

Bahiagrass Regrowth and Physiological Aging

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Highlight: *Pensacola Bahiagrass* (*Paspalum notatum* Flugge) grows by adding new phytomers to the terminal ends of vegetative stolons. A new phytomer and its attached leaf is added on average each 7 to 12 days during growth as long as the tiller is vegetative. The new leaf is supplied with energy primarily for the first 2 to 3 days of growth and, from 3 days of age until fully expanded at 12 days, photosynthates are retained by the leaf. After 12 days, exports are made to other sinks in the sheath, stolon, root, and new tillers. An investigation was completed in which (a) shoot growth (leaves) of plants fertilized with 0, 100, or 300 kg/ha of N were measured for length and clipped at the top of the stolon daily or weekly until the stolons died, (b) photosynthesis rate of leaves of different ages was determined, and (c) photosynthesis was correlated with leaf chlorophyll, and N content by weeks. Thirteen weeks of daily or weekly clipping were required to kill the stolons and regrowth amounted to 749 to 850 kg/ha of dry leaves. Total length of shoot regrowth per square meter ranged between 13 to 22 m for the 13 weeks and was negatively related to N application rate. Photosynthesis started dropping after approximately 25 days, but leaf N and chlorophyll contents were relatively stable for the first 45 days. After 45 days of age all three factors declined rapidly until leaf death occurred 60 ± 6 days after initiation. Stolons live much longer than do leaves.

Pensacola Bahiagrass (*Paspalum notatum* Flugge) is widely grown in the lower South, though effective management for forage purposes continues to be unclear. The degree of defoliation required to eliminate Bahiagrass has never been established and the effect of leaf aging on physiological processes and chemical changes are relatively unknown. Data relative to defoliation tolerance and rate of the aging processes would aid in determining management practices and increase the value of *Pensacola Bahiagrass* as a forage and in nonagricultural uses.

Bahiagrass grows by producing phytomers at the terminal end of vegetative stolons (Fig. 1). Each phytomer consists of an internode, node, leaf sheath, leaf blade, primary root, and usually an axillary bud. At the end of the stolon the leaves of the 6 to 11 youngest phytomers comprise a leaf bundle with the leaf sheath of the oldest of these leaves encircling the outside and leaves decreasing in age toward the center.

The leaves are produced in two ranks along stout stolons that grow along the soil surface. Defoliation by either clipping or grazing removes only a portion of the leaf and flowering culms. Leaves vary in length from 20 to 30 cm (Beaty et al.,

1968) and even when clipped to 5 cm some of the leaf and all of the leaf sheath tissue remain on the stolon. Leaf generation in Bahiagrass apparently requires relatively small quantities of stored energy (Beaty et al., 1974) and photosynthetic sink priorities favor leaf and stolon growth.

With the onset of growth in the spring, a new leaf (entire phytomer) appears at the center of the leaf bundle each 7 to 11 days. After 6 to 11 leaves (phytomers) have appeared, the stolon will have elongated sufficiently to separate the leaf sheath of the oldest leaf from the leaf bundle. The Bahiagrass forage above the soil surface consists primarily of leaves with all ages, from newly initiated to fully expanded and dead leaves represented. Leaves in the leaf bundle will be green and vary from 1 to 2 days in age to fully expanded. Leaves usually

