.49	4.31	10.80			
21	11.15	7.44	18.59	2.38	1.13	2.16
28	10.97	11.36	22.33			
42	20.09	19.26	39.35	2.12	5.26	3.37
57	25.94	30.18	56.11			
63	47.66	14.07	61.73	6.21	2.42	5.07
70	53.16	11.47	64.62			
79	42.81	24.28	67.08	3.61	3.81	6.95

Each figure is the mean of 3 replications.

(b) Autumn.

Day	Herbage yield (dry weight gms/Ft^2)			S.E.		
	Ryegrass	Clover	Total	Ryegrass	Clover	Total
9	0.54	1.22	1.76	0.12	0.17	0.21
16	1.15	2.90	4.06			
23	1.57	4.68	6.25	0.16	0.25	0.17
30	2.62	7.39	10.02			
37	2.25	10.65	12.90	0.39	0.41	0.52
48	3.36	13.79	17.14			
56	3.01	16.94	19.95	0.99	1.62	
63	4.40	17.44	21.84			
71	3.24	16.63	19.87	0.85	1.06	0.21

Each figure is the mean of four replications.

APPENDIX 4

Analyses of Regression of plant populations.

(a) Spring:

Table of data

Ryegrass (tillers) Day	Density (No/Ft^2:Y)	Clover (buds) Day	Density (No/Ft^2:Y)
14	943	14	197
21	613	21	408
28	660	28	244
42	508	42	312
57	307	57	197
63	270	63	150
70	197	70	178
79	156	79	331

Ryegrass $Y = 961.1 - 10.81X$

Source of Variation	Sums of squares (corrected)	D.f.	Mean square	F.	P.
Regression	474,561	1	474,561	53.1	≠≠≠
Error	53,662	6	8,944		
Total	528,223	7			

Clover $Y = 295.3 - 0.923X$

Source of Variation	Sums of squares (corrected)	D.f.	Mean square	F.	P.
Regression	3,455	1	3,455	1	NS
Error	52,716	6	8,786		
Total	56,171	7			

(b) Autumn:

Table of data

Ryegrass (tillers) Day (X)	Ryegrass (tillers) Density (No/Ft^2: Y)	Clover (rooted nodes) Day (X)	Clover (rooted nodes) Density (No./Ft^2:Y)
0	337	0	151
8	227	8	82
16	182	16	110
23	241	23	300
30	185	30	107
37	129	37	243
48	78	48	200
56	152	56	234
63	122	63	283
71	109	71	352

Ryegrass $Y = 269.7 - 2.655 X$

Source of Variation	Sums of squares (corrected)	D.f	Mean square	F.	P.
Regression	36,497	1	36,497	18.07	≰≰
Error	16,161	8	2,020		
Total	52,658	9			

Clover $Y = 133.6 + 2.793 X$

Source of Variation	Sums of squares (corrected)	D.f	Mean Square	F.	P.
Regression	40,381	1	40,381	9.15	≰
Error	35,307	8	4,413		
Total	15,688	9			

APPENDIX 5.

Summary of leaf death data used in calculations of death rate per transect.

(a) Spring (2 day harvest interval)

Day	Dry wt. of dead leaf/transect (mg)		
	Ryegrass	Clover	Total
10	10	5	14
11	9	7	16
14	7	8	16
16	7	7	14
18	12	18	30
20	9	8	17
22	7	17	23
24	5	12	17
26	7	19	26
28	14	25	39
30	8	13	21
32	15	34	48
34	14	29	43
36	18	28	46
38	20	31	51
40	8	7	16
42	25	45	70
44	24	20	44
46	16	33	49
48	24	27	50
50	21	29	50
52	21	34	55
54	25	38	63
56	31	39	70
58	21	50	70
60	15	42	57
62	23	3	27
64	23	27	49
66	12	37	49
68	19	39	58
70	15	57	81
72	20	30	50
74	16	15	31
76	14	12	26
78	10	15	25
80	17	34	50

(b) Autumn (4 day harvest interval)

Day	Dry wt. of dead leaf/transect (mg)		
	Ryegrass	Clover	Total
25	13	6	19
29	14	31	45
33	19	125	144
37	33	116	149
41	54	112	166
45	38	79	118
49	57	96	152
53	42	120	162
57	59	138	196
61	30	146	176

Each figure is the mean of 6 replications in the spring and 4 in the autumn.

