

## LEAF GROWTH IN PASTURE GRASSES

by

J. H. SILSBURY\*

### ABSTRACT

*The pattern of morphogenesis of the grass plant and the influences of environment on leaf growth are reviewed, and some aspects discussed with reference to the author's data from experiments with *Lolium perenne*. In particular, the effects of light energy, temperature and photoperiod on all stages of leaf development from initiation through to maturity are examined and interpreted in relation to leaf growth on a single tiller and in the pasture community.*

### INTRODUCTION

This essay examines the pattern of morphogenesis of the grass plant and describes some of the known effects of environment on leaf growth in plants growing in isolation and as members of a community. An approach of this kind was advocated by Evans *et al.* (1964) who suggested that "a further understanding of the effects of environmental factors on both (grass) swards and single plants will involve an increasing degree of resolution of these effects on the components of grass growth". This suggests that the effects of environmental factors on the growth of the whole plant should be examined in relation to the rates of production of individual organs; their growth rates, ultimate size, senescence pattern and their interrelations. Jewiss (1966) profitably undertook a review along these lines with the belief that improved understanding and appreciation of the basic physiology of grass growth will lead to improved husbandry and higher production.

Original data from experiments with *Lolium perenne* will be used to illustrate specific points. Other examples will be drawn from published papers, mainly those pertaining to the temperate grasses.

### STRUCTURING THE APPROACH

Plant growth as measured by increase in dry weight can be studied in a number of ways. Firstly, we can examine the origin of new organs, their histogenesis, rates of production and early ontogeny. Secondly, we can record the increase in size of particular organs, their growth rates, the final size attained and subsequent life history. The 'growing plant' consists of a population of organs at diverse stages in ontogeny—some embryonic, some expanding, some mature, some senescent, some dead.

Thirdly, we can view a plant as a collection of physically related and physiologically interdependent organs each of which is more or less fixed in position. Here the interrelations between organs are of interest as well as how the environment of each part is modified as the size of the plant or the community increases. Fourthly, we can examine a community as a population of genetically diverse individuals each fixed in position and exploiting a variable environment. Strong selective forces may operate on plants in a sward and changes in number often occur as a consequence of competition.

Finally, it is often profitable to consider a plant community as possessing definable surface attributes despite variation in number, type, kind, size and age of constituent organs and the size and kind of the individuals present. A community exposes to the aerial environment a textured layer of living matter which has specific properties with respect to energy balance and gaseous diffusion prescribed by its absorptive capacity, vertical structure and arrangement of parts. Underground, the root systems

---

\* Waite Agricultural Research Institute, Glen Osmond, South Australia 5064.

penetrate the more physically resistant soil environment tapping a variable pool of water and mineral nutrients.

Each approach calls for separate techniques, skills and resources and it is unlikely that any one will define adequately the plant attributes or environmental factors either limiting or promoting growth. When all are considered it is more probable that plant production can be improved. The ultimate objective is to understand the community. Perhaps this can best be done if it is appreciated that a community consists of a dynamic population of heterogeneous individual plants, each consisting of diversely structured organs having their origins in cellular processes. The study of leaf growth during the vegetative phase is regarded as a step toward understanding the basis for productivity of grass swards.

### THE MORPHOLOGICAL BASIS OF GROWTH

The classic studies of Arber (1934) and Sharman (1942, 1945), the enthusiastic account of the growth of *Poa pratensis* given by Etter (1951), the excellent discussion of form and structure of Barnard (1964) and the recent review of Jewiss (1966) provide a descriptive account of the general architecture of the grass plant. One particular structural feature of grasses which needs to be more fully stressed is the existence of a common segmental unit of growth, the phytomer (see Evans and Grover 1940).

The phytomer originates in the stem apex and consists of four organs—a leaf, an internode, an axillary (tiller) bud and an adventitious root. Leaves, and the internodes which constitute the stem, are finite structures and capable of limited growth. Axillary buds, on the other hand, are (theoretically) capable of unlimited growth since each is a reproduction of the parent apical meristem and, like it, can produce new phytomers until a separate existence is terminated by reproductive development. Each phytomer appears to have the potential for root development but in rosette plants roots are normally confined to the basal nodes of the main stem and tillers originating close to the ground. In rhizomatous plants, rooting at the nodes is a means of vegetative proliferation.

Although this paper is concerned with leaf growth it is necessary to stress that this is only one part of the growth and morphogenesis of the whole phytomer. Leaf production can be studied more or less continuously at the vegetative apex but the development of other organs may be prescribed by the growth stage. Internode elongation occurs as an integrated part of vegetative growth in many grasses whilst in others it is only associated with reproductive development (Silsbury 1964). The axillary bud (tiller) is not foliar in origin and develops in the sub-apical regions. Tillering creates new centres for growth, new meristems, and is important in relation to total dry matter production (Silsbury 1965) and vegetative proliferation.

### LEAF GROWTH

The aspects of leaf growth to be considered are increase in dry weight and increase in surface area of the single leaf lamina. Emphasis on these attributes does not deny the over-all importance of the rate of increase in the total leaf lamina surface to the rate of dry matter production by the whole plant and by the community, but as increase in leaf area is the resultant of the integrated growth of many phytomers it is best considered as a whole-plant phenomenon.

Descriptive accounts of leaf growth in grasses may be found in papers by Sharman (1942), Barnard (1964), Evans *et al.* (1964) and Jewiss (1966). A useful picture of the early vegetative growth of ryegrass is given by Soper and Mitchell (1956). A number of stages in the growth of a grass leaf are clearly discernible, namely: (i) initiation; (ii) pre-appearance; (iii) post-appearance; (iv) maturity; (v) senescence.

The primary event, the initiation of a leaf primordium as a lateral appendage on the apex represents a remarkable piece of cellular engineering. Expansion usually follows initiation as a more or less continuous process but unexpanded leaf primordia may accumulate on the apex in advance of the last expanding leaf. This is commonly a prelude to floral initiation.

The leaf primordium functions at first as a diffuse meristem and increases in size mainly by cell division. When it is 1-2 cm long two localised regions of meristematic activity appear, the one above the ligule giving rise to the lamina, that at the base of the leaf being responsible for the growth of the sheath (Sharman 1942; Esau 1943). Activity by these inter-calary meristems and associated cell expansion result in the lamina elongating upwards so that the tip eventually appears from within the leaf sheaths of the older leaves that surround the apex. This first external indication of leaf growth, leaf appearance (Mitchell 1953), marks the conclusion of pre-appearance growth.

There are good reasons for distinguishing between pre- and post-appearance growth. Begg and Wright (1962) and Friend *et al.* (1962) point out that when enclosed within the sheaths, a leaf is dependent on the rest of the plant for assimilate. Less than 10% of the light incident on the outermost sheath is likely to penetrate to the developing leaf so its potential photosynthesis is very small. The leaf thus grows initially in intense shade; moreover the light it does receive is likely to be of a different spectral composition from that incident on the whole plant. During pre-appearance growth the relative growth rate of the young wheat leaf follows a variety of trends but on emergence a marked decline occurs which continues to zero at maturity (Williams 1960, 1964). Sharman (1942) concluded that cell extension stops when leaf tissue emerges from the sheath. Davidson and Milthorpe (1966) considered that in cocksfoot cell expansion is entirely restricted to regions within the surrounding sheaths. Robson (1967) found in *Festuca arundinacea* that laminae did not increase in length after the ligule had emerged. Cessation of growth may be of a direct result of exposure of the lamina to light. (Begg and Wright 1962.)

On emergence the lamina encounters an entirely new environment: it is able to conduct photosynthesis according to the surface area exposed, the efficiency of its photosynthetic apparatus and the incident light energy. It also commences to transpire and is normally subject to a much more variable humidity environment than when enclosed within the sheaths.

Whilst it is reasonable to consider leaf growth up to the time of appearance as constituting a distinctive stage, it can be argued that 'pre-appearance growth' continues during the actual emergence of the leaf, as a portion of the lamina and all the sheath remain enclosed until the ligule appears. Advantages in making the distinction lie partly with the ease of measurement of the emerged lamina and partly with the fact that the period from appearance to maturity (attainment of final size) denotes the phase during which the leaf contributes by its own growth to increase in dry matter of the whole plant. Williams (1964) has shown that at appearance the dry weight of the wheat leaf is about 10% of the final weight. A similar situation occurs with perennial ryegrass.