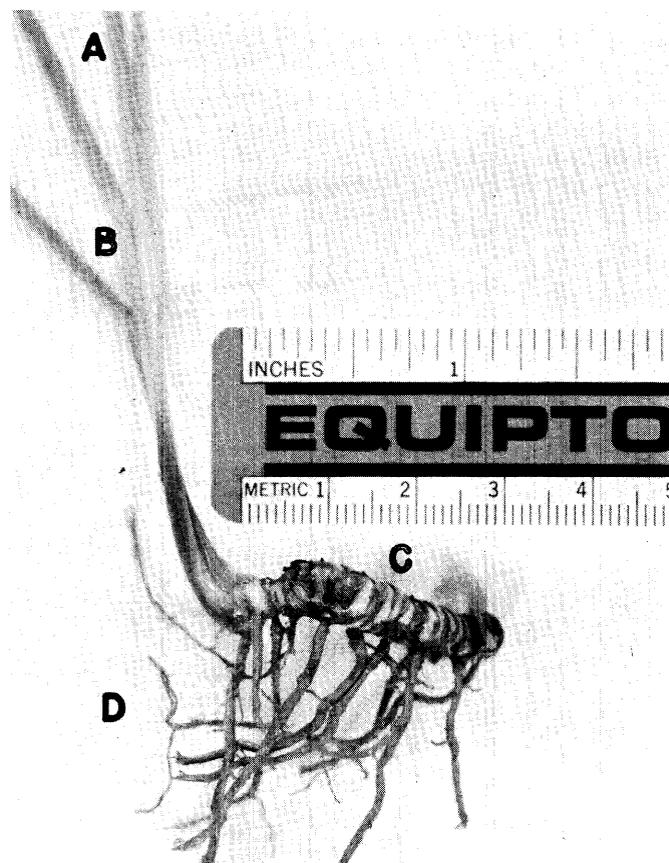


Fig. 1. Bahiagrass tiller showing (A) visible leaves, (B) leaf being separated from leaf bundle, (C) stolon with leaf scars where mature (dead) leaves have been removed, and (D) primary roots.

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die of old age shortly after being separated from the leaf bundle.

The phytomer-producing meristem is located at the base of the stolon tip and is not removed with clipping or grazing. Young leaves continue elongating after defoliation, and new phytomer initiation at the stolon tip continues until the tiller dies or a reproductive flowering culm is produced. It was found previously that organic reserve exports to new leaves is concentrated in the first 2 to 3 days following initiation and from 3 days of age until the leaf is fully expanded, most of the photosynthate produced is retained by the leaf. Following full leaf expansion, CHO exports were primarily to stolons and in general young leaves exported less than did old leaves (Beaty et al., 1974).

The degree of tolerance of Bahiagrass to defoliation is rather surprising. In earlier work Beaty et al. (1963) found that weekly clipping at a 5-cm stubble height reduced yields only slightly as compared to monthly clipping, and Beaty et al. (1970) reported that weekly clipping to 0 cm for 2 years reduced vigor but did not eradicate the stand. Bahiagrass responds to N fertilization, and yield increases for varying N rates have been reported by Beaty et al. (1960).

It is well established that the photosynthesis rate of a young leaf is higher than that of an old leaf, but species differ in the duration of maximum photosynthesis (Jewiss and Woledge, 1967; Osman and Milthorpe, 1971; and Treharne et al., 1968). Some data (Ludlow and Wilson, 1971) are available which describe the changes in photosynthetic rates with leaf age in tropical grasses, but more are needed and the present research was undertaken to establish: (a) leaf clipping intensity required to kill Bahiagrass, (b) photosynthesis rate of Bahiagrass leaves of different ages, and (c) the relationship of photosynthetic rate changes with leaf N and chlorophyll contents.

Procedure

Defoliation Tolerance

On December 3, 1970, Pensacola Bahiagrass plugs 15 cm in diameter and 15 cm deep were taken from an unfertilized field sod and transferred to 1-gallon cans filled with sand. The filled cans were placed in a greenhouse and fertilized uniformly at rates equivalent to 40 kg of P, 50 kg of K, and either 0, 100, or 300 kg of N/ha.

On December 12, after 1 week in the greenhouse, all leaf material above the stolon was removed, N was applied, clipping treatments initiated, and new growth measured for total shoot (leaf) length. Shoot growth was removed at the top of the stolons at: (a) daily and (b) weekly intervals. Clipping was continued until no new growth occurred. Treatments were replicated four times.

The shoot length and weight measurements from the daily and weekly clipped treatments were compared by combining data of 7 daily clippings and comparing with data from a corresponding 7-day period for the weekly clipped treatment. Statistical evaluations by analysis of variance were completed on data for the three N levels and the two clipping frequencies.

