Tillering at the Reproductive Stage in Hardinggrass

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Highlight

Depression of tillering near the onset of flowering is characteristic of several perennial grasses. This was studied in hardinggrass by producing for comparison at one time both vegetative and reproductive plants through manipulation of daylength and temperature. Reduced tillering at the heading stage is associated with some aspect of the reproductive condition, as well as with the increasing dryness and temperature which may exist at this stage of growth in the field. Grazing to remove elongating flowering culms will stimulate tillering if conditions favorable for growth prevail.

The growth of basal axillary shoots, commonly called tillers, provides most of the forage produced by herbage grasses. To a large degree, grass production depends on the numbers and size of grass tillers. The variety of factors affecting tillering, however, is large and success hinges on understanding them individually and collectively. Langer (1963) in a review of tillering literature lists genotype, temperature, light intensity, water supply, mineral nutrition, flowering, photoperiod, and growth regulators as the principal factors affecting tillering. Such an array leads to uncertainty in associating particular factors with observed tiller behavior in the field. As a result, many investigators have studied tillering under controlled environments.

Rate of tiller emergence is not constant if a sufficient span of the life cycle of the plant is observed. Seasonal trends in tiller numbers have been reported for smooth bromegrass (*Bromus inermis*) by Lamp (1952), for S-48 timothy (*Phleum pratense*) and S-215 meadow fescue (*Festuca pratensis*) by Langer (1958) and Langer et al. (1964), and for orchardgrass (*Dactylis glomerata*) by Taylor and Templeton (1966). In each instance a decline in rate of tillering or in tiller numbers is noted near the jointing, heading or anthesis stages with an increase in tillering observed soon thereafter. Although such depression in tillering near the onset of flowering is generally reported, it is not understood whether this is a response to environmental factors, to the reproductive stages of development, or to both.

The present investigation was undertaken to clarify this question, and to consider the importance of reduced tillering during reproductive development in the management of herbage grasses.

Materials and Methods

Hardinggrass (*Phalaris tuberosa var. stenoptera*) was studied in a 3-year-old stand at the Hopland Field Station, and in the greenhouse either on first-year plants grown from seed or on clonal populations from selected mature plants taken from the field at Hopland.

Through the spring of 1962, growth in the field was measured in terms of height, and periodically a plot was cut at 2 inches above ground for measurement of the regrowth during the ensuing 30 days. This regrowth was related to the stage of de-

Table 1. Height of uncut plants and daily increase in regrowth following a single cutting at different stages of development in 1962.

	For 30 days following cutting			
Date of cutting	Average daily regrowth (inches)	Total rainfall (inches)	Average daily maximum temperature (°F)	Height of uncut plants (inches)
March 14	.26	.87	68	7.5
April 2	.38	.57	75	10.3
April 17	.47	.72	71	14.0
May 2[1]	.20	.63	72	16.8
May 16	.14	.48	77	24.5
June 4[2]	.00	.00	88	41.5

[1] Plants in boot.
[2] Plants in anthesis.

velopment of the plants when cut, and to the prevailing temperature and rainfall recorded at a nearby weather station.

Plants in the greenhouse were so manipulated that both vegetative and reproductive individuals were available at the same time within one clone or within one lot of test material, thereby permitting a critical comparison to reveal the differences associated with the reproductive stage of development. This was possible in hardinggrass since it is a long-day plant and usually requires some cold exposure prior to floral induction (Ketellapper, 1960). We found considerable difference among hardinggrass plants in the cold requirement. Therefore, by supplying adequate cold to part of an experimental lot and not to the rest, or by providing cold near the threshold of the amount required, both vegetative and reproductive plants could be obtained under the long daylengths subsequently provided. Furthermore, plants determined to have a lesser cold requirement for induction would flower when subjected directly to 20-hr daylength, whereas those receiving only a 16-hr photoperiod would remain vegetative. The details of each treatment are presented with the results to which they pertain. Records were taken weekly on the vegetative and the reproductive plants indicating the number of new tillers per plant over 1-inch long, the number of dead tillers, and the date of heading, if any. A tiller was considered dead when all leaf blades had turned brown, and heading was marked as that date on which the tip of the inflorescence was visible above the subtending leaf collar. Enumerations of tiller numbers excluded the main culm of the plant.

