Temperature Requirements for Seed Germination in an Annual-Type Rangeland Community[1]

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ABSTRACT

Germination as affected by constant and alternating temperatures was investigated in four species of annual grasses, soft chess (*Bromus mollis* L.); ripgut (*B. rigidus* Roth); slender oat (*Avena barbata* Brot.) and foxtail fescue (*Vulpia megalura* (Nutt.) Rydb.), and in their replacement forage species, seven cultivars and one naturalized population of rose clover (*Trifolium hirtum* All.); hardinggrass (*Phalaris tuberosa* var. *stenoptera* (Hack.) Hitchc.); and perlagrass (*P. tuberosa* var. *hirtiglumis* Bott. & Trobut). Temperature combinations were alternated through a 16 hr (night) and 8 hr (day). All combinations were used for —4, —2, 0, 2, 5, and 5-degree increments through 40 C. The annual grasses germinated under a very broad range of temperatures above a minimum night temperature of 0 C. The rose clover cultivars germinated at lower temperatures, including subzero C (—4 C and —2 C) alternating with 15 to 25 C day temperatures. Seeds of rose clover from a naturalized population had lower germination at low temperatures and higher germination at high temperatures than the seven cultivars tested. In comparison with the annual grasses and rose clover, the perennial grasses were relatively restricted in the temperature regimes that permitted germination. Interpretation of the ecological significance of the results of monitoring seedbed temperatures during germination periods and the juvenile growth rate of the various species is dependent on the results of this investigation.

Additional key words: Improvement of annual ranges, *Phalaris,* Rose clover, Adaptation of alien annuals.

ON annual-dominated ranges in cismontane California, desirable forage species are seeded in the fall. The annual forbs and grasses germinate with the first substantial rain after the summer drought. Treatments for weed control are delayed until the reproductive reserve of the weeds is so committed through germination that the resulting reduction in competition will permit the seeded, desirable forage plants to become established (4). Microenvironmental studies are establishing the parameters of temperature, moisture, and light during the germination period. Interpretation of this information will require knowledge of the inherent responses of both weed and forage species to various germination regimes.

In the study presented here the germination of four annual grasses and their replacement species was compared at constant and alternating temperatures in the laboratory.

METHODS

Four replications of 100 seeds or caryopses were placed in dark germinators at regimes of constant and alternating temperatures from —4, —2, 0, 2, 5, and 5-degree increments through 40 C. The timing was 16 hr at the lower temperature and 8 hr at the higher. The seeds or caryopses were placed on germination pads in 1.5-cm petri dishes and kept moist with tap water. Germinated seeds were counted after 1 and 2 weeks of incubation. Results were totaled for presentation. Caryopses and seeds wer considered germinated when the radicle emerged 5 mm.

Caryopses were collected from the following four dominant grasses of annual-type range in cismontane California: soft chess (*Bromus mollis* L.), ripgut (*Bromus rigidus* Roth), slender oat (*Avena barbata* Brot.), and foxtail fescue (*Vulpia megalura* (Nutt.) Rydb.) (formerly *Festuca megalura* Nutt.). Collections were made at the Sierra Foothills Range Field Station, near Marysville, California, and germination tests were made in 1970 and 1971. The figures presented are mean germination for the 2 years.

The forage species used included rose clover (*Trifolium hirtum* All.) cultivars 'Wilton,' 'Kondinin,' 'Hykon,' 'Sirint,' 'Olympus,' and numbered selections S6 and T02648. In addition, 1970 seed from a naturalized population of rose clover near Marysville, California was collected. This population apparently resulted from seeding of the cultivar 'Wilton' (5) and had probably been established from 10 to 15 years.

The perennial forage grasses tested were hardinggrass (*Phalaris tuberosa* var. *stenoptera* (Hack.) Hitchc.) and perlagrass (*P. tuberosa* var. *hirtiglumis* Bott. & Trobut).

The rose clover and hardinggrass seeds were obtained from a replicated common garden grown at Davis, California in 1969 and 1971. Tests were conducted with seeds 120 days after harvest. The rose clover seeds were harvested and processed mechanically in 1969 without additional scarification. The 1971 seed production and the naturalized population collected in 1970 were harvested and processed by hand. To obtain marked germination of these collections, the seeds were mechanically scarified for 30 seconds. Seeds of the naturalized population were tested for germination in 1970 and 1971, both before and after scarification. The seeds produced in 1971 were tested for germination in September and December 1971, before scarification.

