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THE NATURE OF SUMMER DORMANCY IN PERENNIAL GRASSES

HORTON M. LAUDE

Introduction

The nature of dormancy in herbaceous perennials has received relatively little study. This is particularly true of dormancy during the summer season. Yet herbaceous perennials frequently are subjected to extended periods of summer heat and dryness during which time plant growth may become greatly limited or completely cease. The latter condition is termed "summer dormancy" in this investigation.

In areas of distinctly winter rainfall, such as California, the arid summer period may persist for several months. Summer dormancy in such regions is of great importance in pastures and rangelands, for it limits the seasons of green forage production and affects the maintenance of stands over the severe summer period.

Several external factors have been associated with the initiation and the breaking of dormancy. In studies of winter dormancy the importance of photoperiod has been demonstrated. GARNER and ALLARD (4) proposed that certain perennials may enter a state of dormancy when exposed to particular daylengths. KRAMER (7) found that certain species of trees grew all winter in the greenhouse under long daylengths but ceased growth as early in the greenhouse as outdoors under natural daylengths. GUSTAFSON (5) reported that pine seedlings not subjected to freezing temperatures during the winter made very little summer growth but that those given a photoperiod of 16 hours in the spring grew considerably. The initiation of the

winter rest period in some varieties of strawberries was shown by DARROW and WALDO (3) to be related to short daylength rather than to low temperature, and the rest period was broken by long days and warm temperatures (2). OLMSTED (8) considered that the winter cessation of growth in strains of side-oats grama growing in a warm greenhouse was associated with shortening days and low light intensities.

Summer dormancy generally has been considered to be closely associated with availability of water. That other factors may be involved was recognized by HOWARD (6), who reported that some herbaceous perennials become dormant in the summer months regardless of whether the season is wet or dry, cool or hot. CLAUSEN *et al.* (1) have noted the periodicity of growth in *Poa* species grown at Stanford, California. They reported that *Poa scabrella* from the California Coast Ranges goes dormant as the dry season nears and that *P. secunda* enters dormancy in May irrespective of the soil moisture condition.

The summer growth behavior of *Taraxacum kok-saghyz* has been investigated by SCARTH *et al.* (9). In their studies "dormancy" was used to refer to a condition of limited growth rather than to a complete cessation of growth. These investigators reported, from date-of-planting trials, that growth limitation occurred at a definite stage in ontogeny. Environmental conditions affected the growth rate but did not induce dormancy. Daily watering of the plants from May through August modified the

amount of growth but did not prevent dormancy. Removal of flower buds as they were formed delayed the onset of the period of slow growth but did not prevent it.

On California rangelands the author has observed that *P. scabrella* may enter complete dormancy in the late spring while surrounding annual vegetation is still green and vigorous. *Stipa cernua* may resume rapid growth in mid-September in seasons when the first effective rainfall since spring does not come until October. There is evident need for critical study of the nature of summer dormancy in perennial grasses. The present investigation was undertaken to determine factors involved in the summer dormancy of perennial grasses in California.

Material and methods

The following species of perennial grass were included in this study: *Agropyron desertorum* (Fisch.) Schult.; *Bromus carinatus* Hook. and Arn.; *B. catharticus* Vahl.; *B. stamineus* Desv.; *Dactylis glomerata* L.; *Ehrharta calycina* J. E. Smith; *Elymus glaucus* Buckl.; *Festuca arundinacea* Schreb.; *Lolium perenne* L.; *Melica californica* Scribn.; *Oryzopsis miliacea* (L.) Benth. and Hook. ex Aschers. and Schweinf.; *Phalaris tuberosa* var. *stenoptera* (Hack.) Hitchc.; *Poa ampla* Merr.; *P. bulbosa* L.; *P. compressa* L.; *P. nevadensis* Vasey ex Scribn.; *P. scabrella* (Thurb.) Benth. ex Vasey; *P. secunda* Presl.; *Stipa cernua* Stebbins and Love; and *Stipa pulchra* Hitchc.

