Competition of *Erodium botrys* and *Trifolium Subterraneum* for Phosphorus

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Highlight: *Differential response to phosphorus by broadleaf filaree (*Erodium botrys*) and subclover (*Trifolium subterraneum*) in competition was studied in a phosphorus-deficient soil and in sand culture in pots. The data show the superior competitive ability of filaree, a resident annual forb, over subclover, an introduced annual legume, both at high fertility levels including abundant nitrogen, and in soils low in N, P, and S. Under high fertility, the rapid growth of filaree enables it to develop considerable leaf area and interfere with the light reception of subclover. Since most of the range soils in California are nitrogen-deficient, however, subclover, with its ability to fix atmospheric nitrogen, is able, when P and S are adequate, to outcompete filaree and assume a dominant role. In order to maintain a proper balance among grasses, legumes, and filaree, most California range soils must be topdressed periodically with superphosphate; otherwise, subclover soon becomes subordinate or disappears.*

Phosphorus (P) fertilization of annual grasslands and pastures can have a profound effect on botanical composition, resulting in an undesirable mixture of species. In California a proper balance of legumes, grasses, and filaree (*Erodium* spp.) serves as a buffer against low forage production in unfavorable years. Particular attention must be given, therefore, to judicious use of phosphatic fertilizers. Williams et al. (1956) found that P fertilization favored introduced legumes at the expense of resident annuals, including filaree. In Australia, Meadley (1946) concluded that long-term P applications favored weedy species over subclover (*Trifolium subterraneum*). Rossiter (1964) reported that long-term P fertilization led to differential responses by annuals. At low P levels filaree was dominant and subclover subdominant, at intermediate P levels the species were codominants, and at high P levels both species were suppressed by grasses and capeweed (*Cryptostemma calendula*). Rossiter also reported that botanical composition is related to an infertility of sheep ("clover disease") which occurs on pastures dominated by certain subclover cultivars that are high in estrogens.

Greenhouse and growth-chamber studies have been inconclusive as to whether subclover is more productive than broadleaf filaree (*Erodium botrys*) under conditions of low P. Asher and Loneragan (1967), using a continuous-flow solution culture, found that subclover took up P faster than did filaree at extremely low P concentrations, whereas both species were equal in P uptake at 5 μM P and above. Ozanne et al. (1969) and Keay et al. (1970), using a P-deficient soil, found that filaree was superior to subclover in P uptake at 29 days postemergence, and that subclover at flowering (92 days) had a higher P requirement than filaree.

Additional information is needed for the competitive relationship between these species relative to P nutrition to be defined more clearly.

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Material and Methods

Two experiments were conducted in a walk-in growth chamber to evaluate the relative responses of broadleaf filaree and subclover (cultivar Woogenellup) seedlings to various levels of soil fertility (Experiment 1) and to various levels of P in sand culture (Experiment 2). The competitive relationship between the two species was studied by growing each species alone and in mixed stands with a 1:1 ratio. The plant material was oven-dried at 70°C for 24 hours, weighed, and ground to pass a 40-mesh sieve in a Wiley mill. Total P was determined by the vanadate-molybdate-yellow method of Kittson and Mellon as outlined by Chapman and Pratt (1961). Mean separation was done with Duncan's Multiple-Range Test.

Experiment 1

Three levels of four major nutrients were applied in the following combinations (subscripts are ppm):

Fertility level	Nutrients			
Check	N_0	P_0	K_0	S_0
PKS	N_0	P_{100}	K_{100}	S_{20}
NPKS	N_{100}	P_{100}	K_{100}	S_{20}

The fertilizers were thoroughly mixed into a P-deficient range soil of the Corning series collected at the Ahart Ranch in Butte County, California. The topsoil (15 cm) was removed and screened to remove rocks and gravel larger than 0.6 cm, and air-dried. Quantities (1.8 kg) of fertilized soil were placed in plastic pots (14.6 cm diameter, 17.5 cm depth) lined with polyethylene bags, and free drainage was provided. The clover seed was inoculated with 'Nitragin R' legume bacteria culture. The final population density was 24 plants per pot, 12 of each species in the mixture. Three replications were used and the pots were completely randomized. Nitrogen as NH_4NO_3 was added in solution, half at planting and half 3 weeks after emergence. Soil moisture was maintained near field capacity. The plants were grown for 6 weeks at diurnal ambient temperatures of 25 and 15°C and with a photoperiod of 10 hours at about 1600 ft-c. Three harvests were taken at 2-week intervals by cutting the plants at the soil surface.