RESULTS

Annual Grasses

Soft chess characteristically produced highly viable caryopses that germinated at a wide range of temperatures (Table 1). With night temperatures of 2 C or higher and day temperatures of 10 C or higher, mean germination was 80% or better with day temperatures of 20, 25, and 30 C. Some seed germinated at 2 C alternating with 15 C or at a constant 5 C. Germination was much less at a constant 30 C than when 30 C was alternated with lower night temperatures. Incubation at 40 C inhibited germination.

Just as soft chess caryopses were characteristically highly germinable, collection of slender oat contained many dormant caryopses (Table 1). In addition to generally lower germination, slender oat caryopses required a more restricted temperature regime for that germination than did soft chess. A night temperature of at least 2 C was required for germination with any day temperature, and a night temperature of 5 C was required for germination at 10 C in the day. A constant 30 C inhibited germination, and moderate night temperatures alternating with 30 C depressed germination below that with 25 C day temperatures.

Caryopses of foxtail fescue were highly viable, but their range of germination response was not as great

[1] Cooperative investigations of the Agricultural Research Service, USDA; the Agricultural Experiment Station, University of Nevada, Reno, Nevada, Journal Series Number 232; and the University of California, Davis, California. Received Dec. 4, 1972.

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Table 1. Germination of four annual grasses in relation to constant and alternating temperatures.*

Night temp., C, 16 hr	*Bromus mollis* - soft chess, Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	48e	84cd	80d	80d	0
2		0	24g	80d	96ab	92a-c	90bc	92ab	0
5			22g	84cd	100a	96ab	92a-c	92ab	0
10				84cd	92a-c	96ab	88b-d	100a	0
15					96ab	100a	100a	100a	0
20						92a-c	100a	92a-c	0
25							92a-c	100a	0
30								36f	0
40									0

Night temp., C, 16 hr	Vulpia megalura - foxtail fescue, Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	30g	96ab	50ef	0	0
2		0	0	76d	96ab	92a-c	60e	8h	0
5			0	84cd	96ab	100a	96ab	48f	0
10				100a	100a	96ab	92a-c	96ab	0
15					100a	92a-c	96ab	96ab	0
20						100a	94a-c	88bc	0
25							100a	88bc	0
30								16h	0
40									0

Night temp., C, 16 hr	*Avena barbata* - slender wild oat, Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
2		0	0	0	44e	56d	72c	0	0
5			0	56d	84b	96a	44e	12g	0
10				84b	44e	52de	44e	28f	0
15					72c	72c	44e	24f	0
20						76bc	32f	24f	0
25							16fg	8g	0
30								0	0
40									0

Night temp., C, 16 hr	Bromus rigidus - ripgut, Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-2	0	0	0	0	0	0	0	0	0
0	0	0	0	16l	36ij	74c-e	64e-g	54fg	0
2		0	12lm	64e-g	88ab	92a	90a	68d-f	0
5			30jk	80a-d	92a	84a-c	72de	64e-g	0
10				84a-c	84a-c	84a-c	68d-f	68d-f	0
15					80a-d	76b-e	76b-e	48hl	0
20						56fg	52gh	48hl	0
25							20kl	32jk	0
30								4m	0
40									0

* Means followed by the same letters are significantly different at the 0.01 probability level as determined by Duncan's Multiple Range Test.

as that for soft chess (Table 1). For germination, day temperatures had to reach 10 C with 2 C nights, and 15 C with 0 C nights. A constant 30 C depressed germination, and wide diurnal fluctuations with 30 C greatly depressed or inhibited germination.

The breadth of germination response to temperature was greater in ripgut than in soft chess, although total germination was lower (Table 1). Germination was optimum at relatively cool temperatures.

Rose Clover

There was considerable hard seed in all cultivars of rose clover grown in 1971 (Table 2). Hard seed coats restricted germination to 61% or less, even at optimum temperatures. This seed was not scarified, but the harvesting and threshing method approximated commercial processing. At a given temperature within the optimum germination range, we demonstrated statistically the superiority of one or more cultivars. However, no single cultivar was consistently higher or lower in germination at all temperatures, and under extreme temperature regimes all statistical distinction among the cultivars was lost.

The rose clovers germinated over a much broader range of temperatures than the weedy grasses (Table 2). Germination, at least emergence of the radicle, occurred at a constant 0 C. Diurnal fluctuations from —4 to 15 or 30 C resulted in considerable germination. Germination tended to be depressed by high temperatures, especially by 40 C. Germination was also inhibited by diurnal fluctuations between 30 C and subzero night temperatures.

