Insights into the factors controlling the distributions of the narrow endemic, Helenium virginicum, and its widespread congener, H. autumnale, through a study of their relative competitive abilities and growth rates

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Introduction

Helenium virginicum Blake (Asteraceae) is a narrow endemic perennial herb that is globally limited in distribution to 21 sinkhole ponds in western Virginia (Gleason and Cronquist 1991; Nancy Van Alstine, Virginia Natural Heritage Program, unpublished data). It is protected by the state of Virginia and is a category 1 candidate for federal protection under the endangered species act (Porter and Wieboldt 1991). H. virginicum is morphologically most similar to H. autumnale (Knox 1987, Knox et al. 1995), a highly variable wetland plant indigenous to 47 states in the U.S.A., and seven Canadian Provinces (Synonymized Checklist of the Vascular Flora of the U.S., Canada, and Greenland). Although these two species grow within one km of each other, they are not known to be sympatric (Knox,, unpublished data), and transplant studies show them to be ecologically isolated (Knox et al. 1995). We are interested in determining the causes of the narrow endemism of H. virginicum, and the reasons for its ecological isolation from H. autumnale.

The literature offers several classes of explanations to account rarity in plants. Stebbins (1980) concluded that rarity is most frequently explained by a combination of rare ecological factors, with climatic and genetic factors of secondary importance. Other authors (Kruckeberg and Rabinowitz 1985, Kruckeberg 1991) have also found similar explanations for rarity. The following examples seem to support Stebbins conclusions. In comparing narrow endemics with their associated weedy congeners, Hart (1980) concluded that the two coexisted in a seasonally stressful habitat by the endemic being a stress tolerating plant and the weedy relative being a stress avoiding plant. In this case, Hart (1980) suspected that the endemic plant had special adaptations which permitted it to grow in the presence of high water or nutrient stress, and was restricted by an inability to compete elsewhere and by poor resistance to pathogens which may be more common elsewhere. The associated weedy congeners were found (Hart 1980) to grow rapidly to reproductive maturity at a time when stress was low, and so avoid stress. A similar interpretation of plant ecological data (Grime 1977, Grime and Hodgson 1987) is that with increasing habitat stress, the intensity of competition decreases, and as a consequence, stressful habitats are occupied by plants that have a predictable suite of adaptations, but are unable to compete elsewhere. The stress tolerant plant is described (Grime 1977, Grime and Hodgson 1987) as having a low potential growth rate regardless of soil fertility, lacking a defined growing season, having functional leaves year round, being able to store nutrients when they are present in the soil in excess of need, being well defended against herbivores, allocating a low proportion of resources to seeds, having mutualistic associations, and having little phenotypic plasticity. In contrast, plants of nutrient rich sites are thought to be better competitors and to be possessed of a more robust habit, a greater potential growth rate which is more reflective of the nutrient status of the soil, a shorter life span for roots and leaves, and a higher phenotypic plasticity.

A somewhat different insight into the ecology of rarity is given by Fowler (1982) who found that competition did not increase with increasing soil fertility, and that competitive outcome was very much dependent upon soil fertility and season. Also noteworthy, Rabinowitz et al. (1984) found that sparse species of grass grew largest when they were rare associates of common species, but regardless of relative proportion, the sparse species were the superior competitors.

Some insights into the causes of the narrow endemism of H. virginicum, and the mutually exclusive pattern of distribution of this plant and its most similar congener, H. autumnale, were provided by common garden and transplant studies (Knox 1987; Knox et al. 1995), and long-term field studies (Knox, unpublished data). This work has shown that H. virginicum grows in sites with an unusual soil and lengthy annual period of deep inundation, while H. autumnale grows in more ordinary soils which experience only short periods of shallow inundation. Chemical analysis of the clay soil of 19 of the 21 known H. virginicum sites revealed (Knox, unpublished data) low pH (4.5) and high aluminum levels. These are the combined conditions that are cited (Foy 1974; Taylor 1988) as the most frequent limiting factor to plant growth, because they impair uptake of plant macronutrients. Further increasing the stressful nature of these soils is their low levels of macronutrients, and B, and high levels of As. A nine year demographic study (Knox, unpublished data) found H. virginicum sites to flood annually during winter and spring, with great year to year variation of from four to 16 months of continuous inundation and maximum depths of from 49-59 cm. Garden studies (Knox et al. 1995) found that H. virginicum and H. autumnale survived equally well under lengthy annual deep inundation, when raised singly on potting soil. However, transplant studies found that neither species survived long in the other's habitat. Collectively, these data suggest that H. virginicum is a stress tolerant plant, while H. autumnale appears to be a competitor plant (sensu Grime 1977, Grime and Hodgson 1987).