The final area of the lamina, its photosynthetic efficiency, its angle and position in the canopy and its pattern of senescence determine the potential contribution it can make to the carbon economy of the whole plant. It is well known that the photosynthetic capacity of a leaf declines with age. Hunt and Brougham (1966) have stressed that a community of grass plants displays a dynamic pattern of leaf production and decay and that there is a rapid turnover of leaf material in the canopy as a consequence of ageing, senescence and decomposition.

#### (i) Leaf Initiation

Organisation at the shoot apex has long fascinated students of morphogenesis so that a great deal is now known concerning its histogenesis (Avery 1933; Sharman

1945; Hamilton 1948; Clowes 1961; Barnard 1964; Cutter 1965; Wardlaw 1965 a, b). Interest in the role of the apex in plant productivity however, has more to do with the rate of initiation of leaf primordia by particular genotypes under given conditions than with the histological detail of primordia inception. Even so, there is no doubt that our understanding of environmental effects on leaf initiation will largely be dependent on knowledge derived from studies of histological processes.

Leaf primordia are initiated as lateral appendages on the apex in acropetal succession, the time interval between the appearance of successive units being termed the plastochron (Askenasy 1880). The shoot apex is in a specific morphological stage during each particular time interval (Abbe and Phiney 1951) and the plastochron may be used as a developmental time scale (Sharman 1942; Erickson 1960).

Before discussing effects of environmental factors on leaf initiation, two indirect controls of this process should be mentioned. Firstly, floral induction ultimately exerts complete control over leaf initiation in that commitment of the apex to reproductive development terminates this process. Secondly, Laude (1953) has shown that certain perennial grasses may become dormant and although this state is more properly considered as a property of axillary buds (Silsbury 1964; McWilliam 1968), there is clearly a mechanism whereby the whole of an apex can be 'switched off', or at least temporarily reduced in activity.

Confining our attention to the non-dormant vegetative grass apex, there is surprisingly little data available as to the effects of factors such as light energy and temperature on the plastochron (Clowes 1961; Humphries and Wheeler 1963; Evans *et al.* 1964). Cutter (1965) concluded that with the exception of photoperiod these (environmental) factors have been relatively little studied in relation to the shoot apex itself.

The little information available comes mainly from the cereals. Here study of the effects of light energy and temperature is made difficult by the early onset of floral development. In *Avena sativa*, for example, Hamilton (1948) found that all leaf primordia were initiated in two or three weeks. Sunderland (1961), working with vernalised and unvernalsed 'Petkus' rye, has shown there to be a marked acceleration in the rate of primordium production following transition to reproductive growth. Friend *et al.* (1962) were unable to follow the initiation of primordia on the wheat apex for more than ten days. The rate increased by more than 50% with increase in temperature from 15 to 20°C; increase in light intensity from 200 to 1750 lumen ft<sup>-2</sup> increased the rate from 2.5 per week to 2.8. The relative ineffectiveness of variation in light energy (900 of 3600 lumen ft<sup>-2</sup>) on the plastochron of wheat has been confirmed by Lucas (personal communication).

The barley apex appears to be much more responsive to light energy. Using fluorescent lights which are relatively inefficient in the photoperiodic process, Aspinall and Paleg (1963) found the rate of primordium production of the cultivar 'Prior' to be substantially constant and markedly influenced by light energy over the range 16-67 cal cm<sup>-2</sup> day<sup>-1</sup>. At each of two photoperiods there was a linear response of the plastochron to light energy. Differences in response to energy at the two photoperiods were considered to be real and were attributed to photoperiodic rather than photosynthetic causes. Paleg and Aspinall (1964) showed that the inclusion of incandescent light hastened the onset of reproductive growth and subsequently accelerated the rate of primordium production. Aspinall (1966) was able to keep the apex of unvernalsed 'Pioneer' barley vegetative under fluorescent and incandescent light. The number of primordia produced per day decreased as daylength of constant intensity was reduced from 24 to 14 hr. A further reduction to 10 hr had no further effect.

Leaf initiation in the tomato has been found to increase with temperature (15 to 25°C) and with increase in light intensity from 400 to 1200 lumen ft<sup>-2</sup> (Hussey 1963). Schwabe (1963) recorded only a slight effect of temperature over the range 17 to 27°C in chrysanthemum but a near vernalising temperature reduced pri-

mordium production to a very low level. In these species there was a much more pronounced effect of temperature on the rate of leaf growth than on leaf initiation.

Apical meristems, like other embryonic regions, can develop higher suction forces than other tissues and thus may continue growth when other parts of the plant are wilting (Allsopp 1965). Morton and Watson (1948) found that the production of leaf primordia in sugar beet was not strongly influenced by the external water supply. Aspinall (in press) found that water stress of the barley plant prevented the formation of new primordia but did not prevent the development of lateral primordia.

Effects on the plastochron of variation in the supply of mineral nutrients to grass plants do not appear to have been recorded in the literature.

### (ii) Leaf appearance

Evans *et al.* (1964) and Anslow (1966) have reviewed some of the known effects of environment on the rate of leaf appearance in pasture grasses and variation between genotypes in this attribute. There is little doubt that the rate of leaf appearance is constant with time for a great many species under controlled conditions and that constant rates of leaf production may occur in the field over a considerable part of the growth period. (Humphries and French 1965; Fulford 1965; Burt 1968). Seasonal trends, however, do occur. Anslow (1966) was unable to form a definite view as to the relative importance of such factors as temperature, daylength, total radiation, light flux density or soil moisture status on the rate of leaf appearance. This was undoubtedly due to the occurrence of correlated changes in the level of these factors in the field. Study of the specific effects of single factors can only be achieved under controlled conditions. Seedling plants are frequently utilised for this purpose but here caution is necessary as Taylor, Cooper and Treharne (1968) found that consistent effects of temperature, light energy and genotype did not occur with respect to rate of leaf appearance and leaf lamina area until the fifth or sixth leaf stage. The environmental factors and the interactions between them varied in their effects with position on the shoot.

Table 1 shows data taken from the literature for rate of leaf appearance (days per leaf) for several grass species grown under controlled conditions, in glasshouses and in the field. A wide range of rates within and between species clearly exists.

TABLE 1  
*Rates of leaf appearance in different grasses obtained by various authors under field, glasshouse and controlled conditions*

<i>Species</i>	<i>Author</i>	<i>Conditions</i>	<i>Rate days/leaf</i>
<i>Festuca arundinacea</i>	Robson (1967)	Winter—outdoors	23-70
<i>Festuca pratensis</i>	Patel and Cooper (1961)	Seasonal	6-8
<i>Phleum pratense</i>	Patel and Cooper (1961)	Seasonal	4-10
<i>Lolium multiflorum</i>	Cooper & Edwards (1961)	Glasshouse	6.7-8.1
<i>Lolium multiflorum</i>	Hunt & Brougham (1966)	Seasonal	8-18
<i>Lolium perenne</i>	Beevers & Cooper (1964)	Controlled	6
<i>Lolium perenne</i>	Cooper & Edwards (1961)	Glasshouse	5.4-7.1
<i>Lolium perenne</i>	Patel & Cooper (1961)	Seasonal	5-10
<i>Cenchrus ciliaris</i>	Burt (1968)	Seasonal	2-8

The time course of the appearance of successive leaves on the main stems of 40 plants of *Lolium perenne* cv. Grasslands Ruanui grown in a glasshouse at Adelaide is shown in Figure 1. It can be seen that from leaf 5 to leaf 18 the rate of leaf appearance is constant despite seasonal changes in light energy, temperature and photoperiod during the course of the experiment.

