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PROGRESS IN PASTURE PLANT PHYSIOLOGY

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SUMMARY

Some major achievements of pasture plant physiology are reviewed. Detailed study of growth patterns has provided an understanding of how grasses grow and how they persist in a grazed sward. Genetic variation for physiological characters is shown to offer opportunities for further progress in plant breeding. One of the effects of work on pasture productivity has been to draw attention to the accumulation of dead material, which needs to be harvested before it deteriorates, without however reducing growth rates by too frequent defoliation.

IT MAY APPEAR regrettable to start a review such as this with semantics, but it is important to be clear at the outset that plant physiology, whether dealing with pasture plants, trees or algae, is concerned with biological functions and processes. Given the task, it would be easier to classify plant physiologists according to the processes they study rather than by the plants with which they work. Only a small minority can, by any stretch of the imagination, be properly described as whole plant physiologists, and even among these it is rare to find many whose interests centre around pasture plants. It follows that the position of plant physiology as a discipline predominantly concerned with basic principles largely precludes any direct contribution towards raising productivity. Its main value appears to be to study growth and other functions in relation to the environment and in this way to define and isolate problems for further study in the field. Indeed, it is difficult to envisage purposeful and intelligent field research without the previous dissection of the many complexities encountered under natural conditions. Not only that, but every treatment imposed upon a pasture, be it grazing, treading or nutrient return, can only be interpreted by reference to the physiology of the plants affected by a whole series of changes which will have been set in motion. The role of the pasture plant physiologist then emerges as a provider of basic information, which the agronomist, pasture ecologist and plant breeder require for their endeavours to bring about improvements in forage production for the grazing animal.

GROWTH OF THE GRASS PLANT

The evolution of grasses under the impact of grazing animals has ensured that few other plants are better adapted to repeated defoliation. In the majority of grasses, the stem internodes do not elongate in the vegetative phase, so that the shoot apex normally remains below cutting or grazing height and thus is able to produce new leaves. From buds in the axil of leaves, tillers may arise whose apices also escape removal provided the plant stays vegetative, and consequently grasses recover from each defoliation with all growing centres intact. Leaves elongate through the activity of intercalary meristems and, as long as the leaf has not fully emerged, it will continue its growth even though its tip has been removed (Langer, 1954). This high degree of resistance to grazing receives a setback as soon as flowering begins, for it is then that the shoot apices are carried upwards by elongating internodes into the zone accessible to the animal. Further leaf production stops in these tillers whether they are grazed or not. The important point is that early removal of the apex will favour more continuous tiller formation at the base than allowing the shoot to flower, and in fact pasture management at this time depends very much on the skilful manipulation of physiological principles. Delayed or too lenient grazing will result in a stemmy, unpalatable sward and subsequently in slow recovery, particularly if this period coincides with dry, warm weather, as it often does. In mixed pastures this is the time when changes in botanical composition are initiated, because grasses differ in flowering date and propensity. European plant breeders have been more aware of the importance of flowering in pasture production than have New Zealand workers, as farmers in the drier parts of New Zealand have reason to remember in most seasons.

Persistence of grasses under grazing is also connected with tiller production and performance. Accurate information on seasonal trends is difficult to get, but in timothy swards (Langer *et al.*, 1964) tiller mortality appears to be high in early spring before flowering occurs. Following the onset of flowering, many tillers appear, and these continue to carry the sward through the winter. Autumn tillers become an important constituent by the following spring, but many of them tend to die before mid-summer without reaching the flowering condition. In meadow fescue, tiller replacement seems less complete, but in both grasses there is considerable evidence of continuous dynamic change in sward composition, well above the level suggested by tiller counts (Jewiss, 1966). Among the factors controlling development of tiller buds, the supply of assimilates is of primary importance, and hence high light intensity tends to encourage tiller production (Mitchell, 1953). Seasonal variations in tillering can often be explained in terms of the amount of light reaching the plant, but, perhaps more importantly, frequency and intensity of grazing affect light conditions within a pasture and consequently influence tillering.

