REGROWTH OF RYEGRASS AS INFLUENCED BY
FIVE DIFFERENT REST PERIODS

BY

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A grazing experiment was conducted at the Beef Research Unit, University of Florida, Gainesville, from April through June 1978, with the following objectives: a) to evaluate the feasibility of a pasture system in which ryegrass and clovers were seeded into a bahia-grass sod, b) to follow the development of ryegrass through the production of tillers, and c) to determine the influence of grazing management upon the reseeding of ryegrass.

Five rest periods were imposed from April through May. Starting dates were: 4 April, 18 April, 2 May, 16 May, and 30 May for rest periods 1, 2, 3, 4, and 5, respectively. The total area allocated to the experiment was 1.1 ha, which was subdivided into 22 pastures. The pastures were mob-grazed by cattle from 1 to 4 days to a prescribed residue level.

The number of tillers per $1/4 \text{ m}^2$ decreased linearly with advanced rest periods, at rates of approximately 40 tillers/ $1/4 \text{ m}^2/\text{week}$. The percentage of tillers with seed heads increased linearly with advanced rest periods. The rate of increase in tillers with seed heads/week was about 8.8 percentage units. The percentage of tillers with ripe

seeds increased with later rest periods and reached 98% by rest period 5. Tillers with seed heads in anthesis and milk stage decreased with advanced rest periods and reached 0 and 1.4%, respectively, in rest period 5. Seed weight/tiller also decreased with advanced rest periods. However, estimates indicated that because of the increase in percentage of tillers with ripe seeds with later rest periods, about 100, 83, and 103 kg/ha of ripe seeds were produced in rest periods 3, 4, and 5, respectively. The length of the seed heads decreased linearly with successive rest periods, at the rate of about 1.1 cm/week. This decrease in length of seed head probably was responsible for the decrease in seed weight/tiller. The length of stem showed a curvilinear relationship with successive rest periods. The leaf:stem ratios decreased with later rest periods, but they were low for all. Because samples were cut at ground level and stubble was included, leaf:stem ratios in reality were underestimated.

The relationship between total non-structural carbohydrate (TNC) and rest periods was linear with a rate of decline in carbohydrate content in the grass stubble of about 6 percentage units/week. The crude protein (CP) percentage in stems showed a curvilinear response to time of imposed rest periods. The variation in CP in leaves with rest periods was also erratic; however, based on a linear model, there was a decrease in the CP with advanced rest periods of about 0.6 percentage units/week. The leaf area of the two ryegrass varieties decreased linearly with successive rest periods. The rate of decrease was about $1.0 \text{ cm}^2/10 \text{ tillers/week}$ for Florida Reseeding and about $1.5 \text{ cm}^2/10 \text{ tillers/week}$ for Gulf ryegrass.

There is a great potential for a system with sod-seeding of winter forages; however, in this research, the desired high production of forage during winter was not achieved, probably because of the high grazing intensity used. Ripe seed was produced in satisfactory amounts in three of the five rest periods. However, due to the grazing management used, most of the seed produced was probably ingested and removed from the pasture by animals. The heavy grazing pressure used was also responsible for the low tiller population; forage yield probably decreased at rates similar to that of tiller density.

INTRODUCTION

Pastures in the United States have much more importance today than they had a few years ago. Even today, there is a large movement of feeder calves into the grain-producing regions of the United States where the animals are finished on grain under confinement feeding. Economic considerations during the past several decades have made it more profitable for the farmer to sell his grain crops in the form of beef. It is expected in the years ahead, with an increase in international demand, that the price of grain may make it more profitable for the farmer to sell his grain through the fattened beef animal rather than direct marketing. It is expected that this may create a shortage of grain for dry-lot feeding, which will force the use of pastures and forages in beef feeding systems. The concept now is not only to maintain the animals year-round on pasture, but also to finish them on forages with a minimum of grain feeding. Although the importance of forages has increased, there still exist some very difficult obstacles before pasture and forages alone can supply all of the cattle requirements for a profitable system. A major consideration in the use of pastures and forages to produce marketable animals is the lack of uniformity with which forages are produced during the year.

In cool, subtropical areas, like north-central Florida, low temperatures preclude production of tropical perennial grasses during 4 to 6 months of the year. Intensification of livestock production in Florida is limited by the scarcity of forage production during the winter

months. One alternative for overcoming the deficiency of forage during the winter months is to use winter-annual species for overseeding on dormant permanent pastures. In this way, the productive season for grazing can be increased by producing forages during the winter months.

The concept of overseeding pastures is an old one and has been practiced for more than 30 years. The small grains (oats, barley, and rye) and ryegrass have usually been fall-seeded in tropical perennial pasture sod. Several winter annual legumes have also been utilized in a similar manner. These winter annual species produce high-quality forage during the period of the year when it is most needed. Ryegrass can be established by top-seeding in a perennial sod with a minimum of soil preparation.

The objectives of this research were a) to verify the feasibility of a pasture system in which ryegrass and clovers were seeded into a bahiagrass sod, b) to follow the development of ryegrass through the production of tillers, and c) to determine the influence of grazing management upon the reseeding of ryegrass. The parameters measured on ryegrass included leaf-stem relationships, carbohydrate reserves, and crude protein.

LITERATURE REVIEW

Temporary Winter Pastures

General

The importance and potential for temporary winter forage plants has been recognized for many years. In the Southeastern United States the practice of overseeding cool-season crops such as small grains, clovers, and ryegrass (Lolium multiflorum Lam.) in perennial tropical pastures is increasing in importance. Recently this importance was stressed when Monson and Utley (1977) stated that "any forage program to be successful in the lower South will demand more than one forage species" (p. 393).

The use of two or more species with different temperature requirements will probably fill the gap in forage production during the winter season, thereby providing a more uniform production of forage throughout the year. It may be profitable to use winter-annual grasses and legumes, which are both high in protein and digestibility, to eliminate or at least reduce the shortage of forage during winter when perennial warm-season grasses are low in production. Annual ryegrass is commonly utilized as a forage crop in the Southeast United States to provide winter and spring grazing.

Several factors contribute to a profitable winter-pasture program. Among these are high total yield, provide for a more uniform distribution of forage during the year, a longer grazing season, and better quality forage (Allen et al., 1971). Utley et al. (1976) called attention to a very important point in favor of overseeding winter-annual

grasses into perennial grass sods in that almost no land preparation will be required and an uninterrupted grazing season throughout the year is almost always assured.

One disadvantage of sod seeding is the competitive effect of the perennial grass in the fall establishment of ryegrass. This competition is further complicated by stimulation of the perennial grass by N in starter fertilizer applied in the fall. However, it may be solved by delaying N application, use of herbicides, tillage or intensive grazing of perennial sod (Curl, 1973). However, once established, ryegrass growing under favorable temperature and moisture is highly competitive with other species (McKell et al., 1969).

Small grains generally produce forage earlier than ryegrass following seeding. However, ryegrass will continue producing forage much longer into the spring (Clyde, 1958; Mislevy, 1973a). Roark et al. (1966) pointed out that oats (Avena sativa L.) and rye (Secale cereale L.) supplied most of the grazing during the first half of the grazing season and ryegrass pastures produced similar average daily gain, steer-grazing days/ha and total steer gain/ha. Steers grazing winter annuals grown in prepared seedbeds gained 1.05 kg/head/day compared with 1.12 kg/day for steers grazing sod-seeded pastures. The type of dormant sod in which the winter annuals were grown had a significant effect on animal performance. The total steer gain for the winter annual pastures was 202 kg/ha when grazing in bahiagrass sod, 287 kg/ha when in 'Coastal' bermudagrass sod, and 268 when grazed in 'Coastcross' 1 bermudagrass sod (Utley et al., 1976). On the other hand, Spurway (1975) stressed the capacity of oats for producing large yields, for tolerating repeated

grazings at high stocking rates and producing good liveweight gains. Burton et al. (1949) indicated that oats and rye were the most desirable winter forages.

Winter annuals such as small grains, ryegrasses, and clovers have the capacity to produce 2 to 4 metric tons/ha of highly digestible forage over a 6-month period (Mislevy, 1973a). Clyde (1958) stated that yields vary considerably from year to year. Mislevy (1973a) pointed out that there are definite differences in production of small grain varieties within and between localities. He also found that oat varieties produced higher yields when compared with all other small grains, but all ryegrass varieties outyielded all small grains.

Grazing

Depending upon rainfall and temperature, ryegrass grazing in the Southeast is generally started in late December when growth is 7 to 12 cm high. Livestock feed requirements for late fall may be achieved by fall-seeded oats or rye which can be grazed about 3 weeks earlier than ryegrass (Mislevy, 1973b). Mislevy (1973b) also concluded that even though ryegrass production starts 3 weeks later than small grains, it is one of the highest yielding winter forage crops in Florida.

Winter pastures require more intensive management for profitable return than permanent ones. They should not be overgrazed at any time because they recover slowly from overgrazing (Clyde, 1958). Cook and Lovett (1974) stated that the more severe the defoliation, the longer the period required for recovery; but once active growth was achieved, there was no difference between the growth rates of plants defoliated to different degrees. However, where early seedings are made, increased attention must be given to competition from the old sod. Close grazing

prior to seeding generally is recommended. Much of the N fertilizer for early seedings may have to be withheld until the old sod is less active and the new seeding becomes established (Robinson, 1963).

Mislevy (1973a) recommended that management of small grains should involve initial harvest when plants attained a height of 25 to 45 cm. In South Florida, with adequate moisture and fertility, this height should be reached in about 43 days. Regrowth was removed whenever plants reached a height of 25 to 35 cm. Ryegrass was harvested each time plants attained a height of 30 to 40 cm. Prine and Myers (1974) pointed out that under good grazing management, ryegrass would tend to approach the optimum yield, but the tendency is almost always to overgraze winter pastures. Roark et al. (1966) suggested that one way of improving management of temporary pastures is by controlling the number of animals according to the rate of plant growth. Smith (1969) suggested that more intensive management, such as strip grazing, be used.

Adequate Water Supply

Soil moisture may be one of the most critical factors limiting production of winter pastures in North-Central Florida. Robinson (1963) pointed out that the most important factor associated with variable forage production in the southern region is soil moisture. The first approach to sod seeding in the Southeast United States is to examine climatological data during critical periods in the fall. He also added that soil moisture supply will probably determine whether or not sod-seeding will be successfully achieved. Roark et al. (1966) stressed that there are two critical periods in the production of winter pastures. One is moisture condition of the soil prior to and at planting time, when drought conditions may occur, and the other is during January or February when hard freezes generally occur.

Fertilization

Allen et al. (1971) concluded that with an oat-ryegrass mixture, the most efficient utilization of fertilizer occurred from the application of 100 kg/ha of N. Bertrand and Dunavin (1976) found that a single application of N fertilizer with a slow dissolution rate at the beginning of the grazing season was not different from an equal amount of N from three applications of ammonium nitrate during the grazing season for the production of winter-annual pastures grazed by growing calves. However, the savings in application costs over a season may be considerable.

Raymond (1969) pointed out that the dominant effect of plant age on digestibility cannot be overcome by any effect that N level of fertilization may have on digestibility. However, N fertilization increased CP content in small grains and ryegrass forage (Burton et al., 1949). There was no difference ($P < 0.05$) due to N fertilization in daily gain of calves grazing winter annual pasture forages. The higher gain per hectare of calves grazing a pasture receiving 113 kg/ha of N was due to higher forage production and longer grazing periods indicating that N fertilization did not influence quality of forage as much as it influenced quantity (Bertrand and Dunavin, 1976).

Overseeding Techniques

The advent of sod-seeding goes back into the 1940's when methods of grazing livestock in midwinter and early spring were developed. Thompson (1963) reported that in the late 1940's oats, wheat (Triticum aestivum L.), ryegrass and legumes or mixtures of them were seeded into already established sods of common bermuda (Cynodon dactylon (L.) Pers.) 'Coastal' bermuda, bahiagrass (Paspalum notatum Flugge), and carpetgrass

(Axonopus compressus (Swartz.) Beauv.). Coats (1957) found that a grain crop drilled into permanent pastures was the best alternative for extending the grazing season. Dudley and Wise (1953) indicated that small grains should be drilled approximately 5 cm below the sod; ryegrass or legume seeds should be placed about 1.5 cm deep. They also concluded that the earlier the seeding, the greater the competition between the seedlings and the established sod for moisture, fertilizer, and light. There seems to be a fairly wide range of time when plantings can be made to ensure satisfactory spring production. However, yields from plantings made in late November were lowest (Swain et al., 1965; Coats, 1957). Coats (1957) also noted that clipping the pasture short or burning dormant vegetation favored the winter pasture. Robinson (1963) said that the choice of species seeded for winter grazing may be determined more by the potential for growth during the fall than during winter because even at best, growth during winter is relatively low. In some places disking has been used with success, as well as herbicides to hold back the perennial grass allowing seeding of winter annuals from 4 to 6 weeks earlier (Anon. 1973).

