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COEXISTENCE IN PATCHY ENVIRONMENTS: THE LOCAL, REGIONAL AND CONTINENTAL COEXISTENCE OF MOSSES IN THE FAMILY SPLACHNACEAE

by

PAUL MARINO

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(SIGNED) Paul C. Marino

PERMANENT ADDRESS:

8319 Saskatchewan Dr.

Edmonton, Alberta Canada

DATED 14 October 19 88

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled COEXISTENCE IN PATCHY ENVIRONMENTS: THE LOCAL, REGIONAL AND CONTINENTAL COEXISTENCE OF MOSSES IN THE FAMILY SPLACHNACEAE submitted by PAUL MARINO in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Supervisor

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External Examiner

Date Oct 14, 1988

ABSTRACT

The influence of habitat patchiness on the coexistence of moss species (*Tetraplodon angustatus, T. mnioides, Splachnum ampullaceum* and *S. luteum*: F. Splachnaceae) that use similar resources was studied at the local, regional and continental spatial scales. These mosses grow on the droppings of large mammals and have their spores dispersed to droppings by flies (Diptera).

Patterns of distribution and interaction on a local scale (e.g., on droppings) indicated that a) different species did not commonly co-occur on the same droppings, b) that species appeared to compete for some resource, possibly space, and c) that the relative competitive abilities of species differed and were influenced by differences between dry and wet habitats. The influence of dry and wet habitats on relative competitive ability may be large enough to explain partially the rarity of co-occurrences between species of different genera but not between congeneric species, suggesting that coexistence results from mechanisms operating at larger spatial scales.

On a regional scale (e.g, on several adjacent droppings), Splachnaceae coexist throughout much of temperate and boreal North America and habitat heterogeneity appeared to be important in promoting the coexistence between species of different genera whereas temporal heterogeneity and a tradeoff between relative competitive and dispersal ability may be important in promoting regional coexistence between species of *Tetraplodon* and *Splachnum*, respectively. Simulation results suggested that the independent aggregation of spores on droppings and the availability for colonization, at least periodically, of large numbers of droppings may also be important factors promoting the regional coexistence of species of *Splachnum*.

Because most boreal and arctic species of Splachnaceae have widely overlapping ranges throughout North America, their continental distributions appear to result primarily from the influence of processes promoting regional coexistence.

Therefore, neither historical factors nor the differential sensitivity of species to environmental heterogeneity across large geographic areas appears to strongly influence the coexistence of species on a continental scale.

Overall, habitat patchiness appeared to influence the coexistence of Splachnaceae and coexistence appeared to be the result of several different mechanisms, few of which could be completely understood from the perspective of only one spatial scale.

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I. INTRODUCTION

Habitat patchiness can have a strong influence on the coexistence of species because patches, which are relatively small discrete units in space, can vary in size, location in the environment, internal homogeneity, and discreteness (Elton 1949; Andrewartha and Birch 1954; Huffaker 1958; White and Pickett 1985; Kareiva 1986). However, this influence must be explored at several scales of observation since no single choice of scale allows a complete understanding of species interactions and community patterns (Wiens et al. 1986). Because the area of each scale differs, the ecological processes being examined, the tie scale appropriate to those processes, and an organism's activity or influence during that time period will also differ (Addicott et al. 1987). As a result, different mechanisms of coexistence should apply to interactions between species for each scale of observation, and a single mechanism should not apply to all scales.