Photosynthetic Activity and Chemical Composition

On July 6, 1971, two Pensacola Bahiagrass stolon segments with leaves and roots removed were transplanted into sand-filled gallon cans. The cans were placed in an evaporator-cooled greenhouse and were watered daily with a complete nutrient solution. All newly emerged leaves were identified to establish different age groups as well as age at expiration. Four groups of leaves were identified and apparent photosynthesis

rates of individual leaves in each group were measured using an infrared gas analyzer.

Groups 1, 2, and 3 consisted of eight leaves each, one leaf on eight different plants, and leaves in each group emerged on the same day. Leaves of group 1 emerged on August 26, group 2 on August 29, and group 3 on August 31. The CO₂ fixation rates of leaves in group 1, 2, and 3 were determined weekly from leaf emergence until death. Group 4 consisted of 20 plants, and the CO₂ fixation rates of all leaves on each plant in this group were measured only once and on the same day.

To measure the CO₂ fixation rate of a leaf the middle 8.2 cm of its lamina, still attached to the plant, were enclosed in a 8.2 × 3.1 × 1.2 cm, "flow-thru" plexiglass chamber, with a water jacket in the lower portion. Atmospheric air (336 ppm CO₂) was pumped into the chamber at a flow rate of .51 liter per minute. Samples of the air were pumped to the infrared analyser, at flow rates of .15 liter per minute, before and after passing through the chamber. The air samples were dried by passing through tubes of anhydrous CaSO₄ before being analyzed. The temperature of the chamber was regulated by the water jacket and monitored by a thermocouple. All CO₂ measurements were made at 30°C. Four incandescent 300-w lamps producing 4,400 ft-c were used as the light source. A plexiglass container with circulating water was interposed between the lamps and the chamber to reduce infrared radiation reaching the leaf.

Leaves of different age were analyzed for their N content by a Kjeldahl procedure and for their chlorophyll content according to the procedure of Winterman and Demots (1965). The relationship of these plant constituents to the apparent photosynthesis rates of leaves of the same age was determined.

Results and Discussion

At the start of the investigation in December, the sods had been frosted and were dormant. Stored food reserves in the stolons would be expected to be a maximum. The data collected in the greenhouse were from plants grown in the field and were collected during the season when plants in the field are dormant. Sunshine would be expected to be at a minimum as day length is at a minimum and cloud cover is at a maximum during this time of year. At the beginning of clipping, plants would be expected to reflect maximum stored reserves with minimum photosynthetic inputs during the experiment.

Thirteen weeks were required to eliminate Bahiagrass stolons by daily removal of all leaf tissue. When computed on a hectare basis over the 13-week period, an average of 789 kg of dry forage were harvested when clipped weekly; 689 kg/ha were harvested when clipped daily (Fig. 2). During the investigation total amounts of forage produced at the different N rates were not significantly different. However, plants on high N treatment tended to produce more forage in weeks 1 to 5 and to produce less forage in weeks 6 to 11 than when no N was applied. The 100-kg/ha N treatment produced forage comparably to the high N treatment for the first 6 weeks, and its production was almost identical to that of the low N treatment for the last 6 weeks.

Length of shoot regrowth produced each week for the different N rates is shown in Figure 2. When totaled for the 13-week period and calculated on a square meter area, the sum of shoot growth produced was 16.75, 20.04, and 18.89 m for the 300, 100, and 0 kg/ha N rates at the weekly clipping, respectively. The summed lengths of leaves produced for the same N treatments and daily clipping were 12.25, 13.24, and 13.13 m/m², respectively.

