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Tolerance to Soil Type in Rock Outcrop Plants

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TOLERANCE TO SOIL TYPE IN ROCK OUTCROP PLANTS

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by

Nora Ann Coyne Bennett

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of the requirements for the degree of

Master of Arts

Nora Ann Coyne Bennett

Approved, August 1987

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Dedication

This work is dedicated to my husband, Kenneth S. Bennett. Without his love and encouragement I would have been unable to complete this project.

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I would like to thank Dr. Stewart Ware for his unfaltering encouragement during this project. I would also like to thank Drs. Bradner Coursen and Martin Mathes for their careful review and helpful advice.

Additional thanks to Anne Whitworth for her work on seed germination. This work provided me with seedlings of *Isanthus brachiatus*, *Cyperus granitophilus*, and *C. aristatus*.

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ABSTRACT

Rock outcrops or glades are areas of treeless, shallow soil, where bedrock often breaks the surface. Granite and sandstone bedrock produce acidic soil, while limestone soil is basic. Each of these outcrop types supports a characteristic group of plants, many of which are endemic to one outcrop type. Plant species from acid soils include *Portulaca smallii* and *Cyperus granitophilus* which occur only on granite outcrops; and *Hypericum gentianoides* and *Crotonopsis elliptica* which occur on granite and sandstone outcrops. On basic, limestone soils are found *Sporobolus neglectus* and *Isanthus brachiatus*. *Cyperus aristatus* is an unusual species which occurs on all three soil types. The studied population was from limestone soil.

These experiments were conducted to determine the effect of soil type on the growth of these outcrop species. Each of the above species was grown on all three soil types so that plant growth, as measured in milligrams of dry mass, could be compared for all soil types.

Each species responded differently to the experiments. Soil type appeared to be an important factor in a species' distribution in some cases. Other species grew as well or better on foreign soil types as on their native types. This suggests that some factor or factors other than soil type, such as competition (or lack thereof) or geographic isolation, are more important in that species' distribution.

The glade flora, therefore, are not a group of plants that respond identically to their outcrop environment. Each species is distributed individually, according to its biogeographical and evolutionary history.

TOLERANCE TO SOIL TYPE IN ROCK OUTCROP PLANTS

INTRODUCTION

Throughout the Southeastern United States there are areas where the soil is too shallow to support the deciduous forest characteristic of the region. These areas, known as glades or rock outcrops, support endemic and other characteristic herbaceous plant species which often vary with the soil type. Limestone glades, for example, support a different group of plants than granite outcrops. These areas have been the subject of much descriptive botanical study. The limestone cedar glades of middle Tennessee and northern Alabama (Harper 1926, Quarterman 1950), the granite flatrocks from Virginia to Georgia (McVaugh 1943, Burbanck and Platt 1964), and the sandstone outcrops of the Ozarks (Ladd and Nelson 1984, Jeffries 1985) have all been extensively studied.

All outcrop systems are characterized by bedrock close to the surface. Soil is poorly developed and often less than ten centimeters deep. Rocks often break the surface. Conditions are xeric during the growing season, and outcrops receive full sunlight. Throughout the winter, however, poor drainage often results in saturated soil.

Characteristic outcrop species are tolerant of these extreme environmental conditions which are common to all outcrop systems, yet most species have a range limited to outcrops of one bedrock or soil type. One possible explanation for this phenomenon is the distance separating outcrop systems, which prevents propagules from dispersing between outcrop types across unsuitable forest habitats. If, however, the propagules can reach other outcrop types, as in regions of the Ozark Mountains, where different types of outcrops are only meters apart, and species are still confined to only one outcrop type, other environmental factors must be examined.

Substrate differences such as soil chemistry, soil texture, water holding capacity, and microbial flora and fauna may exist between outcrop types which are otherwise environmentally similar. Soil type, therefore, may be a key factor in a species' restriction to one outcrop type. This study was conducted to determine what, if any, relation exists between soil type and growth of selected outcrop plant species.

MATERIALS AND METHODS

Hypericum gentianoides (L.) BSP (Hypericaceae) was collected from granite soil in Brunswick County, Virginia, and from sandstone in Stone County, Arkansas. *Hypericum gentianoides* is a summer-flowering annual which is characteristic of sandstone and granite outcrops, and is also found in open woodlands and on prairies (Steyermark 1963). This species is actually a winter annual, which germinates in the fall, overwinters as a tiny seedling, and resumes growth in March (Burbanck and Platt 1964).

Portulaca smallii P. Wilson (Portulacaceae) is a winter annual which is found growing in the shallowest soil bordering bare rock. It is endemic to Piedmont granite from Georgia to Virginia. Seeds used in this experiment were collected at this species' northernmost known location in Brunswick County, Virginia.

Cyperus granitophilus McVaugh (Cyperacaceae) is a summer annual found exclusively on granite outcrops in the Piedmont. It grows in shallow soil bordering bare rock. Seeds used in this experiment were collected in Brunswick County, Virginia.

C. aristatus Rottb. occurs commonly on wet sand, gravel or mud bars in streams, and in shallow soil in depressions on limestone, granite, and sandstone outcrops where temporary pools form (Steyermark 1963, McVaugh 1943, Baskin and Baskin 1978, S. Ware, pers. comm.). Seeds used in this experiment were collected from plants growing in the William and Mary greenhouse. These plants were grown from seeds collected from a limestone glade in Rutherford County, Tennessee.

Sporobolus neglectus Nash (Gramineae) is a summer annual which grows on limestone glades, in fields, and along railroads from Texas to Tennessee and north to Maine and North Dakota (Steyermark 1963). Seeds for this experiment were collected from plants grown in the William and Mary greenhouse from seeds collected on a limestone glade in Barry County, Missouri. It is assumed that second generation seeds will not respond differently from field collected seeds.

Crotonopsis elliptica Willd. (Euphorbiaceae) is a summer annual abundant on sandstone and granite glades (Jeffries 1985, Steyermark 1963). Its range is throughout the Piedmont, from Florida to Connecticut, and west to Texas and Kansas (McVaugh 1943, Steyermark 1963). Seeds used in this experiment were collected from sandstone in Stone County, Arkansas.

Isanthus brachiatus (L.) BSP (Labiatae) is a summer annual which is found on limestone glades and along gravel bars of streams (Steyermark 1963). Seeds used in this experiment were collected from a limestone glade in Barry

County, Missouri.

Soil was collected from outcrops at the following locations: Piedmont granite from Brunswick County, Virginia (VA GR), and from DeKalb County, Georgia (GA GR); Pottsville sandstone from Marion County, Alabama (AL SS); Petersburg sandstone from Stone County, Arkansas (AR SS); and Ozark limestone from Barry County, Missouri (MO LS). Ozark granite soil was not available and Piedmont granite soil was used in its place. Data on mineral content and pH for all soil types are in Table 1.