The summer dormancy behavior of these species was noted in field plantings at Davis, California, where a dry summer period of 5–6 months prevails. Based on 40 years of record, the annual average precipitation at Davis is 16.43 inches. From the same records monthly average precipitation in inches for the drier por-

tion of the year has been: April, 0.96; May, 0.48; June, 0.15; July, 0.00; August, 0.01; September, 0.29; and October, 0.68. Relatively high summer temperatures, coupled with this meager rainfall, place most plants under moisture stress by late spring or early summer.

Growth in response to water supplied during the summer was determined in the field, as was autumn growth following the severing of roots at stated depths while the plants were dormant. Tests to determine factors involved in the initiation of dormancy in *P. scabrella* were conducted in the greenhouse with the aid of a controlled environment chamber.

The field plantings were made in November each year for 4 years on a deep, fine sandy loam. These plantings were in replicated rows 3 feet apart and were kept free of weeds. Water during the summer was supplied by sprinklers unless only a few plants were involved, and then surface flooding was used. Portions of the plots were clipped periodically with shears to a uniform level, and summer growth was detected by noting elongation of tissue above the clipped height.

Greenhouse materials were seeded in flats, then transplanted 6 weeks later to 7-inch unglazed clay pots, three plants to a pot. The tests to induce dormancy were conducted during December, January, and February of 4 years. At this season natural daylengths were between 9.5 and 11.5 hours. These natural short photoperiods were used for the short-day condition. Long photoperiods of 16- or 18-hour duration were obtained by prolonging the light period with supplemental illumination provided by incandescent bulbs over the benches. The intensity averaged 100 foot-candles at foliage height. The lights were operated through a time switch to give equal extension of the light period morning and evening.

Greenhouse temperatures were thermostatically set to reach 80° F. for 6 hours daily and 65° F. at night. All greenhouse plantings were watered daily to eliminate possible responses to soil moisture deficiency.

A controlled environment chamber supplied conditions for high-temperature exposures. This unit, with a capacity of

desired air temperature was regained after introducing the plants.

Details of method are presented with each experiment.

Experimentation and Discussion

FIELD STUDIES

Field plantings of the twenty species were used to determine whether vegetative growth would continue throughout the summer at Davis if moisture was supplied. In the spring following the November planting and before moisture deficiency was apparent, half the plots received thorough weekly waterings which were continued until the first effective autumn rain. Certain rows within the watered and unwatered plots were clipped periodically to facilitate detection of vegetative growth.

Growth behavior during the summer following seeding is presented in table 1. Those species listed as continuing vegetative growth when supplied with water differed considerably in the vigor of growth, as well as in the time that the unwatered plants of the same species ceased growth. This group of species would appear to conform with the hypothesis that the summer dormancy period depends primarily on the availability of moisture. In those species not continuing growth throughout the summer with watering, factors other than or in addition to soil moisture supply appear to be involved in the dormancy behavior.

A fall planting of four replications was used the following summer to determine the effect on growth renewal of watering after several durations of dormancy. *Lolium perenne*, *E. glaucus*, *D. glomerata*, *B. catharticus*, *B. carinatus*, *B. stamineus*, *S. cernua*, *S. pulchra*, and *P. scabrella* were included in this planting. The latter three species represented the group failing to continue summer growth when

TABLE 1

EFFECT OF SUPPLYING SOIL MOISTURE AT WEEKLY INTERVALS THROUGHOUT THE DRY SUMMER PERIOD ON VEGETATIVE GROWTH OF TWENTY PERENNIAL SPECIES IN THE FIELD AT DAVIS, CALIFORNIA, 1947-1950

SPECIES CONTINUING VEGETATIVE GROWTH	SPECIES CEASING VEGETATIVE GROWTH	
	Retaining green tissue	Retaining no green tissue
<i>Agropyron desertorum</i>	<i>Melica californica</i>	<i>Poa bulbosa</i>
<i>Bromus carinatus</i> ...	<i>Poa nevadensis</i>	<i>Poa scabrella</i>
<i>Bromus catharticus</i> ..	<i>Stipa cernua</i>	<i>Poa secunda</i>
<i>Bromus stamineus</i> ...	<i>Stipa pulchra</i>	
<i>Dactylis glomerata</i> ...		
<i>Ehrharta calycina</i> ...		
<i>Elymus glaucus</i>		
<i>Festuca arundinacea</i> ..		
<i>Lolium perenne</i>		
<i>Oryzopsis miliacea</i> ...		
<i>Phalaris tuberosa</i> var. <i>stenoptera</i>		
<i>Poa ampla</i>		
<i>Poa compressa</i>		