We undertook a growth and competition study of H. autumnale and H. virginicum to gain insight into the causes of their distributions. We used a multiple de Wit replacement series to study competition, run concurrently with a growth study to identify morphological and physiological characters that might explain competitive outcomes, as was done by Snyder et al. (1994). Our aims were to answer the following questions. 1.) Does H. virginicum have the characteristics of a stress tolerant plant, and does H. autumnale have the characteristics of a competitor plant? 2.) Does each species grow less well on the soil of its congener, than on its own soil, when raised in a common garden? 3.) Is the endemic plant a poorer competitor than its widespread congener? 4.) Does competition decrease with increasing nutrient stress? 5.) Does the endemic plant have a slower growth rate than its congener on a nutrient enriched soil? 6.) Do the patterns of resource allocation in the endemic and its widespread congener help explain their distributions?

Materials and Methods

Seeds for this study were collected in the fall of 1994 from more than 25 plants in each of three natural populations. H. autumnale seeds were from Hidden Valley in Bath County, Virginia. H. virginicum seeds were collected at Twin Ponds, approximately four km north of Stuarts Draft, Virginia, and P. agrostoides seeds came from Kennedy

Mountain Meadow, also four km north of Stuarts Draft, Virginia. The seeds were stratified by exposure to outdoor winter cold while soaking in water in Lexington, Va.

The site of this study was Lexington, Virginia. We germinated seeds in a heated greenhouse on Hyponex commercial potting soil in plastic flats in March, 1995. After they reached seedling stage, we transferred them into 1.3 L plastic pots, 12.5 cm in diameter and 10.5 cm deep. After the seedlings had been transferred, the pots were arranged randomly in an outdoor common garden. All pots received full sunlight and were protected from disturbance by a fence. The pots were placed eight to a plastic flat, and the flats were kept full of water so that the plants could draw up as much as needed through holes in the bottom of the pots. This experiment went on from April 29, 1995 to December 12, 1995. Maximum and minimum daily temperatures were taken. The maximum temperatures ranged from 54.3°C on July 31 to 5.5°C on December 6. The minimum temperatures ranged from 27°C on September 1 to -16.0°C on December 11.

Snyder et al (1994) was used as a model for this study, which followed a de Wit (1960) replacement series, using several densities. The use of several densities and the length of the experiment answer some of the criticisms of the de Wit series (Firbank and Watkinson 1985; Connolly 1987). In the de Wit design, overall density is held constant while the proportions of the two species in the mixture is varied. The yield in mixture is then compared to the yield in monoculture.

Monocultures were grown at densities of 1, 2, 3, 4, 6, 8, 9, and 12 plants per pot. We grew mixtures at densities of 2, 4, 8, and 12 plants per pot. Snyder et al (1994) also grew the plants at a density of 16 plants per pot, but our pots were slightly smaller. Each competition density was grown at three different proportions for the two species (A and B) competing: 25%A:75%B, 50%A:50%B, and 75%A:25%B, except for the density of two plants, which could only be grown at the proportions of 50%A:50%B. There were four replicates of each treatment.

H. autumnale/ H. virginicum mixtures were grown on both H. autumnale and H. virginicum soils, as were H. autumnale and H. virginicum monocultures. P. agrostoides was only grown with H. virginicum on H. virginicum soil, so P. agrostoides monocultures were grown only on H. virginicum soil. There were a total of 280 pots in all. Because many seeds did not germinate, the plants on H. virginicum soil were not planted until eight weeks after those on H. autumnale soil. so they were also harvested eight weeks later. Therefore, the two soil treatments can not be statistically compared.

The plants were harvested and dried at 80° C for 24-48 hours. We then took the dry weights of both roots and shoots. In most pots, some roots had grown outside of the pots. We assumed that each species would contribute the same proportion of root matter outside of the pots as inside, the dry weight of these roots was assigned by the following equation:

total roots per species i =

species i in-pot roots +(species i in-pot roots/all in-pot roots)(outside pot roots)

These dry weights were then used to calculated relative yields (RY), relative yield totals (RYT), and aggressivity (A) for each species, using the equations from Snyder et al (1994). Each calculation was made for the root mass, the shoot mass and for the overall plant mass in each pot.