Ryegrass can be established and maintained as a volunteer stand for pasture. The inherent characteristics for successful natural reseeding of ryegrass pastures are residual seed dormancy (Schafer and Chilcote, 1970) abundant seed production (Weihsing and Evatt, 1960), and germination under water stress (McWilliam and Dowling, 1970). Other techniques for sod-seeding were developed by Coats (1957) in Mississippi; Colman (1966), Wheeler and Campbell (1969) in Australia; and Blackmore (1958) in New Zealand.

Effect on the Permanent Pasture

Thompson (1963) reported that the sods improved each year that sod seeding was done. The main reason for that would have been the use of fertilizer on the winter pasture and/or the use of N-fixing legumes. Welch et al. (1967) reported that the first bermudagrass harvest was low probably because of the effect of shading and competition by the overseeded crop at the time when the perennial pasture was breaking dormancy in the spring. Kalmbacher et al. (1978) considered that sod-seeding may be practical in Florida and that compared to costly land preparation it results in less injury to the perennial grass pasture, reduces soil erosion, and better conserves soil moisture. These authors were, however, concerned with research which indicates that sod-seeding may result in lower small grains or ryegrass yields than in prepared seedbeds. There is no apparent reason why winter grass yields are so low when seeded in bahiagrass sod. They have even considered the possibility that the bahiagrass is holding back winter grasses through the process of "allelopathy."

Utley et al. (1976) reported that the total dry matter produced for the January clipping was about five times larger for ryegrass and ten times larger for oats when grown in prepared seedbeds than when grown in dormant sods. Dudley and Wise (1953) in Mississippi found that the yield of bermudagrass was depressed as much as 18% with top-seeding of ryegrass. They also concluded that the damage to the perennial grass was proportional to the degree of the sod disturbance during the seeding operation and to the competitiveness of the resulting forage.

Quality of Winter Forage

Barnett and Stanley (1976) stated that small grains produce high quality forage when permanent pasture is not available. Cool-season

annual forages have provided quality grazing for growing beef calves in Northwest Florida (Bertrand and Dunavin, 1976). Changes in forage quality that occur during the growing season may be accounted for by time of grazing, management practices, species, and other environmental factors such as climate (Campbell and Dotzenko, 1975).

Roark et al. (1966) pointed out that the CP content of forage mixtures, ryegrass and oats was high while the forage was young but gradually lowered as the season progressed. Protein content of the oats-ryegrass forage ranged from 23.5% early in December to 16.5% at the end of May. Similar conclusions were obtained by Prine and Myers (1974) emphasizing the fact that ryegrass in a vegetative state under good fertilization is one of the highest quality forages, with both digestibility and protein content remaining high.

Barnett and Stanley (1976) stated that most of the differences in chemical composition between cultivars were probably due to differences in the stage of maturity and the time of harvest. In a series of experiments during 4 years, average protein contents were not different. However, Morey (1961) reported that rye was higher in protein than other small grains at similar stages of maturity.

Regrowth

The regrowth of herbage after defoliation by grazing animals can be affected by factors within the sward itself, by factors associated with the grazing animal, and by factors related to the environment, principally climatic conditions. This review will be mainly concerned with factors which influence plant regrowth and are related to within sward conditions. These within sward factors affecting regrowth are leaf area, tillering capacity, and nutrient reserves.

Leaf Area

This factor has been considered as one of the most important affecting plant regrowth. It has been extensively reviewed by many researchers (Watson, 1952; Donald and Black, 1958; Brown and Blaser, 1968).

Watson (1947) defined the area of leaf per unit area of land as the leaf-area index (LAI). The increase in dry matter (DM) per unit of land per unit time is termed the crop growth rate (CGR). If other conditions are optimum for plant growth, there appears to be a close relationship between the LAI and CGR. The point where the CGR reaches its maximum has been termed the optimum LAI (Davidson and Donald, 1958), which is the LAI at which the leaves situated at the base of the canopy are at their compensation point. The optimum LAI, has also been called the critical LAI, the minimum LAI at which the crop is intercepting 95% of the incoming noon radiation. The maximum growth rate often appears to be achieved at LAI values above the minimum for 95% light interception (Pearce et al., 1965), but both terms are usually used as synonyms.

The leaves are the chief organs of photosynthesis, and the area of leaf is usually assumed to be the size-attribute that best measures its capacity for photosynthesis. So the sum of the areas of all the leaf laminae per unit area of land (LAI) can be taken as a measure of the size of the photosynthetic system. A measure of the efficiency of the photosynthetic system is provided by the rate of increase of dry weight per unit leaf area, the net assimilation rate (NAR), which can be estimated from successive determinations of dry weight, and leaf area at short intervals throughout the growth period (Watson, 1956). So far it has been shown that leaf area is relatively much more variable

in agricultural crops and environments than NAR and so is the more potent determinant of dry weight yield. Improvement in yields, is therefore, likely to be affected mainly by an increase in LAI. If NAR were independent of LAI, the rate of increase of dry matter per unit of area of land (CGR) would increase indefinitely with the increase in LAI. But, as LAI increases, mutual shading of the leaves begins to decrease the rate of photosynthesis of part of the foliage and so decreases NAR. Hence, it is to be expected that in the higher range of LAI there will be an inverse relation between NAR and LAI (Watson, 1956). Brown and Blaser (1968) stated that the use of the LAI concept has been oversimplified and interception of light has been overemphasized. They said that higher yield in some cases might be obtained by complete defoliation followed by initiation of new tillers and young leaves. Low LAI values may be desirable at times because they favor tiller production. Values of LAI above optimum may be desirable at other times when regrowth may be dependent on stored reserves.

However, some doubt still remains about the influence of LAI on CGR. Anslow (1965a, b) could find no particular relationship between CGR and LAI. Brougham and Glenday (1967) recalculated Anslow's data, assuming that growth follows a sigmoid curve and concluded that CGR did change with LAI, but it was refuted by Anslow and Back (1967) who considered that their data on regrowth did not follow a sigmoid pattern after defoliation.

Other factors have been considered to affect CGR. Brougham (1961) reported that CGR was found to be more closely related to the amount of chlorophyll per unit ground area than to the critical LAI. The leaf tissue of pastures is subjected to repeated harvesting or grazing over

a long period of time. An understanding of the dynamics of pasture growth during the intervals between defoliation is important to learn about the effects of frequency and intensity of grazing on pasture growth (Brougham, 1955).

Leaf area, light, and regrowth relationships. Numerous researchers have stressed the importance of the interrelationships of light and leaf area for rapid regrowth and high yields of forage plants (Black, 1957; Donald and Black, 1958; and Donald, 1963). Competition for light is probably the most important factor governing the growth of tillers following defoliation. Donald (1963) has commented that competition for light differs from that for nutrients or water in that there is no reservoir of light from which to draw supplies. Light energy is available only in an instantaneous context and it must be instantaneously intercepted or it will be lost as a source of energy for photosynthesis. He also added that the successful plant is not necessarily the plant with more foliage, but the plant which has its foliage in a better position relative to the foliage of its competitors for light interception.

Black (1963) examining the relationship of crop growth rate, leaf-area index, and solar radiation concluded that growth rate increased with increased leaf-area index until a maximal value was reached at the optimum leaf-area index, thereafter, falling. At low levels of radiation, growth rate fell to zero at high leaf-area indices. Both the maximal growth rate and the optimum LAI increased with radiation, and an analysis of the data indicated that these growth indices were dependent on radiation, the effect of temperature being negligible.

Stern and Donald (1961) stated that their results indicated that for any level of radiation there is an optimal LAI at which crop growth

rate will be maximal, and that the value of the optimum index increases as radiation rises. Donald (1963) stated that the ultimate capacity of a plant community to produce dry matter depends on the degree of exploitation of solar radiation. Pearce et al. (1965) stated that net photosynthesis (P_n) should be maximal when the foliage is dense enough to prevent sunlight from striking the soil, but not enough to cause basal leaves to be parasitic. As LAI increases so does light interception, causing increases in P_n up to a critical LAI value. Brougham (1956) has shown that ryegrass-clover mixtures increase in growth rate, with increasing light interception up to 95%. This corresponds to an LAI of 5.0. Additional foliage did not affect growth rate.

Other investigators (Davidson and Donald, 1958; Watson, 1956) reported an optimum LAI beyond which growth rate decreased rapidly. Optimum LAI may be governed by many natural and imposed variables. Leaf arrangement and shape can affect the pattern by which light is intercepted and reflected in plant stands.

Brougham (1958) showed that ryegrass with vertically disposed leaves, intercepted less light per unit LAI than clover, with more horizontal leaves. Leaf age, as well as climatic factors, may alter the optimum LAI. There is evidence that optimum LAI varies seasonally (Stern and Donald, 1961) being higher under high light intensity of summer than at other times of the year. This indicates that such factors as geographic location and diurnal fluctuations (Brougham, 1958) also affect the optimum LAI. At low leaf areas one LAI unit adds significantly to the photosynthesis of the plant stand, but as LAI increases beyond optimum the CO_2 fixed becomes smaller than that lost due to increased shading and respiration (Pearce et al. 1965). Stern and Donald (1962) stated that the growth of clover showed direct dependence on the level of

radiation at the surface of the clover leaf canopy. A relationship was presented between the level of radiation, the LAI, and the CGR. It is shown that the optimum LAI increases with increasing levels of radiation; and further that as the LAI increases, the level of radiation required for maximum growth rate also rises.

As radiation increases and light penetrates more deeply into the canopy, the area of leaves maintained above the compensation point becomes larger. At low LAI, low levels of radiation are as effective as high levels for maximum growth rates (Stern and Donald, 1962).

Stern and Donald (1962) said that their studies confirmed the view that the optimum LAI in crops and pastures will vary considerably between summer and winter, and between cloudy temperate areas and high solar radiation of the tropical zones. It is clear that within certain plant communities growth will be accelerated as either leaf area or radiation moves toward an optimum combination. As various limiting factors to production are overcome, notably by the extension of irrigation and use of fertilizers, the relationship of crop growth to the light regimes becomes increasingly significant in crop and pasture production. It has long been recognized that, between plants, competition occurs for physical environmental factors, and that of these, water, nutrients, and light are of primary significance. Under field conditions, the amount of light falling on a pasture is not controlled by man. The capacity of a species to produce dry matter depends on the degree to which a community of these plants can exploit the incoming light.

Brougham (1955) examined the form of the growth curve in a ryegrass-clover sward following close defoliation, and suggested that an important stage in growth was reached when the leaf area was sufficient

to intercept most of the incident light energy. Until this stage was reached, the growth rate increased; thereafter, it was constant, finally declining. Brougham (1956) reported that a high percentage interception of light energy (95%) occurred at an LAI of about 5, regardless of the intensity of prior defoliation. This LAI was reached 0, 16, and 24 days after defoliating to 12.5, 7.5 and 2.5 cm., respectively. The rate of growth of the pasture was a function of LAI, and hence of light interception, with approximately constant rates when LAI was in excess of 5.

Donald and Black (1958) stated that when light limits growth of pasture plants several relationships will operate. A pasture will have an optimum LAI at which the rate of dry matter production will be maximal; it will have a ceiling LAI at which leaf senescence equals leaf initiation and expansion, and finally it will presumably have a ceiling yield (weight of dry matter per unit area) at which respiration equals photosynthesis. In pasture management, the objective will be to achieve as rapidly as possible the optimum LAI for plant growth and then to maintain it at this level. Early grazing when the LAI is low will delay the achievement of the optimum. The ceiling yield may be increased by the use of alternate species, e.g., clovers with their horizontally disposed leaves may more readily form a canopy and more fully intercept light than grasses. However, the phenomenon of the suppression of those species of dwarf stature by their taller competitors, especially clovers by grasses could be analyzed in terms of LAI (Donald and Black, 1958).

The development of the LAI concept in pasture growth and management is an example of the coordination of physical and physiological

properties of plant communities to help clarify a complicated relationship (Brown and Blaser, 1968). Increased production of plant vegetation requires an increase in utilization of solar energy, other environmental factors being favorable. Efficient utilization of sunlight on a soil-area basis requires a) leaves with high photosynthetic capacity, b) interception of nearly all the incident sunlight, and c) favorable distribution of intercepted light among leaves within a canopy.