Seeds of S. neglectus, Cyperus spp., and I. brachiatus were cold treated for at least six weeks before germination. All seeds were germinated on moist paper towels in Petri plates. Seedlings were transplanted to pots of soil when seedlings showed first green leaves, either cotyledons or primary leaves.

Plastic pots, 10.16 centimeters in diameter, were used. A moist paper towel was placed in the bottom of each, and each was filled with the same volume of dry soil. Three to six seedlings were grown per pot, depending on the species and projected size of the mature plant. This number was kept constant for each species. Since many of the seedlings were very tiny, some may have been damaged during transplanting. Thus, during the first week after transplanting, seedlings that died were replaced. None were replaced after the first week.

Plants were grown in the greenhouse of Solex glass at

TABLE 1: SOIL CHEMISTRY DATA

SOURCE	pH	Ca	Mg	K	P
		PPM OF OXIDES			
DeKalb Co., GA granite	6.6	315	10	15	28
Brunswick Co., VA granite	4.5	165	40	40	13
Stone Co., AR sandstone	5.3	150	15	15	16
Marion Co., AL sandstone	5.3	590	30	32	14
Barry Co., MO limestone	8.3	1350	35	50	6

the College of William and Mary. All plants in any experiment were watered regularly and generously in an attempt to avoid any moisture differences related to soil texture. All pots were weeded regularly to eliminate competition from "volunteer" conspecifics and members of other species.

When the first plants reached flowering stage, the experiment was ended. This time ranged from 43 days for *C. granitophilus* and *C. aristatus* to 158 days with *S. neglectus*. Plants were carefully removed from saturated soil, to preserve most of the roots, and were then dried at 105 C for twenty-four hours. Dry mass, measured to the nearest 0.1 milligram, was the measure of success.

Whenever possible, analyses of variance were used to determine statistically significant variations in plant growth between soil types. Where assumptions of homogeneity of variance were not met, nonparametric tests, the Kruskal-Wallis test and the Mann-Whitney U-Test, were used.

RESULTS

Hypericum gentianoides from Petersburg (AR) sandstone soil was grown on its native soil, on Ozark (MO) limestone soil, and, as a substitute for unavailable Ozark granite soil, on Piedmont (GA) granite soil (Experiment 1). Using a Kruskal-Wallis test, it was shown to grow significantly ($P<0.05$) better on granite soil than on its own native sandstone soil, but still significantly ($P<0.05$) better on sandstone than on limestone soil (Fig Ia). When *H. gentianoides* from Piedmont (VA) granite was grown on its native granite soil and on Pottsville (AL) sandstone (Exp. 3), a Mann-Whitney U-Test showed that the population also grew significantly ($P<0.05$) better on granite (Fig. IIb). Table 2 provides a summary of results for all species. For complete results on this and all other species, see the Appendix.

Because these two experiments were done at different times on different soils, they are not directly comparable. In Experiment 2, however, the two populations were tested on the same soils (Piedmont (GA) granite and Petersburg (AR) sandstone) simultaneously (Figs. Ib and IIa), thus allowing direct comparisons of results. In this experiment the better growth of both populations on granite soil was not

FIGURE I.

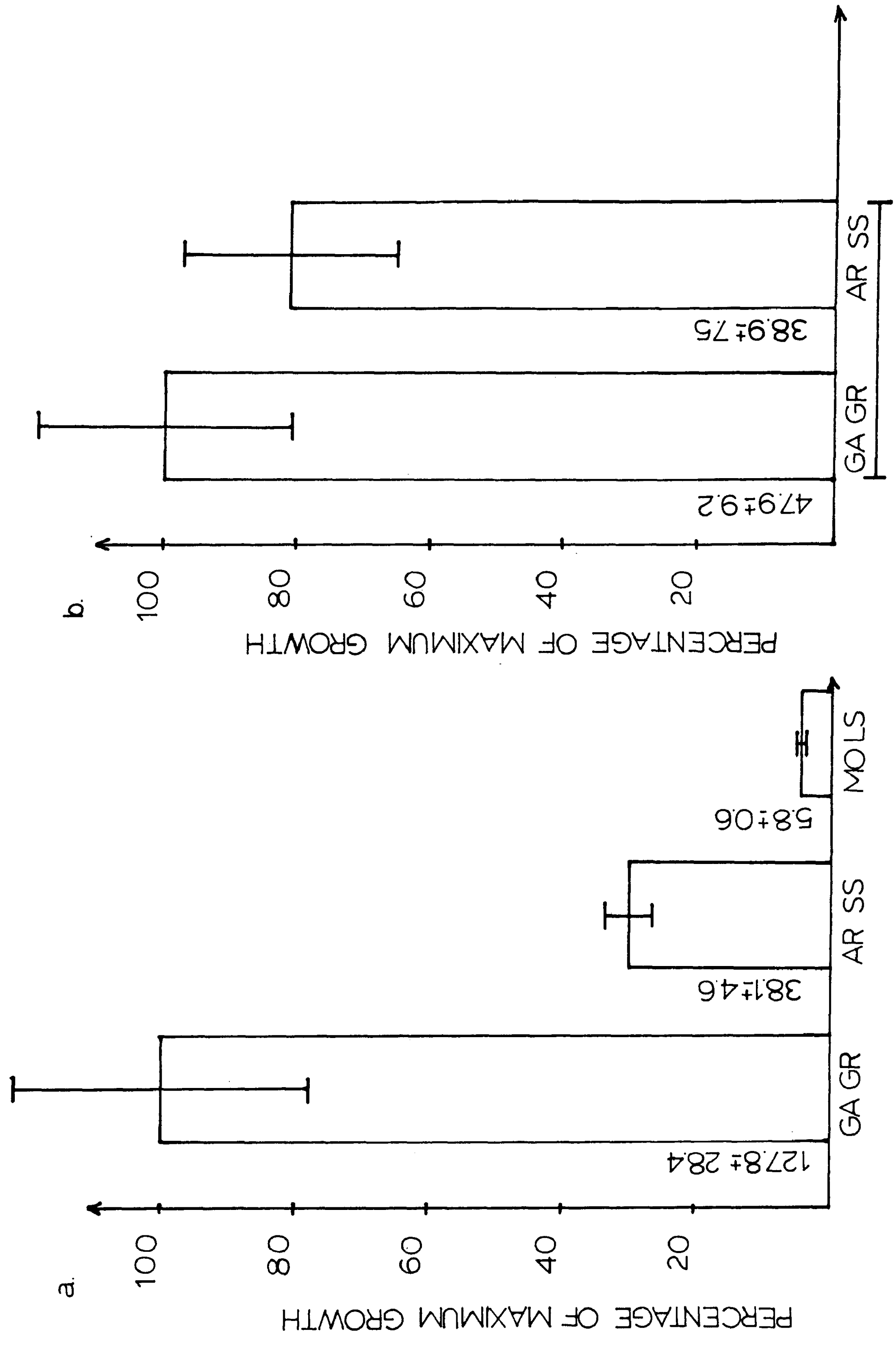

a.
b.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
127.8± 28.4
38.1±4.6
5.8±0.6
47.9±9.2
38.9±7.5
GA GR
AR SS
MO LS

Figure I: Growth of _Hypericum gentianoides_ from Arkansas sandstone: a. Experiment 1: 2/28/85 - 4/25/85; b. Experiment 2: 10/5/85 - 12/8/85. GA GR is Georgia granite soil; VA GR is Virginia granite; AL SS is Alabama sandstone; AR SS is Arkansas sandstone; and MO LS is Missouri limestone. To faciliate visual comparisons between experiments, graphical representations for each experiment are in terms of percentage of maximum growth for that experiment. The range of standard error is also expressed graphically as a percentage of maximum growth. Mean dry mass in milligrams ± standard error are written alongside each bar. Soil types with lines underneath them did not have statistically signifcant differences in growth.