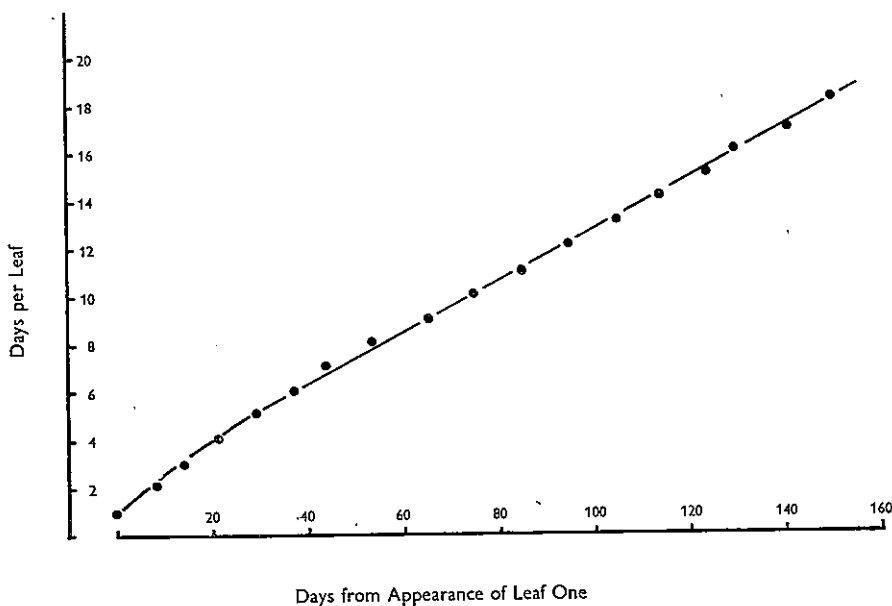


FIGURE 1

The time course of leaf appearance on the main stem of single plants of *Lolium perenne* grown in a glasshouse at Adelaide May–August 1968.

Figure 2 shows data obtained by a number of authors for rate of leaf appearance in *L. perenne* grown at temperatures of 18–23°C but at different levels of visible light energy standardised in  $\text{cal cm}^{-2} \text{day}^{-1}$ . There is reasonable agreement between authors to show that over the range 20–160  $\text{cal cm}^{-2} \text{day}^{-1}$  there is only a small increase in the rate of leaf appearance. Discontinuity is evident at the low energy end in that the rate obtained by Patel and Cooper (1961) is lower than expected from projection from the rest of the data. However it is possible that the relation takes the course of the dotted line in the figure—a rapid decrease in rate occurs as low energy inputs are approached.

The average rate of leaf appearance that may be calculated from Figure 1 is about 10 days per leaf and the energy input over the experimental period averaged 70  $\text{cal cm}^{-2} \text{day}^{-1}$ . This does not agree well with Figure 2 as the temperature during the experiment was lower than the average 20°C on which the data for Figure 2 was based.

Cooper and McWilliam (1966) showed that the rate of leaf appearance in *Phalaris tuberosa* increases with increase in light energy. Burt (1968) grew *Cenchrus ciliaris* in the field at different times of the year and found that the rate of leaf appearance increased with the amount of light energy up to the highest level of about 340  $\text{cal cm}^{-2} \text{day}^{-1}$  visible light.

Temperature exerts a marked effect on the rate of leaf appearance in some species, e.g. wheat (Friend *et al.* 1962), paspalum (Mitchell 1955); but in many there appears to be a relatively broad optimum response to this factor (Mitchell 1953; Beever and Cooper 1964; Templeton *et al.* 1961; Taylor, Cooper and Treharne 1968; Hussey 1963). Burt (1968) suggests that response to high tempera-

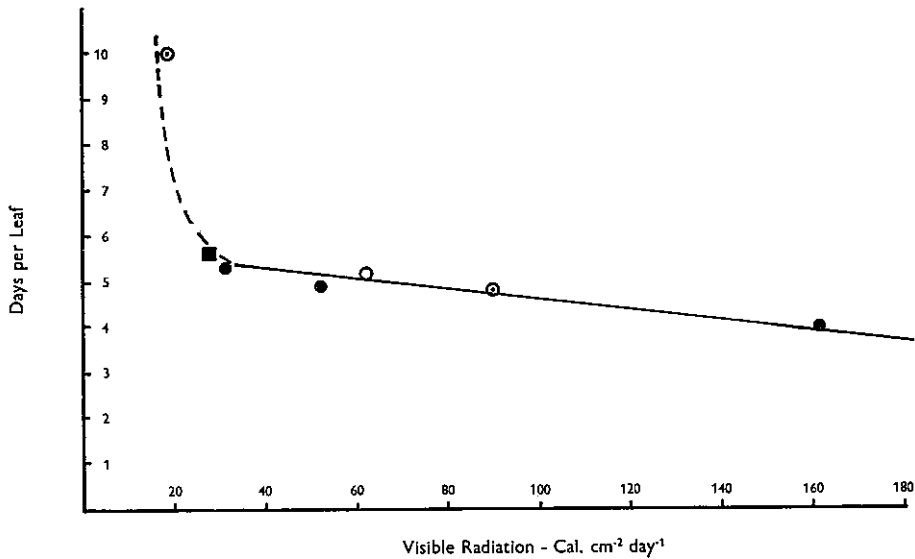


FIGURE 2

Rate of leaf appearance (days per leaf) in *Lolium perenne* as a function of incident visible light energy.

- Silsbury (original data)
- Mitchell (1953)
- Beevers and Cooper (1964)
- ⊙ Patel and Cooper (1961)

ture may be limited by the relatively low flux densities (usually less than 100 watt m<sup>-2</sup>) obtained from artificial sources. Mitchell (1953) found that the rate of leaf appearance in *L. perenne* was relatively unaffected by a temperature rise from 15° to 28°C at 75 watt m<sup>-2</sup> (10 hr daylength and photoperiod). Additional data for this species given in Table 2 confirms Mitchell's results in that response to temperature is similar at the three light flux densities of 22, 38 and 117 watt m<sup>-2</sup>.

TABLE 2

Rate of leaf appearance (days per leaf) in *Lolium perenne* grown as seedling plants at three levels of visible light energy (16 hr day) and at three temperatures

Visible Light Energy watt m <sup>-2</sup>	Temperature °C		
	10	20	30
22	9.5	5.3	5.3
38	7.3	4.9	4.3
117	6.2	3.9	3.9
S.E.	0.3	0.4	0.4

There is evident confusion in the literature as to the effects of photoperiod on the rate of leaf appearance. This arises partly from the frequent occurrence of an accelerating effect of long days on floral initiation and partly from a failure to dis-

tinguish between total energy and true photoperiodic effects. Anslow (1966) tentatively concluded that long photoperiods may reduce the rate of leaf appearance in several species. Cooper and McWilliam (1966) found in *Phalaris tuberosa* that the rate was independent of photoperiod. Robson (1967) did not record effects of photoperiod on the rate of leaf appearance in *Festuca arundinacea*. Humphries (1966) obtained evidence which showed that development of the primordium in *Sinapis alba* is independent of the current environment. He exposed seedlings to different photoperiodic environments for a short period and this treatment affected the rate of leaf production for the next 20 weeks.

Langer (1966) and Anslow (1966) could find little evidence of response in the rate of leaf appearance to variation in nutrient supply.

### (iii) *Post-appearance growth*

In most studies of leaf expansion increase in lamina dimensions or increase in area are measured, these attributes being much more readily determined than increase in lamina dry weight. Lamina area and lamina weight are often highly correlated (Robinson and Massengale 1967; Baker and Jung 1968; Silsbury unpub.), but it is nevertheless hazardous to extrapolate from one attribute to the other under variable environmental conditions and during ontogeny.

The central problem in measuring the growth rate of a single leaf is that of variation between plants in the time of appearance of the leaf under consideration. A series of destructive harvests of samples of an emerging leaf population can provide data for the average dry weight but this will only reflect the growth rate of a single leaf if all leaves to be measured emerge together and reach maturity at the same time. Synchronous development of leaves is likely to occur only during seedling growth. For later formed leaves careful matching of time of emergence on separate plants is necessary, or some attribute reliably correlated with dry weight can be measured repetitively on the same leaf. Niffenegger, Mills and Davis (1965) have shown the leaves of barley to increase in length at a constant rate during emergence, and Baker and Jung (1968) have shown leaf length to be correlated with dry weight. Data given by Williams and Rijven (1965) for wheat show that there may be a good correlation between length and weight in some species. It is therefore possible that lamina length could provide a suitable measure of lamina dry weight although care should be taken when comparing leaves grown in different environments.

Scott (1961) found that most of the growth of a tussock was confined to the youngest leaf of a tiller. He found the rate of elongation to be relatively accurate as a measure of the dry weight gain of the whole plant. The rate of elongation showed diurnal fluctuation. This latter conclusion is supported by evidence of Allison (1963). Williams and Biddiscombe (1965) used recording instruments to measure extension growth of grass tillers under outdoor conditions. Variation in the rate of extension growth was high; it was highly correlated with temperature while poorly correlated with light energy.