twenty 7-inch pots, precisely controlled air temperature and relative humidity. Light intensity of 600 foot-candles at foliage height was provided by a fluorescent light panel within the chamber. Positional effects were eliminated by placing the pots on a slowly revolving turntable. In operation the chamber was brought to the desired conditions, then opened, and the plants were introduced. The duration of each high-temperature exposure was timed from the moment the

supplied with supplemental water in previous tests. By July 20 the nine species had ceased growth, but some green tissue was still visible in all but *L. perenne* and *P. scabrella*.

One replication was thoroughly watered on July 20, the second on August 10, the third on September 7, and the fourth on September 29. In each instance decided growth was obtained 7–10 days after a watering in all species except the two species of *Stipa* and the *Poa*. The former made appreciable growth only after the September waterings, while *P. scabrella* did not break dormancy until cool weather prevailed coincident with the first fall rain. This suggests that those species in which summer growth may be prolonged by watering will also break dormancy when watered after being dormant a portion of the summer.

Stipa cernua, *O. miliacea*, and *P. tuberosa* var. *stenoptera* have been observed to make vigorous vegetative growth at Davis in September before autumn rains and after a period of dormancy or of greatly reduced growth during the summer. Such fall growth prior to precipitation was noted in a stand of 2-year-old spaced plants of *P. tuberosa* in 1949. The plots had been mowed to a 3-inch height on June 1 about 2 weeks after the last spring shower. By July 12 there had been no new growth, and the plant bases were nearly devoid of green tissue. Growth evidenced by green leaves 6–8 inches tall was noted on all plants on September 13. Dry weights of this growth, clipped on September 25, averaged 6.75 gm. per plant. The first fall rain did not come until November 9.

In 1950 the same stand, then in its third year, was used to investigate the source of moisture for the growth made prior to autumn precipitation. The plants were mowed to a 3-inch height on May

26 after the last effective precipitation of the spring. *P. tuberosa* produced a negligible amount of growth until early September. Between July 24 and 26, trenches which severed all lateral roots 18 inches from the center of the row were dug around three-plant blocks. Vertical roots were severed at 2- or 4-foot depth by cuts under the blocks. In one instance the lateral roots were cut by trenching, but those roots extending directly downward were left intact. The trenches were filled with dry soil tamped into place, and plant tops were clipped at a 3-inch height. Soil moisture samples taken on August 3 to a depth of 6 feet indicated that the soil was dry to the permanent wilting percentage to that depth.

Vegetative growth in September was compared in the root-pruned and control plants. All undisturbed plants showed 3–4 inches of leaf elongation by September 12, while those plants with roots cut at a 2- or 4-foot depth resumed growth only after rainfall the last of October. The trenched sample with uncut vertical roots resumed growth in September as vigorously as did the undisturbed plants. In this species early fall growth prior to precipitation appears to depend upon moisture procured by roots at a considerable depth. Additional studies of this nature are needed.

Poa scabrella exhibited such precision in its summer dormancy behavior that the species was selected for critical study of the factors involved. When dormant in the field, this plant is devoid of visible green tissue. When entering dormancy, it first shows a bronzing of the leaf tips and then loses all green coloration in a period of approximately 2 weeks. In breaking dormancy in the field, it produces green shoots about 4 days after suitable conditions prevail.

Indications as to the probable factors

involved in the summer dormancy of *P. scabrella* were obtained from field observation. Over a 5-year period this species entered complete dormancy (recorded as the date by which all green coloration had disappeared) at approximately the same time regardless of the date of the last spring precipitation. This suggested the possibility that photoperiod might play a part in the response. Normally rising spring temperatures also could be involved. The breaking of dor-

TABLE 2

SUMMER DORMANCY IN *POA SCABRELLA* AT
DAVIS, CALIFORNIA

Year	Date of last spring rain exceeding 0.25 inch	Date of dormancy	Date of first fall rain exceeding 0.50 inch	Date of first visible fall growth
1947...	June 7	May 25	Oct. 8	Oct. 13
1948...	June 5	May 24	Oct. 11	Oct. 13
1949...	May 14	June 6	Nov. 9	Nov. 14
1950...	April 8	June 1	Oct. 25	Oct. 30
1951...	May 4	June 1	Oct. 25	Oct. 29

mancy followed the first fall rains by a few days, suggesting that moisture coupled with the cooler temperatures then prevailing might be instrumental in this response.