If p = proportion of species i in a mixture and q = proportion of species j in a mixture so that p+q=1, then

$$RY_{ij}=Y_{ij}/(pY_i) \text{ and } RY_{ij}=Y_{ji}/(qY_j)$$

where RY_{ij} is the relative yield of species i in mixture with j, Y_{ij} is the absolute yield of species I in competition with species j, and Y_i is the yield of species i in monoculture. RY_{ij} (or $_{ji}$) values less that 1.0 indicate that species i (or j) competes better intraspecifically than interspecifically. If RY_{ij} (or $_{ji}$) is greater than 1.0, then species i (or j) competes better interspecifically. An RY_{ij} (or $_{ji}$) of 1.0 implies no difference between intraspecific competition and interspecific competition with species j (or i).

Relative yield total is the weighted average of the relative yields of the species mixture:

$$RYT = p\,RY_{ij} + qRY_{ji}.$$

Values greater than 1.0 imply avoidance of competition. If the RYT is less than 1.0, the species are antagonistic. If the RYT equals 1.0, the species compete for the same resources but do not actively harm each other.

Aggressivity measures the gain or loss of biomass by individuals of each species in competition. Aggressivity is obtained by :

$$A_i = RY_{ij}\text{-}RY_{ji} \text{ and } A_j = RY_{ji}\text{-}RY_{ij}.$$

The higher the values, the more aggressive the species is.

We calculated the difference of the values of each of these indices from 1.0, using Student's t-test.

Results

We observed a constant final yield at two plants per pot, so we will only present data for densities of 4, 8, and 12 where the variance between replicates was low. In H. autumnale soil, H. autumnale showed RY_{av}'s greater than 1.0 in all but two treatments. Shoot RY_{va}'s remained below 1.0 in all but two treatments, but root and overall RY_{va}'s were greater than 1.0 for all proportions at density 8 and for the 50:50 proportion at density 12. In all treatments on H. autumnale soil, RY_{av} was greater than RY_{va} (Tables 1, 2, and 3). Within a density, the shoot RY_{av} was highest at the 25:75 proportion and lowest at the 50:50 proportion (Table 1). The shoot RY_{va}'s increased with higher proportion of H. virginicum, with one exception (Table 1).

For root RY's , the trends were markedly different. RY_{av}'s within a proportion were highest at density 8 and lowest at density 4. Within a density, RY_{av}'s rise with decreasing proportion of H. autumnale, with one exception. The RY_{va}'s are likewise highest at density 8 and lowest at density 4, with one exception. The patterns for overall RY's followed root RY's exactly (Tables 2 and 3).

On H. virginicum soil, all RY_{va}'s were above 1.0. Root and overall RY_{av}'s were less than 1.0 in all but one treatment. All RY_{va}'s were greater than RY_{av}'s on H. virginicum soil. Within a proportion, RY_{va}'s are highest at density 4, lowest at density 8. RY_{va}'s decreased with increasing proportion of H. virginicum.

Following Harper's (1977) classification, the de Wit diagrams of all competitions were model II (Fig. 1 and 2). On H. autumnale soil, total RYT's at all proportions were highest at density 8, lowest at density 4 (Table 7). The total aggressivities of H. virginicum were all negative, whereas all the H. autumnale aggressivities were positive (Tables 8 and 9). On H. virginicum soil. the highest total RYT's were at density 4, lowest at density 8 (Table 10). H. virginicum had positive aggressivities and H. autumnale had negative aggressivities on H. virginicum soil (Tables 11 and 12).

Discussion

On H. autumnale soil, H. autumnale is the better competitor, as supported by RY's, RYT's, and A's. The de Wit diagrams for that soil are all model II (Harper 1977), which indicate that intraspecific competition is stronger than interspecific competition for one species (H. autumnale) and weaker than interspecific competition for the other species. It is interesting that some RY_{va}'s were greater than 1.0 even on the H. autumnale soil, indicating that H. virginicum is not hurt as much by competition with H. autumnale as it is by intraspecific competition. Since all the RYT values except one are greater than 1.0, it appears that the two species avoid competition (Harper 1977, Snyder et al 1994). These results could indicate that H. virginicum shows the same pattern found in sparse grasses (Rabinowitz et al 1984), where improved growth was observed with decreasing proportion of the sparse grass. However, the results of the competition with P. agrostoides, which grows with H. virginicum, do not seem to support this, as RY_{vp}'s were less than 1.0 for all but two treatments (Tables 4, 5, and 6), indicating that H. virginicum is hurt by competition with P. agrostoides. The coexistence of H. virginicum and P. agrostoides in nature seems to fit the pattern described by Hart (1980) in which the widespread plant avoided stress by limiting its growth and reproduction to a favorable window of time, while endemics grew during the period of stress as well as during the favorable time. For this habitat, the more favorable time during which P. agrostoides grows is during the dry part of the year, while H. virginicum grows continually throughout the year.