A number of aspects of the growth of the grass leaf are illustrated in Figure 3 which shows growth curves of leaf number four on the main stem of perennial ryegrass grown at 20°C and 30°C with visible light flux densities of 22, 38 and 117 watt m<sup>-2</sup>. Leaf four showed synchronous development in these experiments and was initiated on the apex after exposure to the specified conditions.

The general pattern of dry matter increase of the emerging leaf lamina can be seen to be S-shaped with a substantial middle phase when growth is essentially linear with time. This pattern is largely to be expected as the ryegrass lamina is a long, narrow, rectangular structure. Effects of temperature and light energy on the time of leaf appearance are readily apparent. Of more immediate interest is that the growth rate of the lamina appears to be independent of the level of radiation and is only reduced at low temperature. Linear regressions of lamina dry weight on time show



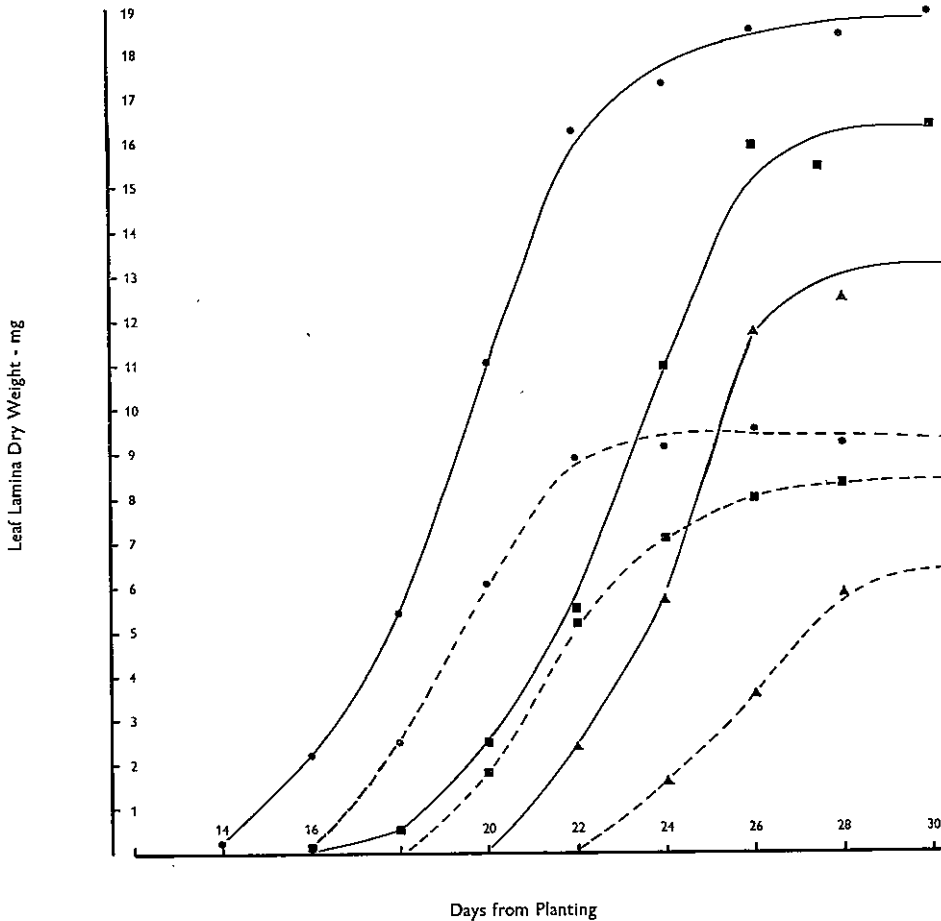


FIGURE 3

Growth curves of leaf 4 of *Lolium perenne* grown at 20°C (continuous line) and at 30°C (broken line) under 117 (closed circles) 38 (squares) and 22 (triangles) watt m<sup>-2</sup> visible light energy for 16 hr each day

no significant effect of light energy level for leaf four and also for leaf five. This suggests that the leaf is not dependent for growth on its own supply of photosynthate and that an amount adequate for this purpose can be supplied by the rest of the plant. Measurements of rates of photosynthesis of the ryegrass lamina show that when leaf five has reached half its final area at 20°C and 117 watt m<sup>-2</sup>, the amount of carbohydrate synthesised by the exposed portion would be only about one third of that required for growth. Thus, in contrast to the cucumber leaf which exports sucrose during expansion (Hopkinson 1964) the ryegrass leaf appears to be an importer of carbohydrate during the major part of its growth. It may be that even at low levels of light energy the supply of assimilate to the leaf meristem from the rest of the plant is adequate and it is for this reason that the growth rate of the single lamina is relatively independent of the prevailing light energy.

Some support for this view is provided by work of Forde (1965) who found that when C<sup>14</sup>O<sub>2</sub> was fed to young ryegrass leaves little or no movement occurred into the remainder of the plant. Forde considered that this could be due to all the assimilate being used completely by the young leaf or that there was some blockage

of carbohydrate movement out of the leaf. He produced anatomical evidence to show that the translocation pathway across the meristematic region could become temporarily blocked during leaf development. Milthorpe (1959) found that the level of radiation had no effect on the *rate* of expansion (increase in area) of the individual cucumber leaf.

#### (iv) Leaf Size

It may be readily observed that the final size obtained by a leaf is related to the level of insertion on the shoot (Borrill 1959; Saha 1960). Increase in the size of successive laminae up the shoot is associated with increase in size of the leaf initial and the dimensions of the shoot apex (Abbe and Phiney 1951; Yamazaki 1963), but the apical meristem does not always increase in size as the plant develops (Allsopp 1965) and final leaf size does not always parallel increasing apex size (Humphries 1967). Forde (1966b) found that variation in the size of the apical meristem of ryegrass brought about by defoliation had little effect on the size of the leaves produced from it.

Blackman (1956, 1961) drew attention to the plasticity of leaf sizes in many species. Jones (1956) has shown that great variation in leaf shape can be induced environmentally.

Responses in leaf size to light energy are often recorded in shading experiments and it is unfortunate that in many of the studies reported the absolute energy inputs both as peak flux density and total amount were not recorded. More precise data is available from controlled environments although these suffer from the disadvantages of relatively low light energy levels and often unspecified spectral composition. The latter may be important for processes such as leaf unfolding which are controlled by the phytochrome system (Virgin 1962).

Light energy and temperature influence the dimensions of the mature lamina, its area and its dry weight. No clear picture can at present be drawn to show responses in these attributes to absolute energy units expressed either as flux density or total daily amount. As a broad generalisation it seems that responses are greatest below about 200 watt m<sup>-2</sup> visible light energy. Species differ in the detail of their responses but certain general trends are clear.

Decreased light energy usually results in increased lamina area although an optimum relation with this factor sometimes occurs (Newton 1963; Dale 1965; Friend 1966). The increased area is usually associated with increased lamina length, 'low' light grown leaves being longer, narrower and thinner than those grown under 'high' light (Friend 1966). Forde (1966) found 10- and 20-fold differences in lamina length of ryegrass and cocksfoot grown under different shading and temperature regimes. Friend (1966) attributed the increased length of wheat leaves to increased cell division along the length of the lamina. Evans (1964) and Forde (1966a) found the epidermal cell length of ryegrass to be increased by shading.

Leaf area often also shows an optimum relation with temperature (Cooper 1964; Cooper and McWilliam 1966; Friend 1966). Marked interactions between the effects of temperature and light energy on leaf area in *Salvinia natans* have been shown by Blackman (1961). Wheat leaves become narrower and thinner with increased temperature (Friend 1966).

Data on variation in leaf weight induced by light energy and temperature are more difficult to find in the literature. Mitchell (1954, 1956) found leaf weight of ryegrass to decrease with decrease in light energy; it is believed that this response may be a general one.

Leaf size data for the fourth leaf of *L. perenne* grown at three levels of light energy and at two temperatures given in Table 3, illustrate the nature and magnitude of the responses possible in one species. A rise in temperature from 20 to 30°C reduced both lamina area and lamina weight; at both temperatures decreased radia-

tion increased area relatively more than it decreased dry weight. Response to light energy in this species appears to vary with the temperature.

TABLE 3  
Final dry weights and areas obtained for leaf 4 of *Lolium perenne* grown at two temperatures and at three levels of visible light energy (16 hr day length)

Light Energy watt m <sup>-2</sup>	Weight — mg		Area — cm <sup>-2</sup>	
	20°C	30°C	20°C	30°C
22	55.4(4.8)	28.2(2.4)	24.7(1.2)	12.9(0.6)
38	65.8(3.8)	38.5(3.1)	21.7(1.2)	13.4(0.4)
117	73.3(7.5)	33.9(3.7)	15.0(0.8)	8.2(0.6)

Standard errors are given in parenthesis.