I have studied the coexistence of the mosses *Tetraplodon angustatus*, *T. mnioides*, *Splachnum ampullaceum* and *S. luteum* (F. Splachnaceae) by examining mechanisms of coexistence at the local, regional and continental spatial scales. These mosses grow primarily on the droppings of large mammals and have their spores dispersed to droppings by flies (Diptera). In this the first chapter, I will: 1) introduce the main concepts of coexistence theory; 2) define the spatial scales used to examine mechanisms of coexistence in Splachnaceae; and 3) discuss mechanisms of coexistence at each scale. The second chapter examines local coexistence of Splachnaceae by determining whether different species can coexist on a homogeneous resource and whether resource heterogeneity influences coexistence. The third chapter examines regional coexistence by determining whether there is a tradeoff between dispersal and competitive ability. In the fourth chapter, the influence of spore aggregation on regional coexistence is examined with simulation modeling. The fifth chapter examines the continental distributions of Splachnaceae in North America. The sixth chapter is a general discussion synthesizing the

results of this study.

A. COEXISTENCE THEORY

Coexistence theory based on equilibrium solutions was first developed mathematically by Volterra (1926), who showed that in situations where the growth and reproduction of two species are resource-limited, only one species can survive per resource. This is known as the competitive exclusion principle. The competitive exclusion principle was extended to discrete resources by MacArthur and Levins (1964), who showed that indefinite coexistence is not possible if n species exist on fewer than n resources, niches, or limiting factors.

The competitive exclusion principle was extended to a continuum of resources by the theory of limiting similarity (MacArthur and Levins 1967). Limiting similarity is defined as the maximum level of similarity in the use of a set of resources that are in short supply that will allow competing species to coexist (Abrams 1983). Levins (1968) further suggested that the number of coexisting species in a community depends on the mean and variance of overlap, and the dissimilarities of niche breadths. Although broader limits to similarity can be attained under conditions of equilibrium predation and spatial variation (Chesson and Case 1986), competition theory based on equilibrium solutions suggests, overall, that several species cannot coexist on the same resources unless they use those resources differently.

However, coexistence theory based on equilibrium solutions is often inappropriate (Levins 1979) because environmental variation is an important factor in the dynamics of real populations and communities (Andrewartha and Birch 1954; Hutchinson 1961; Wiens 1977; Grubb 1977; Connell 1978; Strong 1985). Numerous empirical studies have shown that species using the same resources do coexist in what appear to be nonequilibrium situations (e.g., Denno and Cothran 1975; Rathcke 1976; Hanski 1980; Strong 1982; Hanski and Ranta 1983). A

nonequilibrium situation is one in which species densities do not remain constant over time at each spatial location, often as a result of environmental variation. Nonequilibrium theories of coexistence can be separated into four approaches: those that assume 1) fluctuations and continuous competition; 2) fluctuations and discontinuous density-dependence or competition; 3) changing environmental mean; and, 4) slow competitive displacement (Chesson and Case 1986).

In the first approach, the relative competitive abilities of species vary through time and space (Chesson and Case 1986). Such variation occurs in two ways. First, dispersal rates into particular patches may fluctuate, causing fluctuations in the numerical advantage of a species in a particular patch. This may occur, for example, through differences among species in dispersal ability (Skellam 1951; Hutchinson 1975; Hanski and Ranta 1983). Secondly, competitive abilities of species may be environmentally dependent and, therefore, fluctuate with local environmental changes. Different species will be favored under different sets of environmental conditions, allowing each species to have periods of strong recruitment. This results in positive growth rates at low densities for competing species implying that they will coexist (Chesson 1986). Coexistence can result from environmental variation in time (Chesson and Warner 1981), space (Chesson 1986; Comins and Noble 1985) or both (Chesson 1985).

In the second approach, fluctuations in environmental factors reduce the densities of potentially competing species to levels where competition is weak and population growth is for a time insensitive to density (Koch 1974; Chesson 1983). Therefore, the intensities of intra- and interspecific competition fluctuate with time, and competing species are able to coexist (Chesson and Case 1986).

In patchy environments, local extinctions or population reductions resulting from predators (Caswell 1978) or environmental fluctuations (Slatkin 1974; Hanski 1983) can allow species to colonize and grow for some time in patches in the absence of competition. In this way even inferior competitors can persist if they

are, for example, relatively less susceptible to predation or are relatively better dispersers.