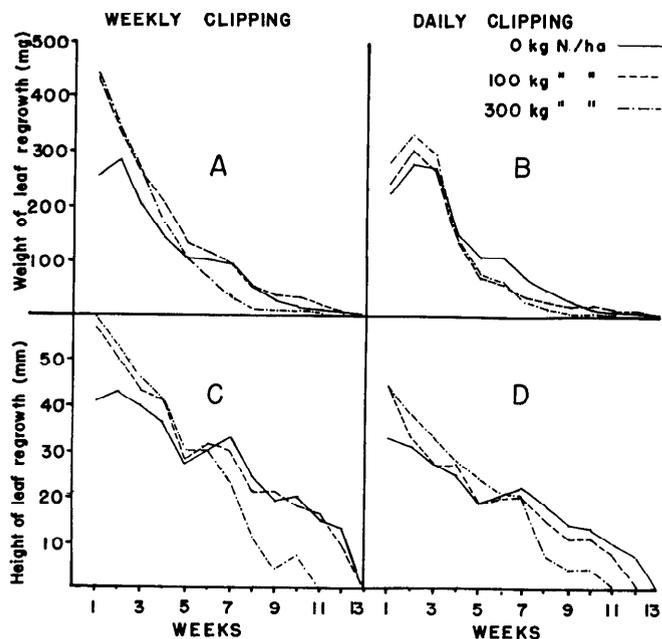


Fig. 2. Weight and height of *Pensacola Bahiagrass* leaf regrowth in 15 cm diameter sods clipped daily or weekly to stolon top until regrowth stopped.

Stolon weight per ha on treatments used in this investigation usually ranged between 10,000 and 12,000 kg (Beaty et al., 1964). The 789 kg of dry shoot produced before expiration of the stolons therefore represents only about 8% of gross stolon weight. While it has been concluded that vegetative growth causes organic reserves to decline (Brown and Ashley, 1974) the 13 weeks of intense defoliation required for elimination suggest Bahiagrass conserves its energy reserves rather carefully. The work of Beaty et al. (1974) shows that new leaves are initiated on each stolon one at a time, at 9- to 12-day intervals, and that energy export to the new leaf is concentrated in the first 3 days. The time involved in this investigation (13 weeks) would suggest that 9 to 10 leaves would be generated and energy export to the young leaves would be active for 27 to 30 days. Each new leaf produced would be part of a new phytomer, including internode, node, axillary bud, and primary root, in addition to the leaf sheath and blade. All of these would require organic reserve exports. Therefore energy import to the leaf represents only a part of the total energy required for plant growth.

The survival mechanism of Bahiagrass appears to be minimal exposure of storage organs (stolons) to defoliation by grazing and intermittent generation of new photosynthetic tissue (leaves) over a long period of time. In contrast Leafe et al. (1974) describes a growth pattern in orchardgrass (*Dactylis glomerata*) and ryegrass (*Lolium* spp.) characterized by the near simultaneous generation of large numbers of tillers and leaves per tiller, with stem elongation following the basal leaf rosette stage. It is assumed there is a corresponding major drop in organic reserves. Presumably in such grasses leaf growth is stimulated by light saturation of the meristems, and over utilization of the forage produced is prevented by the flush of growth exceeding the endemic capacity of fauna to consume it. During early growth periods when energy supplies become low, such grasses survive by growing faster than animals present can graze them.

Bahiagrass, in contrast, has a forage production pattern of a new leaf being produced in a measured cadence of a new one each 7 to 12 days on each tiller. Periods of high leaf production occur after N applications have stimulated new tiller production.

From a pasture management view, grasses with growth patterns whose maximum vegetative growth periods result in low levels of organic reserves are subject to stand losses from clipping or grazing unless organic reserves are allowed to be resupplied. Bahiagrass, in contrast, does not have early periods of maximum growth, and organic reserves are not stressed over short periods and can be resupplied as photosynthetic production exceeds current plant energy and grazing needs.

Complementing the husbanding of energy reserves in Bahiagrass is the systematic initiation of leaves, and before reserves are exhausted 9 to 10 leaves will have been produced. The data in Figure 3 show that from the time of emergence until the leaf was 30 days old, CO₂ fixation rates were stable at approximately 30 mg CO₂/dm²/hour. There was a small drop in CO₂ fixation in leaves between 30 and 40 or 45 days of age. Leaves 45 days old or more showed an accelerating decline in CO₂ fixation until the 60th (±6) day, when photosynthesis ceased. Stolons on which leaves are produced live much longer than do the leaves. Leaf chlorosis followed cessation of photosynthetic activity and desiccation followed chlorosis by 2 to 3 days.