TABLE 2: Relative growth of each species on all soil types. Those soils connected by an underbar showed no significant difference in growth for that species. Abbreviations for soil types as in Figure I.

SPECIES and SOURCE	RELATIVE GROWTH
Hypericum gentianoides from Arkansas sandstone (also found on granite)	Exp. 1: GAGR > ARSS > MOLS Exp. 2: GAGR > ARSS
Hypericum gentianoides from Virginia granite (also found on sandstone)	Exp. 2: GAGR > ARSS Exp. 3: VAGR > ALSS
Portulaca smallii from Virginia granite	Exp. 4: VAGR > ARSS > MOLS Exp. 5: VAGR > ALSS > MOLS
Cyperus granitophilus from Virginia granite	Exp. 6: ARSS > VAGR > MOLS Exp. 7: VAGR > ARSS > MOLS
Cyperus aristatus from Tennessee limestone (also found on GR and SS)	Exp. 6: ARSS > MOLS > VAGR ----------- Exp. 7: VAGR > ARSS > MOLS
Sporobolus neglectus from Missouri limestone	Exp. 8: VAGR > ALSS > MOLS Exp. 9: VAGR > ALSS > MOLS
Crotonopsis elliptica from Arkansas sandstone (also found on granite)	Exp. 10: VAGR > ARSS > MOLS
Isanthus brachiatus from Missouri limestone	Exp. 11: VAGR > MOLS > ARSS

FIGURE II.

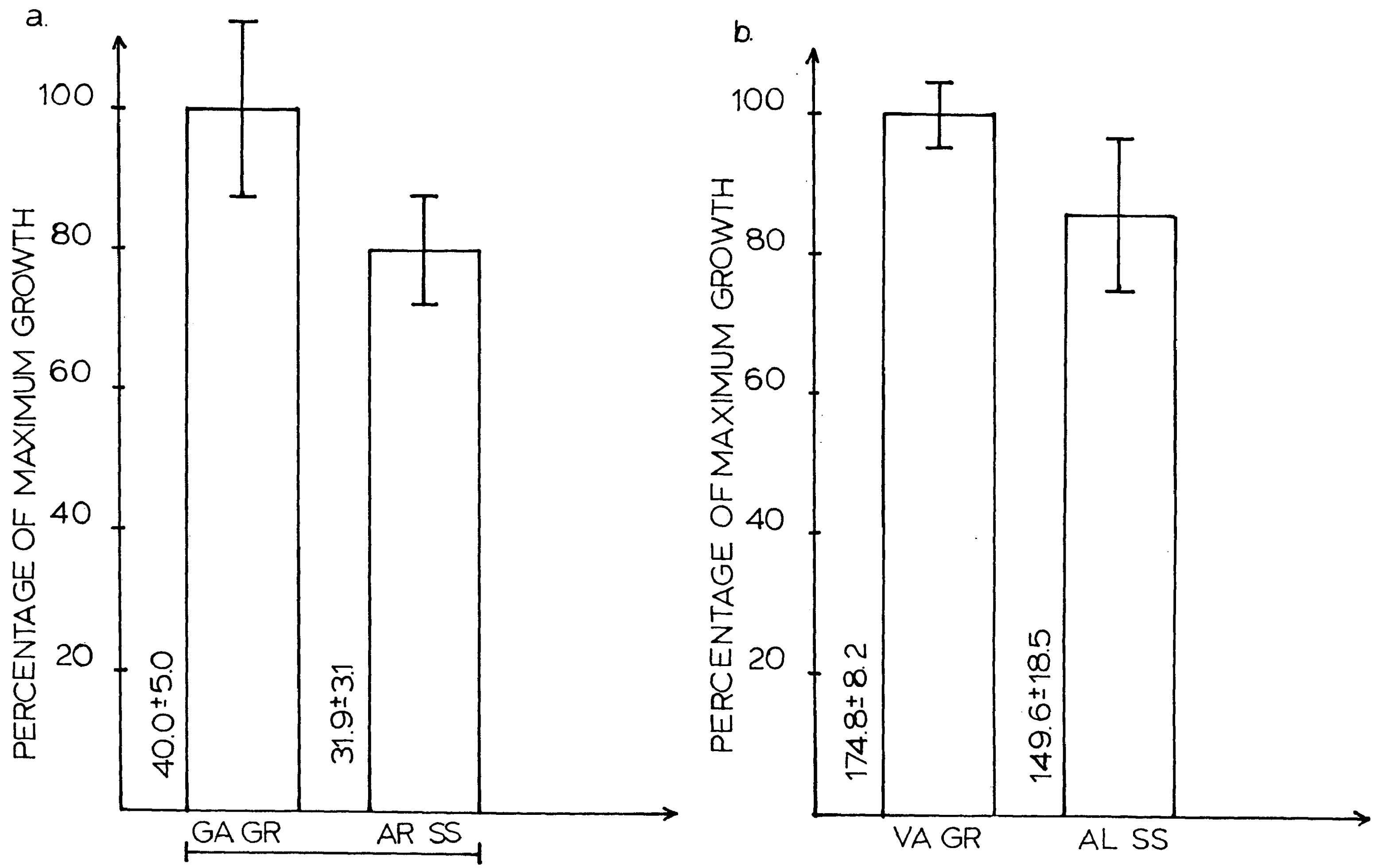

a.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
40.0±5.0
31.9±3.1
GA GR
AR SS
b.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
174.8±8.2
149.6±18.5
VA GR
AL SS

Figure II: Growth of *Hypericum gentianoides* from Virginia granite: a. Experiment 2: 10/5/85 - 12/8/85; b. Experiment 3: 4/28/86 - 8/23/86. Legend as in Figure I.

statistically significant.

In Experiment 4, Portulaca smallii was grown its native Piedmont (VA) granite soil, on Petersburg (AR) sandstone soil, and on Ozark (MO) limestone soil (Fig. III). The population grew significantly ($P<0.05$) better on its native granite soil than on either of the other two, although it grew significantly ($P<0.05$) better on sandstone than on limestone. In Experiment 5, P. smallii was grown in its native granite, Pottsville (AL) sandstone, and Ozark (MO) limestone soil. In this experiment, the better growth on granite than on sandstone was not statistically significant. Growth on Pottsville (AL) sandstone was, as with Petersburg (AR) sandstone, significantly ($P<0.05$) better than on Ozark (MO) limestone. A one-way ANOVA was used in Experiment 4, and a Kruskal-Wallis test was used in Experiment 5.