Table 2 summarizes this field behavior. Obviously rainfall prior to the last spring precipitation greater than 0.25 inch will affect available soil moisture. The spring season of 1948 was relatively wet, whereas that period for 1949 and 1950 was considerably drier than normal. The fall rains listed mark the beginning of precipitation of 1 inch or more. In all years except 1948 these dates represent the first autumn rain of any consequence. The exception was a shower of 0.35 inch on September 17, 1948, which, however, was not followed by growth in dormant *P. scabrella* unless additional water was supplied.

Efforts to break summer dormancy in the field by watering had failed with *P. scabrella* until temperatures had moderated toward autumn, at which time the plant had been dormant 4-5 months. A test was devised to determine whether dormancy could be broken in midsummer with water if cooler temperatures prevailed. Plants in the field approaching their third summer were potted in 12-inch clay pots in late February. The pots were sunk to the rim in soil among undisturbed plants. Top growth of the potted plants was similar to that of the undisturbed ones until early April, but the potted plants, with greatly restricted root systems, entered dormancy 4 weeks earlier. On August 4 ten potted plants were moved to a laboratory where maximum room temperatures averaged 76° F., while daily maximum field temperatures were averaging 87° F. Plants in both laboratory and field were thoroughly watered, this being done periodically to maintain available soil moisture. On the fourth day after the initial watering, plants in the laboratory commenced to break dormancy, and by the sixth day all were growing. There was no resumption of growth in the field.

Cooler temperatures in the field without precipitation were ineffective in breaking the dormancy. An instance was noted in which daily average temperatures near 65° F. prevailed for 3 weeks prior to the first effective autumn rain, and *P. scabrella* failed to resume growth unless watered.

GREENHOUSE STUDIES WITH *POA SCABRELLA*

These experiments were conducted to determine the factors involved in the induction of dormancy in *P. scabrella*. In view of its field behavior, particular attention was given to the effects of day-length and of temperature. Responses re-

sulting from deficient soil moisture were eliminated by daily watering of the plants.

Effort was made to induce dormancy in December, January, and February, when this species normally makes vigorous vegetative growth in the greenhouse. The daylength conditions used were those of the prevailing short winter days or of longer photoperiods of 16 or 18 hours obtained by prolonging the natural day with incandescent light. The temperature conditions employed were either the established greenhouse temperatures of 80° F. day and 65° F. night or these greenhouse temperatures with a series of brief exposures to higher temperature at intervals in the controlled environment chamber.

Exposures to high temperature in the control chamber were sought which would visibly affect, but not kill, the plants. Two, three, and four exposures to air temperatures from 120° F. to 135° F. for periods of 4–5½ hours were tried on successive days, alternate days, and at intervals during a 2-week period. The most precise response was obtained following heat stresses of 130° F. and 50% relative humidity for 4-hour exposures applied on 3 alternate days. These conditions were used in the tests to be described. Soil temperatures of 114° F. were reached at ¾-inch depth in the center of the pots by the end of such an exposure. Between these exposures the plants were returned to their respective daylength conditions at greenhouse temperatures. Such high-temperature treatments induced wilting of the plants while in the chamber and resulted in the death of some of the older leaf tissue, especially in the plants under short day. The younger leaves and basal portions of the older leaves remained green, however, and the plants were not killed by these exposures.