The third approach involves historical factors, and emphasizes that the mean of environmental fluctuations does not remain constant over ecological time. Neither approaches 1 or 2 or any of the equilibrium models consider this possibility (Chesson and Case 1986). In this view, communities of species are constantly adjusting to new environmental conditions but never competely adjust before conditions change again. Historical factors are mainly important in understanding the relationships between species of long-lived individuals. Because population dynamics of short-lived organisms are fast relative to changes in the mean environment, present-day populations and communities can be understood on the basis of contemporary environmental fluctuations without considering historical changes in the environment (Chesson and Case 1986).

The overall similarity of species and their long-term coexistence is emphasized in the fourth approach (Chesson and Case 1986). The biotic interactions between species are not important in shaping specialized niches; rather, they appear to shape broad adaptive zones amongst guilds of species. Species diversity is a result of regional species richness and availability of potential immigrants, which in turn are dictated by the interaction of climate, the biogeography of particular species, local dispersal and speciation processes on a regional and subcontinental scale. Species occupying similar niches are able to coexist because competitive exclusion is slow. This is not a theory of stable community structure since species composition will show no tendency to recover following a perturbation (Chesson and Case 1986).

In summary, in approaches 1 and 2, species must differ from one another if they are to coexist, as in equilibrium theories. However, unlike equilibrium theories, the focus is not on how species coexist by partitioning resources, but rather on how species can coexist on the same resources if they have different

responses to fluctuating environments. Approaches 1 and 2 also consider fluctuations in the environment about some mean value, and generally the mean and variance of these environmental fluctuations are assumed to be constant over time (Chesson and Case 1986). Approaches 3 and 4 differ considerably from 1 and 2 by considering the roles of chance, variability and historical factors in promoting coexistence (Chesson and Case 1986).

B. SPATIAL SCALE AND MECHANISMS OF COEXISTENCE

In divided habitats, such as those occupied by Splachnaceae, I have identified three levels of scale in which mechanisms of coexistence can be examined: the local, regional and continental spatial scales. The local scale is the distribution of and interaction between species on individual patches. Direct interactions, such as intra- and interspecific competition for resources, occur at this scale. There are two kinds of interaction of interest between species: those occurring on homogeneous patches (i.e., patches of similar size, composition and/or location in the environment) and those influenced by patch heterogeneity (i.e., patches differing in size, composition and/or location in the environment). The regional scale is the distribution of and interaction between species across several adjacent patches. The region encompassed is defined by the dispersal range of the species. This is approximately the area in which different local populations are able to disperse to the same patches and therefore to interact with one another. The continental scale is the distribution of species across biomes; in different areas, species are influenced by differences in climate, syntopic species and historical influences. In the context of these spatial scales, I will discuss mechanisms of coexistence pertinent to the Splachnaceae system.

Local and Regional Coexistence

Habitat and resource heterogeneity that is a permanent part of the environment can influence the relative ability of species to establish or compete for resources, and thus promote local and regional coexistence (MacArthur and Levins 1964,1967; Lawlor and Maynard Smith 1976). If the relative establishment or competitive abilities of species differ between patches as a result of the location or composition of the patch, then local and regional coexistence is possible. Local coexistence will occur when the location or composition of a patch permits several species to establish and grow in that patch. Regional coexistence will occur either as a result of local coexistence or, if species are unable to coexist in the same patches, through their ability to occupy different patches in the same region. For example, in carrion (Hanski 1976), dung (Merritt and Anderson 1977), and rocky intertidal communities (Denley and Underwood 1979) the species composition of patches at the extremes of environmental gradients differ thereby promoting regional coexistence whereas the species composition of patches in intermediate habitats overlap thereby also promoting local coexistence.