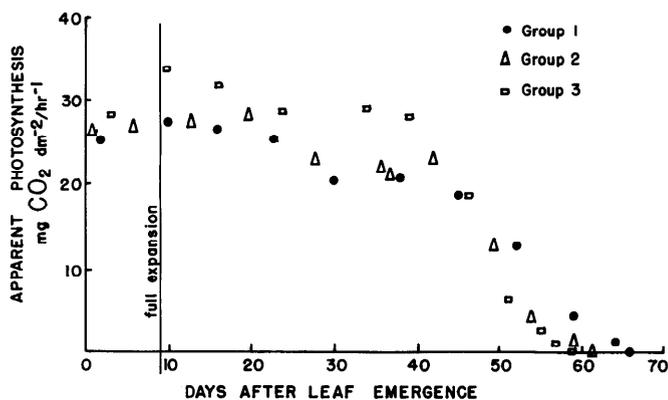


Fig. 3. Apparent photosynthesis rate of *Pensacola Bahiagrass* leaves as affected by leaf age. Each value represents average rate of 8 leaves.

Leaf chlorophyll levels of more than 3 mg chlorophyll per dm², and N levels of more than 2% of dry matter, were maintained for approximately 45 days after leaf emergence and neither was correlated with photosynthetic rate during that period. Chlorophyll and N in leaves more than 45 days of age decreased very rapidly, and the rates of decline for both N content and chlorophyll were significantly correlated with CO₂ fixation.

The data in Figure 4 that show a lack of significant correlation between forage N content and apparent photosynthesis indicate that photosynthesis activity is independent of N content. Forage N content appears to be a tissue age factor while photosynthesis is physiological and may well explain there being no clear-cut association between forage N content, which was stable in green leaves, and digestibility, which was found to decrease linearly with tissue age (Miller et al., 1965). In this investigation N content of Bahiagrass leaves was stable for the first 45 days following emergence. The pattern between leaf N and chlorophyll content appears to be

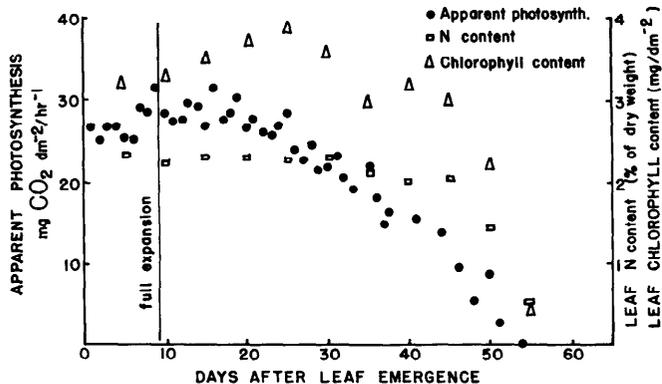


Fig. 4. Apparent photosynthesis rate, chlorophyll and N content of Pensacola Bahiagrass leaves as affected by leaf age.

similar, as chlorophyll content was stable for some 45 days also. Leaf photosynthetic activity began dropping 25 to 30 days after emergence and by the time leaf N started dropping, photosynthesis had been reduced by approximately half. The data of Miller et al. (1965) showed a steady erosion of the dry matter digestibility of Coastal Bermudagrass (*Cynodon dactylon*) forage (leaves and stems) as it aged from 21 to 49 days. This is the same time when photosynthetic activity of Bahiagrass leaves was decreasing significantly but leaf N and chlorophyll contents were stable.

Bahiagrass management would appear to be more related to forage quality considerations (keeping leaves young and digestible) than to regrowth, as continuous and severe defoliation over 13 weeks were required to kill it. Bahiagrass is not likely to be eliminated by grazing or mowing, and management should put greater emphasis on producing young growth higher in digestibility.

Photosynthetic activity of individual Bahiagrass leaves was high over the relatively long period of 30 to 40 days and was not correlated with N or chlorophyll content. The photosynthetic aging process of leaves appeared to be rather slow, and when combined with the low energy expenditure in leaf generation helps to explain the persistence of Bahiagrass in grazing or clipping. Large quantities of photosynthates are not used in growing stems for flowering culm development. The

tiller never has a large number of uniformly young leaves in a clump (rosette) at one time, and stem energy requirements are limited to the short stolon segment.

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