Cyperus granitophilus, in Experiment 6, was grown on its native Piedmont (VA) granite, on Petersburg (AR) sandstone, and on Ozark (MO) limestone soil. Cyperus aristatus, from Tennessee limestone, was grown on the same soils, simultaneously (Figs. IVa and Va). Both species showed best growth on sandstone soil. Growth of C. granitophilus on granite was not significantly different from on sandstone, while growth of C. aristatus on granite was significantly ($P<0.05$) poorer than on sandstone. Both species grew most poorly on limestone. Only two individuals in the C. granitophilus population survived on limestone until the end of the experiment, and their growth was

FIGURE III.

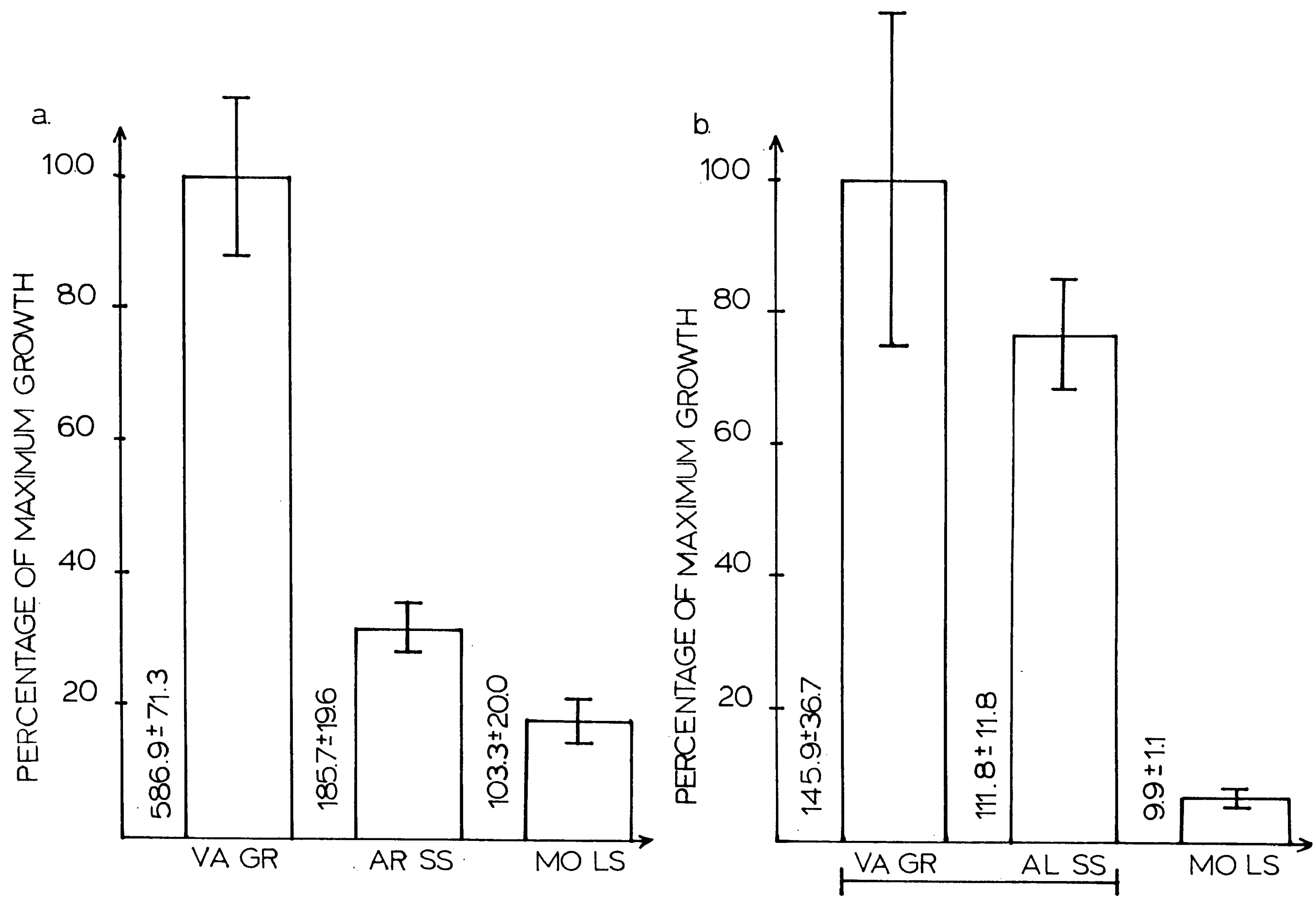
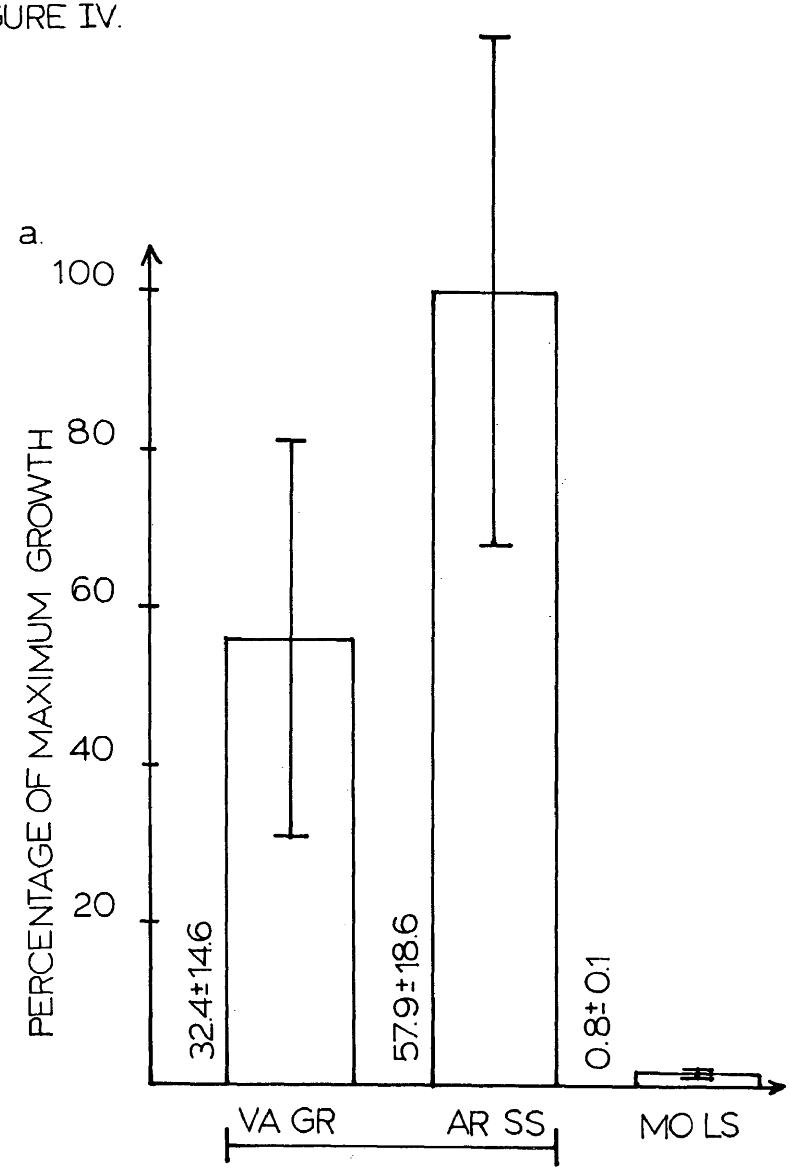