Perhaps the most striking as well as the most commonly demonstrated response in leaf size attributes to variation in light energy is a marked increase with decrease in radiation in the ratio between leaf area and leaf weight, the specific leaf area of Hughes (1959b). Specific leaf area provides a quantitative measure of the 'sun'-'shade' effect of classical literature and its response to radiation is documented in the results of Blackman (1956, 1961), Hughes (1959a), Templeton *et al.* (1961), Hughes and Evans (1962), Bean (1964), Dale (1965), Friend *et al.* (1965), Cooper (1967), and many others. In perennial ryegrass grown at 20°C specific leaf area increases from about 200 cm<sup>2</sup> g<sup>-1</sup> at 120 watt m<sup>-2</sup> to 500 cm<sup>2</sup> g<sup>-1</sup> at 20 watt m<sup>-2</sup>, i.e. at the lower light energy level unit dry weight is spread over about 2.5 times the area. The morphological basis of this response is not clearly known but it is believed to be associated with increase in cell size (see above) and with a decrease in cell wall thickness. Hughes (1959a) found that sun and shade leaves of *Impatiens parviflora* were fundamentally similar in meristematic activity and that differences in structure at maturity lay in the greater expansion of the shade leaf. The physiological basis of the response is also not clearly known but it could be related to increased auxin levels in the leaf as a consequence of reduced destruction of that substance by photo-oxidation.

Silsbury (1967) has shown the light saturated rate of photosynthesis in *Lolium* to be inversely related to the specific leaf area and it is of interest to see to what extent the increased area of a low light grown leaf can compensate for reduced photosynthetic rate. A mature fourth leaf of *L. perenne* grown at 117 watt m<sup>-2</sup> could be expected to fix (at normal CO<sub>2</sub> concentration) about 0.11 mg CO<sub>2</sub> hr<sup>-1</sup>. A similar leaf grown at 22 watt m<sup>-2</sup> on the other hand would fix about 0.06 mg CO<sub>2</sub> hr<sup>-1</sup>. Thus although net photosynthesis is reduced from about 30 to about 10 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>, the total CO<sub>2</sub> fixed by the whole leaf per hour is reduced only by about one half.

Little information is available concerning the specific effects of mineral nutrition on leaf size (Langer 1966), although it is well known that the total leaf lamina area is markedly responsive to the level of nutrient supply.

### GROWTH AT THE APEX

Although a great deal is known about organisation at the shoot apex (Wardlaw 1965b), there still appears to be much to learn about apex physiology with respect both to its internal metabolism and responses to environmental factors. Wardlaw (1965a) takes an essentially holistic view of the apex and there is little doubt that the initiation of new primordia and their growth into mature leaves make an interacting system of great complexity. Cutter (1965) considers that the growth of new

primordia is controlled by the apex and existing primordia and that there is 'probably a complex combination of hormonal relationships and requirements for nutrients and other substances' mediated through the organisation and physiological activity of the apex as a whole and the distribution of growth within it.

The importance of the apical meristem as the primary controlling region of the shoot can not be too highly emphasised. Growth of each vegetative grass tiller in the absence of internode elongation is largely a matter of the initiation and expansion of leaves. The rate of growth of a single tiller is the outcome of a number of processes occurring at the apex.

Perhaps the most important feature of growth at the vegetative apex is that leaves are initiated and expanded in a strict linear sequence. The rate of initiation is related to rates of cell division which may be slower than in other kinds of meristematic tissue (Clowes 1961). In general, the rate of initiation appears to be relatively independent of the environment. Responses to temperature occur, but over the range 15-30°C these are comparatively small. Positive responses to light energy are also known but a wide range of energy inputs appears to have fairly small effects on the plastochron and on the rate of leaf appearance. It may be that the absolute demand for nutrients by the apex is small and the existence of a priority system always ensures that it has an adequate supply of assimilate and mineral nutrients. However, as Williams (1960) has pointed out, there is abundant scope for limitation in the supply of essential requirements as transport to the site is by diffusion.

Milthorpe (1959), Milthorpe and Newton (1963) and Newton (1963) have interpreted environmental effects on leaf growth of the cucumber in terms of competition between leaf primordia for assimilates and mineral nutrients. Caution should be adopted in applying their results to other species as it appears that during early growth the cucumber produces a large number of leaves at the apex but only a relatively small proportion of these unfold and actually expand. Friend *et al.* (1962) in their study of leaf growth in wheat regarded the morphogenetic effects of temperature, light intensity and photoperiod as being more probably related to changes in the concentration of growth substances.

The existence of a strict hierarchical relation between the growth of one leaf and that of its neighbours has been stressed by Robson (1967). He found the duration of growth of any leaf to be closely correlated with the interval between the appearance of successive laminae, a sequence occurring so that only one lamina expands on a shoot at any time. Clearly the duration of growth of each leaf and the start of growth of the next leaf must be synchronised. The physiological basis for this association is not clear but competitive effects could be involved. Cooper and Edwards (1961) found in *Lolium* that where selection for rate of leaf appearance was effective, smaller laminae were produced. Milthorpe (1959) found in the cucumber that conditions which induced a high rate of unfolding of leaves favoured small individual areas at maturity. He suggested that this was due to increased competition for mineral nutrients but in a later paper (Milthorpe and Newton 1963) it was shown that, provided the nutrient supply to the plant was high, the ultimate areas of individual leaves were greater the higher the radiation; the rate of leaf production also increased with increased radiation. Friend *et al.* (1962) found with wheat that increase in light intensity from 200-1750 lumen ft<sup>-2</sup> increased the rates of primordial initiation, emergence, and expansion and also increased final leaf areas at maturity. Cooper and Edwards' results may have been due to the use of relatively low levels of light energy.

The suggestion made in this paper that the growth rate of the emerging lamina is relatively independent of the level of light energy should be interpreted with caution. It could well be that the amount of assimilate produced by a leaf constitutes only a relatively small proportion of that required for its growth, but the total supply

to the leaf from the rest of the plant will depend on the leaf area already expanded and the level of light energy incident on the whole plant.

Gregory (1956) summarised what he considered to be the (internal) determinants of leaf size as: (i) the number of primordial cells; (ii) the rates of cell division; (iii) duration of the phase of cell division; and (iv) size of the mature cells. Gregory was probably thinking mainly of the dicotyledon leaf and apparently did not subscribe to what was then the more common view of leaf growth consisting of a stage of cell division followed by one of cell enlargement. It seems reasonable that these four sequential aspects of leaf growth also could provide a convenient basis for the examination of the growth of the grass leaf.

The contribution made by each 'partial process' could well differ between genotypes and each could respond to environment in a different way. It is thus unlikely that environmentally induced variation in leaf size can be wholly associated with either variation in cell number or with that in cell size. Cell division is now considered to be pre-eminent during the growth of the dicotyledon leaf (Humphries and Wheeler 1963; Humphries 1967), but the position with the grasses is by no means clear. The rate of cell division at the intercalary meristems is likely to respond to temperature, nutrient supply and to growth regulators. The supply of assimilate to the developing leaf could be limited by the lack of vascular connections at early stages (Sharman and Hitch 1967).

It is clear that at present the environmental control of leaf size in the grasses can be sketched only in the briefest terms. A major problem is to resolve how the process of cell division and the final size attained by the cells are separately influenced by both internal mechanisms and the level of external factors. The role of the size of the stem apex as a determinant of leaf size is also not clear. It is evident that the final dry weight attained by a leaf is a function of both age and environment and that variation of this attribute in response to environment represents a component of the response in dry matter yield.

### GROWTH OF THE SINGLE TILLER

The initiation of leaves in a strict linear time sequence, expansion in a hierarchical order by elongation rather than isodiametric growth and the attainment of a limited size by each leaf suggest that the growth of a single vegetative tiller should follow an essentially linear trend with time. If each leaf attained the same final size we would expect very close agreement with a linear growth curve but increases in leaf size with the level of insertion will contribute curvilinearity to the time trend. Initially this will be large as the proportionate increase in leaf size up the shoot decreases with the level of insertion.

