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Influence of Temperature on the Growth of *Erodium botrys* and *Trifolium subterraneum*[1]

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ABSTRACT

Temperature effects on the vegetative growth of broad-leaf filaree, *Erodium botrys* (Cav.) Bertol., and subterranean clover, *Trifolium subterraneum* L., were studied at three diurnal temperature regimes: low (5 to 15 C), medium (10 to 20 C), and high (15 to 25 C). The objective of this study was to evaluate the response of these species to temperatures that reflect the conditions of the annual grassland type during the seedling stage. Chamber-grown plants were harvested periodically over a 5-week period.

Filaree was less sensitive to low temperatures and exhibited a temperature optimum between 10 to 20 C and 15 to 25 C, whereas subclover showed a linear increase in relative growth rate with temperature up to 15 to 25 C.

Although subclover demonstrated a more efficient photosynthetic system, i.e., a greater net assimilation rate, filaree had a higher photosynthetic capacity as shown by a greater leaf area ratio. Filaree partitioned more assimilate into leaf tissue than subclover which in turn produced more stem and root tissue than filaree. These results indicate that filaree is favored when late fall rains occur along with lower temperatures.

Additional index words: **Seedling growth, Broadleaf filaree, Subclover, Growth analysis, Relative growth rate, Net assimilation rate, Specific leaf area.**

THE establishment of winter annual legumes has led to improved forage quality and an increase in the carrying capacity of considerable acreage in California's annual grasslands (Murphy et al., 1973). Although various difficulties such as cultivar selection, proper strains of *Rhizobium,* and soil infertility, have been surmounted, numerous pasture establishments have failed. Sumner and Love (1961) have attributed some of the failures to competition from resident vegetation during the seedling stage. Depending on climatic conditions, competition may be most intense from various graminaceous spp. or from *Erodium* spp. The latter are highly adapted to arid environments and through early germination, large cotyledons, and rapid root development (McCown and Williams, 1968) often dominate the annual vegetation early in the season.

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Aspect dominance by one of these groups results in a "good grass year," "good filaree year," or "good clover year" (Rossiter, 1966). Differential response by these species to environmental factors (mainly temperature and precipitation) seems to determine which will dominate, and of course competition for limited resources influences the botanical composition. Competition is usually for water, nutrients, and light (Donald, 1963), and the effectiveness of a competitor lies in its capacity to obtain a disproportionate share of the limiting resource. Seedling vigor serves as an index of competitive ability and is characterized by dry weight accumulation over a given period of growth. Since low temperatures limit the growth of annual legumes (McKell, Wilson, and Williams, 1962) and winter annuals in general (Bentley and Talbot, 1951), an evaluation of this factor on the growth of a widely used legume, subclover, and a wide-spread forb (filaree) would help to elucidate the competitive relationship between these "cohabitants" (i.e., potential competitors).

Leaf area and yield/plant have been used to assess seedling vigor. In addition there are various growth parameters which are useful, especially relative growth rate (RGR). Radford (1967) defines RGR as "the increase of plant material per unit of material present per unit of time." It is the product of the net assimilation rate (NAR) and leaf area ratio (LAR) which can be regarded respectively, as measures of the efficiency and of the capacity of a plant photosynthetic system (Watson, 1952). NAR is "the increase of plant material per unit of assimilatory material per unit of time" and LAR is "the ratio of the assimilatory material per unit of plant material present" (Radford, 1967). Blackman (1962) suggested that any factor which influences RGR does so by altering NAR, LAR, or both.

According to Watson (1952) the size of a plant is a function of: i) relative growth rate, ii) the initial capital (seed reserve), and iii) the duration of growth.

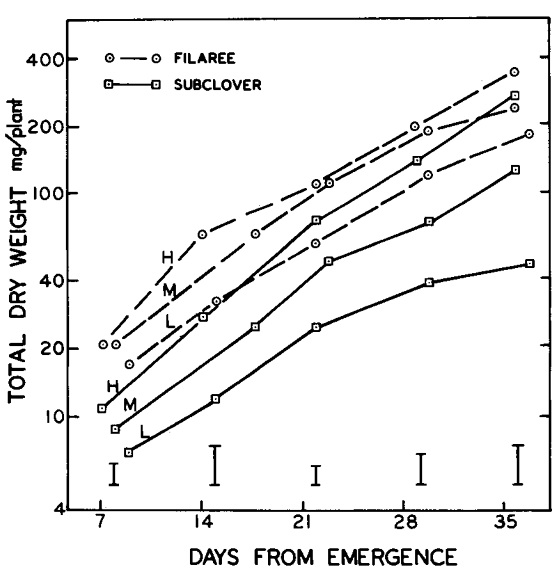

Fig. 1. Filaree and subclover grown under three temperature regimes: 5 to 15 C (L), 10 to 20 C (M), and 15 to 25 C (H). Vertical bars are L.S.D. values at 1% levels.