Hart (1980) found that stress tolerator plants were not good competitors on non-stressful soil. She found that the endemics did not grow well on normal soils. H. virginicum did not follow this pattern, as it grew very well on H. autumnale soil. Although it did not compete as well as H. autumnale, its RY's were significantly smaller than 1.0 in only three treatments (Tables 1, 2, and 3), so competition never stunted it much.

It has been found that changing soil chemistry can reverse dominance (Fowler 1982, Hart 1980) although Grimes (1977) believed these changes were caused by some noncompetitive effect. This could very well be true of this experiment, as the competition on H. virginicum soil was started later than the rest of the experiment. However, our results do follow the pattern mentioned above. H. virginicum is a better competitor on its own soil. The deWit diagrams for this soil are also model II, this time indicating that H. virginicum competes better on its own soil. The RY_{va} values were less than 1.0 in only one treatment. Again, the results seem to follow Rabinowitz et al (1984), in that H. virginicum grows best in small proportions (Tables 4, 5, and 6). RY_{av}'s are consistently less than 1.0, indicating that H. autumnale competes better interspecifically than intraspecifically on H. virginicum soil. However, the RYT's are greater than 1.0 in all but two treatments, indicating avoidance of competition.

It is interesting that the patterns were set mostly by root biomass. There are indications that stress tolerant plants have a larger investment in roots than other types of plants (Grime 1977). Perhaps more competition studies should be done that look at roots of plants, rather than merely shoots.

Literature Cited

Fowler, N. 1982. Compettiion and coexistence in a North Carolina grassland III. Mixtures of component species. J. Ecol. 70: 77-92.

Foy, C. D. 1974. Effects of aluminum on plant growth. pages 601-642 in The plant root and its enviromnent, ed. E. W. Carson. University Press of Virginia, Charlottesville.

Gleason, H. A. and A. Cronquist. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd ed. Bronx: New York Botanical Garden.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

Grime, J. P., and J. G. Hodgson. 1987. Botanical contributions to contemporary ecological theory. New Phytol., suppl. 106: 283-295.

Harper, John L. 1977. Population Biology of Plants. New York: Academic Press.

Hart, R. 1980. The coexistence of weeds and restricted native plants on serpentine barrens in southeastern Pennsylvania. Ecology 61: 688-701.

Knox, J. S. 1987. An experimental garden test of characters used to distinguish Helenium Virginicum Blake from H. autumnale L. Castanea 52: 53-58.

Kruckeberg, A. R. 1991. An essay: geoedaphics and island biogeography for vascular plants. Aliso 13: 225-238.

Kruckeberg, A. R. and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. Ann. Rev. Ecol. Syst. 16: 447-479.

Porter, D. M., and T. E. Wieboldt. 1991. Vascular plants. pages 51-171 in Virginia's endangered species: proceedings of a symposium, coordinated by K. Terwilliger. Blacksburg, Virginia: McDonald and Woodward Publishing Co.

Rabinowitz, D., J. K. Rapp, and P. M. Dixon. 1984. Competitive abilities of sparse grass species: means of persistence of causes of abundance. Ecology 65: 1144-1154.

Snyder, K. M., J. M. Baskin, and C. C. Baskin. 1994. Comparitive ecology of hte narrow endemic Echinacea tennesseensis and two geographically widespread congeners: relative competive ability and growth characteristic. Int. J. Plant Sci. 155: 57-65.

Stebbins, G. L. 1980. Rarity of plant species: a synthetic viewpoint. Rhodora 82: 77-86.

Taylor, G. J. 1988. The physiology of aluminum phytotoxicity. pages 123-163 in Metal Ions in Biological systems vol. 24: Aluminum and its Role in Biology, ed. H. Sigel and A. Sigel. Marces Dekker, New York.

Table 1

Mean relative shoot yields of H. autumnale (HA) and Helenium virginicum (HV), growing in paired competition at different proportions and densities on H. autumnale soil. Each mean relative yield was compared with the yield in monoculture (1.0) using the t-test. * P < .10, ** P < .05; *** P < .01; **** P < .001

Proportion	Density					
	4		8		12	
HA:HV	RY_{av}	RY_{va}	RY_{av}	RY_{va}	RY_{av}	RY_{va}
75:25	2.97	.68**	2.49**	.84	1.92**	.86
50:50	1.31	.74	1.99	.92	1.47	1.09
25:75	5.05**	.85	4.57***	1.20	2.80**	.83

Table 2

Mean relative root yields of H. autumnale (HA) and Helenium virginicum (HV), growing in paired competition at different proportions and densities on H. autumnale soil. Each mean relative yield was compared with the yield in monoculture (1.0) using the t-test. * P < .10, ** P < .05; *** P < .01; **** P < .001