The rose clover cultivars were grown under similar conditions at Davis, California in 1972, but the seed was harvested and threshed by hand. Germination of this hand-processed seed was less than 5% in all cultivars at all temperatures. With scarification, however, germination of all cultivars was dramatically increased (Table 2). There was no clear distinction among cultivars in germination response to the various temperatures. As noted for the seed production in 1971, germination of a cultivar could be significantly higher at a given temperature, but no germination of any cultivar was consistently higher or lower at all temperatures or was consistently highest at a given temperature both years.

Scarification of 1972 seeds permitted germination at temperature regimes that inhibited germination of seeds not deliberately scarified in the previous year (Table 2). Apparently there is an interaction between hard seed and incubation temperatures; seeds that can germinate at extreme incubation temperatures tend to have hard seed coats.

The naturalized population of rose clover also had an extremely high percentage of hard seed. Germination at any temperature was elss than 5% even after 1 year's storage. Scarification greatly increased germination (Table 3). The range of temperatures at which seeds germinated and the total germination at optimum incubation temperatures were similar for the naturalized population and the mean of the cultivars. At extreme temperatures allowing germination, there was a striking difference between the naturalized population and the cultivars (Table 4). Selection

Table 2. Mean germination of seven cultivars of rose clover in relation to constant and alternating temperatures, year of production, and scarification.*

Night temp., C, 16 hr	1971 seed - no scarification, Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-4	0	0	0	0	17j-l	24j	0	0	0
-2	0	0	2m	14kl	28ij	32hl	8lm	0	0
0	2m	30hl	32hl	44fg	44fg	50d-f	40gh	5m	0
2		44fg	50d-f	52b-e	57a-c	58ab	32hl	17j-l	0
5			56a-d	57a-c	59a	56a-d	52b-e	41gh	0
10				59a	58ab	57a-c	59a	39gh	5m
15					59a	61a	59a	35h	15kl
20						51c-f	48ef	39gh	0
25							46ef	22jk	0
30								12l	0
40									0

Night temp., C, 16 hr	1972 seed - scarification required for germination, Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-4	0	0	2i	28ef	48d	32e	4i	0	0
-2	0	0	12g-i	84a	86a	84a	62c	2i	0
0	8hl	64c	80a	84a	86a	88a	84a	46d	8hi
2		77ab	79ab	80a	82a	82a	83a	73b	17h
5			79ab	84a	84a	82a	85a	82a	67c
10				88a	87a	86a	89a	88a	88a
15					85a	80a	84a	82a	55d
20						59cd	64c	56cd	43de
25							22e-g	21e-g	19fg
30								23e-g	15g-l
40									2i

* Means followed by the same letter are not significantly different at the 0.01 probability level as determined by Duncan's Multiple Range Test.

Table 3. Germination of seeds of rose clover collected from a naturalized roadside population. Scarification required to obtain significant germination.*

Night temp., C, 16 hr	Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-4	0	0	0	0	12fg	14fg	2g	0	0
-2	0	0	0	44d-f	60a-f	26fg	8g	0	0
0	4g	36fg	34fg	80a-d	84a-c	76a-e	72a-e	32fg	0
2		55b-f	56b-f	80a-d	86ab	85a-c	79a-e	76a-e	47d-f
5			76a-e	76a-e	73a-e	77a-d	77a-d	80a-d	80a-d
10				89ab	85a-c	77a-e	82a-c	79a-e	80a-d
15					79a-e	75a-e	74a-e	92a	79a-e
20						79a-e	70a-e	86ab	60a-f
25							44ef	60a-f	78a-e
30								71a-e	33fg
40									5g

* Means followed by the same letter are not significantly different at the 0.01 probability level as determined by Duncan's Multiple Range Test.

Table 4. Comparison of mean germination of a naturalized population and of seven cultivars of rose clover in relation to constant and alternating temperatures. 0 indicates no difference; L indicates naturalized population significantly (0.01 probability level) lower; and H indicates significantly higher.

Night temperature, C, 16 hours	Day temperatures, C, 8 hours								
	0	2	5	10	15	20	25	30	40
-4			0	L	L	L			
-2			0	L	L	L	0	0	
0	0	0	L	0	0	0	0	0	0
2		L	L	0	0	0	0	0	H
5			0	0	0	0	0	0	H
10				0	0	0	0	0	0
15					0	0	0	0	H
20						H	0	H	H
25							H	H	H
30								H	H
40									0

pressure among the cultivars has apparently been for the genotypes to germinate at low temperatures, whereas the pressure for the naturalized population was the opposite.