a.
b.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
586.9 ± 71.3
185.7±19.6
103.3±20.0
145.9±36.7
111.8 ± 11.8
9.9 ± 1.1
VA GR
AR SS
AL SS
MO LS

Figure III: Growth of Portulaca smallii from Virginia granite: a. Experiment 4: 3/8/86 - 7/1/86; b. Experiment 5: 4/21/86 - 7/5/86. Legend as in Figure I.

FIGURE IV.


a.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
32.4±14.6
57.9±18.6
0.8±0.1
VA GR
AR SS
MO LS

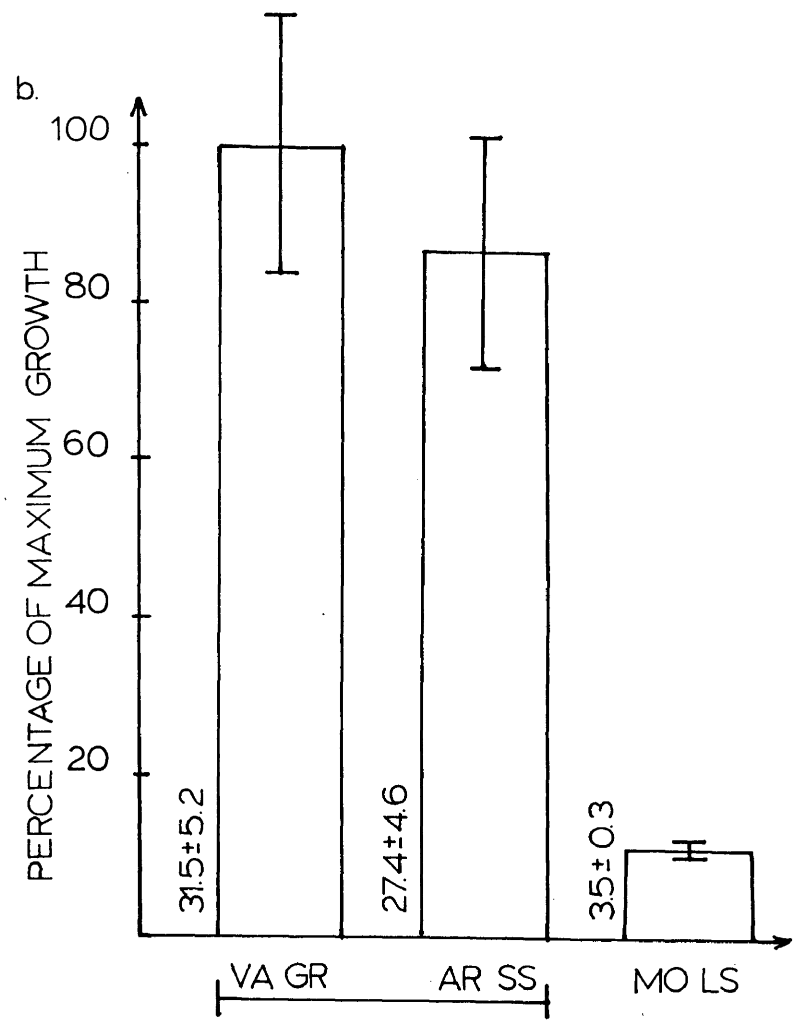

b.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
31.5±5.2
27.4±4.6
3.5±0.3
VA GR
AR SS
MO LS

Figure IV: Growth of *Cyperus granitophilus* from Virginia granite: a. Experiment 6: 12/8/85 - 3/17/86; b. Experiment 7: 3/23/86 - 10/5/86. Legend as in Figure I.

FIGURE V.