Youngner (1972) considered the relationship between growth and light and said that a young sward with well-spaced plants may use only a small part of the total light falling on it. As the sward grows, an increasing amount of the light is intercepted by the leaf canopy until the amount of light reaching the soil is negligible. Then, if all leaves receive adequate light and no other factor becomes limiting, the sward will grow at its maximum rate. As the density of the leaf canopy increases, lower leaves receive insufficient light, their contribution to the growth of the sward decreases, and the growth rate of the sward declines. Eventually old leaves die and a time is reached when leaf-death rate equals leaf-emergence rate. At this point, maximum sward yield is reached. Defoliation will change the light relationships and thus growth rates. Forage yields can be greatly increased through grazing or mowing practices that maintain growth rates as near the maximum as possible. The alteration in light relations will increase as the amount of leaf removed is increased. After very severe defoliations, competition for light could almost disappear and the variability in light within the sward is likely to be smaller than after light grazing. However, the variability within the sward

is different at different stages of plant growth. Stern and Donald (1962) stated that the situation of small tillers tends to be better during the reproductive phase since leaves responsible for a large proportion of shading are disposed over a greater vertical range.

It seems that the most important effect of defoliation is the rapid decrease in leaf surface and in photosynthesizing tissue. Although animals remove less leaf when low grazing pressures are applied, they select young and leafy material (Hodgson, 1966; Morris, 1969) and long shoots are defoliated more frequently than short ones (Hodgson and Ollerenshaw, 1969). These are also the most important plant tissues for growth since younger leaves are more photosynthetically efficient than older ones (Begg and Wright, 1964; Brown et al., 1966b; Mitra and Wright, 1966; Jewiss and Woledge, 1967) and laminae are likely to be more efficient than sheaths (Thorne, 1959). Therefore, grazing tends to decrease the efficiency of sward photosynthesis (Anslow, 1968).

The depressive effects of defoliation on herbage production may be due to a reduction in the substrate for leaf growth, but may also be explained in part by changes in growth regulating substances due to the removal of plant parts (Bignoli, 1950).

Leaf appearance and expansion. Mitchell (1953a) stated that the rate of leaf appearance is so responsive to external factors that it would be dangerous to make any generalization. These differences in rate of leaf appearance have wider implications than variation in number of leaves formed on a stem in a given time. Until a leaf on any stem has developed, its axillary bud may not produce a new tiller.

The rate of appearance of leaves varies with the environment, but remains constant for any given set of conditions (Mitchell, 1953a). In contrast, however, there are marked changes in leaf size (Borrill, 1961) the blades of successive leaves become progressively larger until about the time of inflorescence formation, when leaf blades up the flowering stem become progressively shorter. The reduction in length of successive leaf blades is indicative of the increased competitive demand for assimilates by the developing inflorescence and the elongating stem. Leaf removal affects subsequent herbage growth more by slowing the rate of leaf appearance than by depressing the rate of leaf expansion.

Koller and Kigel (1972) suggested that at least three independent factors control leaf expansion. Two of these are components of the light environment, photoperiod and level of radiation, while the third is ontogenetic and is related to the nodal position of the leaf on the shoot. Leaf dimensions are determined by the growth rate and the duration of the growth period of the leaf. Jewiss (1966) stated that in general the rate of leaf death is about equal to the rate of leaf appearance. The number of living leaves on a tiller is a direct result of the rate of leaf appearance and the length of life of these leaves.

Davidson and Milthorpe (1966) found that 7 to 8 days after defoliating orchardgrass (Dactylis glomerata L.) plants to 2.5 cm, the rate of leaf appearance was one-quarter and the rate of expansion of new leaves was one-half of the rates in uncut plants. Langer (1954) found that cutting did not stimulate new growth of leaves which were already fully expanded.

Leaf parasitism and senescence. In the absence of stem elongation, the new canopy is a relatively shallow horizontal layer fairly close to the ground, able to intercept a large proportion of the incoming light although it is generally formed by narrow leaves. The role of old leaves in herbage production has received increasing attention. In undefoliated stands, bottom leaves were assumed to be parasitic since their photosynthetic activity declined as a result of aging and shading, but they continued to respire. It is now known that respiration rates also decline with age (Begg and Wright, 1964; Hopkinson, 1966) and that the rate of decline is accelerated by shading (Alburquerque, 1968). In addition the rate of decline in photosynthetic activity is much slower in dim than in bright light (Woledge, 1971).

It was supposed that when leaves situated at the bottom of the canopy were exposed to better light conditions after cutting, they were unable to utilize solar energy efficiently at least initially (Pearce et al., 1965; Brown et al., 1966a; Brown et al., 1966b). More recently, Woledge (1971) found that old leaves of large tillers and leaves of small tillers, those previously shaded, increased their photosynthetic rate when they were exposed to light and thus became useful to the growth of the whole sward. Nutrients are released from old leaves which will be used in other sites for further growth (Hopkinson, 1966). It has also been suggested that old leaves may produce growth regulators which may be important in herbage growth after defoliation (Carlson, 1966). In view of these findings it can be concluded that the concept of parasitism of old leaves can no longer be supported. Shading may be one of the causes of senescence, death and decay of plant material situated at the bottom of the sward, but

evidently this is not the only cause. Leaf senescence may be caused by other factors like moisture and flowering. Immediately after severe defoliation, the rate of leaf death is minimal but increases later (Bean, 1964; Hunt, 1971). Hunt (1965) has pointed out that the increase in the senescence, death and decomposition of plant material during growth depends largely on the moisture status. Therefore, seasonal differences may be very marked.

The rates of decay, average leaf age (Pearce et al., 1965), and sheath to lamina ratio (Hunt and Brougham, 1967) all increase at advanced stages of growth.

Tillering Capacity

Although the grass plant is a complex of many shoots, the individual tiller has been considered to be the growth unit of grasses. Productivity depends upon the ability of a plant to initiate tillers and on their development. Within the limits set by genotype, growth of tillers is responsive to the environment. The pattern of tillering of grass swards and the influences of management have been recently reviewed by Langer (1963), Booyesen et al. (1963) and Williams (1970). One of the most important features of tillering is the elevation of the stem apex in flowering tillers in spring. The consequent vulnerability of the apex to removal by grazing or mowing is very important and it has a strong influence on the future development of the sward. Jewiss (1966) stated that stem internodes seldom elongate during vegetative growth; thus the stem apex remains below cutting or grazing height and continues to produce new leaves and tillers. In consequence, dense population of tillers occur in one place and a characteristic tufted habit is formed. An adverse environment may reduce the rate of tillering more than that of leaf production.

During the growing phase the growing point of the shoot remains largely inaccessible and the effect of defoliation may only alter the pattern of tillering by improving the light conditions near the base of the sward. In addition to management and developmental differences in tillering, there are also important genetic differences. The reproductive tiller is also of importance in the total production of swards because in that period a large proportion of the total annual yield is concentrated. This is because of a large increase in the weight of reproductive tillers (Langer, 1958, 1959) since the total number per unit area decreases by the death of weak vegetative tillers under increasing competition. Estimates of relative growth rates of individual tillers show that these are initially higher than that of the whole plant and that this is due to a high initial net assimilation rate (Langer, 1957b). It is believed, that at this stage, part of the dry matter accumulating in the tiller is derived from the parent shoot and is not the product of photosynthesis of its own leaves (Jewiss, 1966). Williams (1964) using labeled CO_2 , has demonstrated that young, fully expanded leaves translocate assimilates to young tillers in the axils of older leaves, and this may continue until four or five leaves are visible on the tiller.

Tillering rates. Milthorpe and Davidson (1966) stated that during the development of a grass sward, tillers are continually emerging, growing, and dying at rates which differ, depending on environmental conditions and stage of development. At any time, there may be a population of tillers ranging in size from dormant buds to elongating flowering stems.

Anslow (1965a) said that when the rate of production of herbage is compared with the number and size of tillers, it appears that in timothy

(Phleum pratense L.), the rate of herbage production is closely related to the size of the tillers at harvest. The lowest rate of production occurred simultaneously with the lowest value of weight per tiller.

Langer et al. (1964) stated that, although new tillers were produced throughout the year the largest monthly total, in both timothy and meadow fescue (Festuca elatior L.) appeared at about the time of ear emergence. Changes in total tiller numbers are affected by variations not only in the rate of production of new tillers, but also in the death rate of tillers and by the interaction of these two factors. Reasons for differences in tillering response to clipping are related to photosynthate supply and to apical dominance (Youngner, 1972). Leopold (1949) stated that cutting of stem apices stimulates tillering by removing the major source of auxin which inhibits lateral bud development. Inactive lateral buds are then free to develop.

Youngner (1972) concluded that defoliation to remove leaves only retards tillering through a reduction of photosynthetically active tissue with a resulting reduction in carbon assimilation. Available carbohydrate supplies may be used first for renewal of the leafage and only after this need has been met are they used for tiller growth. With no further defoliation as new leaves develop, the normal tillering rate is resumed. Compared to no defoliation, stimulation of tillering in these cases could result from creation of a more favorable light environment for tillering. As growth accumulates, tillering may be reduced because of shading of the basal part of the plants or of young tillers by older shoots. Removal of part of the top growth at regular intervals would maintain satisfactory light conditions. Troughton (1957) showed that the number

of tillers produced by a plant was reduced by defoliation. The greater the severity of defoliation, the greater was the decrease in tiller number. However, Jameson and Huss (1959) studying tillering following clipping of elongated and unelongated culms of little bluestem (Andropogon scoparius Michx.) stated that tillering was stimulated by clipping of elongated culms at both mid-summer (July 30) and late summer (August 23) compared to that in the unclipped control. No increase in tillering resulted from the midsummer clipping of unelongated culms but there was a slight increase from the late summer clipping. Mitchell (1954, 1955) reported that leaf emergence rates, as well as tillering rates, were retarded by defoliation. Lambert (1962) stated that defoliation of grasses in closed stands under field conditions may stimulate tillering even though stem apices remain intact. Mitchell (1953a) examined a series of plants and showed that a tiller does not appear until there is one mature leaf above it on the stem. This minimum requirement is little affected by treatment or genotype. Total increment of tillers per week is the product of rate of tillering and the rate of leaf appearance. Alberda (1966a) working with Lolium did not find tillers with more than four healthy leaves. When the fifth leaf emerged the first became yellow and died, even when it was fully illuminated.

Lateral buds. Mitchell (1953b) stated that apical dominance, which is defined as the limitation or complete inhibition by a vigorous terminal bud of the development of lateral buds, has long been recognized. If the terminal bud is removed, one or more of the lateral buds close to the top of the stem usually commence development. Once growing vigorously, these in their turn limit the growth of lateral buds below them. Mitchell (1953b) stated that there is indication that it is not

so much the rate of substrate formation in the leaves as controlled by photosynthesis, or the potential rate of utilization, as controlled by temperature; but the balance between the two, which can determine lateral bud development. This balance is in terms of general level of energy substrate in the plant. If energy level falls, bud inhibition tends to occur, but growth of the tillers already present continues, though at a reduced rate. This implies that the meristematic centers at the apices of the existing tillers receive priority for the limited supply of energy substrate. With young ryegrass plants in the vegetative phase of development, there is little inhibition of lateral buds when the plants are under conditions favoring vigorous growth. Inhibition of the lateral buds tends to be induced by shading or reduction of the period of illumination partial defoliation, or high temperature.

Temperature. Mitchell (1956) using climate control cabinets with the same regime of daylength and light intensity, determined the growth of several species of grass at constant temperatures from 7.2° to 35° C. He concluded that the growth rate of the tillers of most species changes little over a comparatively wide range of temperatures, although there are distinct differences among species.

Mitchell and Lucanus (1960) studied combinations of day temperatures of 15.5, 11.4, and 7.2° C with night temperatures of 7.2, 4.4, and 1.7° C. Within these ranges, lowering the day temperature reduced the growth of individual tillers more than did lowering night temperature. The rate of tillering, however, was little affected by reducing day temperature, whereas with some species lower night temperatures were associated with increased rates of tillering.

Light. Intensity and duration of light has been studied probably more than any other factor in relation to tillering. Pritchett and Nelson (1951) grew brome grass (Bromus inermis Leyss.) in the greenhouse under different light intensities. The plants experienced no moisture stress but were with and without supplemental N fertilization. Top growth and tillering were increased by the higher light intensities. Nitrogen fertilization stimulated tillering only if the light intensity was above the 422 foot candle level.

Auda et al. (1966) concluded that orchardgrass responded both to reduced light intensity and to long day by a decline in tillering. When a 9-hour photoperiod was extended to 18-hour by low-intensity illumination, the rate of tillering was reduced by more than 50% during 6 weeks of growth. These authors suggested that tillering was more associated with light energy than with photoperiod. Mitchell (1953a) stated that the quantity of light energy appears to be the chief determinant of number of tillers formed. Ryle (1966a, b) investigated the effects of photoperiod on growth and tillering using S.37 cocksfoot, (Dactylis glomerata L.), S.215 meadow fescue and S.24 perennial ryegrass (Lolium perenne L.) grown vegetatively either in greenhouse or in growth cabinet. In both situations the results were similar, showing that the number of tillers decreased with increase in photoperiod. Plants under long days tended to have fewer but larger tillers than those under short days. He observed a relationship between increase in leaf surface expansion and decrease in tillering as photoperiod increased. This general relationship suggested a correlated effect of photoperiod on growth of the entire plant.