Seed size determines the initial cotyledonary area, and in annuals early growth is proportional to seed size (Black 1956). Cooper (1967) has suggested that RGR is useful in studying differences in seedling vigor because it is based upon initial weight; therefore, difference in seed weight between species is compensated.

Other useful parameters are specific leaf area [SLA = leaf area (LA)/leaf weight (LW)] and leaf weight ratio (LWR = LW/total weight). The product of these two components is LAR.

MATERIALS AND METHODS

A series of three experiments was conducted in ventilated, temperature-controlled, growth chambers. Three different temperature regimes were used to simulate the diurnal maximum-minimum temperatures which may occur during the fall in the California annual-type.

Two growth chambers were used (i.e., a cabinet type and a walk-in type). The following summarizes the environmental variables of these experiments.

Variables	Night	Day	Night	Day	Night	Day
Temperature regimes, C	5 to 15		10 to 20		15 to 25	
Mean relative humidity, %	42 to 78		40 to 70		35 to 60	
Photoperiod, hours	12	12	12	12	12	12
Light intensity, lux	23,400±300		23,400±300		19,350±1,500	
Emergence date, 1972	27 Nov.		10 Oct.		18 Oct.	
Growth chamber	cabinet		cabinet		walk-in	

The containers (pots) for growing the plants were wax-coated Lily cups (no. 24) with a 9-cm top diameter and a 17.5-cm depth. The pots were filled with 1,035 g of inert, fine-grained, white sand. The mean weight of the seed without seed coat was 6.1 mg for filaree and 5.1 mg for 'Woogenellup' subclover. Sufficient seed was sown to permit eventual thinning to five uniform seedlings/pot. The seed was covered with an additional 85 g of sand, and paper towels were placed over the pots to retard evaporation and then removed at time of emergence.

The pots were arranged in a randomized, complete block design in three replications. Periodic rotation of the pots (in blocks) reduced the variability in light. A 0.5 Hoagland nutrient solution was applied weekly to ensure adequate fertility. The plants were watered daily and free drainage was provided.

Five harvests were made at about weekly intervals. The plants were removed carefully by washing away the sand with a jet of water and additional rinsing was accomplished by floating the plants in a bucket of clean water. The plants were placed in moist paper towels, covered, and stored at 10 C for future measurements, which were completed within 16 hours. The seedlings were divided by cutting them into shoots and roots. The shoots were further divided into leaves (laminae only) and stems (including petioles). Leaf area, including cotyledonary area, was obtained using an air-flow planimeter, and number of leaves/plant was recorded. Plant material was dried to a constant weight at 70 C.

Additional measurements taken were: LW, stem weight (SW), root weight (RW), and total plant weight (W = LW + SW + RW). With these and previously mentioned measurements, it was possible to calculate RGR, NAR, LAR, and SLA. Statistical analyses showed highly significant differences among temperatures, species, and harvests for LW, SW, RW, and W; LA; and LAR. The other derived parameters were not analyzed statistically.

RESULTS

Both species showed a significant yield increase as a function of temperature (Fig. 1). However, the production of filaree was almost as great at 10 to 20 C as at 15 to 25 C, while growth of subclover increased more uniformly over the temperature range used.

The mean RGR values (slopes of best fitting $\log_e$-linear functions) over the 5-week period are as follows.

Temperature range	Yield	Temperature range	Yield
C	mg/g/day	C	mg/g/day
Filaree		Subclover	
5-15	87 b	5-15	71 a
10-20	89 b	10-20	94 b
15-25	92 b	15-25	111 c

where values followed by the same letter do not differ significantly at the 1% level. The RGR for filaree was very similar among the three temperature regimes, while the RGR for subclover increased significantly with increasing temperature. The RGR of subclover was higher than that of filaree at the highest temperature regime, but fell to a lower level than filaree for the lowest temperature regime.

No temperature trend was evident from partitioning of the total dry weight into leaf, stem, and root. However, filaree partitioned 7% more of its assimilates into leaf tissue than subclover.