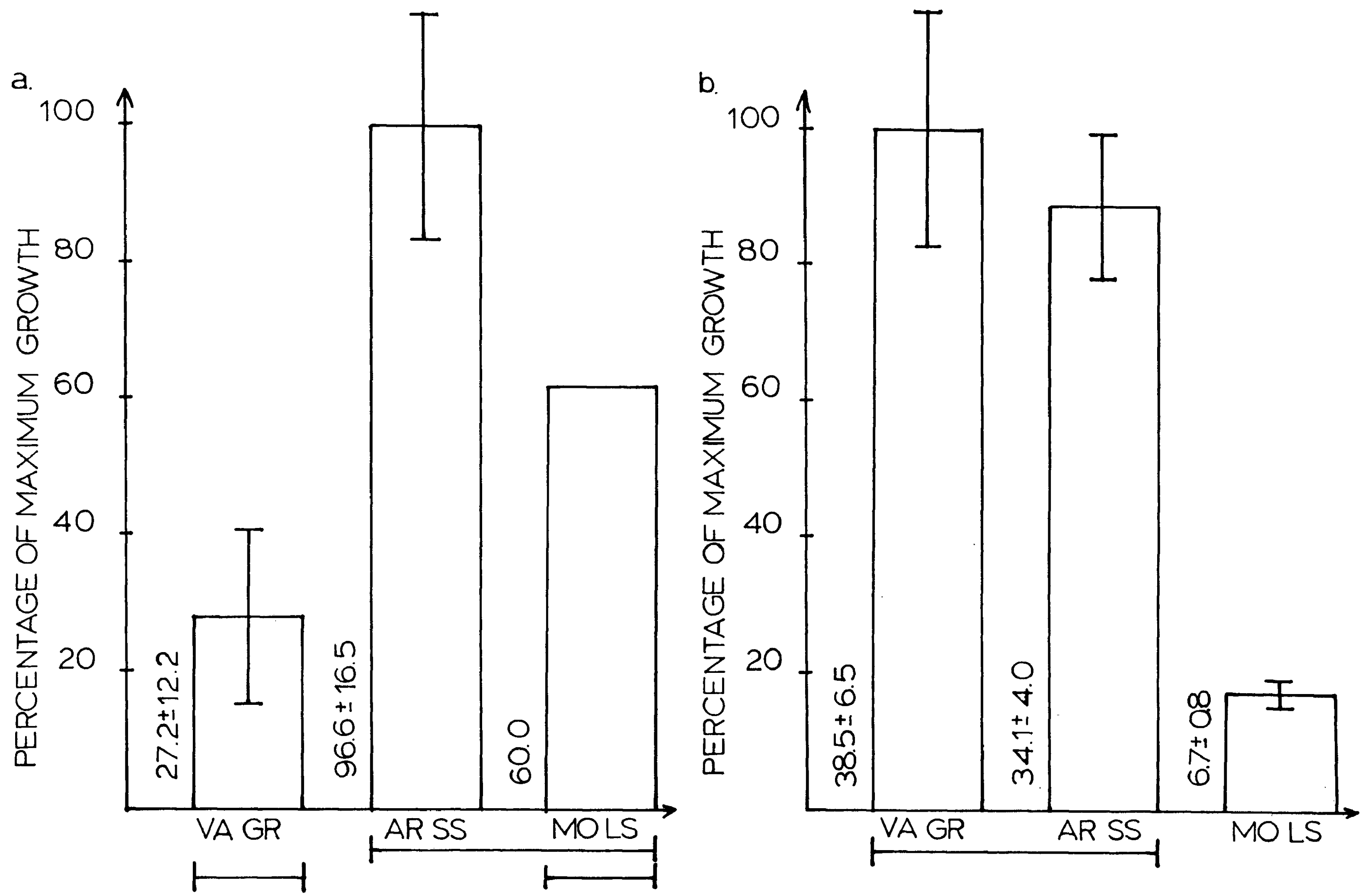

a.
b.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
27.2±12.2
96.6±16.5
60.0
38.5±6.5
34.1±4.0
6.7±0.8
VA GR
AR SS
MO LS

Figure V: Growth of *Cyperus aristatus* from Tennessee limestone: a. Experiment 6: 12/8/85 - 3/17/86; b. Experiment 7: 8/23/86 - 10/5/86. On MO LS, in Figure Va, there is no standard error, as N = 1. Legend as in Figure I.

significantly ($P<0.05$) less than growth on sandstone or granite. Only one individual in the C. aristatus population on limestone soil (the type of soil from which it came) survived to the end of the experiment, thus preventing statistical comparison with the other soil types.

In Experiment 7, the same species and soil types were used as in Experiment 6 (Figs. IVb and Vb). In this case, however, both species grew best on granite, although the difference between granite and sandstone was not statistically significant. Growth on sandstone was, in both cases, significantly ($P<0.05$) better than on limestone soil. One-way ANOVAs were used in Experiments 6 and 7.

Sporobolus neglectus, in Experiments 8 and 9, was grown on its native Ozark (MO) limestone, on Piedmont (VA) granite, and on Pottsville (AL) sandstone soil (Fig VI). In both experiments, the populations grew best on granite soil, significantly ($P<0.05$) better than on either sandstone or the species' native limestone soil. Also in both experiments, a one-way ANOVA showed the plants' better growth on sandstone than on limestone to be statistically insignificant.

Crotonopsis elliptica, from Petersburg (AR) sandstone, was grown on Piedmont (VA) granite, its native sandstone, and Ozark (MO) limestone soil, in Experiment 10. The population grew best on granite, intermediate on sandstone, and most poorly on limestone (Fig. VIIa). Differences between all three groups were significant ($P<0.05$), using a

FIGURE VI.

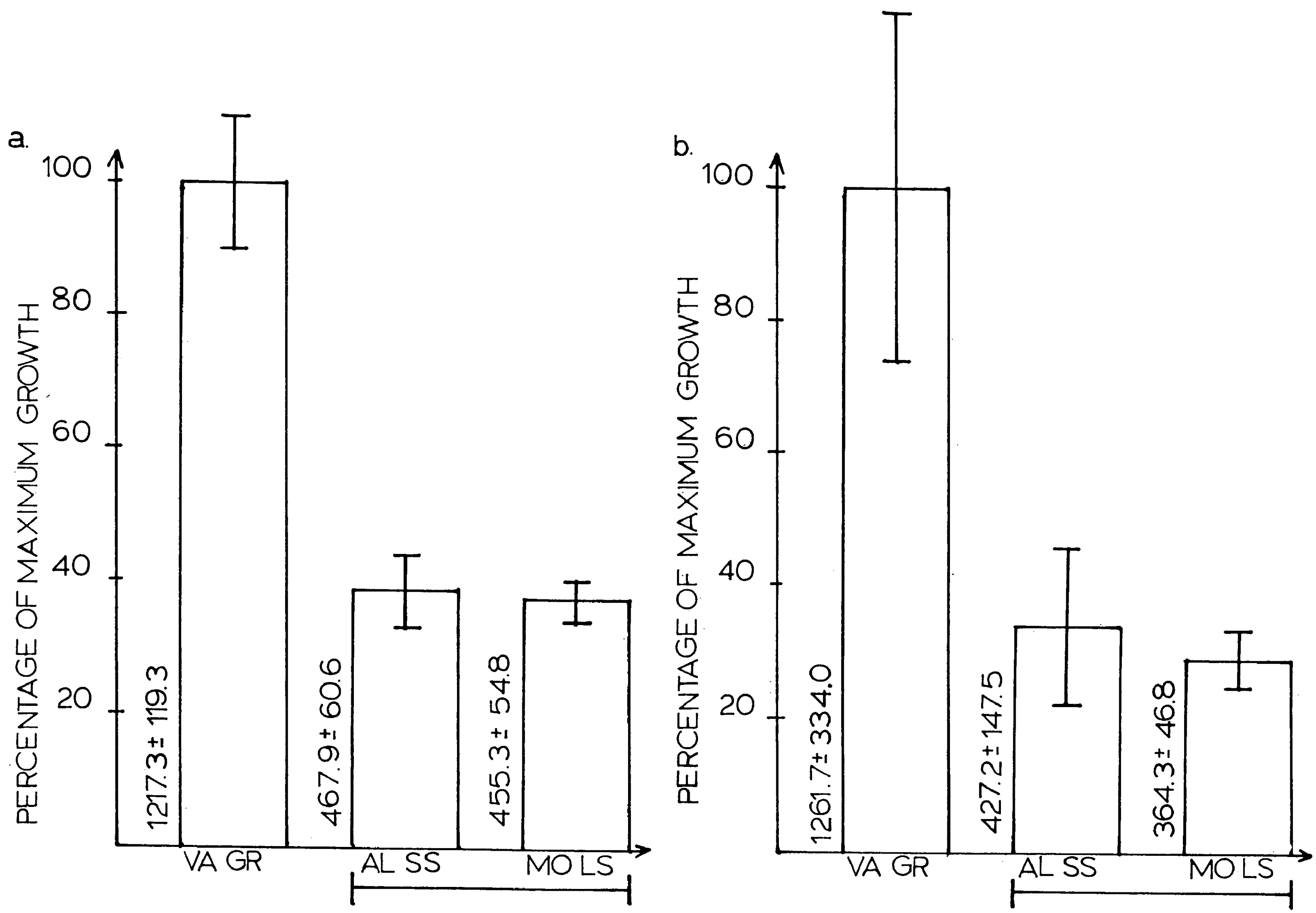

a.
100
80
60
40
20
PERCENTAGE OF MAXIMUM GROWTH
1217.3± 119.3
467.9± 60.6
455.3± 54.8
VA GR
AL SS
MO LS
b.
100
80
60
40
20
PERCENTAGE OF MAXIMUM GROWTH
1261.7± 334.0
427.2± 147.5
364.3± 46.8
VA GR
AL SS
MO LS

Figure VI: Growth of Sporobolus neglectus from Missouri limestone: a. Experiment 8: 3/5/86 - 7/30/86; b. Experiment 9: 4/21/86 - 9/26/86. Legend as in Figure I.

one-way ANOVA. This experiment could not be repeated, as no more seeds were available.