Interaction of factors. Mitchell (1953b) presented evidence to show that a rise in temperature, reduction in light quantity, or partial defoliation can induce bud inhibition in ryegrass. He noted that a change in any one factor is conditioned by the level of the other environmental factors and by genotype. Templeton et al. (1961) studied the effects of light and temperature on early growth of tall fescue (Festuca arundinacea Schreb.). They found interactions among environmental and genetic factors. With regard to tillering, the following interactions were important: photoperiod x temperature, photoperiod x age of plant, photoperiod x plant source, temperature x age of plant, and temperature x duration of treatment. Nittler et al. (1963) stated that light intensity was associated with greater differences in number of tillers than was temperature. Varietal distinctions were small when light was abundant but were increased under regimes of reduced light obtained either by low intensity or short photoperiod.

Stage of plant development. It has generally been accepted that a tiller which gains advantage will dominate and even cause the death of some smaller tillers due to competition for light. However, Sagar and Marshall (1965) indicated that tillers within a plant during vegetative growth do not compete but encourage each other to some extent. Langer (1957b) stated that the smaller the tiller, the greater is its relative growth rate (R.G.R.).

The growth of other types of tillers is inhibited by hormonal influences from the primary reproductive tillers to which they are attached (Leopold, 1964). As the sward nears reproductive maturity, these inhibiting influences diminish and disappear leading to the production of new tillers (Langer, 1956). When the apices of stem tillers

are elevated much above ground level, they may be removed by severe grazing. This also removes any inhibition and regrowth can come from buds and from tillers with undamaged apices. Booysen et al. (1963) indicated that in most species elevation of the apex occurs early in reproductive growth, but there are some species in which elevation of apices occurs during vegetative growth.

Regrowth of herbage may be slower if it depends on regrowth from secondary reproductive tillers or smaller vegetative tillers rather than from partially defoliated primary reproductive tillers with intact apices (Milthorpe and Davidson, 1966). The reason for this is the larger growth rates of elongating reproductive shoots. However, swards units do not have a uniform growth rate over a long period of time, for example, reproductive tillers have much higher growth rates when elongating than after flower emergence.

If all of the apices of the primary reproductive tillers are removed and environmental conditions remain favorable for flowering, some of the vegetative apices may differentiate (Langer, 1957a). The reproductive stage in plants develops in response to environmental conditions among which temperature and photoperiod are especially important. Depression of tillering near the onset of heading, therefore, may be in part a response to external factors (Laude, 1972). Laude et al. (1968) investigated tillering in Hardinggrass (Phalaris tuberosa Batt. & Trab. var. stenoptera) in a greenhouse by comparing at the same time vegetative and reproductive plants from the same clone. Rate of tillering was alike in both lots until 2 weeks before head emergence. Then for approximately 4 weeks from the time of head emergence, the reproductive plants developed no new tillers while the vegetative plants continued

to initiate tillers at near the previous rate. Resumption of tillering in headed plants occurred about 2 weeks after heading. Substantial number of tillers died near the onset of heading.

Management. There are several ways to influence tillering in grasses. One of these is plant spacing. Kaukis and Reitz (1955) reported that oats with two different spacings in the row (6.3 and 12.5 cm), 75% more grain was produced at the 12.5 cm spacing; they attributed 77% of this increase to increased tillering. One of the most important external factors in tillering is the effect of the animal on the plant. Grazing and defoliation studies have provided useful information on herbage removal effects. Edmond (1958, 1962, 1963) studied the effect of animal trampling on plants. Trampling was noted to reduce herbage yields by reduced plant vigor and fewer tillers. Direct effects of trampling on the plant were root damage, plants buried in mud, and crushing of leaves and stems. Damage was greatest when the soil was wet.

Langer et al. (1964) stated that like plant populations the tiller numbers were significantly higher under frequent cutting than under hay management. With timothy, infrequent cutting resulted in little more than half the plant population of frequently cut swards. Within each species the number of plants per m^2 was roughly inversely related to the number of tillers/plant in frequently cut swards; there were more plants and tillers per unit area, but significantly fewer tillers/plant than in those cut for hay. Smith (1968) stated that defoliation of tall tillers may improve the position of small ones for further growth, not only by removal of smaller amounts of tissue but also by improvement of light conditions.

Seed yield. Ryle (1966c) considered as components of final seed yield, (a) number of fertile tillers per unit area, (b) number of florets per ear, (c) seed set and seed weight. The time of flowering in nearly all grasses is determined by the length of day. However, the effect of daylength can be modified by temperature. Even after flower initiation has taken place, daylength and temperature continue to influence the rate of inflorescence development and the rate of stem elongation. In most grasses the time from initiation to ear emergence ranges from 25 to 70 days, depending on photoperiod, temperature, and genotype (Langer, 1972). The environment not only determines the time of ear emergence but also the size of the individual inflorescence.

Langer (1972) stated that tillers arising in the autumn and early winter tend to accumulate leaf primordia and, by the time the days are long enough in the spring for induction to occur, they possess many sites at which spikelets can be formed. Later formed tillers are induced at the same time, but because of their later start, will not have as many sites available for conversion. The largest number of spikelets is thus commonly found in the oldest tillers and the smallest in those which do not arise until the advent of flower-inducing photoperiods (Ryle, 1966c). Thus, the number of seeds produced by an inflorescence will depend on the number of spikelets formed.

The number of ear-bearing or fertile tillers is a very important topic related to seed yield. Langer and Ryle (1959) stated that when it comes to ability to flower and the size of the inflorescence, the position of the tiller appears to be very important. In timothy, primary tillers were found to have a higher probability of producing an ear than

secondary tillers arising at the same time and in the same environmental conditions.

In studies with single plants of several species, it has been found that severe lack of N will prevent ear production, although vegetative growth may continue at a lower rate. Increasing the N supply stimulates tiller and inflorescence production (Langer, 1972).

Langer and Lambert (1959) stated that tillers formed in the early autumn provide the bulk of the ear-bearing tillers the following spring. Tillers arising at successively later dates have a proportionally smaller chance of developing an ear. The total number of florets in the inflorescence depends on the number of spikelets. The date of origin of the shoot also appears to affect the number of florets developed. In ryegrass, shoots arising in early autumn developed ears with more florets per spikelet than comparable shoots appearing in spring (Ryle, 1966c).

Two other factors which exert effects on final ear size are temperature and daylength. In single plants of timothy (Ryle and Langer, 1963) and ryegrass (Ryle, 1965) the total number of florets in main-stem ears decreased as daylength or temperature increased. When initiation is delayed by either unfavorable daylength or temperature, the inflorescence is subsequently found to contain more spikelets.

Analyses of the proportion of florets which set seed in ears of ryegrass in the field showed a slight fall in fertility from the base to the tip of the ear, and much more marked fall from the base to the tip of each spikelet (Anslow, 1963). Even under favorable conditions, the proportion of florets which set seed seldom exceeded 70% and was often less (Ryle, 1966c). Anslow (1964) has shown that within the

inflorescence of ryegrass, the basal spikelets developed slightly heavier seed than the more terminal ones, and within spikelets, seeds from the basal florets were heavier than comparable ones developed in terminal florets. It has been shown that generally only a small proportion of total tillers produced an inflorescence, and this proportion decreased with increases in the number of tillers per plant (Lambert and Jewiss, 1970).

Nutrient Reserves

It has been generally accepted that the rate of recovery of a defoliated plant depends on the level of nutrient reserves, especially carbohydrate reserves. The role of reserve substances in plant regrowth has been reviewed by May (1960) and Milthorpe and Davidson (1966). The former author doubted the importance of water soluble carbohydrates in supporting plant regrowth. However, Ehara et al. (1966) showed that carbohydrate reserves assimilated as labeled CO_2 by bahiagrass were used in the formation of leaves for 6 days after herbage removal. Davies (1965) and Ward and Blaser (1961) have established beyond doubt that the concentration of soluble carbohydrates in herbage does influence regrowth after defoliation.

Smith and Silva (1969) found that between the day when tops were removed and the date of lowest carbohydrate level in the roots, 15% of the total nonstructural carbohydrates (TNC) was used in root respiration, and 66% was used in production of new roots and crown. Smith and Marten (1970) found that 40% of the TNC in alfalfa roots had been translocated to the shoots by the time they were 15 cm tall.

Plants that are defoliated by grazing or clipping several times a year must have energy in readily accessible form to generate new

tillers. Carbohydrate reserves are thought to be used by plants as substrate for growth and respiration. Graber et al. (1927) concluded that new top growth, especially in the early stages of regrowth of alfalfa (Medicago sativa L.) plants, was initiated and developed largely at the expense of previously accumulated organic reserves. Adequate carbohydrate reserves are important in perennial plants for winter survival, early spring growth initiation, and regrowth after herbage removal when photosynthesis is not enough to meet demands. Bula and Smith (1954) and Graumann et al. (1954) found that as much as 50% of the available carbohydrate stored in the roots during fall was used in respiration during winter. Thus, plants low in carbohydrate reserves are most likely to be injured or killed (Smith, 1964).

Smith (1969) suggested that the term "total nonstructural carbohydrates" (TNC) be used because it is more applicable to both animal and plant investigations. Nonstructural carbohydrates—reducing sugars (glucose and fructose), nonreducing sugar (sucrose), fructosans and starches—are the major reserve constituents. Structural carbohydrates—hemicellulose (pentosans and Hexosans), and cellulose—are not considered to provide significant reserves (McCarty, 1938; Sullivan and Sprague, 1943; Weinmann, 1948).

Predominant carbohydrate reserves stored by temperate grasses are sucrose and fructosans, whereas those of subtropical or tropical grasses are sucrose and starch (Weinmann and Reinhold, 1946; Smith, 1968; and Ojima and Isawa, 1968). Nonstructural carbohydrates may be stored temporarily in all plant parts. Troughton (1957) concluded that the underground organs were the major storage parts for carbohydrate

reserves. However, many other studies have revealed that the major storage part is generally in the stem bases (Sullivan and Sprague, 1943; Baker and Garwood, 1961). Plants go through periods when carbohydrates are used and when they are stored; a cyclic pattern occurs between early growth and maturity. The accumulation of carbohydrate reserves in plant tissue is a dynamic system of energy balance between photosynthesis and respiration. Blaser et al. (1966) reported that carbohydrate reserves of orchardgrass and bermudagrass grown in growth chambers decreased when growth and respiration demands were greater than photosynthesis rates and increased otherwise.

Temperature and the availability of water and nutrients affect the seasonal variation of carbohydrate reserves as much as they affect growth. Robison and Massengale (1968, 1969) and West and Prine (1960) reported an association between high temperatures and low accumulation of carbohydrate reserves due to high respiration losses.

Nitrogen applied at low to moderate rates increased carbohydrate reserves through its effect on increasing leaf area, and hence increased photosynthesis (Murata, 1969). The effects of grazing and clipping on carbohydrates are similar but not identical. Grazing may be less detrimental than clipping if some ungrazed tillers are left on a plant while others are removed, thus allowing for the transfer of carbohydrates from ungrazed to grazed tillers. Carbohydrate reserves of tall fescue grass in Missouri increased as the unclipped tillers per plant increased from 0 to 30% (Matches, 1966) and carbohydrate reserves of dallisgrass (*Paspalum dilatatum*, Poir) in Mississippi also increased as the unclipped tillers increased from 0 to 10% (Watson and Ward, 1970).

Begg and Wright (1964) gave the following order of priority in the utilization of assimilates in vegetative swards (a) leaf initiation and expansion, (b) shoot growth and internode elongation, and (c) accumulation of reserves. The maximum import of assimilates to a single leaf coincides with the period of its maximum growth rate (Doodson et al., 1964). Before the leaf has fully expanded, importation stops and the export of product begins. Thus, fully expanded leaves normally do not import assimilates (Williams, 1964). After defoliation the use of the stored materials for further growth will depend largely on the amount of leaf tissue remaining and on the level of reserves. Although individual tillers in vegetatively undisturbed swards may behave as if they were independent, with little transference of assimilates between them (Sagar and Marshall, 1965), defoliation demonstrates the presence of organic interconnections because there is a considerable increase in translocation between the different plant parts, either leaves (Hartt et al., 1964) or tillers (Sagar and Marshall, 1965). Thus, growth may come either from products direct from photosynthesis or from reserves stored in the stems (Matches, 1966). Radio-carbon studies (Marshall and Sagar, 1965) have confirmed that substantial translocation from intact to defoliated tillers is fairly short-lived. However, it occurs at the important initial stage of regrowth and may have a particularly important role before new centers of active metabolic activity can be developed. Youngner and Nudge (1976) stated that the accumulation of nonstructural carbohydrate appears to be directly related to conditions that affect the incorporation of photosynthate into structural elements. In unclipped plants lowest percentages of nonstructural carbohydrates

were obtained at temperatures that yielded the highest weights of shoots dry-matter. Frequent defoliation reduces nonstructural carbohydrate accumulation and restricts all aspects of growth by reducing the plants ability to assimilate carbon.