Constancy in the amount of dry matter produced per day by a single tiller of several grasses grown under controlled conditions has been proposed by Mitchell (1955, 1956). In a longer-term study in a glasshouse at Adelaide, perennial ryegrass plants were grown singly in large pots with favourable fertiliser treatment, May through August. The dry weights of the main stem and tillers one and two were determined by harvesting all leaves produced by those tillers at weekly intervals. Figure 4 shows that the growth rates of each tiller were near constant for several weeks.

Constancy in the growth rate of a single tiller is believed to be relevant to the growth pattern displayed by grass swards. Tiller number per unit area in an established sward may fluctuate seasonally but is often fairly stable during periods of uninterrupted growth (Mitchell and Glenday 1958; Langer 1958; Langer, Ryle and Jewiss 1964). When this occurs leaf production will be restricted to a constant number of sites and at each of these growth will also be constant. The growth rate of the sward can thus be expected to be constant. Ample evidence to support this view is provided by data of Brougham (1955, 1956), Bean (1964), Alberda (1965) and Sibma (1968). Indeed it can be proposed as a general thesis that a grass sward will,

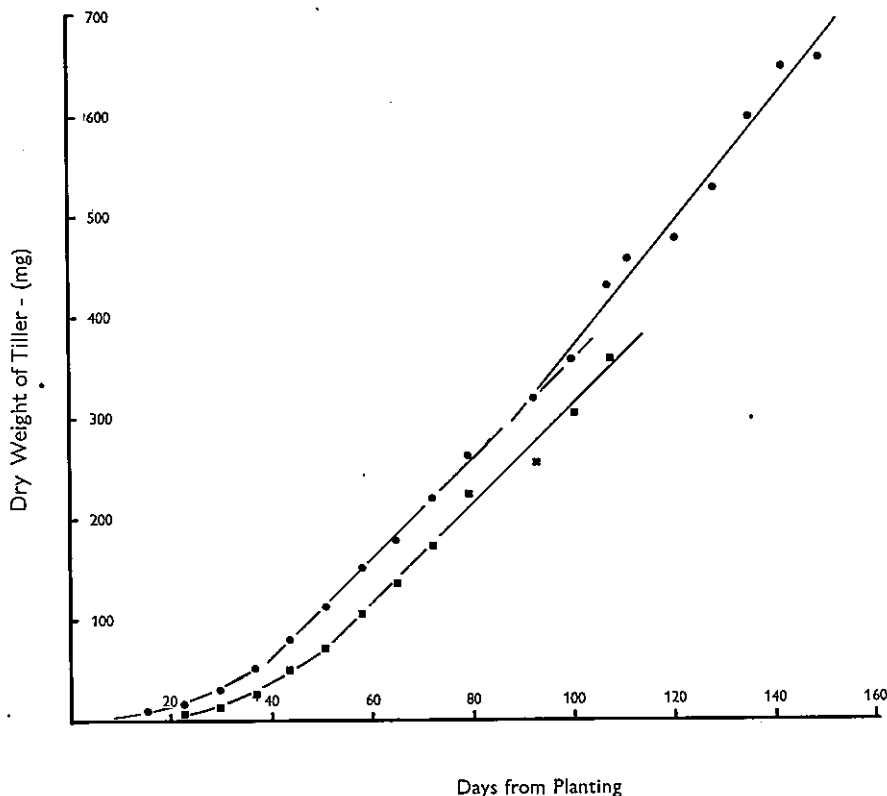


FIGURE 4

Dry matter growth curve of the main stem (closed circles) and tillers one and two (squares) of *Lolium perenne* grown in a glasshouse at Adelaide May–August 1968.

at least during the short term in a 'normal' season, show a constant growth rate once complete light interception has been achieved. This is directly attributable to the suppression of tillering and the control of growth on each established tiller by the sequence of events occurring at the vegetative apex. It is as though the processes of leaf initiation and leaf extension constitute a morphological bottleneck which limits dry matter growth to a series of extension processes that are more or less self regulatory and originate as a linear function of time. In fashionable terms, each leaf constitutes a single sink for assimilate. When other sinks come into play (e.g. internode extension or tillering) a new pattern of growth occurs.

#### LEAF GROWTH IN THE COMMUNITY

Studies of leaf growth in relation to the productivity of grass swards have been concerned more with leaf growth by the community than with leaf growth in the community. The area of the total leaf lamina surface has been recorded in a great many growth experiments and dry matter growth rate related to this attribute either as net assimilation rate in the case of single plants or as crop growth rate per unit leaf area index in that of communities. Very little is known on the other hand concerning the behaviour of individual leaves within the community and how leaf

physiology is modified in response to change in environment induced by increases in plant size or by change in plant density.

Brougham (1958) has drawn attention to the rapid rate of turnover of leaves in a white clover sward. Hunt and Brougham (1966) obtained data for an Italian ryegrass pasture which showed that the actual amounts of young leaf, mature leaf, sheath, and senescent and dead material were fairly constant for the major part of the growing season. They concluded that one third of the canopy was replaced every 18-20 days under the conditions of this experiment.

Bean (1964) studied cocksfoot swards grown at 100, 60 and 40% of the natural daylight. He found the rate of leaf production and the rate of senescence of mature leaves and therefore the number of leaves per tiller to be unaffected by the light regime.

Kloot (1967) established ryegrass plants at densities of 27, 108, 432 and 1728 plants  $m^{-2}$  (D1, D2, D3, D4), and followed the dry weight attributes of the first formed leaves for 60 days from plant emergence. The first attribute to be affected by density was time (rate) of leaf appearance. This was first evident at plastochron 4. Leaf 4 at all densities reached the same final size and grew at nearly the same rate in each treatment. As leaf 5 emerged its growth rate at D4 was very much slower than at D1 although this leaf at all densities appeared to reach the same final size. Leaf 6 was not followed to full emergence in all treatments. Full emergence had occurred at D1 before it had even appeared at D4. Its growth rate and probably its final size appeared to be markedly affected by density.

It is clear that there is still much to be learned about leaf growth in grass communities, but it is believed that what is already known of the biology of the single lamina can provide a useful basis for understanding the role of leaf growth in grass swards.

#### REFERENCES

- ABBE, E. C. and PHINNEY, B. O. (1951)—The growth of the shoot apex in maize: external features. *Amer. J. Bot.* **38**: 737-744.
- ALBERDA, Th. (1965)—The influence of temperature, light intensity and nitrate concentration on dry-matter production and chemical composition of *Lolium perenne* L. *Neth. J. Agric. Sci.* **13**: 335-360.
- ALLSOPP, A. (1965)—Heteroblastic development in cormophytes. *Encyclopedia of Plant Physiology* Vol XV: 1172-1221.
- ALLISON, R. M. (1963)—Phasic growth of the leaves of cereals. *Nature* **198**: 809-810.
- ANSLow, R. C. (1966)—The rate of appearance of leaves on tillers of the Gramineae. *Herb. Abst.* **36**: 149-155.
- ARBER, A. (1934)—'The Gramineae: A study of cereal bamboo and grass.' Cambridge University Press.
- ASKENASY, A. (1880)—Ueber eine neue methode, um die vertheilung der wachstumsintensität in wachsenden theilen zu bestimmen. *Verhandl. Naturhist.—Med. Ver Heidelberg (N.F.2.)* **2**: 70-153.
- ASPINALL, D. (1966)—Effects of daylength and light intensity on growth of barley. IV. Genetically controlled variation in response to photoperiod. *Aust. J. Biol. Sc.* **19**: 517-34.
- ASPINALL, D. and PALEG, L. G. (1963)—Effects of daylength and light intensity on growth of barley. I Growth and development of apex with a fluorescent light source. *Bot. Gaz.* **124**: 429-437.
- AVERY, George S. (1933)—Structure and development of the tobacco leaf. *Amer. J. Bot.* **20**: 565-592.