Proportion	Density 4		Density 8		Density 12	
HA:HV	RY_{av}	RY_{va}	RY_{av}	RY_{va}	RY_{av}	RY_{va}
75:25	1.18	.78*	1.55	1.27	1.38***	.90
50:50	.86	.72	1.80	1.02	1.57**	1.24
25:75	1.45	.82	3.15**	1.39	2.69**	.88

Table 3

Mean relative total plant yields of *H. autumnale* (HA) and *Helenium virginicum* (HV), growing in paired competition at different proportions and densities on *H. autumnale* soil. Each mean relative yield was compared with the yield in monoculture (1.0) using the t-test. * P < .10, ** P < .05; *** P < .01; **** P < .001

	Density					
Proportion	4		8		12	
HA:HV	RY_{av}	$_{va}$	RY_{av}	RY_{va}	RY_{av}	RY_{va}
75:25	1.45	.77**	1.77*	1.21	1.50****	.89
50:50	.93	.72	1.84	1.01	1.55*	1.22
25:75	1.99*	.82	3.48***	1.36	2.72**	.87

Table 4

Mean relative shoot yields of H. autumnale (HA), Helenium virginicum (HV), and Panicum verrucosum (PV) growing in paired competition at different proportions and densities on H. virginicum soil. Since PV plants were not harvested and weighed, mean relative yields for them could not be calculated. Each mean relative yield was compared with the yield in monoculture (1.0) using the t-test. * $P < .10$, ** $P < .05$; *** $P < .01$; **** $P < .001$

	Density					
Proportion	4		8		12	
HA:HV	RY_{av}	RY_{va}	RY_{av}	RY_{va}	RY_{av}	RY_{va}
75:25	1.13	4.64	.86	1.52	1.41	2.50**
50:50	1.14	2.94	.41**	1.28	1.08	1.70**
25:75	.07****	2.65****	.85	1.01	0.83	1.60**
HV:PA	RY_{vp}		RY_{vp}		RY_{vp}	
75:25	1.04		.71		.28***	
50:50	1.10		.39***		.21***	
25:75	.82		.49**		.20***	

Table 5

Mean relative root yields of H. autumnale (HA), Helenium virginicum (HV), and Panicum verrucosum (PV) growing in paired competition at different proportions and densities on H. virginicum soil. Since PV plants were not harvested and weighed, mean relative yields for them could not be calculated. Each mean relative yield was compared with the yield in monoculture (1.0) using the t-test. * P < .10, ** P < .05; *** P < .01; **** P < .001

	Density					
Proportion	4		8		12	
HA:HV	RY_{av}	RY_{va}	RY_{av}	RY_{va}	RY_{av}	RY_{va}
75:25	.79	4.62	.99	1.35	1.24	2.05**
50:50	.79	2.90**	.48*	1.12	.88	1.41**
25:75	.04****	2.89*	.68	.86	.83	1.37
HV:PA	RY_{vp}		RY_{vp}		RY_{vp}	
75:25	.75		.41**		.16****	
50:50	.90		.20****		.10****	
25:75	.55*		.31***		.10****	

Table 6

Mean relative total plant yields of H. autumnale (HA), Helenium virginicum (HV), and Panicum verrucosum (PV) growing in paired competition at different proportions and densities on H. virginicum soil. Since PV plants were not harvested and weighed, mean relative yields for them could not be calculated. Each mean relative yield was compared with the yield in monoculture (1.0) using the t-test. * $P < .10$, ** $P < .05$; *** $P < .01$; **** $P < .001$

	Density					
Proportion	4		8			
HA:HV	RY_{av}	RY_{va}	RY_{av}	RY_{va}	RY_{av}	RY_{va}
75:25	.87	4.62*	.96	1.37	1.29	2.11**
50:50	.87	2.90**	.46	1.14	0.94	1.45**
25:75	.04****	2.86*	.73	.88	0.83	1.40
HV:PA	RY_{vp}		RY_{vp}		RY_{vp}	
75:25	.79		.45**		.18****	
50:50	.93		.22****		.11****	
25:75	.59*		.33***		.11****	

Table 7

Mean relative yield totals of the entire plants of H. autumnale and H. virginicum, growing in paired competition at different proportions and densities on H. autumnale soil. Each value was compared with 1.0 using the t-test. *P<.10, **P<.05, ***P<.01, ****P<.001

	Density		
Proportion HA:HV	4	8	12
75:25	1.28	1.63*	1.35***
50:50	0.82	1.43	1.38**
25:75	1.11	1.89***	1.33

