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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 herbivores 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 occurred 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 rufor*, *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 (1958) 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 susceptibility 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 (1954) 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 susceptibility 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. Leaves 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 m² (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 m² per day (8.9 lb per acre per day) for the uplands and 3 g. per m² (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 m² on "uplands", 417 g per m² 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).