Experiment 2

Plants were grown for 6 weeks in a sand-nutrient culture solution at ambient diurnal temperatures of 25 and 15°C and with a photoperiod of 12 hours at 1800 ft-c. Population density was 10 plants per pot, 5 of each species in the mixture. The containers, wax-coated cups (8.8 cm diameter, 17.5 cm depth), were filled with 1.2 kg of pure white fine-textured sand, and free drainage was provided. Four replications were arranged in a randomized block fashion. The basal nutrient solution was a 0.25-strength modified Hoagland with P omitted. Phosphorus as $NaH_2PO_4 \cdot H_2O$ was added to the basal solution at concentrations of 25, 125, 625, and 1250 μM (equivalent to 0.8, 4, 20, and 40 ppm). On alternate days 100 ml of the solution was applied to each pot, and every sixth day prior to fertilization distilled water was applied in ten 50-ml portions to leach accumulated nutrients from the sand. A single harvest was done by splitting the containers lengthwise and carefully washing away the sand with a jet of water. The plants were separated into shoots and roots.

Results

Experiment 1

In pure stand, filaree plants were somewhat heavier than subclover plants under the NPKS treatment at all harvest dates, whereas in mixture filaree plants were much heavier than subclover plants (Table 1). In pure stand, filaree yields were very low under the PKS treatment, whereas subclover after a slow start approached the yields in the NPKS treatments. In mixture, subclover yielded 4.5 times as much as filaree under the PKS treatment by the final harvest. In pure stand, filaree yield was as low in the check as with PKS at all times, whereas subclover in the check yielded more than filaree by the final harvest, although not so high as with PKS. In mixture, subclover yielded more than filaree in the check only at the final harvest.

Filaree accumulated more P than subclover for all treatments and harvests (Table 2). Both species accumulated more P under the NPKS treatment. When expressed as percent P in tissue, however, both species had higher values under the PKS treatment, with the filaree enhanced more. Combined total P uptake in mixture was intermediate between individual uptakes of the species pure stands. In general, the greater the yield the greater the total uptake of P per pot, and, in the P treatments, the greater the yield the lower the tissue concentration of P.

Table 1. Absolute and relative top growth (mg/plant) of filaree and subclover in pure and mixed stands under three fertility treatments, Experiment 1.

Weeks from emergence and component		Fertility treatment: Check	PKS	NPKS
Two weeks				
Pure	filaree	13 ef (100)[1]	14 e (100)	31 b (100)
	subclover	11 f (100)	13 ef (100)	24 c (100)
Mixed	filaree	13 ef (100)	14 e (100)	43 a (139)
	subclover	10 f (91)	14 e (100)	18 d (75)
Four weeks				
Pure	filaree	31 gh (100)	31 gh (100)	115 b (100)
	subclover	39 fg (100)	71 d (100)	99 c (100)
Mixed	filaree	24 hi (77)	22 i (71)	137 a (119)
	subclover	25 hi (64)	55 e (77)	45 f (45)
Six weeks				
Pure	filaree	37 g (100)	43 g (100)	210 b (100)
	subclover	72 f (100)	166 d (100)	190 c (100)
Mixed	filaree	38 g (103)	44 g (102)	286 a (136)
	subclover	73 f (101)	195 b (117)	129 e (68)

[1] Values in parentheses are percent relative to yield of species in pure stands for a harvest within a fertility treatment. Values (within a harvest and among fertility treatments) followed by the same letter do not differ significantly at the 5% level.

Table 2. Tissue concentration and uptake of P by filaree and subclover tops grown in pure and mixed stands under three fertility treatments, Experiment 1.

Weeks from emergence and component		Check %	Check mg/pot	PKS %	PKS mg/pot	NPKS %	NPKS mg/pot
Two weeks							
Pure	filaree	0.27	0.84	0.69	2.32	0.35	2.60
	subclover	0.15	0.40	0.42	1.31	0.29	1.67
Mixed	filaree	0.29	0.45	0.68	1.14	0.37	1.91
	subclover	0.15	0.18	0.38	0.64	0.27	0.58
Total P in mixed			0.63		1.78		2.49
Four weeks							
Pure	filaree	0.20	1.49	0.79	5.88	0.30	8.28
	subclover	0.13	1.22	0.31	5.28	0.21	4.99
Mixed	filaree	0.23	0.66	0.97	2.55	0.30	4.93
	subclover	0.13	0.39	0.31	2.05	0.23	1.24
Total P in mixed			1.05		4.61		6.17
Six weeks							
Pure	filaree	0.23	2.04	0.97	10.01	0.31	15.62
	subclover	0.13	2.25	0.30	11.95	0.28	12.77
Mixed	filaree	0.22	1.00	1.14	6.02	0.33	11.32
	subclover	0.15	1.31	0.31	7.25	0.27	4.18
Total P in mixed			2.31		13.27		15.50

Experiment 2

In pure stand, filaree had greater shoot yields and subclover had greater root yields at all P levels (Fig. 1). Growth of both species in pure stand was enhanced by 125 μM P, and in total weight they equaled each other. Growth was not increased further by higher levels of P. In mixture, subclover growth was reduced at the lowest P level (25 μM), and filaree growth was reduced at the 125- and 625-μM P levels. The root:shoot ratio of subclover was significantly greater than filaree at all levels of P (Table 3). The root:shoot ratio of subclover declined more with increasing P in mixture than in pure stand. This may be related to the seemingly anomalous growth reduction of subclover in mixture at the 1250-μM P level.