Table 8

Mean aggressivities of the entire plants of H. autumnale (HA) growing in paired competition at different proportions and densities with H. virginicum on H. autumnale soil. Each value was compared with 1.0 using the t-test. *P<.10, **P<.05, ***P<.01, ****P<.001

	Density		
Proportion HA:HV	4	8	12
75:25	0.68	0.56	0.61**
50:50	0.21	0.83	0.32
25:75	1.16	2.11	1.84

Table 9

Mean aggressivities of the entire plants of H. virginicum growing in paired competition at different proportions and densities with H. autumnale on H. autumnale soil. Each value was compared with 1.0 using the t-test. *P<.10, **P<.05, ***P<.01, ****P<.001

	Density		
Proportion HA:HV	4	8	12
75:25	-0.68**	-0.56**	-0.61****
50:50	-0.21**	-0.83**	-0.32**
25:75	-1.16**	-2.11***	-1.84***

Table10

Mean relative yield totals of the entire plants of *H. autumnale* and *H. virginicum*, growing in paired competition at different proportions and densities on *H. virginicum* soil. Each value was compared with 1.0 using the t-test. *P<.10, **P<.05, ***P<.01, ****P<.001

	Density		
Proportion	4	8	12
HA:HV			
75:25	1.81	1.06	1.50
50:50	1.89**	0.80	1.19
25:75	2.15*	0.84	1.26

Table 11

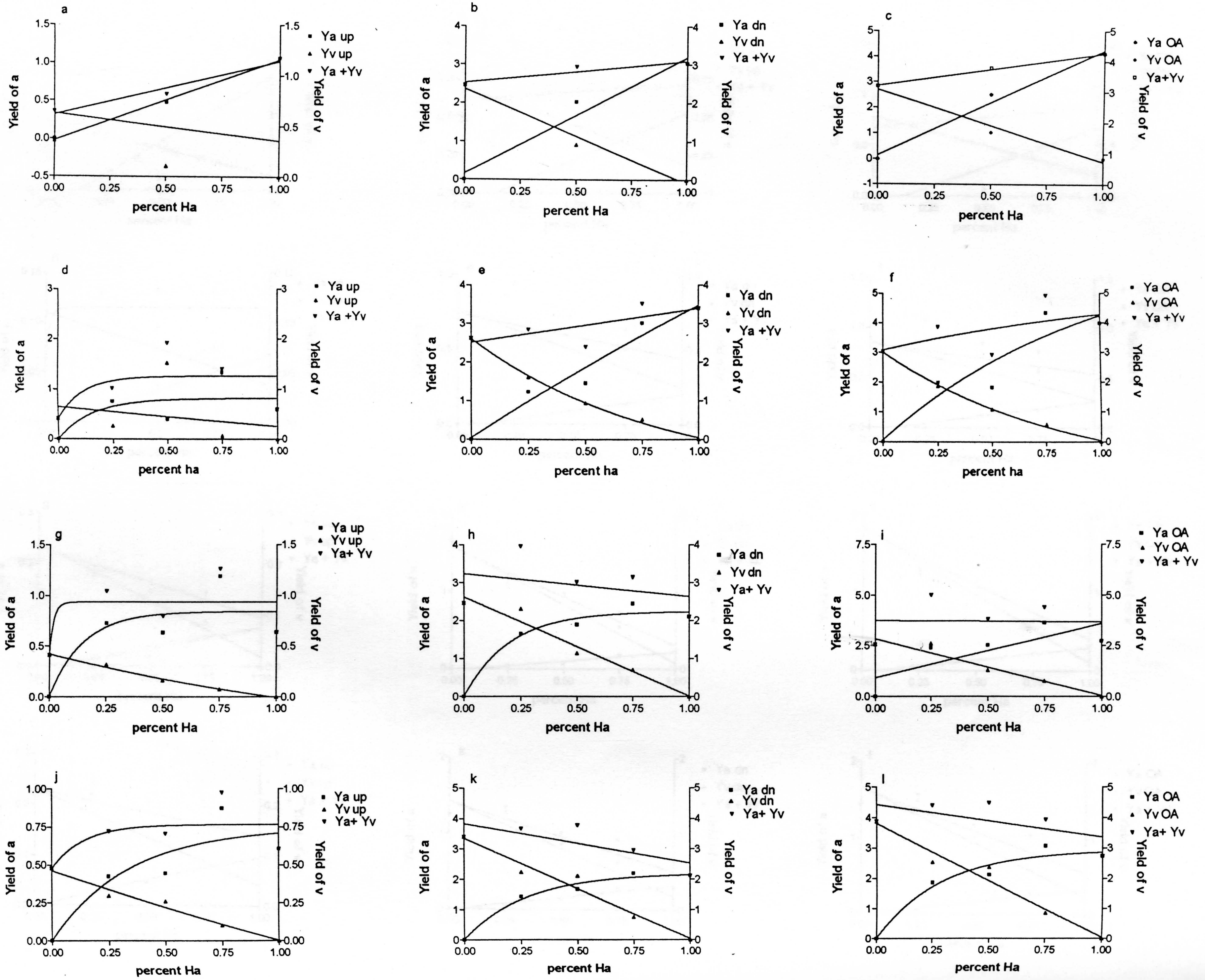
Mean aggressivities of the entire plants of H. autumnale growing in paired competition at different proportions and densities with H. virginicum on H. virginicum soil. Each value was compared with 1.0 using the t-test. *P<.10, **P<.05, ***P<.01, ****P<.001