Perlagrass and hardinggrass. The caryopses of the perennial forage grasses required higher minimum temperatures for germination than seeds of the rose clovers (Table 5). Caryopses germinated at 2 C night temperature if day temperatures reached 10 C but did not exceed 30 C. Germination of perlagrass and hardinggrass was optimum at a constant 10 C.

DISCUSSION

Germination of soft chess, the ubiquitous dominant of annual grass communities in cismontane California, is near optimum over a very wide range of temperatures. The same is generally true for foxtail fescue and ripgut. Temperature-related germination requirements of slender oat are more restrictive. Seedbed temperature quite possibly controls the establishment of these annuals, especially if the first rains are late in the season and followed by low temperatures. Evidence of this is the restricted distribution of slender oat, found mostly on south slopes or other sites with generally higher temperatures. This species is one of the dominants in the annual grasslands of southern California but is only a minor component of most stands in central and northern California.

Partly as a result of temperature effects on seed germination, the establishment of annual plants is controlled selectively by the heterogeneity of the soil (2, 3) and is further affected by germination of caryopses in litter (7) and by litter coverage of seeds and caryopses (1).

The rose clovers (not scarified) had a lower percentage of germination and a more restricted germination response to temperature than did cultivars of subterranean clover (*Trifolium subterranean* L.) grown in the same environment (8). The rose clovers will germinate under lower temperature regimes than the annual grasses. This should provide an advantage because the forage species cannot be planted until after the annuals germinate and are destroyed by weed control treatments (4).

Comparative rates of growth must also be considered. Studying seedling growth of subterranean clover at temperatures from 10 to 25 C, Raguse, Fianu, and Menke (6) determined that the time required from water imbibition by the seed to development of the first trifoliate leaf varied with temperature from 10 to 34 days. Adjusting our criterion for germination from 5 mm to 10 mm of radicle emergence would eliminate rose clover germination below 2 C within a 2-week incubation period. Root elongation of the annual grasses is much faster at low temperatures (7). Buried in the soil of a cold seedbed, the rose clover seeds may initiate germination but not emerge until higher temperatures favor elongation. Laboratory-obtained germination data taken alone are therefore difficult to correlate with observations of field establishment of seedlings.

Experience in the field over numerous trials has shown that the rose clovers usually, but not always, do not establish well if planted after early November. In contrast, the perennials, perlagrass and hardinggrass, can be planted successfully until February. The opposite would be expected if the limiting factor was the effect of cold seedbed temperatures on germination. Temperature may not be limiting for the perennials. The perennial grasses will not germinate at temperatures near or below 0 C, whereas germination at 10 C night and 20 C day temperatures was not significantly lower than optimum. Analysis of the results of monitoring seedbed temperatures on cismontane rangelands in California will tell us how temperature in the seedbed affects the establishment of perennial grasses and introduced clovers.

The lower germination of seeds from a naturalized rose clover population at relatively low temperatures and the markedly greater germination of these seeds

Table 5. Germination of perlagrass and hardingrass in relation to constant and alternating temperatures.*

Night temp., C, 16 hr	Perlagrass: Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-4	0	0	0	0	0	0	0	0	0
-2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
2		0	0	5lm	17kl	22i-l	31f-k	27h-k	0
5			0	30f-k	25i-k	40d-j	39e-j	20i-k	0
10				68a	48b-g	54a-e	46b-l	41e-l	15kl
15					60a-c	56a-b	47b-g	54a-e	21i-k
20						64a	61ab	60a-c	22e-l
25							60a-c	61ab	6lm
30								29g-k	2m
40									0

Night temp., C, 16 hr	Hardinggrass: Day temperatures, C, 8 hr								
	0	2	5	10	15	20	25	30	40
-4	0	0	0	0	0	0	0	0	0
-2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
2		0	0	17hi	32f-h	48b-f	66a-c	38e-g	0
5			0	26gh	42d-g	64a-d	52a-f	37e-h	0
10				74a	58a-c	60a-e	68ab	64a-d	11i
15					58a-e	72a	66a-c	44d-g	16hi
20						28gh	54a-f	40e-g	4j
25							32f-h	40e-g	0
30								17hi	0
40									0

* Means followed by the same letter are not significantly different at the 0.01 probability level as determined by Duncan's Multiple Range Test.

at high temperatures may relate to the paradox in clover establishment. As previously mentioned, clover can be seeded 2 weeks to 1 month after fall rains initiate germination of the resident annual population. This delay is necessary if weed control is practiced to reduce competition. During this time lag, temperatures are lowering with the onset of winter. Once the annual clover is established and reproduces, its progeny must germinate at the same time as the resident annual population, under the warmest conditions, in order not to be at a competitive disadvantage.

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