In Experiment 11, Isanthus brachiatus was grown on its native Ozark (MO) limestone soil, on Petersburg (AR) sandstone, and on Piedmont (VA) granite soil (Fig. VIIb). A one-way ANOVA showed none of the differences between groups to be statistically significant, although the plants grew best on granite, followed by limestone, then sandstone. A dearth of seeds also prevented repetition of this experiment.

FIGURE VII.

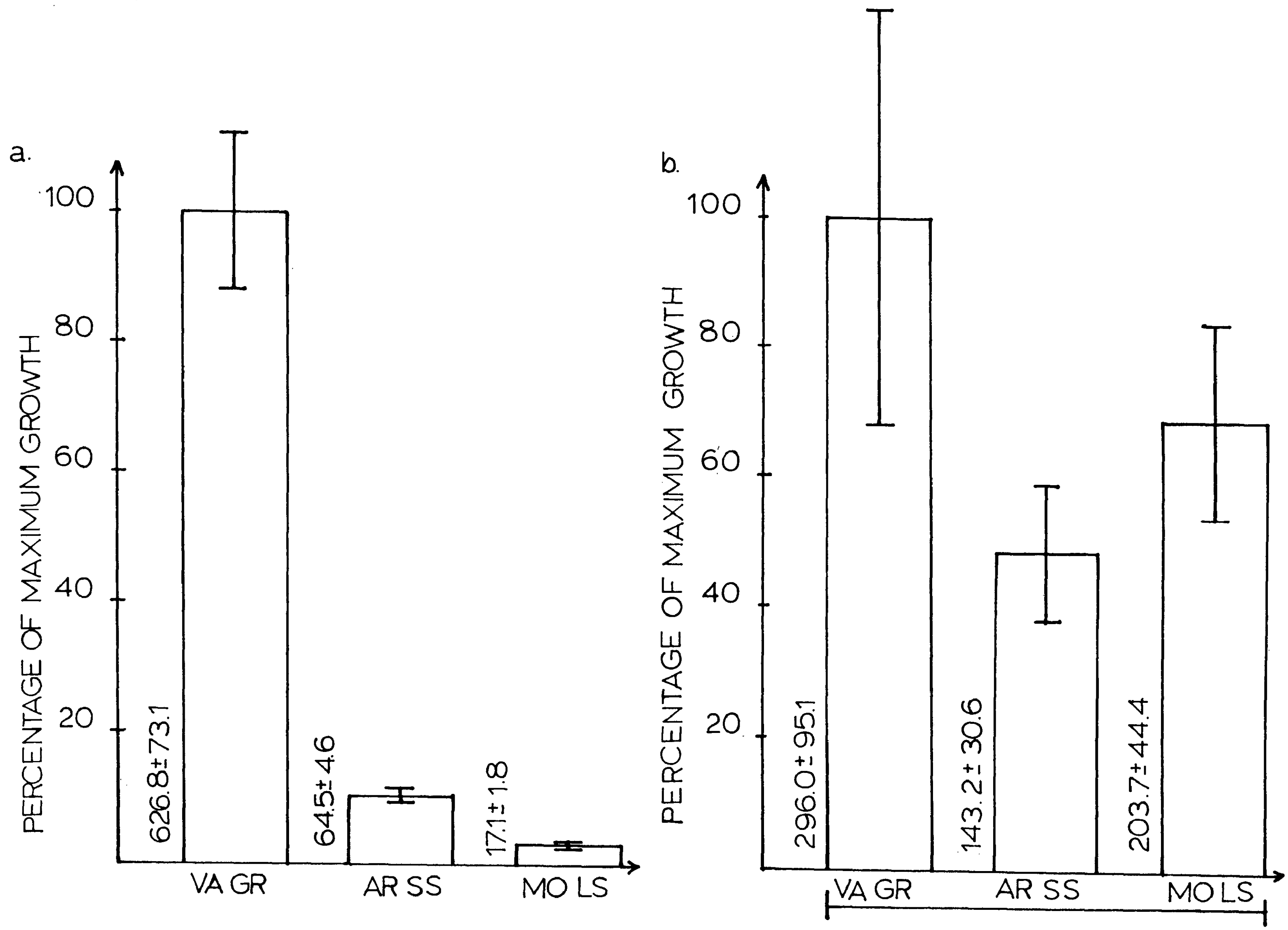

a.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
626.8±73.1
64.5±4.6
17.1±1.8
VA GR
AR SS
MO LS
b.
PERCENTAGE OF MAXIMUM GROWTH
100
80
60
40
20
296.0±95.1
143.2±30.6
203.7±44.4
VA GR
AR SS
MO LS

Figure VII: a. Growth of *Crotonopsis elliptica* from Arkansas sandstone: Experiment 10: 4/25/85 - 7/6//85; b. Growth of *Isanthus brachiatus* from Missouri limestone: Experiment 11: 12/10/85 - 3/12/86. Legend as in Figure I.

DISCUSSION

Hypericum gentianoides occurs both on granite and sandstone outcrops, and is a dominant species on both (McVaugh 1943, Jeffries 1985). Plants on both of these soils grew much better than on limestone, suggesting that soil type is a factor in the restriction of *H. gentianoides* to sandstone and granite soils. This species is greatly inhibited by limestone soil, and would be unlikely to invade limestone outcrops even if its seeds reached there often.

Plants from sandstone and from granite grew better on granite soil than on sandstone. In two of four cases, however, the difference in growth was not statistically significant. This suggests that *H. gentianoides* from either soil type may be better adapted to granite than to sandstone, although it is quite capable of success on either. Experiment 2 shows that sandstone and granite populations are not ecotypically differentiated: their responses to the two soil types are remarkably similar.

Since *Portulaca smallii*, a granite outcrop endemic, grew significantly better on granite than on limestone soil in both experiments, limestone soil clearly inhibits the growth of this species. It would be unlikely that any seeds reaching a limestone outcrop would successfully invade that habitat.