Both species produced more leaves and a greater leaf surface with increasing temperature (Table 1). The average leaf area of filaree was four times that of subclover at the lowest temperature, and it was two times that of subclover at the highest temperature. Overall, filaree had as much as three times the leaf area of subclover during the first 3 weeks.

Several other derived measures of growth are shown in Table 2. The NAR of subclover, especially at the two temperatures, was greater than that of filaree.

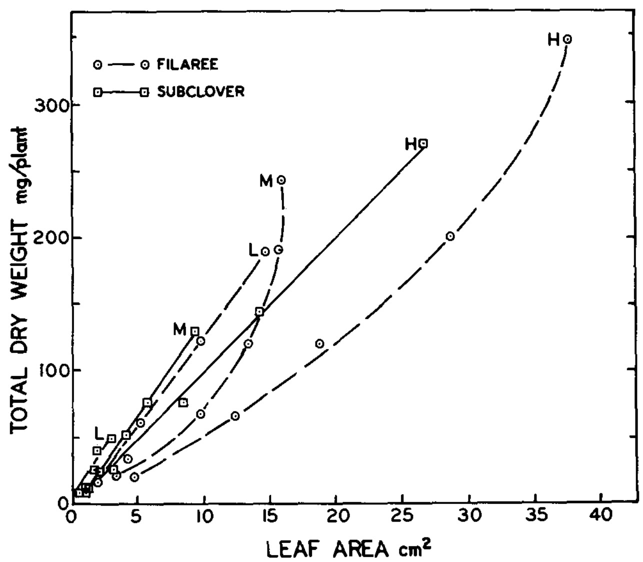

Fig. 2. Filaree and subclover grown under three temperature regimes: 5 to 15 C (L), 10 to 20 C (M), and 15 to 25 C (H).

Filaree displayed a greater range in leaf area as it had a higher LAR and a higher SLA than subclover.

Figure 2 shows that the relationship between plant dry weight and LA was not linear for filaree at the two higher temperature regimes necessitating the use of an exponential component for calculating NAR (Evans, 1972).

Table 1. Filaree and subclover grown under three temperature regimes and harvested over a 5-week period.

Harvest	Filaree, temperature range in °C				Subclover, temperature range in °C			
	5-15	10-20	15-25	Avg.	5-15	10-20	15-25	Avg.
			Leaves/plant					
1	2.0	2.0	2.7	2.2 a*	0.9	1.0	1.9	1.3 a*
2	3.0	5.1	6.5	4.9 b	1.9	3.0	3.2	2.7 b
3	4.4	6.6	9.5	6.8 c	2.9	4.1	6.5	4.5 c
4	5.9	8.4	12.2	8.8 d	3.8	6.0	10.0	6.6 d
5	7.5	9.6	13.9	10.3 e	4.4	9.5	16.8	10.2 e
Avg.	4.6 w*	6.3 x	9.0 z		2.8 v	4.7 w	7.7 y	
			Leaf area/plant, cm²					
1	1.9	3.3	4.9	3.4 a*	0.6	1.0	1.3	1.0 a*
2	4.2	9.7	12.5	8.8 b	1.2	2.1	3.1	2.1 b
3	5.1	13.3	18.8	12.4 c	1.6	4.0	8.4	4.7 c
4	9.7	15.6	29.0	18.1 d	2.0	5.6	14.1	7.2 d
5	14.7	15.8	37.9	22.8 e	3.1	9.2	26.9	13.1 e
Avg.	7.1 x*	11.5 y	20.6 z		1.7 v	4.4 w	10.8 y	

* Averages within a column or row followed by the same letter do not differ significantly at the 1% level (FLSD--Carmer and Swanson, 1971).

DISCUSSION

Various authors have shown that subclover has a fairly high temperature optimum (McKell et al., 1962; Bouma and Dowling, 1969; Sumner, Raguse, and Taggard, 1972). There is very little prior information on the effects of temperature on the growth of filaree, although Heady (1958) found that low temperatures in the spring favored filaree over the grasses. We have demonstrated here that filaree grows more vigorously than subclover at low temperatures in the seedling stage. While at higher temperatures the magnitude of the difference is decreased.

The physiological mechanism responsible for the differential response to temperature by subclover and filaree is not known. However, the magnitude and

Table 2. Average values for various growth parameters.