- BAKER, B. S. and JUNG, G. A. (1968)—Effect of environmental conditions on the growth of four perennial grasses. I. Response to controlled temperature. *Agron. J.* **60**: 155-158.
- BARNARD, C. (1964)—Form and structure. In 'Grasses and Grasslands' Ed. Barnard (McMillan): pp. 47-72.
- BEAN, E. W. (1964)—The influence of light intensity upon the growth of an S.37 Cocksfoot (*Dactylis glomerata*) sward. *Annal. Bot. (N.S.)* **28**: 427-443.
- BEEVERS, L. and COOPER, J. P. (1964)—Influence of temperature on growth and metabolism of ryegrass seedlings. I. Seedling growth and yield components. *Crop Sci.* **4**: 139-143.
- BEGG, J. E. and WRIGHT, M. J. (1962)—Growth and development of leaves from intercalary meristems in *Phalaris arundinacea*. *Nature* **194**: 1097-1098.
- BLACKMAN, G. E. (1956)—Influence of light and temperature on leaf growth. In 'The Growth of Leaves', Ed. Milthorpe (Butterworths). Proc. 3rd Easter School in Agric. Science, University of Nottingham. pp. 151-169.
- BLACKMAN, G. E. (1961)—Responses to environmental factors by plants in the vegetative stage. In 'Growth in Living Systems', Ed. Zarrow (Basic Books), pp. 525-556.
- BORRILL, M. (1959)—Inflorescence initiation and leaf size in some Gramineae. *Ann. Bot.* **23** (N.S.): 217-27.
- BROUGHAM, R. W. (1955)—A study in rate of pasture growth. *Aust. J. Agric. Res.* **6**: 804-812.
- BROUGHAM, R. W. (1956)—Effect of intensity of defoliation on regrowth of pasture. *Aust. J. Agric. Res.* **7**: 377-387.
- BROUGHAM, R. W. (1958)—Leaf development in swards of white clover (*Trifolium repens* L.) *New Zeal J. Agric. Res.* **1**: 707-18.
- BURT, R. L. (1968)—Growth and development of buffel grass (*Cenchrus ciliaris*). *Aust. J. Expt. Ag. An. Hus.* **8**: 712-719.
- CLOWES, F. A. L. (1961)—'Apical Meristems'. (Blackwell).
- COOPER, C. S. (1967)—Relative growth of alfalfa and birdsfoot trefoil seedlings under low light intensity. *Crop Sc.* **7**: 176-178.
- COOPER, J. P. (1964)—Climatic variation in forage grasses. I. Leaf development in climatic races of *Lolium* and *Dactylis*. *J. Appl. Ecol.* **1**: 45-61.
- COOPER, J. P. and EDWARDS, K. J. R. (1961)—The genetic control of leaf development in *Lolium*. I. Assessment of genetic variation. *Heredity* **16**: 63-82.
- COOPER, J. P. and McWILLIAM, J. R. (1966)—Climatic variation in forage grasses II. Germination, flowering and leaf development in Mediterranean populations of *Phalaris tuberosa*. *J. Appl. Ecol.* **3**: 191-212.
- CUTTER, E. G. (1965)—Recent experimental studies of the shoot apex and shoot morphogenesis. *Bot. Rev.* **31**: 7-113.
- DALE, J. E. (1965)—Leaf growth in *Phaseolus vulgaris*. 2. Temperature effects and the light factor. *Ann. Bot. (N.S.)* **29**: 293-308.
- DAVIDSON, J. L. and MILTHORPE, F. L. (1966)—The effect of defoliation on the carbon balance in *Dactylis glomerata*. *Annal Bot. (N.S.)* **30**: 185-198.
- ERICKSON, R. O. (1960)—Nomogram for the plastochron index. *Amer. J. Bot.* **47**: 350-351.
- ESAU, K. (1943)—Ontogeny of the vascular bundle in *Zea mays*. *Hilgardia* **15**: 327-368.
- ETTER, A. G. (1951)—How Kentucky bluegrass grows. *Ann. Missouri Bot. Gard.* **38**: 293-367.
- EVANS, L. T., WARDLAW, I. F. and WILLIAMS, C. N. (1964)—Environmental control of growth. In 'Grasses and Grasslands' Ed. Barnard (McMillan) pp. 102-125.



- EVANS, M. W. and GROVER, F. O. (1940).—Developmental morphology of the growing point of the shoot and inflorescence in grasses. *J. Agric. Res.* **61**: 481-520.
- EVANS, P. S. (1964).—A comparison of some aspects of the anatomy and morphology of Italian ryegrass (*Lolium multiflorum* Lam.) and perennial ryegrass (*L. perenne* L.) *New Zeal. J. Bot.* **2**: 120-130.
- FORDE, B. J. (1965).—Differentiation and continuity of the phloem in the leaf intercalary meristem of *Lolium perenne*. *Americ. J. Bot.* **52**: 953-961.
- FORDE, B. J. (1966a).—Effect of various environments on the anatomy and growth of perennial ryegrass and cocksfoot. 1. Leaf growth. *New Zeal. J. Bot.* **4**: 455-468.
- FORDE, B. J. (1966b).—Effect of various environments on the anatomy and growth of perennial ryegrass and cocksfoot. 2. Apical and sub-apical growth. *New Zeal. J. Bot.* **4**: 469-478.
- FRIEND, D. J. C. (1966).—The effects of light and temperature on the growth of cereals. In 'The Growth of Cereals and Grasses' Ed. Milthorpe and Ivins (Butterworths). Proc. 12th Easter School in Agric. Sc., University of Nottingham. pp. 181-199.
- FRIEND, D. J. C., HELSON, V. A. and FISHER, J. E. (1962).—Leaf growth in Marquis wheat, as regulated by temperature, light intensity, and daylength. *Canad. J. Bot.* **40**: 1299-1311.
- FRIEND, D. J. C., HELSON, V. A. and FISHER, J. E. (1965).—Changes in the leaf area ratio during growth of Marquis wheat, as affected by temperature and light intensity. *Canad. J. Bot.* **43**: 15-28.
- FULFORD, R. M. (1965).—The morphogenesis of apple buds. I. The activity of the apical meristem. *Ann. Bot. (N.S.)* **29**: 167-180.
- GREGORY, F. G. (1956).—General aspects of leaf growth. In 'Growth of Leaves' Ed. Milthorpe. pp. 3-17 (Butterworths).
- HAMILTON, H. H. (1948).—A developmental study of the apical meristem in four varieties of *Avena sativa* grown at two temperatures. *Amer. J. Bot.* **35**: 656-665.
- HOPKINSON, J. M. (1964).—Studies on the expansion of the leaf surface. IV. The carbon and phosphorous economy of a leaf. *J. Exp. Bot.* **15**: 125-137.
- HUGHES, A. P. (1959a).—Effects of the environment on leaf development in *Impatiens parviflora* D.C. *J. Linn. Soc. Lond. Bot.* **LVI**: 161-165.
- HUGHES, A. P. (1959b).—Plant growth in controlled environments as an adjunct to field studies. *J. Agric. Sc.* **53**: 247-259.
- HUGHES, A. P. and EVANS, G. C. (1962).—Plant growth and the aerial environment II. Effects of light intensity on *Impatiens parviflora*. *New Phytol.* **61**: 154-174.
- HUMPHRIES, E. C. (1966).—Internal control of rate of leaf production in sugar beet. *Physiol. Plant.* **19**: 827-829.
- HUMPHRIES, E. C. (1967).—Leaf growth of white mustard (*Sinapis alba*) in different environments. *Planta* **72**: 223-231.
- HUMPHRIES, E. C. and FRENCH, S. A. W. (1965).—A growth study of sugar beet treated with gibberellic acid and (2-chloroethyl) trimethylammonium chloride (CCC). *Ann. Appl. Biol.* **55**: 159-173.
- HUMPHRIES, E. C. and WHEELER, A. W. (1963).—The physiology of leaf growth. *Ann. Rev. Plant Physiol.* **14**: 385-410.
- HUNT, L. A. and BROUGHAM, R. W. (1966).—Some aspects of growth in an un-defoliated stand of Italian ryegrass. *J. Appl. Ecol.* **3**: 21-28.
- HUSSEY, G. (1963).—Growth and development in the young tomato. I. The effect of temperature and light intensity on growth of the shoot apex and leaf primordia. *J. Exp. Bot.* **14**: 316-25.