APPENDIX 6

Summary of the Number of leaves that Died per Transect.

(a) Spring No. of leaves/transect			(b) Autumn No. of leaves/transect		
Day	Ryegrass	Clover	Day	Ryegrass	Clover
10	8.0	2.2	25	8.3	5.6
12	6.9	3.2	29	7.0	12.3
14	6.6	3.5	33	7.5	42.8
16	7.2	3.2	37	11.2	31.0
18	12.5	7.3	41	15.5	23.3
20	7.2	2.8	45	10.3	17.3
22	4.7	4.3	49	18.5	21.5
24	6.3	5.0	53	10.3	23.5
26	5.8	5.5	57	15.5	28.5
28	9.3	6.0	61	9.8	22.8
30	4.7	4.7			
32	8.2	7.5			
34	8.2	7.2			
36	8.8	5.3			
38	10.5	6.3			
40	3.7	2.0			
42	10.3	7.5			
44	9.2	3.5			
46	7.2	5.2			
48	9.2	3.5			
50	5.7	3.7			
52	7.2	3.3			
54	6.0	3.2			
56	6.8	3.3			
58	4.5	3.5			
60	3.0	3.0			
62	4.7	0.8			
64	3.3	1.8			
66	1.8	1.7			
68	2.3	2.2			
70	2.3	2.0			
72	2.8	1.3			
74	1.8	1.2			
76	1.2	0.8			
78	1.2	4.0			
80	1.5	4.0			

Each figure is the mean of 6 replicates in the spring and 4 in the autumn.

APPENDIX 7

Analysis of Variance on the effect of sward Disturbance on Light Penetration

7.3.67 (21 days from defoliation)

Table of Data

		Replication 1	2	3	4	Treatment totals
Treatment	4	373.4	234.5	392.0	302.4	1302.3
Intervals (days)	8	334.0	237.8	310.6	228.1	1110.5
between	16	304.9	394.8	301.9	266.6	1268.2
Disturbances	24	306.5	209.8	324.8	229.8	1070.9
Rep totals		1318 .8	1076.9	1329.3	1026.9	4751.9

Each figure is the sum of the % Light Penetration of 6 measurements

Analysis of Variance

Source of Variation	Sums of squares (corrected)	D.f.	Mean square	F.	P.
Replication	3140.44	3	1046.81		
Treatment	1633.96	3	544.65	1.25	NS
Error 1	3919.10	9	435.46		
Error 2	56085.03	80	701.06		
Total	64778.53	95			

Error 1 = Residual error.

Error 2 = Variation between measurements within transects.

Mean % Light Penetration = 49.50%

Mean % Light Interception = 50.50%

13.3.67 (27 Days from defoliation)

Table of Data

		Replication 1	2	3	4	Treatment totals
Treatment:	4	116.7	38.5	200.3	120.5	476.0
Intervals (days)	8	218.0	64.0	136.6	185.5	604.1
between	16	123.3	124.7	165.8	176.0	589.6
Disturbances	24	192.3	187.2	176.1	168.1	723.7
Rep totals		650.1	414.4	678.8	650.1	2393.4

Analysis of Variance

Source of Variation	Sums of squares (corrected)	D.f.	Mean square	F.	P.
Replication	1902.75	3	634.25		
Treatment	1282.99	3	427.66	1.3	NS
Error 1	2959.24	9	328.80		
Error 2	53942.99	80	674.28		
Total	60087.97	95			

Mean % Light Penetration = 24.9%

Mean % Light Interception = 75.1%

18.3.67 (32 days from defoliation)

Table of Data

		Replication				Treatment totals
		1	2	3	4	
Treatment:	4	36.5	25.6	64.1	14.4	140.6
Interval (days)	8	58.8	36.9	111.6	64.0	271.3
between	16	139.4	27.7	39.4	94.3	300.8
Disturbances	24	70.6	62.7	23.7	43.4	200.4
Rep totals		305.3	152.9	238.8	216.1	913.1

Analysis of Variance

Source of Variation	Sums of squares (corrected)	D.f.	Mean square	F.	P.
Replication	494.63	3	164.88		
Treatment	648.87	3	216.29	1.09	NS
Error 1	1784.63	9	198.29		
Error 2	13529.42	80	169.12		
Total	16457.55	95			

Mean % Light Penetration = 9.5%
Mean % Light Interception = 90.5%

<u>27.3.67</u> (41 days from defoliation)