	Density		
Proportion	4	8	12
HA:HV			
75:25	-3.75*	-0.41**	-0.81**
50:50	-2.04**	-0.68***	-0.50**
25:75	-2.81***	-0.15	-0.57***

Table 12

Mean aggressivities of the entire plants of H. virginicum growing in paired competition at different proportions and densities with H. aurumnale on H. virginicum soil. Each value was compared with 1.0 using the t-test. *P<.10, **P<.05, ***P<.01, ****P<.001

	Density		
Proportion HA:HV	4	8	12
75:25	3.75	0.41	0.81
50:50	2.04	0.68**	0.50
25:75	2.81*	0.15	0.57*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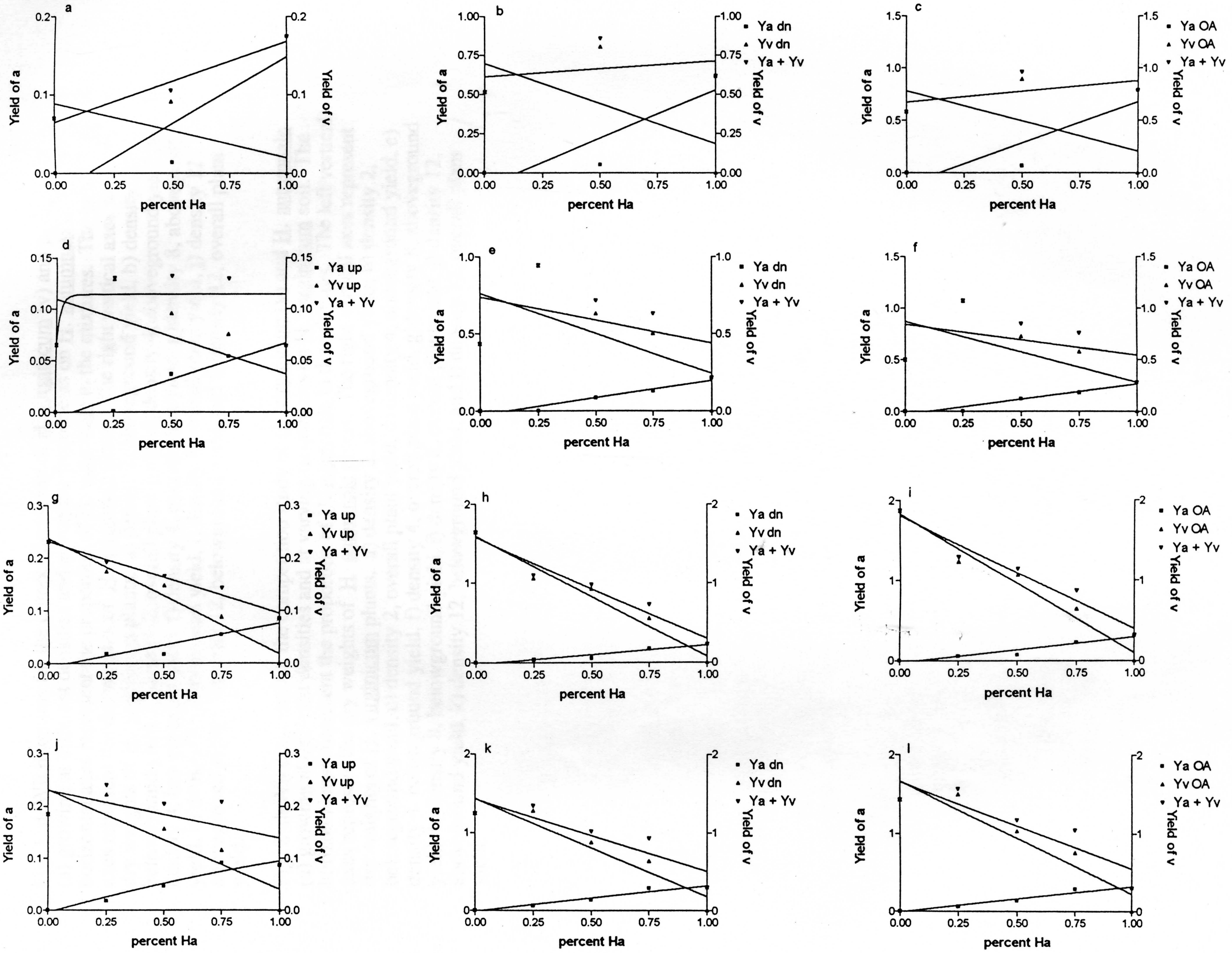a
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1.0
1.5
1
2
Ya dn
Yv dn
Ya + Yv
Ya OA
Yv OA
Ya up
Yv up