In both tests (Experiments 4 and 5), the species grew best on granite soil. Also in both tests, however, the number of individuals to survive to maturity was higher on sandstone than on either of the other soil types. The AR and AL sandstone may not be directly comparable, for the difference in growth on granite and on AL sandstone was not statistically significant in the second test (Experiment 5). The number blooming on sandstone was also higher than on granite in the second test. This suggests that, while the plants may not grow as rapidly on sandstone as on granite, they are still perfectly able to survive to maturity and to reproduce. Soil type might play a role in excluding P. smallii from limestone outcrops, but geographical separation may be more important in the absence from sandstone outcrops.

Cyperus granitophilus is a granite endemic, believed to have evolved from the more widespread C. aristatus (Murdy 1968). It would be expected that C. granitophilus would show its best growth on granite, as was the case in Experiment 6, yet in Experiment 7 better growth was seen on sandstone soil. In both cases, however, differences in growth between sandstone and granite were not statistically significant. The results show clearly that C. granitophilus does not grow well on limestone soil, and suggest that soil type is a factor in the species' exclusion from limestone soil. Results suggest that geographic isolation rather than soil type is responsible for the exclusion of _C._ _granitophilus_ from sandstone soil, since plants did grow well there.

Contrary to expectations, _Cyperus_ _aristatus_ did not grow well on limestone soil. Since only one plant grew until the end of Experiment 6 on limestone soil, results on limestone can not accurately be compared with other soils. This poor survival suggests that in fact the plants grow more poorly on limestone than on the other soil types although statistical analysis showed no significant difference in growth between granite and limestone soils. Best growth and greatest number of plants surviving until the end of the experiment occurred on sandstone soil. This suggests that this population has no ecotypic adaptation to limestone soil, although it is abundant there. It somehow manages to survive on limestone soil, although it is better adapted to sandstone and granite soils. This species grows in very shallow soil, where there is essentially no competition. It may, therefore, do well in that niche, even on limestone, because no other species can exploit that habitat.

During Experiment 7, _C._ _aristatus_ grew better on granite than on sandstone, a reversal from Experiment 6. In this case, however the difference in growth was not statistically significant. Further experimentation must be done before conclusions can be drawn regarding the relative growth of _C._ _aristatus_ on sandstone and granite.

Sporobolus neglectus occurs on limestone outcrops and several non-outcrop habitats (Steyermark 1963). It does not occur on sandstone or granite glades. Results of these experiments showed that S. neglectus grew significantly better on granite than on either sandstone or limestone in both tests. This is quite unexpected, and suggests that soil type is not the major factor affecting the distribution of S. neglectus. An investigation should be made of the possiblilty that exclusion from acid subtrate might be the result of competition with some other species which has pre-empted its potential niche on those outcrops. For example, Coreopsis lanceolata is a dominant species in deeper soil on sandstone outcrops, yet it does not occur in outcrop areas where the pH is greater than 6.1 (Jeffries, 1985).

Crotonopsis elliptica showed significantly better growth on granite soil than on its native sandstone soil. Since this species occurs on granite, as well as on sandstone glades, these results are not unexpected. Plants grown on sandstone and on granite grew significantly better than plants on limestone soil, suggesting that soil type is a factor in the species' exclusion from limestone soil. Because this experiment could not be repeated, further experimentation must be done before firm conclusions can be made.

Isanthus brachiatus occurs on limestone glades and in several habitats other than outcrops. It does not occur on granite or sandstone outcrops. Surprisingly, _I. brachiatus_ showed its best growth on granite soil, and the highest number of individuals survived to maturity on sandstone soil. This suggests that some factor other than soil type controls the distribution of _I. brachiatus_. Because this experiment could not be repeated, however, no firm conclusions can be drawn until further experimentation is done on this species.

It is clear from these results that no general explanation exists for the distribution of all glade flora. Although certain species tend to occur together on each type of outcrop, the reasons for their occurrence may be different. These reasons may include adaptation to soil type, geographic isolation, and competitive interactions. Each species is distributed according to its individual evolutionary and ecological history.

APPENDIX

SPECIES and SOURCE	DATES	NO. DAYS	SOIL TYPE	N	MEAN	S.D.	S.E.
Hypericum gentianoides from Arkansas sandstone	2/28/85-4/25/85	56	GA GR	11	127.8	94.1	28.4
			AR SS	12	38.1	15.9	4.6
			MO LS	12	5.8	2.1	0.6
	10/5/85-12/8/85	61	GA GR	16	47.9	37.0	9.2
			AR SS	16	38.9	29.9	7.5
Hypericum gentianoides from Virginia granite	10/5/85-12/8/85	61	GA GR	16	40.0	19.8	5.0
			AR SS	15	31.9	12.0	3.1
	4/28/86-8/23/86	117	VA GR	16	174.8	32.9	8.2
			AL SS	16	149.6	73.9	18.5
Portulaca smallii from Virginia granite	3/8/86-7/1/86	115	VA GR	15	586.9	276.1	71.3
			AR SS	18	185.7	83.2	19.6
			MO LS	14	103.3	74.8	20.0
	4/21/86-7/5/86	75	VA GR	14	145.9	137.2	36.7
			AL SS	19	111.8	51.5	11.8
			MO LS	16	9.9	4.3	1.1
Cyperus granitophilus from Virginia granite	12/8/85-3/17/86	99	VA GR	9	32.4	43.9	14.6
			AR SS	9	57.9	55.8	18.6
			MO LS	2	0.8	0.1	0.1
	8/23/86-10/5/86	43	VA GR	11	31.5	17.2	5.2
			AR SS	13	27.4	16.5	4.6
			MO LS	15	3.5	1.1	0.3

SPECIES and SOURCE	DATES	NO. DAYS	SOIL TYPE	N	MEAN	S.D.	S.E.
Cyperus aristatus from Tennessee limestone	12/8/85-3/17/86	99	VA GR	6	27.2	29.8	12.2
			AR SS	9	96.6	47.8	15.9
			MO LS	1	60.0	--	--
	8/23/86-10/5/86	43	VA GR	13	38.5	23.4	6.5
			AR SS	15	34.1	15.3	4.0
			MO LS	15	6.7	3.0	0.8
Sporobolus neglectus from Missouri limestone	3/5/86-7/30/86	147	VA GR	16	1217.3	477.3	119.3
			AL SS	16	467.9	242.4	60.6
			MO LS	14	455.3	205.2	54.8
	4/21/86-9/26/86	158	VA GR	7	1261.7	883.7	334.0
			AL SS	13	427.2	531.8	147.5
			MO LS	8	364.3	132.3	46.8
Crotonopsis elliptica from Arkansas sandstone	4/25/85-7/6/85	72	VA GR	7	626.8	193.4	73.1
			AR SS	8	64.5	13.0	4.6
			MO LS	5	17.1	4.1	1.8
Isanthus brachiatus from Missouri limestone	12/10/85-3/12/86	92	VA GR	5	296.0	212.7	95.1
			AR SS	8	143.2	86.5	30.6
			MO LS	6	203.7	108.7	44.4

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