Table of Data

		Replication				Treatment totals
		1	2	3	4	
Treatment:	4	9.8	16.4	84.9	15.5	126.6
Interval (days)	8	20.6	47.0	32.7	25.6	125.9
Between	16	13.8	8.7	7.5	14.4	44.4
Disturbances	24	65.2	13.5	19.8	13.6	112.1
Rep totals		109.4	85.6	144.9	69.1	409.0

Analysis of Variance

Source of Variation	Sums of squares (corrected)	D.f	Mean square	F.	P.
Replication	135.26	3	45.09		
Treatment	191.50	3	63.83	0.65	NS
Error 1	882.61	9	98.07		
Error 2	7424.78	80	92.81		
Total	8634.15	95			

Mean % Light Penetration = 4.3%
Mean % Light Interception = 95.7%

APPENDIX 8

Summary of polynomials fitted to the cumulative data of Leaf Death per Unit Area

Form of polynomial:

$$y = a + bx + cx^2 + dx^3 + ex^4$$

($y = mg/Ft^2$, x = days from defoliation, a,b,c,d, and e = Power coefficients)

Data	Polynomial
Spring:	
Total (1)	$y = -3495.8 + 519.75x - 20.960x^2 + 0.4167x^3 - 0.0023x^4$
Ryegrass(2)	$y = -1535.6 + 249.23x - 10.128x^2 + 0.2089x^3 - 0.0013x^4$
Clover (3)	$y = -1882.0 + 261.87x - 10.705x^2 + 0.2053x^3 - 0.00104x^4$
Autumn:	
Total (4)	$y = 15649.0 - 1768.6x + 68.926x^2 - 1.0822x^3 + 0.0064x^4$
Ryegrass(5)	$y = 1928.7 - 179.4x + 5.206x^2 - 0.0380x^3$
Clover (6)	$y = 14364.0 - 1653.6x + 66.119x^2 - 1.0826x^3 + 0.0066x^4$

Analyses of variance

Source of Variation	Sums of squares	D.f.	Mean square	F.	P.
(1)					
Mean	26074×10^5	1	26074×10^5		
Linear	17419 x "	1	17419 x "		
Quadratic	1322 x "	1	1322 x "		
Cubic	0	1	0		
Quartic	30 x "	1	30 x "	32	≠≠
Residual	29 x "	31	94077		
Total	44875×10^5				

≠ = P 0.05

≠≠ = P 0.01

Source of Variation	Sums of squares	D.f.	Mean square	F.	P.
(2)					
Mean	55819 x 10^4	1	55819 x 10^4		
Linear	28934 x "	1	28934 x "		
Quadratic	917 x "	1	917 x "		
Cubic	71 x "	1	71 x "		
Quartic	93 x "	1	93 x "	168.8	≠≠
Residual	17 x "	31	55206		
Total	85852 x 10^4	36			
(3)					
Mean	74129 x 10^4	1	74129 x 10^4		
Linear	60822 x "	1	60822 x "		
Quadratic	7248 x "	1	7248 x "		
Cubic	1050 x "	1	1050 x "		
Quartic	58 x "	1	58 x "	6.7	≠
Residual	267 x "	31	86269		
Total	142630 x 10^4	36			
(4)					
Mean	86736 x 10^3	1	86736 x 10^3		
Linear	44184 x "	1	44184 x "		
Quadratic	548 x "	1	548 x "		
Cubic	2 x "	1	2 x "		
Quartic	44 x "	1	44 x "	5.9	0.10-
Residual	267 x "	31	7423		0.05
Total	131550 x 10^3	36			
(5)					
Mean	7375 x 10^3	1	7375 x 10^3		
Linear	3110 x "	1	3110 x "		
Quadratic	12 x "	1	12 x "		
Cubic	18 x "	1	18 x "	37.1	≠≠
Quartic	0 x "	1	0 x "	0.1	NS
Residual	2 x "	31	493		
Total	10518 x 10^3	36			

Source of Variation	Sums of squares	D.f.	Mean square	F.	P.
(6)					
Mean	43530 x 10^3	1	43530 x 10^3		
Linear	23853 x 10^3	1	23853 x "		
Quadratic	397 x "	1	397 x "		
Cubic	32 x "	1	32 x "		
Quartic	47 x "	1	47 x "	7.1	≠
Residual	33 x "	31	6588		
Total	67892 x 10^3	36			