Results and Discussion

The growth behavior of one stand of mature hardinggrass in the field at Hopland is presented in Table 1. Through April 17, growth in overall

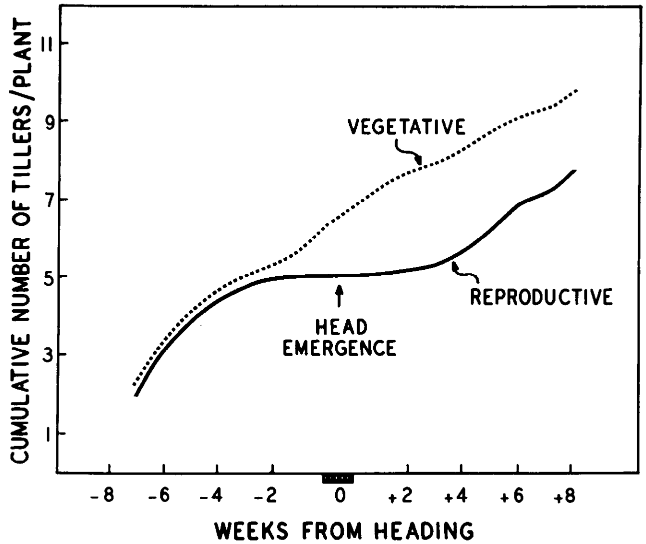

Fig. 1. Cumulative production of tillers over 1-inch long in first year growth of hardinggrass.

height and regrowth following cutting was vigorous, and both temperature and precipitation conditions were favorable. By early May the uncut plants showed reproductive development, being in the boot stage, and the subsequent rapid increases in height depict the elevation of the flowering culms. However, regrowth rates declined rapidly following the May 2 and later cuttings, and at the same time moisture became meager and temperatures increased. No regrowth was measurable after the June 4 cutting. Clipping the plants when in boot or later obviously removes many of the growing points. The termination of growth in height by a culm which loses its growing point has been pointed out by Branson (1953), Cook and Stoddart (1953), and Laude (1957). Regrowth in these cases is attributable mainly to the elongation of vegetative shoots and of new tillers. Among the factors which may be involved, therefore, in the reduced regrowth commencing in early May are not only the increasing dryness and temperature, but also possibly the stage of reproductive development at that time and the amount of new tillering. This possibility was studied further in the greenhouse.

It had been determined in previous greenhouse plantings of hardinggrass that subjecting the seedlings to 5 weeks of 36 F and short daylengths prior to exposure of these plants to 17-hr photoperiod, would result in approximately half of the plants heading and the rest remaining vegetative. Seedlings 35 days old were exposed to 5 weeks of such cold conditioning. They were then placed under 17-hr daylength in a greenhouse averaging 82 F in the daytime and 70 F at night, and were watered daily. Fig. 1 depicts the cumulative production of tillers in reproductive and in vegetative plants.

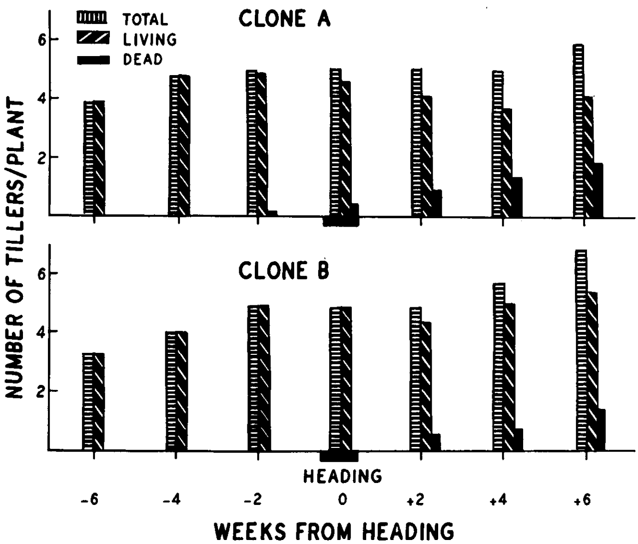

FIG. 2. Average numbers of tillers (total, living, and dead) on reproductive plants of two clones before and after heading.