Davidson and Milthorpe (1965) concluded that the amount of growth made during the first few days is related to amounts of carbohydrates present but over long periods other factors dominate. Defoliation by grazing or cutting reduces the amount of the leaf surface and, thereby, the income from photosynthesis. The reserve carbohydrates then provide one pool which is a possible source of substrates for growth and respiration. The extent of the contribution from this source would be expected to depend upon the size and activity of photosynthetic system. A greater contribution would be expected from severe than from light defoliation, and immediately following rather than some days after defoliation, and at optimum rather than low temperatures, and with high rather than with low contents of N.

MATERIALS AND METHODS

In October 1977, seeds of two varieties of ryegrass (Lolium multiflorum Lam.), two of white clover (Trifolium repens (L.)), and one of red clover (Trifolium pratense (L.)) were prepared for seeding in November. The species used in this experiment and their combinations are shown in Table 1.

Experimental Area

The area used was a typical flatwoods site, located at the Beef Research Unit (BRU) approximately 24 km northeast of Gainesville, Florida, 30° N latitude and 82°5' W longitude. The experimental area was oriented north-south with a very gentle slope. The soil is classified as Myakka fine sand (sandy, siliceous, hyperthermic Aeric Haplaquod).

The fertility of the area is generally low. The average organic matter content of the soil from the experimental area on April 1976 was 2.77; the average pH was 4.0; and NH_4OAc (pH 4.8), extractable nutrients were for Ca, 75; Mg, 24; P, 0.75; and K, 15 ppm. Climatological data for the experimental period and for the last 70 years are shown in Fig. 1 and Fig. 2, respectively.

Table 1. Ryegrass-clover combinations and varieties seeded in each treatment in November 1977.

Treatment	Varieties and Combinations
1	Florida reseeding ryegrass and Florida selection white clover
2	Florida reseeding ryegrass and Nolin's white clover
3	Florida reseeding ryegrass and Nolin's red clover
4	Florida reseeding ryegrass alone
5	Gulf ryegrass and Florida selection white clover
6	Gulf ryegrass and Nolin's white clover
7	Gulf ryegrass and Nolin's red clover
8	Gulf ryegrass alone
9	Florida selection white clover alone
10	Nolin's white clover alone
11	Nolin's red clover alone
12	Check (no clover or ryegrass)

Land Preparation

Recently cleared land at the Beef Research Unit was cultivated and leveled in the summer of 1976. Ground calcitic limestone was applied at the rate of 3400 kg/ha and dolomitic limestone was also applied at 3400 kg/ha on 9 November 1976. Nitrogen fertilizer was applied on 25 July 1977, 13 December 1977, and 7 March 1978 for a total N application of 83.3 kg/ha. Mineral fertilizers were applied on two occasions, 10 November 1976 and 13 December 1977, for a total of 47.7 kg/ha of P, 90.6 kg/ha of K, and 31 kg/ha of FTE.[†] After

[†] Contains B, 0.066; Cu, 0.107; Fe, 0.291; Mn, 0.175; Mo, 0.024; Zn, 0.167%.

Fig. 1. Climatological data for the Beef Research Unit during the period (October through July). Monthly average for 1977-1978.

Fig. 2. Climatological data for the Beef Research Unit during the period (October through July). Monthly average for the last 70 years.

liming and the first application of fertilizer, the area was tilled with a rototiller to assure a more uniform distribution of the material.

Size of the Experimental Area

The total area was 1.1 ha. Twenty-two pastures, each 10 x 50 m were provided. The entire experimental area was seeded to 'Pensacola' bahiagrass at the rate of 28 kg/ha during the spring prior to the seeding of ryegrass and clover. The borders and areas between pastures were seeded to 'Argentine' bahiagrass.

Pasture Establishment and Management

On 31 October 1977 before seeding the ryegrass-clover, the area was sprayed with paraquat at the rate of 1.2 l/ha. On 18 November, the area was burned, and on 21 November 1977, the area was chopped with one pass of a 'Marden Chopper.' The ryegrass-clover combinations were then seeded in plots 2 x 10 m across each pasture. The seeding operation required 2 days. The first replication was seeded on 22 November, and the second replication on 28 November 1977. The appropriate amount of seed for each plot was weighed into a separate envelope. The seeding rates used are shown in Table 2. On the seeding day, the seeds were distributed by being broadcast with a mixture of sand in their appropriate plots, which had been previously randomized. The legumes were inoculated with wide-spectrum inoculant B (Nitragin Company, Milwaukee) in the field. The legume seeds were wetted with a pellet gel, and a rhizobia powder was applied, shaken, and left to dry in the closed envelope. After being mixed with sand, the seeds were broadcast. After broadcasting the seed, one pass of a culti-packer seeder was made.

During the period from 28 November 1977 until 22 March 1978, the area was mob-grazed by cattle to a prescribed residue level in from 1 to 4 days. The experiment was designed to study the effect of five

rest periods during the April through May period, and grazing pressure applied during the following September through October period. The experimental design was a modified central composite response surface with two experimental variables, each at five different levels. Since only certain design points were replicated, the part of the research reported in this dissertation has unequal numbers of replications. The data were analyzed as a split-split plot design and includes only the effects of rest period on treatments 1, 4, 5, and 8 (Table 1).

Table 2. Seeding rates used in the different combinations of ryegrass and clover.

Species		Seeding rates
		kg/ha
Ryegrass	in mixture	16.8
	alone	33.6
Nolin's red clover	in mixture	8.9
	alone	17.9
Nolin's white clover	in mixture	3.4
	alone	6.8
Fl. sel. white clover	in mixture	3.4
	alone	6.8

The five rest period dates used and the pasture numbers in which each one was assigned are shown in Table 3. Each pasture was grazed until the day before each rest period. For example, pasture numbers 5, 7, 9, 11, 15, and 22 were grazed until 3 April 1978. In the afternoon of that day the animals were removed from these pastures and the pastures were allowed to rest for 5 weeks. After 5 weeks the pastures were again grazed. This same procedure was repeated in each of the five rest-period dates. All pastures were grazed under the same grazing pressure.

Table 3. The five rest-period starting dates applied from April through May 1978, and their respective pastures assignments.

Rest period starting date	Code	Pasture numbers
April 4	1	5, 7, 9, 11, 15, 22
April 18	2	18, 20
May 2	3	2, 8, 10, 13, 17, 21
May 16	4	6, 19
May 30	5	1, 3, 4, 12, 14, 16

Field Measurements

No measurements were taken until April 1978. The experimental measurements were started on 25 April 1978 when samples for percentage crude protein (CP) and total nonstructural carbohydrates (TNC) were collected for laboratory analysis. On the same day, samples for leaf-area measurements were also collected. On 2, 3, and 4 May 1978, the number of tillers per $1/4 \text{ m}^2$ were counted as well as the number of tillers with seed heads. Lengths of the seed heads were also measured.

For the first rest period starting 4 April 1978, samples for CP, TNC, and leaf area were collected on the last day of the third week after the start of the rest period. All other measurements were taken on the first two or three days of the fifth week after the beginning of the rest period. All samples collected and measurements taken refer to the ryegrass component of treatments 1, 4, 5, and 8 mentioned above. The same procedure was followed for the other rest periods starting on 18 April, 2 May, 16 May, and 30 May 1978. The samples for CP, TNC, and leaf area were

collected on 25 April for the first rest period; on 9 May for the second rest period; on 23 May for the third rest period, on 6 June for the fourth rest period, and on 14 June for the fifth rest period.

Sampling Procedure

Carbohydrate, CP, and Leaf:Stem Ratio

These samples were collected on the last day of the third week after each rest period had started. Carbohydrate, CP, and leaf:stem ratio were analyzed from the same sample. This plant material was collected for all five rest periods always in the same manner. These samples were also collected about the same time of the day for the different rest periods. The general procedure used was as follows: Tillers of ryegrass were collected throughout each plot of each of these treatment combinations (1, 4, 5, and 8; Table 1).

The tillers were cut off at ground level, placed in paper bags, and then into an iced styrofoam chest. Immediately after the four samples from each pasture had been collected, they were stored in a freezer until the different samples were prepared for the laboratory analyses. The length of 20 tillers out of 120 tillers from each sample was measured to the nearest cm. These samples were stored in a freezer to arrest any respiratory enzymatic activity which could have occurred. The same procedure was followed when collecting this kind of sample in each subplot within the 22 pastures.

Leaf Area

Four samples were taken in each pasture-rest period combination. For each ryegrass variety two samples were collected, one from the

subplot where the grass was growing alone and the other from the subplot with grass-clover mixture. These samples were collected and immediately brought to the laboratory. In the laboratory the leaves were separated from each tiller; the leaves were passed through a leaf area meter, where the leaves from 10 to 15 groups of 10 tillers were measured in cm^2 .

Tiller Measurements

During the fifth week following initiation of each rest period a set of ryegrass samples was collected for tiller measurement. The total number of ryegrass tillers per $1/4 \text{ m}^2$ was counted, as well as the number of tillers with seed heads. A subsample of 15 seed heads was collected and the head length was measured to the nearest cm. The number of seed heads with ripe seeds, in milk stage, and in anthesis were also recorded for each treatment, but only during rest periods 3, 4, and 5. No records were made during rest periods 1 and 2 because no ripe seeds were found in these rest periods. The average weight of seeds/head and weight/100 seeds were also recorded for each treatment in rest periods 3, 4, and 5.

Sample Preparation and Analyses for Carbohydrate, CP, and Leaf:Stem Ratio

Each sample consisted of 120 tillers, and each sample was subdivided into three at this stage. Each of the 120 tillers per sample was separated from their leaves. These leaves were used for CP determination.

The carbohydrate samples were taken from the 10 cm of the bottom part (stubble) of each of the 120 tillers. After this 10 cm had been cut from each tiller, they were stripped of leaf sheath and only the clean stem was used for the TNC determination. The remainder of each tiller (tops) was used for CP in the stem portion. Each of these three portions was then placed in a paper bag and dried in a forced-air drier at 65° C for 48 hours.

Later, each portion was weighed and its dry-matter recorded. The dry-matter weight of stubble plus tops made up the stem dry-matter which was used with the dry-matter weight of the leaves to obtain the leaf: stem ratio relationship. After weights were taken, all samples were ground in a Christy-Norris mill to pass a 1-mm screen. The ground samples were placed in whirl-pak plastic bags, sealed, and stored at room temperature for subsequent analyses.

The samples were analyzed for TNC and total N. Crude protein (CP) was obtained by multiplying total N by 6.25 and the results were expressed on dry-matter basis. The procedure for N as outlined by Schuman et al. (1973) was used with the following modifications: a 0.1 g dried and ground sample was placed in each digestion tube along with 3.4 g of prepared catalyst (90% anhydrous K_2SO_4 + 10% anhydrous $CuSO_4$) 2 or 3 Alundum Boiling chips, and 10 ml of concentrated H_2SO_4 . The contents were mixed in a vortex and a total of 2 ml of 30% H_2O_2 was carefully added in 0.5, 0.5, and 1 ml increments. The samples were allowed to stand until reaction of H_2O_2 ceased. The samples were digested at 420° C in the digestion block for 2 hours, after which the samples were diluted, brought to 75 ml volume, and the N concentration was read in the Auto Analyzer.

Extraction of TNC from dried, ground plant stubble followed the enzymatic procedure modified by Carter et al. (1973). The general procedure used was as follows: a 0.1 g ground sample was placed into a 50 ml Erlenmeyer flask and heated in boiling water bath with 5 ml deionized water for 10 min. to gelatinize the starch. Five milliliters of 0.2 M acetate buffer, pH 4.8 were added to bring the volume in the flask to 10 ml of 0.1 M acetate buffer, One milliliter of the following enzyme mixture was placed in each flask to digest the 0.1 g of ground tissue. The enzyme mixture consisted of 1 ml invertase concentrate in glycerol; 1 g amyloglucosidase; 0.30 g takadiastase; 10 ml of 0.1 M (pH 4.8) acetate buffer; 2.0 ml, 80% ethyl alcohol solution with a few grains of thymol dissolved; and 37 ml of deionized water. This enzyme mixture is enough for 48 flask. The thymol solution is used to prevent microbial growth during incubation. After enzyme addition, all samples were incubated at $40^{\circ} \text{C} \pm 1^{\circ} \text{C}$ for 48 hours. After which 1.1 ml 1N HCl acid was added and the flasks were heated in a boiling water bath for 20 min. The samples were then centrifuged at 1500 rpm for 15 min. and at 2000 for 30 min. The supernatant liquid containing the TNC extract was decanted and immediately analyzed using the Nelson-Somogyi copper reduction method (Nelson, 1944; Somogyi, 1945). Duplicate analyses were performed on each field sample.