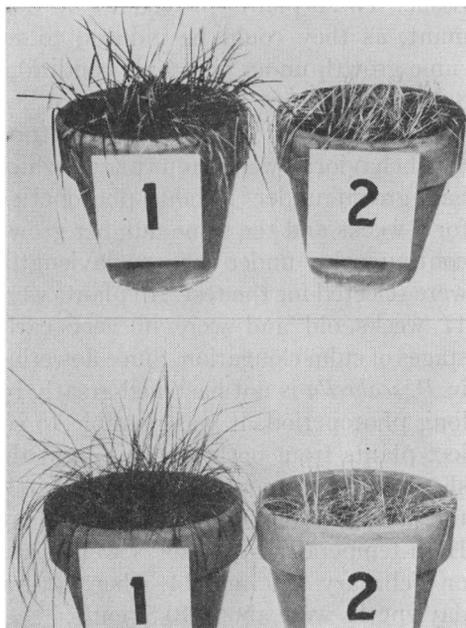
It was found that plants grown under short day at greenhouse temperatures continued vegetative growth, as did those plants under short day subjected to the high-temperature stresses. With long photoperiod and greenhouse temperatures plants continued active growth, but those grown under long photoperiod and subjected to the high-temperature stresses ceased growth and within 1 week after the last exposure to high temperature lost all, or virtually all, visible green tissue. These plants proved to be dormant, as they could be induced to resume growth under favorable conditions 8–12 weeks later.

A typical test will serve to illustrate this behavior. Twenty-four plants which had grown under 18-hour photoperiod for 8 weeks and the same number grown continuously under short daylengths were selected for the test. All plants were 17 weeks old and were in very early stages of culm elongation. Since flowering in *P. scabrella* is not hastened greatly by long photoperiod, it was possible to select plants from both the long- and the short-day treatments in approximately the same apparent stage of development. High-temperature exposures were given on February 7, 9, and 11, when natural daylengths were about 10.5 hours.

On the day following the third heat stress all plants were living as evidenced by turgid green leaves, but some leaves of the plants of the group on long photoperiod exhibited a noticeably pale-green coloration. By February 13 all plants under short day showed abundant normal green leaves while two of the long-day group had lost all visible green tissue, and in the remainder the amounts of distinctly pale-green leaves had been reduced. Three days later increase in both length and numbers of green leaves was apparent in all plants on short photoperiods, while those on long photoperiods

showed no new shoots and still greater reduction in amount of green tissue. One week after the third heat stress plants in the long-day group were either completely brown or retained only traces of pale-green leaves, even though they were being watered daily. Figure 1 was taken 28 days after the third heat exposure.

On April 1 all plants of this test were moved outside the greenhouse, where cooler temperatures and natural day-length prevailed. By April 8 some plants



FIGS. 1, 2.—Fig. 1 (above), *Poa scabrella* plants 28 days after third high-temperature exposure. Pot 1 is from group on natural short day, and pot 2 from group on 18-hour daylength. Fig. 2 (below), *P. scabrella* plants dormant 20 months in greenhouse. Watering of pot 1 resumed 28 days before photograph was taken. Pot 2 received no water and is still dormant.

of the long-photoperiod, high-temperature treatment showed the first indications of growth. Two days later 66% of these plants had produced green shoots. By April 15 all plants had resumed

growth, thus demonstrating that these plants were previously in a dormant condition. It was noted that resumption of growth under favorable conditions after dormancy was slower in plants such as these, watered daily while dormant. From 1 to 2 weeks were required generally to break dormancy in such plants compared with 4 or 5 days for plants in dry soil during dormancy.

The same heat stresses were applied to plants varying in age from 10 to 24 weeks and having been grown under conditions of long photoperiod for 1–8 weeks prior to testing. Under the test conditions employed it was found that growth ceased in those plants subjected to long photoperiods and high temperatures only when the plants were at least 15 weeks old. Additional trials will be necessary, however, to determine precisely the earliest stage of development and the minimum duration of long photoperiod required to permit the induction of dormancy. A 16-hour photoperiod was used in some tests and appeared as effective as the 18-hour photoperiod.

If *P. scabrella* is permitted to grow in a warm greenhouse under natural day-length and without the exposure to high temperature, the plant will go dormant by early June even though watered daily. This is similar to the field behavior. Two weeks after such dormancy had set in, watering was stopped on a series of these plants. The pots then remained dry on greenhouse benches for 5, 7, 11, 17, and 20 months. At the end of each interval, six pots were removed to a section of greenhouse having daily maximum temperatures not exceeding 75° F., and daily watering was resumed. All plants of the groups dormant 5, 7, 11, and 17 months resumed growth by the fifth day after the resumption of watering. The majority of

these plants had developed vigorous new shoots 1–2 cm. long by the fourth day. In the group dormant 20 months, only two plants (out of eighteen) failed to grow.