In Experiment 2, accumulation of P was greater in the shoot in filaree and greater in the root in subclover (Fig. 2). Total P uptake was similar for the two species at the three highest P levels. At 25 μM, however, filaree took up more P than subclover in both pure and mixed stands. Table 4 shows the values for P concentration in the tissue. Both species had extremely low concentrations of P at the 25-μM level. With increasing levels of P, both species accumulated greater concentrations of P.

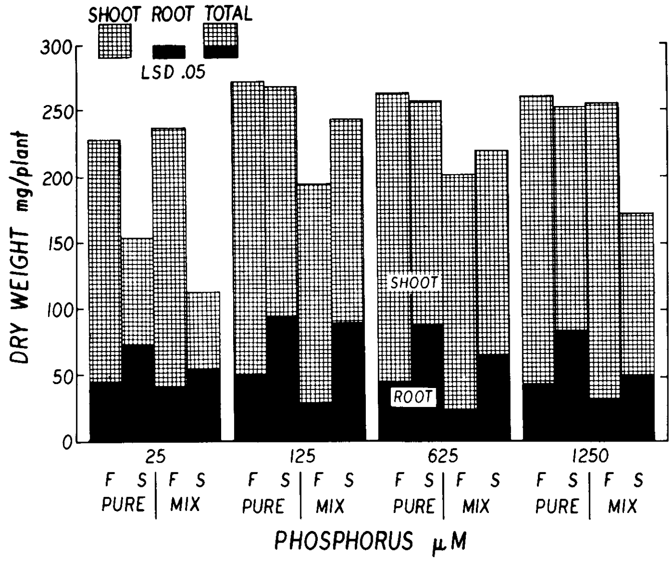

Fig. 1. *The effect of P on the root and shoot dry weight of filaree (F) and subclover (S) grown in pure and mixed stands, Experiment 2.*

Table 3. Relative total plant weight and root:shoot ratio for dry matter of filaree and subclover grown in pure and mixed stands at four P levels, Experiment 2.

Component		P levels (μM) 25	125	625	1250	Mean
Relative total yield (%)[1]						
Pure	filaree	84	100	97	96	94
	subclover	56	98	95	93	86
Mixed	filaree	87	71	74	94	82
	subclover	41	90	81	63	69
Mean		67	90	87	87	
Root:shoot ratio[2]						
Pure	filaree	0.25 g	0.23 g	0.21 gh	0.20 gh	0.22 b
	subclover	.88 a	.55 bc	.50 bcd	.49 bcd	.61 a
Mixed	filaree	.21 gh	.18 gh	.14 h	.14 h	.17 c
	subclover	.95 a	.57 b	.43 def	.40 f	.59 a
Mean		.57a	.38 b	.32 c	.31 c	

[1] Values are percent relative to filaree yield at the phosphorus concentration of 125 μM.
[2] Values followed by the same letter do not differ significantly at the 5% level.

Discussion

The results in Experiment 1 are similar to the behavior of these species observed under field conditions. Large responses to N fertilization by annual vegetation, especially grasses and forbs, have been reported by Martin and Berry (1970). Jones and Evans (1960) observed that legumes tend to decrease with added N, whereas grasses and forbs increase. The suppression of subclover under the NPKS treatment of Experiment 1 can be attributed to the greater seedling vigor of filaree. The rapid production of leaf area, and especially the large cotyledons, enables filaree to interfere with light reception by the smaller subclover plants.

With N limiting, subclover quickly becomes dominant because of its N-fixing ability, if other required nutrients are supplied. Without P, K, and S (check), however, the significant decrease in subclover yields can be attributed to its high nutrient requirement. Whereas filaree, since N is its primary limiting factor, is able to maintain productive rates similar to those when P, K, and S are supplied. Tissue concentration of P supplies the evidence that filaree has a greater ability to utilize limited amounts of P (Table 2, check).

In Experiment 2, both species had low yields when grown at 25 μM P, and the tissue-analysis data indicate that P was limiting (Table 4). The slightly higher yields of filaree and significant suppression of subclover grown in mixture indicates again that filaree is the better competitor under P-deficient conditions. The luxury uptake of P with increasing levels of P beyond where plant growth had reached a maximum (125 μM) is consistent with data of various workers (Asher and Loneragan, 1967; Ozanne et al., 1969; Snaydon and Bradshaw, 1962).