The data were analyzed by analysis of variance and regression. Because rest period varied with respect to time of the year at which it was applied, regression analysis was also performed in an attempt to understand better the variation of the different parameters throughout the season. Attempts to find a predictive polynomial model which

would fit the data were abandoned because the best fitting polynomial was of fourth degree and was biologically meaningless. A linear or a quadratic equation was used as a first approximation model. The quadratic model was used only if it provided acceptably higher r^2 than that of the linear model. For the regression analysis all sources of variations other than rest period were pooled in the error term. Since they were not significant ($P < 0.05$) in the analysis of variance, it was assumed that the relationship would be the same in the regression analysis. However, the proposed equations should be used with caution since they were considered only as a first approximation model and because the test for lack of fit was significant. Better models may exist.

In all regression equations the independent variable (X) is always equal to two weeks, because the interval between two rest-period starting dates was always 14 days.

RESULTS AND DISCUSSION

Number of Tillers per Unit of Area

The statistical analysis detected an interaction ($P < 0.01$) between rest period and legume (Appendix Table 1). The number of tillers per $1/4 \text{ m}^2$ ranged from 387 (rest period 1) to 46 (rest period 5) whenever the two ryegrass varieties were grown alone, and from 263 (rest period 1) to 26 (rest period 5) when grasses were grown with white clover (Appendix Table 2). The means of number of tillers/ $1/4 \text{ m}^2$ for legume (present or absent) were subjected to Duncan's multiple range test at the 0.05 level for each rest period (Appendix Table 2).

Since rest period interacted with the legume, separate analyses were performed for grasses grown alone and for grasses with white clover. These analyses appear in Appendix Table 3, and suggest that the relationship between rest period and number of tiller per unit of area is linear, at least as a first approximation (Fig. 3).

Grasses grown alone. The general trend was to decrease the number of tillers/ $1/4 \text{ m}^2$ as the season advanced (Fig. 3). Even though the test for lack of fit was significant ($P < 0.05$), the linear equation was considered a good predictor since $r^2 = 0.82$ (Appendix Table 3).

Grasses grown with white clover. There was also a decline in the number of tiller/ $1/4 \text{ m}^2$ with later rest periods. Despite the fact that the test for lack of fit was also significant ($P < 0.05$) the data were also fitted to a straight line since $r^2 = 0.79$ (fig. 3 and Appendix Table 3).

Fig. 3. Relationship between tiller density and rest period during the experimental period (April through June 1978).

Looking at both estimated equations (Appendix Table 3 and Fig. 3) for number of tillers per unit of area, one can see that the decline in number of tillers was faster when the grasses were grown alone ($45 \text{ tillers}/1/4 \text{ m}^2/\text{week}$) than when grasses were grown with the legume ($31 \text{ tillers}/1/4 \text{ m}^2/\text{week}$). This explains why the tiller density of the grasses did not differ ($P < 0.05$) after rest period 3, even though this density was 387 and 263 tillers/ $1/4 \text{ m}^2$, respectively, for grasses alone and for grasses with the legume. The decline in the number of tillers was more noticeable between rest period 3 and rest period 4 and the tiller population almost stabilized after that (Fig. 3).

This decline in the number of tillers per unit of area in the sward is supported by Albuquerque (1966) who found a decrease in the number of tillers of tall fescue during the growing season. He concluded that this decrease coincided with increase in stem elongation of the grass. Langer et al. (1964) working with timothy and meadow fescue found sharp decreases in the number of tillers from April to June. He also concluded that changes in total tiller numbers were affected by variation in the rate of production of new tillers and the death rate of tillers. Dead tillers were found in largest amount before ear emergence, and the death of tillers was attributed to depletion of carbohydrate reserves by frequent removal of leaf area. Alberda (1966b) stated that decreased carbohydrate in perennial ryegrass tillers caused marked reductions in tillering.

Probably several factors were interacting to cause the decrease in tiller number during spring. Mitchell (1953b, 1955) and Bean (1964) found that decrease in the number of tillers was caused by reduction in light intensities. Langer (1958) reported that total number of

of tillers per unit of area decreased continuously and by 7 July it had fallen to about one-half of the level measured on 14 April. In our research, the number of tillers in the rest period 1 was 9 times the number of tillers in rest period 5. Langer (1959) concluded that the decline in tiller numbers from early spring to mid-summer could be reduced by frequent defoliation.

Lambert (1962) and Langer et al. (1964) related higher tiller population and increased tillering to herbage removal and less light competition in frequently cut swards of timothy and meadow fescue. However, this desirable effect of frequent defoliation may be overcome by the undesirable effect of severity of defoliation. Troughton (1957) showed that the number of tillers produced by a plant was reduced as severity of defoliation was increased.

In this research, all pastures were severely grazed, perhaps overgrazed, and this may be the reason why tiller population stability at the end of the grazing season was reached at relatively low tiller densities. The number of tillers in the sward remained almost constant for rest period 4 (54 and 46 tillers/ $1/4 \text{ m}^2$) and rest period 5 (41 and 26 tillers/ $1/4 \text{ m}^2$) for grasses growing alone or with white clover, respectively. This was an equilibrium of tiller populations at about the same tiller density found by Huokuna (1966) in meadow fescue. However, tiller density was low, and consequently the dry matter yield could not support sufficient animals for a profitable system.

Percentage of Tillers with Seed Heads

The interaction (Appendix Table 1) between rest period and legume was found to be significant ($P < 0.05$). Tillers with seed heads ranged from 30.4 (rest period 1) to 100% (rest period 5) for grasses alone

and from 35 (rest period 1) to 100% (rest period 5) for grasses grown with white clover. The means of percentage of tillers with seed heads for legume (present or absent) were subjected to Duncan's multiple range test at the 0.05 level for each rest period (Appendix Table 2).

Results of the regression analysis are presented in Appendix Table 4. The relationship between percentage of tillers with seed heads and rest periods was very similar whether the grasses were grown alone or with the legume (Fig. 4).

Grasses grown alone. The percentage of tillers with seed heads increased with later rest periods (Appendix Table 4 and Fig. 4). A linear equation was fitted to the data, and in spite of the test for lack of fit had been significant ($P < 0.01$), the equation was considered a good predictor since $r^2 = 0.89$.

Grasses grown with white clover. The general trend was to increase the percentage of tillers with seed heads as rest periods advanced into the season (Appendix Table 4, and Fig. 4). The variation in the percentage of tillers with seed heads was well explained by a linear equation ($r^2 = 0.90$).

The rate of increase in tillers with seed heads/week was about 8.8 percentage units.

Percentage of Tillers in the Anthesis Stage

Results of the statistical analysis showed that the percentage of tillers in the anthesis was not the same ($P < 0.05$) for the two ryegrass varieties (Appendix Table 5). Florida Reseeding and Gulf ryegrass had respectively 4.1 and 7.8% of their tillers in the anthesis stage for the three rest periods (3, 4, and 5). There were 4.9 and 7.0% of

Fig. 4. Relationship between percentage of tillers with seed heads and rest period during the experimental period (April through June 1978).

the tillers in anthesis when grasses were grown alone and with white clover, respectively. The percentage of tillers in the anthesis increased from 8.7 (rest period 3) to 15.9 (rest period 4) and then decreased to 0 in rest period 5 (Fig. 5).

Percentage of Tillers with Seed in the Milk Stage

Results of the statistical analysis showed that the percentage of tillers with seed in the milk stage was not the same ($P < 0.01$) for all rest periods (Appendix Table 5). The general trend was to decrease the percentage of tillers with seed in the milk stage with later rest periods (Fig. 5). Grasses subjected to rest periods 3, 4, and 5 had 72.1, 18.6, and 1.4% of their tillers with seeds in the milk stage. Grasses growing alone averaged 34.6% of their tillers with seed in the milk stage and 33.7% when growing with the legume.

Percentage of Tillers with Ripe Seeds

The percentage of tillers with ripe seeds was not the same ($P < 0.01$) for all rest periods (Appendix Table 6). Grasses from rest periods 3, 4, and 5 had 19.2, 65.5, and 98.5% of their tillers with ripe seeds (Fig. 5). The two ryegrass varieties had 60.4 and 59.3% of the tillers with ripe seeds when they were grown alone and with the legume, respectively.

Since percentage of tillers with seed heads in anthesis, in milk stage, and with ripe seeds are all interdependent, and an increase in one necessarily requires a decline in the other, they will be discussed together. Measurements on these parameters were started only on rest period 3. In Fig. 5 the averages for each rest period were plotted and the points for each parameter were connected in an attempt to show the trend of each one. As expected, the percentage of tillers with

Fig. 5. Relationship between percentage of tillers with seed heads in anthesis, in milk stage and with ripe seeds, and rest period during the experimental period (April through June 1978).

Fig. 6. Relationship between seed weight/tiller and rest period during the experimental period (April through June 1978).

ripe seeds increased with later rest periods. The percentage of tillers with seeds in the milk stage decreased sharply between rest periods 3 and 4 and moderately between rest periods 4 and 5, and tillers in anthesis increased from rest period 3 to 4 and then decreased to 0 in rest period 5. However, it did not follow a regular pattern like the others; tillers in anthesis always made up less than 20% of the total, throughout the three rest periods in which they were counted.

Seed Weight/Tiller

Results of the statistical analysis showed that the seed weight/tiller was not the same ($P < 0.05$) for all rest periods. A difference ($P < 0.05$) was detected between the two ryegrass varieties as well as an interaction ($P < 0.05$) between rest period and the legume (Appendix Table 6). The Florida Reseeding and the Gulf ryegrass seeds weighed 0.076 g/tiller and 0.081 g/tiller, respectively. The means of seed weight/tiller for legume were subjected to Duncan's multiple range test at the 0.05 level for each rest period (Appendix Table 7). Measurements were only started in rest period 3, and because of that no prediction equation was attempted due to the reduced number of points. The general trend in the seed weight/tiller was to decrease as the time of imposed rest period advanced into the season (Fig. 6). The seed weight decreased from 0.084 g/tiller (rest period 3) to 0.074 g/tiller (rest period 5). The weight/100 seed was 0.17, 0.13, and 0.11 g, respectively, for rest periods 3, 4, and 5.

Length of the Seed Head

Results of the statistical analysis showed that length of seed heads was not the same ($P < 0.01$) for all rest periods (Appendix Table 8). The length of the seed head ranged from 14.5 (rest period 1) to 6.1 cm (rest period 5). Seed head of the grasses was shorter when grown

alone (9.6 cm) than when grown with the legume (10.4 cm). There was no difference ($P < 0.05$) in length of seed head for the two varieties of ryegrass. The length of seed head of the two ryegrass varieties declined with later rest periods (Fig. 7) at a rate of about 1.1 cm/week during April through June. As a first approximation a linear model was selected ($r^2 = 0.85$), even though the test for lack of fit had been significant at the 0.01 level (Appendix Table 9). The decline in length of the seed head was relatively constant after rest period 3, the sharpest decline between rest periods 1 and 3 (Fig. 7).

Length of Stem

The stem length of the grasses was also affected by the different rest periods (Appendix Table 8 and Fig. 8). The stem length ranged from 27.2 (rest period 3) to 21.3 cm (rest period 5). Contrary to what happened with the length of seed head, length of the stem was not affected ($P < 0.05$) by the presence of white clover. The length of stem was 23.8, and 24.2 cm long for grasses alone and with white clover, respectively.

Length of the stem of the two ryegrass varieties did not follow a linear relationship with rest periods, and as a first approximation, a quadratic equation was used (Appendix Table 9 and Fig. 8).

Percentage of tillers with seed heads; percentage of tillers with seed heads in anthesis, milk stage, and with ripe seeds as well as seed weight/tiller; length of seed head; and length of stem are all related to flowering. Because of these interrelationships they will be discussed together.

Cooper (1950) reported that in perennial herbage grasses like timothy, the apical meristem normally remains vegetative and produces

Fig. 7. Relationship between length of seed head and rest period during the experimental period (April through June 1978).