The rapidity of the new shoot growth was striking. The early growth of marked shoots of the group dormant 20 months was measured daily. The average length of eight shoots measured on the fourth, fifth, sixth, and seventh days after watering was resumed was 1.2, 2.8, 4.1, and 5.5 cm., respectively. Seven days after the first watering the more vigorous plants averaged twenty-seven green shoots per plant. The appearance of such plants 4 weeks after the resumption of watering compared with those still dormant is shown in figure 2.

The greenhouse studies with *P. scabrella* demonstrate that in this species the initiation of summer dormancy is associated with long photoperiods and high temperatures. Both conditions prevail in the late spring at Davis and appear to be related to the field behavior. Growth resumption after extended periods of dormancy was obtained when the plants were subjected to relative coolness and were watered. Coolness and availability of water are factors of the field environment when the species breaks dormancy in the autumn after the first effective fall rains. The experiments indicate that these conditions are associated with the resumption of growth in the field.

Summary

1. The summer dormancy behavior of twenty species of perennial grass was investigated in the field at Davis, California, where the climate is a winter-rain-fall, arid-summer type.

2. Of the twenty species, seven became summer dormant in the field even

though supplied with water throughout the dry season.

3. Those species which continued growth as long as water was available were found to resume growth in summer if watered after a period of dormancy. This was not true of the species going dormant while watered.

4. *Stipa cernua*, *Oryzopsis miliacea*, and *Phalaris tuberosa* var. *stenopectera* were observed to make vigorous vegetative growth in September after being summer dormant and before effective autumn rains. Portions of the root system of *P. tuberosa* were severed while the plant was dormant. The typical September growth occurred following such treatment only when the roots at depths below 4 feet were left intact.

5. *Poa scabrella* was selected for critical study of the factors, other than moisture, involved in the summer dormancy behavior of a species becoming dormant though watered throughout the dry season. Field observations indicated that high temperatures and long day lengths were related to the initiation of dormancy in this plant and that moderating temperatures and availability of water were associated with the breaking of dormancy. Greenhouse studies confirmed these deductions.

6. Dormancy in *P. scabrella* was induced in the greenhouse in midwinter while soil moisture was available by subjecting plants at least 15 weeks of age to an 18-hour photoperiod and to high-temperature stresses in a controlled environment chamber. The conditions of the most effective high-temperature treatments were 130° F. and 50% relative humidity, the plants being illuminated by fluorescent light while in the chamber. Three such exposures each of 4-hour duration were given on alternate days.

7. Dormancy was broken by relative coolness and water. Plants of *P. scabrella* dormant 20 months in the greenhouse resumed growth 5 days after being placed

at temperatures not exceeding 7° F. daily and receiving water.

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FUNGICIDAL PROPERTIES OF SOME CARBONIC AND THIOCARBONIC ACID DERIVATIVES OF HYDRAZINE¹

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Introduction

The biological activity of hydrazine and its derivatives has been noted by a number of investigators (1). Aldehyde derivatives of semicarbazide and thio-

semicarbazide have been found to be useful insecticides; the tuberculostatic character of the p-acetamido benzaldehyde derivative of thiosemicarbazide has led to development of this material as a pharmaceutical. Maleic acid hydrazide has been found to have application as a plant growth-regulator. The objects of the preliminary tests summarized in this paper were to ascertain fungicidal properties of some carbonic and thiocarbonic acid derivatives of hydrazine.

Material and methods

The fungi, *Helminthosporium sativum*, *Rhizoctonia* sp., and *Pythium* sp., were cultured at room temperature on potato dextrose agar to which had been added

¹ The results published here are based upon a cooperative investigation sponsored by the Departments of Agronomy and Chemistry of the University of Illinois. The fungicidal tests were carried out by H. W. GAUSMAN, C. L. RHYKERD, and H. R. HINDERLITER and were supported by a research grant made available through the Graduate College of the University of Illinois. The investigation and preparation of the various hydrazine compounds were carried out by E. S. SCOTT and L. F. AUDRIETH under a fellowship grant made available to the University of Illinois by the Western Cartridge Company Division of Olin Industries of East Alton, Illinois.

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