Since the root:shoot ratios for yield and P concentration in tissue were greater for subclover than for filaree it appears that subclover is more sensitive to P deficiency than is filaree. Table 5 shows that the uptake of total and shoot P per unit final

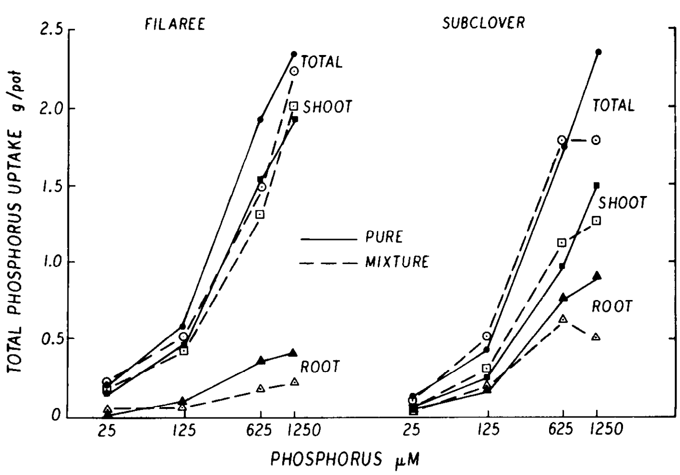

Fig. 2. *Total uptake of P by filaree and subclover as a function of P concentration (log scale) in sand culture. Plants were grown in pure and mixed stands, Experiment 2.*

Table 4. P concentration in shoot and root and root:shoot ratio for P concentration of filaree and subclover grown in pure and mixed stands at four P levels, Experiment 2.

Component		P levels (μM) 25	125	625	1250
Shoot P (%)					
Pure	filaree	0.09 a[1]	0.22 c	0.71 f	0.89 g
	subclover	.09 a	.15 b	.57 e	.89 b
Mixed	filaree	.10 ab	.27 d	.73 f	.90 g
	subclover	.11 ab	.21 c	.73 f	1.30 h
Root P (%)					
Pure	filaree	.07 a	.21 bc	.84 e	.93 efg
	subclover	.09 ab	.19 abc	.88 ef	1.02 g
Mixed	filaree	.09 ab	.23 c	.82 e	.69 d
	subclover	.11 ab	.22 bc	.98 fg	1.03 g
Root:shoot ratio of P					
Pure	filaree	.76	.93	1.18	1.05
	subclover	1.03	1.27	1.55	1.15
Mixed	filaree	.99	.86	1.12	.77
	subclover	1.04	1.09	1.34	1.01

[1] Values followed by the same letter do not differ significantly at the 5% level. No significant interaction for root:shoot ratios.

Table 5. P uptake (mg/pot) and root weight (mg/pot) for 25 μM P treatment, Experiment 2.

Component		Root P	Shoot P	Total P	Root weight
Pure	filaree	31	167	198	448
	subclover	67	74	141	717
Mixed	filaree	39	185	224	416
	subclover	62	63	125	542

weight of roots was greater for filaree than for subclover at the lowest P level.

Such a differential response may be the results of variation in "phosphate feeding capacity," the ability to extract relatively insoluble P from the soil. This is facilitated by the excretion of various organic compounds by the root (Fried, 1953). Fried's hypothesis is supported by work of Keay et al. (1970), who evaluated the comparative rates of P absorption by eight annuals growing in a P-deficient soil. They reported that the relationship between rate of uptake and level of applied P was sigmoid for subclover and less so for filaree, and they suggested that the species with the more sigmoid-shaped response curve has the higher P requirement. Richardson et al. (1931) found that filaree displayed a highly efficient utilizaton of insoluble P. Conversely, Rossiter and Ozanne (1955) reported that subclover yields decreased as the insolubility of the P source increased.

The mechanism by which filaree is able to outcompete subclover at low levels of phosphorus cannot be attributed to a difference in root surface since subclover in all experiments had a much greater root:shoot ratio. Therefore filaree's ability to do well in phosphorus-deficient soils is likely related to some root exudation properties which break down the insoluble phosphate complex and release phosphorus. No data in these studies indicate that, although filaree in sand-nutrient solutions depressed yields of subclover at extremely low levels of phosphorus, indicating that filaree has a lower phosphorus requirement than subclover.

Our practical conclusion is that the suggested rates of single superphosphate (Murphy et al., 1973) should be followed. That management practice, however, should include grazing with the aim of limiting growth and seed production by the resident grasses and forbs. Otherwise, through utilization of the nitrogen made available by the legumes, the nonlegumes will become dominant and the pasture will revert to a more natural condition. The reduction in the legume component will allow production of less-nutritious forage.

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