Range in temperature regimes	Harvest interval: Filaree 1-2	Filaree 2-3	Filaree 3-4	Filaree 4-5	Filaree Avg.	Subclover 1-2	Subclover 2-3	Subclover 3-4	Subclover 4-5	Subclover Avg.
°C					Net assimilation rate, mg/dm² day					
5-15	95	86	106	79	92	99	131	105	52	97
10-20	76	92	68	55	73	106	163	75	123	111
15-25	78	42	50	63	58	117	113	86	92	102
					Leaf area ratio, dm²/g					
5-15	1.22	1.05	0.81	0.78	0.97	0.90	0.81	0.57	0.56	0.71
10-20	1.50	1.27	0.96	0.73	1.11	0.97	0.81	0.77	0.73	0.82
15-25	2.10	1.73	1.51	1.35	1.67	1.16	1.11	1.03	0.97	1.07
					Specific leaf area, dm²/g					
5-15	2.1	1.6	1.5	1.7	1.7	2.1	1.9	1.4	1.3	1.7
10-20	4.3	3.9	2.4	2.0	3.1	2.5	2.1	2.1	2.2	2.2
15-25	4.3	3.3	2.9	2.7	3.3	2.7	2.7	2.5	2.7	2.7

timing of photosynthetic partitioning into assimilatory rather than nonassimilatory material is the major difference between the two species (i.e., filaree partitions more photosynthate into leaf tissue than subclover). It does so earlier in the seedling stage and is able to do so at low temperatures. Much of filaree's advantage in seedling vigor can be attributed to this.

The light intensity to which the plants were subjected at the high temperature was about 17% lower than at the other two temperatures. Although not measured, it is possible that a light-temperature interaction occurred.

Although the seed weight ("initial capital") of filaree was slightly greater than subclover, the difference did not account for the great difference in various leaf characters (e.g., by the first harvest filaree had an LAR almost twice that of subclover). Williams (1972) attributed differing growth responses to root temperature among subclover cultivars to differential leaf expansion, and suggested that either nutritional or hormonal factors were involved. In the same vein, Esau, Currier, and Cheadle (1957) reported that the major effect of low temperature on plant growth is a reduction in carbohydrate translocation in the phloem; it is known that growth regulators and nutrients are also transported in the phloem.

Blackman (1962) has suggested that any factor which brings about a change in RGR does so by altering either NAR or LAR or both. In order to consider the effects of temperature on RGR and its components (LAR and NAR) it is convenient to discuss their averages over all harvest intervals (Table 2). There is a positive association for subclover among RGR, LAR, and temperature. Morley (1958) also found that all cultivars of subclover tested exhibited an increase in RGR with increasing temperature except 'Bacchus March,' which is insensitive. The RGR of filaree remained about the same at all temperatures. The declining NAR of filaree with increasing temperature was compensated by an increasing LAR. In comparison, subclover exhibited a higher and more stable NAR along with a lower and moderately increasing LAR with increasing temperature. According to Watson (1952) dry matter yield depends more on variation in leaf area than on NAR. Therefore, emphasis is placed on the ability of filaree to increase LAR, which it does by increasing SLA to a greater degree than subclover at the two higher temperature regimes. We deduce that filaree gains in photosynthetic capacity by utilizing thinner leaves.

The superior growth of filaree early in the seedling stage (at all temperatures) can be attributed to rapid development of cotyledonary surface. Although cotyledons of subclover are very important as photosynthetic organs (Black, 1956; Machado, Williams, and Tucker, 1974), the advantage in size belongs to filaree. Guerrero (1974) found that the mean areas of cotyledons of filaree and subclover were 121 mm^2 and 32 mm^2 per cotyledon, respectively, 11 days after emergence.

Other adverse effects of low temperature on subclover are a reduction in rate of morphological development (Sumner et al., 1972) and a reduction in N fixation by nodulating bacteria (Jones, Lawler, and Murphy, 1971). Also Sumner et al., (1972) suggest that continued low temperatures during the fall and winter could seriously reduce seed production by subclover since the runners producing flowers are initiated in the axillary buds.

In conclusion, the greater tolerance of filaree to low temperature enables it to assume a dominant role in the annual pasture in the event of a "late break" with its concomitant low temperatures. This differential response to temperatures could also profoundly influence the botanical composition of the pasture on a long-term basis such that failure to select subclover cultivars with sufficient cold tolerance could result in a reversion of a seeded pasture to its natural condition.

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