Long-day exposure began 7 weeks before head emergence. Until 2 weeks before heading both lots tillered at the same rate. Then for 4 weeks, centering on 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. By 1 week after head emergence, this divergence in tiller numbers had become statistically significant at the 5% level. Resumption of tillering in the headed plants occurred some 2 weeks after heading. First tiller mortality was observed 1 week after heading in the reproductive plants but tiller mortality in the vegetative plants did not commence until 5 weeks later.

In order to eliminate genetic variability as a factor in the comparison between vegetative and reproductive plants, clonally propagated material was used in further comparisons. Clones were selected which possessed no obligatory cold requirement for induction, and therefore, in the absence of prior cold conditioning, would flower in the greenhouse under 20-hr photoperiod but remain vegetative under 16 hr of light. One clonal segment was established per 6-inch pot filled with a 1 to 1 mixture of loam soil and sand. No nutrient additions were provided during the experiment. Six weeks was allowed for the establishment and early growth of the segments before commencement of the photoperiod treatment and by this time the plants supported 3 tillers.

The behavior of the vegetative and reproductive plants was in agreement with the curves presented in Fig. 1. Vegetative plants continued to produce tillers at a relatively constant rate. The reproductive plants developed no new tillers for a period of 4 to 6 weeks centering on the time of heading, and numbers of tillers died commencing near the onset of heading. The cumulative total of tillers produced, together with the number living or dead at 14-day intervals is presented in Fig. 2 for the reproductive plants of two clones. Six weeks before heading the rate of tiller production was alike in plants destined to head or to remain vegetative. Divergence in tillering behavior became apparent 3 to 4 weeks before head emergence. At this time new tillers ceased to appear on the reproductive plants. Near the time of head emergence, tiller mortality commenced on reproductive plants, but no tiller mortality was evident on the vegetative plants for another 8 weeks. The number of living shoots on vegetative plants became significantly greater than on the reproductive plants within 2 weeks after head emergence of the latter. A resumption of tillering by the reproductive plants was evident 3 to 4 weeks after they had headed. The tillering behavior depicted in Fig. 2 was obtained on plants subjected to a 20-hr photoperiod, and was compared to that of vegetative plants receiving a 16-hr photoperiod. It was considered possible that this difference in photoperiod may have produced the tillering responses noted. Preliminary trials with clone B had revealed that following a 5-week cold conditioning, the plants would head under 17-hr daylength. Accordingly, both reproductive and vegetative plants of this clone were obtained under 17-hr photoperiod after the former had received cold treatment and the latter had not. Again the vegetative plants continued to tiller while the reproductive plants near the heading stage did not, but exhibited some tiller mortality. These results would support the contention that the depression of tillering at the heading stage is associated with some aspect of the reproductive condition, and not the daylength employed. Since the divergence in tillering behavior commences well before head emergence, it would appear further that factors are involved other than the mobilization of metabolites to the seed.

The depression in tillering and the tiller mortality noted in hardinggrass near the onset of heading is associated with the stage of development of the plant, as well as with the environmental factors of increasing dryness and temperature which often prevail. That depression of tillering in hardinggrass which centers on the heading stage is transitory in nature. If favorable conditions for growth persist, tillering will resume soon after heading. The decline in rate of tillering when flowering culms are elongating can be offset to a degree by grazing or clipping the flowering stalks. Such terminal bud removal is followed by renewed tillering. Grazing the plants to accomplish this appears to be a sound practice when seed production is not desired. At the Hopland Field Station, sheep have been observed to take the heads almost preferentially between the anthesis and seed shattering stages of maturity. Grazing heavily at these stages also eliminates growth which can become coarse and stemmy.

It is not known at this time whether hardinggrass exhibits a tillering pattern generally found in perennial grasses, nor exactly what causes the reduced tillering near the onset of heading. These questions should receive additional study.

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