ENVIRONMENTAL EFFECTS

In general, the growth rate of grasses, apart from tillering, increases with light intensity, both in single plants and in swards, depending on the level of other environmental factors. Shading has a deleterious effect, particularly on the roots, and this is shown particularly well in plants establishing under the cover of a nurse crop. Although season and weather determine the level of radiation reaching a pasture, the proportion which penetrates is variable, depending on the amount of foliage that is left to intercept the light, and thus grazing management affects plant growth profoundly. A further and most important illustration of light conditions within the pasture is, of course, the proportion of grasses to clovers.

On a practical scale day length cannot be controlled, but physiologically this factor plays an important part by causing flowering to occur. Initially, this process appears to be accompanied by higher growth rates (Langer, 1958), although whether this can be explained by improved illumination as the leaf canopy rises through stem elongation or whether more subtle changes in carbohydrate distribution are involved, is not certain at present. In view of the suggestion that non-flowering grasses could have considerable advantages, further work on this aspect is clearly desirable. As matters stand, unchecked flowering leads to stemmy growth with high fibre content and low digestibility, which again highlights the necessity for more research in this area. In this connection it is interesting to note an interaction of changing day length with time of tiller appearance. In some species, notably timothy and cocksfoot, tillers appearing after mid-summer are stimulated to produce an inflorescence, but as the days shorten during the autumn, vegetative shoots or proliferations appear from the florets without a seed having set (Langer and Ryle, 1958).

Many of the common Festucoid grasses grow well at relatively low temperature. Just above 25°C an optimum is often reached, but higher temperatures tend to decrease growth markedly (Mitchell, 1956). Soil temperatures frequently have a more pronounced effect than air temperatures, even if water supply is kept constant. On the other hand, non-Festucoid grasses grow poorly below 15°C, but they come into their own at temperatures of 30°C and above. Although grazing management influences temperatures within a pasture through an effect on radiation and re-radiation, the more important application of these responses lies in the ability to predict the suitability of various grasses for different climatic regions. The adaptability of existing genotypes may be known well enough from practical experience, but in the realm of plant breeding and plant introduction these temperature responses are of greater relevance than is generally realized.

GENETIC VARIATION OF PHYSIOLOGICAL CHARACTERS

At relatively low light intensities, the rate of photosynthesis varies with the amount of energy received, but as light input rises photosynthesis does not increase proportionately and eventually it reaches saturation. In many species, such as cocksfoot and red clover, light saturation occurs when the visible radiation reaches about 10 cal/sq. cm/hr, but in maize more than three times this level is required before the leaf is saturated, and the rate of photosynthesis is correspondingly greater (Hesketh, 1963). Conversely, there are species adapted to shade with lower light saturation values than cocksfoot and red clover. These data suggest that genotypic differences in this respect are probably greater than has been assumed hitherto, and that pasture species should be examined for their photosynthetic efficiency over the range of light climates to which they are exposed in the sward. Although at Lincoln College it has not so far been possible to measure photosynthesis directly, it has been found, for example, that the growth rate of prairie grass suffers much less from reduction in light intensity than that of short-rotation ryegrass. This difference appears to account for the winter growth of prairie grass, because both grasses responded similarly to decreasing temperatures. It remains to be seen whether these species differ in photosynthetic activity or whether leaf arrangement and distribution are more important. Genetic variation exists for these and other physiological characters which relate to the efficiency of energy utilization, and it is tempting to think that further physiological work may lead to greater precision in plant breeding objectives than at present.

When it comes to temperature, more meaningful and immediately useful results have been obtained, particularly in Mediterranean varieties, some of which already figure in plant breeding programmes. Few differences in the optimum temperature for leaf expansion have been found in ecotypes of ryegrass, cocksfoot and tall fescue, but at 5°C plants of Mediterranean origin grow more actively than those from northern Europe (Cooper, 1964). Unfortunately, ability to grow at low temperature is not associated with frost resistance. The time of flowering in Mediterranean grasses is also geared to the climate of the region in which winter growth is followed by summer dormancy (Knight, 1963). Inflorescences are produced in fairly short photoperiods, and there is little or no need for previous exposure to cold or to short days. Conversely, northern European ecotypes are relatively winter dormant, and flowering is normally delayed until the longer days of summer. It follows that it is possible to determine the requirements of pasture plants for optimum growth and flowering by standard physiological techniques. On the basis of such tests the suitability of plants for various climatic zones can be predicted, but a more important advantage is that plants can be screened for selection by the plant breeder. A wealth of desirable genes awaits to be identified and utilized.