- JEWISS, O. R. (1966)—Morphological and physiological aspects of growth of grasses during the vegetative phase. In 'Growth of Cereals and Grasses' Ed. Milthorpe, Ivins (Butterworths). Proc. 12th Easter School in Agric. Science, University of Nottingham. pp. 39-54.
- JONES, H. (1956)—Morphological aspects of leaf expansion, especially in relation to changes in leaf form. In 'Growth of Leaves' Ed. Milthorpe (Butterworths). Proc. 3rd Easter School in Agric. Science, University of Nottingham. pp. 93-106.
- KLOOT, P. M. (1967)—Effects of heavy shading and density on the vegetative development and morphology of perennial ryegrass (*Lolium perenne* L.) Honours Thesis, University of Adelaide.
- LANGER, R. H. M. (1958)—A study of growth in swards of timothy and meadow fescue. I. Uninterrupted growth. *J. Agric. Sci.* **51**: 347-352.
- LANGER, R. H. M. (1966)—Mineral nutrition of grasses and cereals. In 'The Growth of Cereals and Grasses' Ed. Milthorpe and Ivins (Butterworths). Proc. 12th Easter School in Agric. Sciences, University of Nottingham. pp. 213-226.
- LANGER, R. H. M., RYLE, S. M. and JEWISS, O. R. (1964)—The changing plant and tiller populations of timothy and meadow fescue swards. I. Plant survival and the pattern of tillering. *J. Appl. Ecol.* **1**: 197-208.
- LAUDE, H. M. (1953)—Nature of summer dormancy in perennial grasses. *Bot. Gaz.* **114**: 284-292.
- MILTHORPE, F. L. (1959)—Studies on the expansion of the leaf surface. I. The influence of temperature. *J. Exp. Bot.* **10**: 233-249.
- MILTHORPE, F. L. and NEWTON, P. (1963)—Studies of the expansion of the leaf surface. III. The influence of radiation on cell division and leaf expansion. *J. Exp. Bot.* **14**: 483-95.
- MITCHELL, K. J. (1953)—Influence of light and temperature on the growth of ryegrass (*Lolium* spp.) I. Pattern of vegetative development. *Physiol. Plant.* **6**: 21-46.
- MITCHELL, K. J. (1954)—Growth of pasture species. I. Short rotation and perennial ryegrass. *New Zealand J. Sci. Tech.* 'A'. **36**: 193-206.
- MITCHELL, K. J. (1955)—Growth of pasture species II. Perennial ryegrass (*Lolium perenne*), cocksfoot (*Dactylis glomerata*) and paspalum (*Paspalum dilatatum*). *New Zeal. J. Sc. Tech.* **A**: **37**: 8-26.
- MITCHELL, K. J. (1956)—Growth of pasture species under controlled environment I. Growth at various levels of constant temperature. *New Zeal. J. of Sci. Tech.* **A**: **38**: 203-216.
- MITCHELL, K. J. and GLENDAY, A. C. (1958)—The tiller population of pastures. *New Zeal. J. Agric. Res.* **1**: 305-318.
- MORTON, A. G. and WATSON, D. J. (1948)—A physiological study of leaf growth. *Annal. Bot. (N.S.)* **12**: 281-310.
- McWILLIAM, J. R. (1968)—The nature of the perennial response in Mediterranean grasses. II. Senescence, summer dormancy and survival in phalaris. *Aust. J. Agric. Res.* **19**: 397-409.
- NEWTON, P. (1963)—Studies on expansion of the leaf surface II. The influence of light intensity and day length. *J. Exp. Bot.* **14**: 458-82.
- NIFFENEGGER, D., MILLS, I. K. and DAVIS, D. J. (1965)—Effects of barley stripe mosaic virus upon growth of infected barley plants. *Crop Sc.* **5**: 227-229.
- PALEG, L. G., and ASPINALL, D. (1964)—Effects of daylength and light intensity on growth of barley. II. Influence of incandescent light on apical development. *Bot. Gaz.* **125**(3): 149-155.

- PATEL, A. S. and COOPER, J. P. (1961)—The influence of seasonal changes in light energy on leaf and tiller development in ryegrass, timothy and meadow fescue. *Brit. Grassl. Soc. J.* **16**: 299-308.
- ROBSON, M. J. (1967)—A comparison of British and North African varieties of tall fescue, (*Festuca arundinacea*). I. Leaf growth during winter and the effects on it of temperature and day length. *J. Appl. Ecol.* **4**: 475-484.
- ROBINSON, C. D. and MASSENGALE, M. A. (1967)—Use of area-weight relationship to estimate leaf area in alfalfa (*Medicago sativa* L. cultivar 'Moapa'). *Crop Sc.* **7**: 394-395.
- SAHA, B. (1960)—Relative lengths of leaf sheath and blade with reference to the developmental stages of the rice plant. *Nature* **187**: 259-260.
- SCHWABE, W. W. (1963)—Morphogenetic responses to climate. In 'Environmental Control of Plant Growth' Ed. Evans (Academic Press). pp. 311-336.
- SCOTT, D. (1961)—Methods of measuring growth in short tussocks. *New Zeal. J. Agric. Res.* **4**: 282-5.
- SHARMAN, B. C. (1942)—Developmental anatomy of the shoot of *Zea mays* L. *Ann. Bot. (N.S.)* **6**: 245-82.
- SHARMAN, B. C. (1945)—Leaf and bud initiation in the Gramineae. *Bot. Gaz.* **106**: 269-289.
- SHARMAN, B. C. and HITCH, P. A. (1967)—Initiation of procambial strands in leaf primordia of bread wheat, *Triticum aestivum* L. *Ann. Bot. (N.S.)* **31**: 229-243.
- SIBMA, L. (1968)—Growth of closed green crop surfaces in The Netherlands. *Neth. J. Agric. Sc.* **16**: 211-216.
- SILSBURY, J. H. (1964)—Tiller dynamics, growth, and persistency of *Lolium perenne* L. and of *Lolium rigidum* Gaud. *Aust. J. Agric. Res.* **15**: 9-20.
- SILSBURY, J. H. (1965)—Interrelations in the growth and development of *Lolium* I. Some effects of vernalization on growth and development. *Aust. J. Agric. Res.* **16**: 903-13.
- SILSBURY, J. H. (1966)—Interrelations in the growth and development of *Lolium* II. Tiller number and dry weight at low density. *Aust. J. Agric. Res.* **17**: 841-7.
- SILSBURY, J. H. (1967)—Variation among ryegrasses in rates of apparent photosynthesis. Carnegie Institution of Washington Yearbook 1967, Report of the Director, Department of Plant Biology. pp. 491-493.
- SOPER, K. and MITCHELL, K. J. (1956)—The developmental anatomy of perennial ryegrass (*Lolium perenne* L.) *New Zeal. J. Sci. & Tech. 'A'* **37**: 484-504.
- SUNDERLAND, N. (1961)—Cell division and expansion in the growth of the shoot apex. *J. Expt. Bot.* **12**: 446-57.
- TAYLOR, T. H. COOPER, J. P. and TREHARNE, K. J. (1968)—Growth response orchardgrass (*Dactylis glomerata* L.) to different light and temperature environments. I. Leaf development and senescence. *Crop Sc.* **8**: 437-440.
- TEMPLETON, W. C., MOTT, G. O., and BULA, R. J. (1961)—Some effects of temperature and light on growth and flowering of tall fescue, *Festuca arundinacea*. Schreb. I. Vegetative Development. *Crop. Sci.* **1**: 216-219.
- VIRGIN, H. I. (1962)—Light-induced unfolding of the grass leaf. *Physiol. Plant.* **15**: 380-389.
- WARDLAW, C. W. (1965a)—The morphogenetic rôle of apical meristems: fundamental aspects (illustrated by means of the shoot apical meristem). *Encyclopedia of Plant Physiology*: Vol XV: 443-451.
- WARDLAW, C. W. (1965b)—Organisation and development of the shoot. (a) The organization of the shoot apex. *Encyclopedia of Plant Physiology*: Vol XV: 966-1076.

- WILLIAMS, C. N. and BIDDISCOMBE, E. F. (1965)—Extension growth of grass tillers in the field. *Aust. J. Agric. Res.* **16**: 14-22.
- WILLIAMS, R. F. (1960)—The physiology of growth in the wheat plant. I. Seedling growth and the pattern of growth at the shoot apex. *Aust. J. Biol. Sc.* **13**: 401-428.
- WILLIAMS, R. F. (1964)—The quantitative description of growth. In 'Grasses and Grasslands' Ed. Barnard (McMillan). pp. 89-101.
- WILLIAMS, R. F. and RIJVEN, A. H. G. C. (1965)—The physiology of growth in the wheat plant. II. The dynamics of leaf growth. *Aust. J. Biol. Sc.* **18**: 721-43.
- YAMAZAKI, K. (1963)—Studies on leaf formation in rice plants. II. The development of leaves in relation to their position on a stem. *Crop Sci. Soc. Japan (Proc.)* **32**: 81-88.