Fig. 8. Relationship between length of the stem and rest period during the experimental period (April through June 1978).

foliage leaves until a critical daylength is reached. The growing point then changes to the reproductive condition. The internodes begin to elongate and the ear develops. The size of the inflorescence of perennial ryegrass plants increased as daylength of temperature decreased. The larger ears had more spikelets and more florets in each spikelet (Ryle, 1965). Increasing daylength or temperature accelerated the development of the ear (Ryle, 1965). Langer (1957a) stated that plants cut early would probably proceed normally to flower production. However, a late cut will induce newly formed tillers to flower, if daylength and other conditions remain favorable. Based on population studies of seed crops, Stoddart (1959) concluded that the abundant small heads (less than 4 cm in length) contributed very little to seed yield.

In our research, head emergence on tillers started on rest period 1 when 32% of the tillers headed, and it continued until rest period 5 when practically 100% of the tillers had seed heads. The number of tillers decreased linearly with rest periods, and so did length of seed heads, resulting in a linear decrease in the seed yield as rest period advanced into the growing season. Ripe seeds were found only in rest periods 3, 4 and 5. Grasses at rest period 3 had 75.9% of their tillers with seed heads but only about 20% had ripe seeds. The total number of tillers with ripe seed were 30, 27, and 35 per $1/4 \text{ m}^2$ in rest periods 3, 4, and 5, respectively. The seed weights per tiller in each of these rest periods were 0.084, 0.077, and 0.074 g, respectively. The production of ripe seeds in each rest period was roughly 100, 83, and 103 kg/ha for rest period 3, 4, and 5, respectively. This seed production was more than three times the seeding rates used for establishing the experiment. Even considering ant damage and other hazards to seed

left in the pasture, there appeared to be enough seed for a self-reestablishment of the pasture during the following winter.

Leaf:Stem Ratio

There was a difference ($P < 0.01$) in the leaf:stem ratio of the grasses due to the time of the season in which the rest period was applied (Appendix Table 10 and Fig. 9). It ranged from 0.21 (rest period 1) to 0.07 (rest period 5). The leaf:stem ratio was also affected by the presence (0.13) or absence (0.11) of the legume. The presence of the legume improved significantly ($P < 0.01$) the leaf:stem of the grasses. There was no difference ($P < 0.05$) between the two ryegrass varieties; both had a value of 0.12.

The relationship between leaf:stem ratio and rest period was well explained by a quadratic equation ($r^2 = 0.82$). The test for lack of fit was not significant at the 0.05 level (Appendix Table 11). The leaf:stem ratios were low for all rest periods; this may be explained by the fact that stubble was included because samples were cut at ground level; leaf:stem ratios in reality were underestimated. Another factor which contributed to the low ratios was that a high percentage of the tillers had seed heads when samples were collected, and these were included in the stem portion.

Langer (1958) reported that timothy and meadow fescue species had considerably more leaf than stem in the vegetative stage, but by the time of ear emergence, the weight of stem was about twice that of leaves. After full ear emergence the ratio had dropped to about 0.1. Something like this probably occurred in the present study, since the percentage of tillers with seed heads increased linearly with later rest periods.

Fig. 9. Relationship between leaf:stem ratio and rest period during the experimental period (April through June 1978).

Total Non-Structural Carbohydrates

A difference ($P < 0.01$) in total non-structural carbohydrate contents (TNC) in the stubble of the grasses was found due to rest periods (Appendix Table 10), and it varied from 51.49% (rest period 1) to 2.70% (rest period 5). There was no difference ($P < 0.05$) in the TNC contents of the grasses whether or not white clover was present, nor were the two ryegrass varieties different. The TNC contents were 27.2% for grasses grown alone and 28.0% for grasses with white clover. Florida Reseeding and Gulf ryegrass averaged 27.4, and 27.8%, respectively.

The general trend was to decrease the TNC content in the grasses stubble with later rest periods, and a linear model ($r^2 = 0.96$) fits the data well (Appendix Table 11 and Fig. 10). The test for lack of fit was significant at the 0.01 level. This steady decline in the TNC content of the grasses was expected since the grasses were annuals and by the last rest period most of the sward was dead. The rate of decline in the TNC content was about 6 percentage units/week during the April through June period. The high concentration of TNC during the initial rest periods may have been due to fertilization with a low N rate which probably limited plant growth and favored carbohydrates accumulation. Milthorpe and Davidson (1966) stated that any factor which retards growth—low photosynthesis activity, low temperatures, low availability of mineral nutrients—will lead to an increase in soluble carbohydrates.

Crude Protein in Stem

Results of the statistical analysis showed the crude protein (CP) content of the grass stems was not the same ($P < 0.01$) for all rest periods (Appendix Table 12). It ranged from 12.86 (rest period 2) to 7.85% (rest period 5). There was no difference ($P < 0.05$) between the

Fig. 10. Relationship between total non-structural carbohydrate reserves and rest period during the experimental period (April through June 1978).

two ryegrass varieties, Florida Reseeding (9.3%) and Gulf (9.4%). The CP content of the grasses was not different ($P < 0.05$) whether they were grown alone (9.3%) or with white clover (9.4%).

As a first approximation model, a quadratic equation ($r^2 = 0.33$) was selected, since it fitted the data better than a straight line with a $r^2 = 0.14$ (Appendix Table 13 and Fig. 11).

Crude Protein in Leaves

A difference ($P < 0.01$) in the CP content of the grass leaves was found due to rest periods (Appendix Table 12). The CP content ranged from 14.69 (rest period 2) to 8.24% (rest period 5). There was no difference ($P < 0.05$) between the two ryegrass varieties, and there was no difference ($P < 0.05$) due to the legume. The grasses averaged 11.1 and 10.5%, respectively, for Florida Reseeding and Gulf ryegrass. The CP content for grasses with or without white clover was 10.5 and 11.0%, respectively.

The linear relationship between CP in the leaves and rest period accounted for 73% of the rest period sum of squares, hence was considered a satisfactory first approximation model (Appendix Table 13 and Fig. 12). In addition to that there was no improvement in the $r^2 = 0.37$ when a quadratic equation was tried. Based on this linear equation, there was a decrease in CP with later rest periods of about 0.6 percentage units/week. Even though CP in stems or in leaves of the grasses varied erratically through the different rest periods, the variation of CP in stems followed the same pattern as for leaves. The CP content in both plant tissues was relatively high at all rest periods and was never below 7%. The CP in leaves was higher than in stems for all rest periods.

Fig. 11. Relationship between crude protein in stems and rest period during the experimental period (April through June 1978).

Fig. 12. Relationship between crude protein in leaves and rest period during the experimental period (April through June 1978).

Leaf Area

Regression analysis for the two ryegrass varieties showed that their leaf areas decreased linearly with later rest periods (Fig. 13). The rate of decline was different for Florida Reseeding ($1.0 \text{ cm}^2/10$ tillers/week) and Gulf ryegrass ($1.5 \text{ cm}^2/10$ tillers/week). Gulf ryegrass leaf area ranged from $10.5 \text{ cm}^2/10$ tillers (rest period 1) to $2.2 \text{ cm}^2/10$ tillers (rest period 4), whereas Florida Reseeding ranged from 7.2 to 1.4 cm^2 , respectively, for the same rest periods. Both varieties had no green leaves by rest period 5 that could be collected for leaf area measurements, they had completed their life cycles and were dead. The slopes of the two equations showed a higher rate of decline in leaf area for Gulf than for Florida Reseeding ryegrass which explains the closeness of the leaf area for the two varieties after rest period 2. The two cultivars had different leaf area values in rest period 1, their rates of decline differed so that their regression lines converged reaching a value of near zero at rest period 4.

This decline in the leaf area of the grasses with advance of the growing season was due to variations in the physiology with plant age. Borril (1961) found marked changes in leaf size on Lolium temulentum tillers. The blades of successive leaves became larger until the time of inflorescence, after which leaf blades on flowering stems became progressively shorter. Langer (1958) also observed a decrease in leaf area after ear emergence in swards of timothy and meadow fescue. Borrill (1961) suggested that the reduction in length of successive leaf blades is indicative of the increased competitive demand for assimilates by developing inflorescence and elongating stems.

We may conclude that the decrease in the leaf area of the grasses was probably related to the plant's physiology—age, competition for

Fig. 13. Relationship between leaf-area and rest period during the experimental period (April through June 1978).

assimilates—and it occurs whenever the plants are headed toward the end of their life cycle.

However, the rate of decrease of leaf area may vary due to other factors. It could be increased by an increase in the rate of leaf death which generally occurs with reduction in light penetration to the lower part of the canopy. The rate of decrease of leaf area could be increased by frequent defoliations or by the intensity of defoliation.

Leaf area remaining after defoliation interacts with another important factor, carbohydrate reserves, and they affect tiller regrowth in a pasture. The relationship between leaf area and changes in stubble carbohydrates indicates that carbohydrate starts to accumulate when there is sufficient leaf area per tiller or per unit of area. Milthorpe and Davidson (1966) concluded that the carbohydrate concentration at defoliation significantly influenced the rate of regrowth during the first few days. However, the amount and type of leaf area remaining after defoliation also greatly influences regrowth. High carbohydrates content in the tiller supplied energy for regrowth and leaf area development.

Baker (1957) found severe reduction in regrowth as the carbohydrate content of tillers was less than about 16%. Brougham (1956) found that the rate of recovery of a pasture after defoliation depends on the proportion of incident light intercepted by the remaining foliage, i.e., recovery depends on the amount of remaining leaf area. There seems to be no doubt about the importance of leaf area and carbohydrate content and their interactions in the regrowth of a sward. In our research, leaf area and carbohydrate reserves of the tillers decreased with advanced rest periods. The leaf area remaining in the pasture after grazing was generally low in all rest periods; however, the carbohydrate content

was high in the initial rest periods. The tiller density of the initial rest periods, even though decreasing still maintained a satisfactory density. After rest period 3 when the carbohydrate content started to decrease more sharply and was about 20%, the tiller population reached lower densities and stabilized. In the late rest periods when the plants were reaching senescence, carbohydrate contents and leaf area were very low. This was expected since the plants were near the end of their life cycles.

SUMMARY AND CONCLUSIONS

A grazing experiment was conducted at the Beef Research Unit, University of Florida, Gainesville. The objectives were. a) to evaluate the feasibility of a pasture system in which ryegrass and clovers were seeded into a bahiagrass sod, b) to follow the development of ryegrass through the production of tillers, and c) to determine the influence of grazing management upon the reseeding of ryegrass.

There were two varieties of ryegrass (Lolium multiflorum Lam.), Florida Reseeding and Gulf, two white clover varieties (Trifolium repens L.), and one red clover (Trifolium pratense L.). Five rest periods were imposed during April through May. Starting dates were 4 April, 18 April, 2 May, 16 May, and 30 May for rest periods 1, 2, 3, 4, 5, respectively. The total area allocated to the experiment was 1.1 ha, which was subdivided into 22 pastures. The pastures were mob-grazed by cattle from 1 to 4 days to a prescribed level. The same grazing pressure was used for all rest periods.

Parameters measured for ryegrass included number of tillers/1/4 m²; percentage of tillers with seed heads; percentage of tillers with seed heads in anthesis, milk stage, and with ripe seeds; seed weight/tiller; length of seed heads and stems; leaf:stem ratio relationships; carbohydrate reserves; crude protein in the stem and leaf portions; and leaf area. The experimental design used was a split-split plot.

Samples for carbohydrate, CP, and leaf:stem ratio were collected on the last day of the third week after each rest period had started. During the fifth week following initiation of each rest period, the number of ryegrass tillers/ $1/4 \text{ m}^2$ was counted, as well as the number of tillers with seed heads. The length of the seed head and of the stem were also measured to the nearest centimeter. The number of seed heads with ripe seeds, in milk stage, and in anthesis were also recorded for each treatment in all five rest periods. The weights of seeds/tiller were also recorded.

From the results of this experiment the following conclusions appear to be justified:

The number of tillers per $1/4 \text{ m}^2$ decreased linearly with advanced rest periods whether the two ryegrass varieties were grown alone or with white clover. The number of tillers decreased at higher rates for grasses grown alone (45 tillers/ $1/4 \text{ m}^2/\text{week}$) than for grasses grown with the legume (31 tillers/ $1/4 \text{ m}^2/\text{week}$).

The percentage of tillers with seed heads increased linearly with advanced rest periods. The relationship between percentage of tillers with seed heads and rest periods was very similar whether the grasses were grown alone or with the legume. The rate of increase in tillers with seed heads/week was about 8.8 percentage units.

Percentage of tillers with seed heads in anthesis, milk stage, and with ripe seeds were all dependent on each other, and an increase in one necessarily required a decrease in the other/others. As expected, the percentage of tillers with ripe seeds increased with advanced rest periods and reached 98% by rest period 5. Tillers

in anthesis and milk stage decreased with later rest periods and reached 0 and 1.4%, respectively, in rest period 5.