Fig. 1 deWit diagrams for the competition study of H. virginicum (v) and H. autumnale (a) growing at different densities and at varying frequencies on H. autumnale soil. The horizontal axes represent the proportion of H. autumnale in the mixtures. The left vertical axes represent the dry weights of H. autumnale plants. The right vertical axes represent dry weights of H. virginicum plants. a) density 2, aboveground yield, b) density 2, belowground yield, c) density 2, overall plant yield, d) density 4, aboveground yield, e) density 4, belowground yield, f) density 4, overall plant yield, g)density 8, aboveground yield, h) density 8, belowground yield, i) density 8, overall plant yield, j) density 12, aboveground yield, k) density 12, belowground yield, and l) density 12, overall plant yield.

Fig. 2 deWit diagrams for the competition study of H. virginicum (v) and H. autumnale (a) growing at different densities and at varying frequencies on H. virginicum soil. The horizontal axes represent the proportion of H. autumnale in the mixtures. The left vertical axes represent the dry weights of H. autumnale plants. The right vertical axes represent dry weights of H. virginicum plants. a) density 2, aboveground yield, b) density 2, belowground yield, c) density 2, overall plant yield, d) density 4, aboveground yield, e) density 4, belowground yield, f) density 4, overall plant yield, g)density 8, aboveground yield, h) density 8, belowground yield, i) density 8, overall plant yield, j) density 12, aboveground yield, k) density 12, belowground yield, and l) density 12, overall plant yield.

Literature Cited

Fowler, N. 1982. Competttiion and coexistence in a North Carolina grassland III. Mixtures of component species. J. Ecol. 70: 77-92.

Foy, C. D. 1974. Effects of aluminum on plant growth. pages 601-642 in The plant root and its enviromnent, ed. E. W. Carson. University Press of Virginia, Charlottesville.

Gleason, H. A. and A. Cronquist. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd ed. Bronx: New York Botanical Garden.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

Grime, J. P., and J. G. Hodgson. 1987. Botanical contributions to contemporary ecological theory. New Phytol., suppl. 106: 283-295.

Harper, John L. 1977. Population Biology of Plants. New York: Academic Press.

Hart, R. 1980. The coexistence of weeds and restricted native plants on serpentine barrens in southeastern Pennsylvania. Ecology 61: 688-701.

Knox, J. S. 1987. An experimental garden test of characters used to distinguish Helenium Virginicum Blake from H. autumnale L. Castanea 52: 53-58.

Kruckeberg, A. R. 1991. An essay: geoedaphics and island biogeography for vascular plants. Aliso 13: 225-238.

Kruckeberg, A. R. and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. Ann. Rev. Ecol. Syst. 16: 447-479.

Porter, D. M., and T. E. Wieboldt. 1991. Vascular plants. pages 51-171 in Virginia's endangered species: proceedings of a symposium, coordinated by K. Terwilliger. Blacksburg, Virginia: McDonald and Woodward Publishing Co.

Rabinowitz, D., J. K. Rapp, and P. M. Dixon. 1984. Competitive abilities of sparse grass species: means of persistence of causes of abundance. Ecology 65: 1144-1154.

Snyder, K. M., J. M. Baskin, and C. C. Baskin. 1994. Comparitive ecology of hte narrow endemic Echinacea tennesseensis and two geographically widespread congeners: relative competive ability and growth characteristic. Int. J. Plant Sci. 155: 57-65.

Stebbins, G. L. 1980. Rarity of plant species: a synthetic viewpoint. Rhodora 82: 77-86.

Taylor, G. J. 1988. The physiology of aluminum phytotoxicity. pages 123-163 in Metal Ions in Biological systems vol. 24: Aluminum and its Role in Biology, ed. H. Sigel and A. Sigel. Marces Dekker, New York.