Reference must also be made to the mineral content and nutritive value of pasture plants, for here again considerable genotypic differences have been discovered. For example, Butler *et al.* (1962) found significant differences in the content of 10 ions among clones of ryegrass, and in the case of iodine diallel crosses demonstrated a high degree of heritability (Butler and Glenday, 1962). Digestibility has been shown to decline rapidly after ear emergence (Minson *et al.*, 1961), so that genetic variability in the date of flowering will affect the value of herbage consumed at any one time. In addition, there appear to be varietal differences at the same stage of development. The type of rumen fermentation ultimately relates to the soluble and structural carbohydrates of the plant, for which genetic variation exists. For instance, the content of soluble carbohydrates is greater in tetraploid than in diploid Italian and perennial ryegrass (Dent and Aldrich, 1963). Despite these advances and the prospects arising from them, far too little is still known of the characteristics of pasture plants which affect voluntary intake, and it is in this area that plant physiology could play an important part.

PASTURE PRODUCTIVITY

Work in New Zealand and elsewhere has demonstrated the relationship between light interception and crop growth. Following germination or defoliation, dry matter production is limited because inadequate foliage is present to utilize the incident radiation. As leaf area index increases the crop growth rate also rises until a critical, or optimum, leaf area index is reached. Following this, since no further light can be intercepted, crop growth rate ceases to increase or declines (Brougham, 1958, 1960a). Critical leaf area index values have been determined for a number of species, depending on penetration of light through the canopy and the level of radiation. These relationships have already been refered to (Campbell, 1967), so that it now remains to discuss their significance. Although work in this area can rightly be claimed as one of the major recent contributions of plant physiology to pasture agronomy, it would be misleading to think, nor was it ever intended, that precise recipes for pasture management could be derived from it. Responses to grazing management can in part be explained and certain principles elucidated (Brougham, 1960b), but perhaps the main value of this approach has been in predicting maximum obtainable levels of productivity. Actual production often falls far short of potential production, and hence new systems of plant culture and utilization have been proposed. This in itself has been a stimulating exercise, although it illustrates only part of the value of these researches.

One of the important results of these and similar studies has been to draw attention to the accumulation in pastures of dead and unproductive material of low nutritive value. This may amount to some 2,000 to 6,000 lb/acre at any one time, depending on season, type of pasture and management. For example, in undefoliated Italian ryegrass, the dead matter present increased from about 840 lb/acre in May to over 2,000 lb/acre in August (Hunt and Brougham, 1966). In interpreting these losses to productivity, it must be remembered that leaves are organs of limited growth, which appear, unfold, senesce and die. How long they live is determined by the environment, notably moisture and mineral supply, light and temperature, but, just as the tiller population undergoes continuous change, so does the leaf complement experience perpetual renewal. At any one time each tiller carries relatively few leaves whose number fluctuates within narrow limits, determined by the rates of leaf appearance and death. As one would expect, senescence and decay reach a high level in dense swards in which little light reaches the lower layers of the canopy. Leaf death cannot be avoided, even though its rate and magnitude are variable. Theoretically, close and frequent defoliation would be expected to reduce these losses, but this conflicts with the requirement for adequate foliage to be retained to obtain fast recovery growth. Frequent lenient defoliation does not provide a satisfactory solution. As pointed out by Hunt (1965), management systems which achieve a desirable balance between losses of dry matter by decay and gains by photosynthesis may differ from one environment to another. One could go further than this by saying that more information is required on the effects of nitrogen temperature, light and humidity on leaf longevity, and on how these factors operate in the sward, before it is possible to suggest how to harvest more effectively the material produced by pasture plants.

CONCLUSION

Although plant physiology is concerned with plant processes and functions, it can be claimed with some force that it has contributed materially towards solving problems basic to pasture production. Within the last ten or twenty years, a great deal of vital information has come to hand, and what previously was inferred or surmised is now known with precision. The major application of this body of knowledge is threefold: it explains in detail how pasture plants grow and how they react to pasture management, it offers to the plant breeder promising objectives for selection and hybridization, and it leads to the definition of production potentials and how they might be achieved.

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