The seed weight/tiller decreased with later rest periods. However, estimates indicated that because of the increase in percentage of tillers with ripe seeds with advanced rest periods, about 100, 83, and 103 kg/ha of ripe seed were produced in rest periods 3, 4, and 5, respectively. No seed was produced in periods 1 and 2.

The length of the seed heads decreased linearly with advanced rest periods. The length of the seed heads decreased at a rate of about 1.1 cm/week during the April through June period. This decrease in ear size had a negative effect on seed production. The decrease in length of the seed heads probably explains the decrease in seed weight/tiller. However, it was compensated by an increase in the percentage of tillers with ripe seeds with advanced rest periods.

The length of stem showed a curvilinear relationship with later rest periods, indicating that stem length increased with advancement into the growing season. It reached a maximum in rest period 3 and decreased with further advancement of the season.

The leaf:stem ratios were low for all rest periods. This may be explained by the fact that stubble was included because samples were cut at ground level; leaf:stem ratios in reality were underestimated.

The relationship between TNC and rest periods was linear. The rate of decline in the carbohydrate content in the grass stubble was about 6 percentage units/week, during the April through June period. The high concentration of TNC during the initial rest periods may have been due to fertilization with a low N rate which probably limited plant

growth and favored carbohydrate accumulation. The low TNC content at the last rest period was expected since the grasses were annuals and were dying or dead.

The CP percentage in stems showed a curvilinear response to the time of imposed rest periods. It increased to a maximum in rest period 2 and then decreased with advanced rest periods into the season. The variation in CP in leaves with rest periods was also erratic and as a first approximation a linear equation was used. Based on this linear model there was a decrease in the CP in leaves with advanced rest periods of about 0.6 percentage units/week.

The leaf area of the two ryegrass varieties decreased linearly with advanced rest periods. The rate of decline was different for Florida Reseeding ($1.0 \text{ cm}^2/10 \text{ tillers/week}$) and Gulf ryegrass ($1.5 \text{ cm}^2/10 \text{ tillers/week}$). However, both varieties had no green leaves by rest period 5; they had completed their life cycles and were dead.

There seems to be a great potential for a pasture system based on seeded winter forages into a warm-season perennial sod. However, in this research the desired high production of forage during winter was not achieved, probably because of the high grazing intensity used. Leaf area of the components of the sward was depleted which delayed their regrowth, thus regrowth relied mainly on tiller carbohydrates. The low level of fertilization applied also limited plant regrowth.

Ripe seed was produced in satisfactory amounts in three of the five rest periods. However, due to the grazing management used, most of the seed produced was grazed and removed from the pasture by the animal.

In the future, alternatives for improving this research may be:

- to increase the length of the rest periods thus allowing the seed produced to shatter before grazing the pasture again,
 - to allow the pasture to rest until seed is produced,
 - to use mechanical devices for shattering the seed produced before again grazing.
- to utilize lighter grazing pressure to avoid the consumption of the major portion of the seed by the grazing animal.

The heavy grazing pressure used was also possibly responsible for the decrease in tiller density and for the low tiller population when the sward stability was reached. Since the remaining leaf area after grazing was low, tiller regrowth was associated with amounts of carbohydrates. Young tillers with low carbohydrate reserves died which resulted in a decrease in tiller population. Forage yield probably decreased at rates similar to that of tiller density.

APPENDIX

Appendix Table 1. Analysis of variance for (a) number of tillers per unit of area, and (b) percentage of tillers with seed heads.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (RP)	4	313402.15**	16815.37**
Error (a)	17	3150.04	81.24
Grass (G)	1	3.40	143.29
RP x G	4	9411.76	54.36
Error (b)	17	3831.62	53.54
Legume (L)	1	70778.24**	5.47
RP x L	4	10539.79**	100.86*
G x L	1	2766.34	16.39
RP x G x L	4	1772.69	7.87
Error (c)	34	1720.11	35.30

*Significant at the 0.05 level.

**Significant at the 0.01 level.

Appendix Table 2. Duncan's multiple range test for (a) number of tillers per unit of area, and (b) percentage of tillers with seed heads for legume by rest period.

Rest period	Legume	Means*	
		(a)	(b)
1	Absent	387.5 ^a	30.4 ^a
	Present	263.8 ^b	35.0 ^a
2	Absent	334.2 ^a	34.7 ^a
	Present	233.7 ^b	42.8 ^a
3	Absent	253.7 ^a	77.5 ^a
	Present	179.8 ^b	74.4 ^a
4	Absent	54.5 ^a	95.1 ^a
	Present	46.5 ^a	88.3 ^a
5	Absent	45.9 ^a	100.0 ^a
	Present	26.2 ^a	100.0 ^a

* Means within the same column and within the same rest period followed by the same letter are not significantly different at the 0.05 level.

Appendix Table 3. Regression analysis for number of tillers per unit of area for (a) grasses grown alone, and (b) grasses grown with the legume.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (X)	4	218902.27	105039.67
Linear	1	834856.96**	400024.04**
Lack of Fit	3	13584.04*	6711.54*
Error	39	3515.11	2223.79

* Significant at the 0.05 level.

** Significant at the 0.01 level.

Fitted equations:

$$\hat{Y}(a) = 491.55 - 89.60 X \quad r^2 = 0.82$$

$$\hat{Y}(b) = 339.68 - 62.02 X \quad r^2 = 0.79$$

Appendix Table 4. Regression analysis for percentage of tillers with seed heads for (a) grasses grown alone, and (b) grasses grown with the legume.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (X)	4	9425.03	7491.21
Linear	1	35153.51**	29152.13**
Lack of Fit	3	848.87**	270.90**
Error	39	42.15	59.76

** Significant at the 0.01 level.

Fitted equations:

$$\hat{Y}(a) = 13.34 + 18.38 X \quad r^2 = 0.89$$

$$\hat{Y}(b) = 18.82 + 16.74 X \quad r^2 = 0.90$$

Appendix Table 5. Analysis of variance for (a) percentage of tillers in the anthesis stage, and (b) percentage of tillers with seeds in the milk stage.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (RP)	2	910.43**	31082.80**
Error (a)	11	30.14	92.78
Grass (G)	1	16.85*	132.12
RP x G	2	99.43	72.41
Error (b)	11	31.36	36.01
Legume (L)	1	79.81**	0.016
RP x L	2	24.94	32.38
G x L	1	6.57	60.71
RP x G x L	2	2.07	25.86
Error (c)	22	11.46	37.89

* Significant at the 0.05 level.

** Significant at the 0.01 level.

Appendix Table 6. Analysis of variance for (a) percentage of tillers with ripe seeds, and (b) seed weight/tiller.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (RP)	2	37935.62**	0.000619*
Error (a)	11	154.57	0.000153
Grass (G)	1	1.41	0.000206*
RP x G	2	55.68	0.000065
Error (b)	11	21.71	0.000039
Legume (L)	1	77.54	0.000250**
RP x L	2	55.93	0.000150*
G x L	1	27.34	0.000003
RP x G x L	2	13.72	0.000012
Error (c)	22	27.10	0.000036

* Significant at the 0.05 level.

** Significant at the 0.01 level.

Appendix Table 7. Duncan's multiple range test for seed weight/
tiller, for legume by rest period.

Rest period	Legume	Means*
3	Present	0.089 ^a
	Absent	0.078 ^b
4	Present	0.079 ^a
	Absent	0.075 ^a
5	Present	0.074 ^a
	Absent	0.073 ^a

* Means within the same rest periods and followed by the same letter are not significantly different at the 0.05 level.

Appendix Table 8. Analysis of variance for (a) length of the seed head, and (b) length of the stem.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (RP)	4	266.22**	111.70**
Error (a)	17	1.78	10.39
Grass (G)	1	4.04	5.36
RP x G	4	2.24	3.52
Error (b)	17	1.61	3.17
Legume (L)	1	7.82**	2.05
RP x L	4	1.04	2.43
G x L	1	0.43	0.85
RP x G x L	4	1.29	0.40
Error (c)	34	0.80	2.07

** Significant at the 0.01 level.

Appendix Table 9. Regression analysis for (a) length of the seed head, and (b) length of the stem.

Source of variation	d.f.	<u>Mean square</u> (a)	d.f.	<u>Mean square</u> (b)
Rest period (X)	4	266.22	4	111.70
Linear	1	1009.36**	1	115.65**
Quadratic			1	229.93**
Lack of Fit	3	18.51**	2	50.62**
Error	83	1.54	83	4.06

** Significant at the 0.01 level.

Fitted equations:

$$\hat{Y}(a) = 16.58 - 2.20 X \quad r^2 = 0.85$$

$$\hat{Y}(b) = 20.37 + 4.56 X - 0.89 X^2 \quad r^2 = 0.44$$

Appendix Table 10. Analysis of variance for (a) leaf:stem ratio, and (b) total non-structural carbohydrates.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (RP)	4	0.0705**	7543.78 **
Error (a)	17	0.0009	35.96
Grass (G)	1	0.0005	3.18
RP x G	4	0.0007	4.82
Error (b)	17	0.0004	6.91
Legume (L)	1	0.0045**	21.14
RP x L	4	0.0001	2.19
G x L	1	0.0004	1.42
RP x G x L	4	0.0006	1.60
Error (c)	34	0.0008	12.28

** Significant at the 0.01 level.

Appendix Table 11. Regression analysis for (a) leaf:stem ratio, and (b) total non-structural carbohydrates.

Source of variation	d.f.	Mean square (a)	d.f.	Mean square (b)
Rest period (X)	4	0.0705	4	7543.78
Linear	1	0.2342**	1	29997.62**
Quadratic	1	0.0470**		
Lack of Fit	2	0.0005	3	59.17**
Error	83	0.0007	83	14.47

** Significant at the 0.01 level.

Fitted equations:

$$\hat{Y}(a) = 0.30 - 0.11 X + 0.012 X^2 \quad r^2 = 0.82$$

$$\hat{Y}(b) = 63.64 - 12.01 X \quad r^2 = 0.96$$

Appendix Table 12. Analysis of variance for (a) crude protein in the stem, and (b) crude protein in the leaves of the grasses.

Source of variation	d.f.	Mean square	
		(a)	(b)
Rest period (RP)	4	39.42**	91.15**
Error (a)	17	4.26	6.28
Grass (G)	1	0.001	4.43
RP x G	4	1.59	9.09
Error (b)	17	1.15	4.24
Legume (L)	1	0.12	0.06
RP x L	4	0.75	4.91
G x L	1	1.97	2.69
RP x G x L	4	0.58	1.86
Error (c)	34	1.002	2.64

** Significant at the 0.01 level.

Appendix Table 13. Regression analysis for (a) crude protein in the stem, and (b) crude protein in the leaves of the grasses.

Source of variation	d.f.	Mean square (a)	d.f.	Mean square (b)
Rest period (X)	4	39.42	4	91.15
Linear	1	42.14**	1	266.07**
Quadratic	1	56.03**		
Lack of Fit	2	29.75**	3	52.36**
Error	83	1.68	83	4.26

** Significant at the 0.01 level.

Fitted equations:

$$\hat{Y}(a) = 7.80 + 2.18 X - 0.44 X^2 \quad r^2 = 0.33$$

$$\hat{Y}(b) = 14.19 - 1.13 X \quad r^2 = 0.37$$

Appendix Table 14. Means for all response variables measured for the five rest periods.

Rest period	Number of tillers/unit area	Number of tillers with seed heads/unit area	Number of tillers without seed heads/unit area	Percentage of tillers with seed heads	Number of tillers/unit area with seed heads in:		
					Anthesis	Milk stage	Ripe seeds
1	326	101	225	32.7	--	--	--
2	284	105	179	38.8	--	--	--
3	262	163	99	75.9	13	120	30
4	51	46	5	91.7	9	10	27
5	36	36	0	100.0	0	1	35

Appendix Table 14 - continued

Rest period	Percentage of tillers with seed heads in:			Seed weight/ tiller (g)	Weight/ 100 seeds (g)	Length of seed head	Length of stem	Leaf: stem ratio	CP stem %	CP leaves %	TNC %	Leaf area cm ² /10 tillers	
	Anthesis	Milk stage	Ripe seed									Fla. res.	Gulf
1	--	--	--	--	--	14.54	24.21	0.21	9.23	12.56	51.49	7.2	10.5
2	--	--	--	--	--	13.70	24.02	0.13	12.86	14.69	36.49	5.8	9.0
3	8.7	72.1	19.2	0.084	0.17	9.04	27.18	0.09	9.79	10.16	29.24	2.0	3.7
4	15.9	18.6	65.5	0.077	0.13	6.81	22.19	0.08	9.44	11.23	17.00	1.4	2.2
5	0.0	1.4	98.5	0.074	0.11	6.14	21.28	0.07	7.85	8.24	2.70	--	--

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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