Temporal heterogeneity that is a permanent feature of the environment (e.g., seasonal differences) can also promote regional coexistence. Identical resources can become occupied by different communities of organisms because these resources become available for colonization during different seasons. Such seasonal differences have been shown to occur in carrion (Hanski and Kuusela 1980), dung (Laurence 1954; Merritt and Anderson 1977), and early successional intertidal algal communities (Paine 1977). However, in relatively persistent patches, such as unoccupied space in the rocky intertidal, patches created in different seasons eventually come to be dominated by the same long-lived organisms (Sousa 1985).

Variation in relative competitive ability through time and space can promote local and regional coexistence (Chesson 1985; Comins and Noble 1985).

Relative competitive abilities may fluctuate because of either differences in relative dispersal ability that affects the numerical advantage of species in patches or environmental variability. Processes that may cause the numerical advantage of species in patches to fluctuate include 1) priority effects, 2) the independent aggregation of propagules on apparently identical resources, and 3) an inverse relationship between competitive and dispersal ability.

First, priority effects, in which initial abundances determine which species survives in a patch, may promote local and regional coexistence by allowing an inferior competitor to establish with superior competitors in patches (Slatkin 1974; Hanski 1983). Regional coexistence can also be promoted in the absence of local coexistence if priority effects are more extreme and allow an otherwise inferior competitor to prevent the establishment in patches of otherwise superior competitors. Hanski (1976), for example, argues that the outcome of competition between carrion flies on individual carcasses depends upon the order in which fly species arrive.

Second, in a simulation study examining independent aggregation of propagules on identical resources, Atkinson and Shorrocks (1981) showed that increasing the aggregation of competitors and increasingly dividing resources can prolong the regional coexistence of competitors in a two-species system. Predictions of the model have been verified experimentally in carrion fly communities (Ives 1988). Similarly, a generalist predator may promote the coexistence of potentially competing prey items if the prey aggregate independently in patches and generalist predators forage non-randomly, congregating in high-density patches (Hanski 1981).

Finally, tradeoffs between local competitive ability and dispersal ability both within and between regions can promote coexistence of species that use similar resources (Skellam 1951; Hutchinson 1975; Hanski and Ranta 1983). Within regions, creation of new patches or local population extinctions can provide establishment opportunities for species that are relatively poor competitors in

patches but better dispersers. If regions are relatively isolated from one another, a similar process can occur between regions.

Environmental variation that causes the competitive abilities of species to fluctuate with environmental changes can promote local and regional coexistence. This may cause strong recruitment for different species at different times and allow several species to establish in the same patches or in different patches in the same region (Chesson and Warner 1981; Chesson 1983; Warner and Chesson 1985). If environmental variation causes large fluctuations in the relative competitive abilities of species in patches, local competive exclusion may occur resulting in regional but not local coexistence. However, smaller fluctuations in relative competitive ability may permit local coexistence by allowing several species to establish and grow in the same patches. Species using the same limiting resources can coexist only because they have different responses to environmental fluctuations. The relationship between environmental and recruitment variation in promoting species coexistence has been examined, for example, in fish communities (Sale 1977), forest trees (Comins and Noble 1985) and long lived perennial herbs (Grubb 1985).

Continental Coexistence

Species using similar resources may coexist on a continental scale because of historical factors or differential sensitivity to environmental heterogeneity between large geographic areas. In both mechanisms the ranges of potentially competing species overlap little and species, therefore, segregate resources spatially.

Environmental heterogeneity, such as differences between biomes, can be climatic and involve differences between assemblages of species. The interaction between climate and life history traits or physiology can promote continental coexistence by restricting the ranges of species to certain geographic areas thereby allowing other species access to similar resources in areas with an unfavorable

climate (Hokanson 1977; Noble 1978, 1980; Shuter et al. 1980). Differences between assemblages of species living in different geographic areas can promote continental coexistence because the presence or absence of other species may restrict the ranges of species that use similar resources to different geographic areas. For example, parasites well adapted to one host species, but pathogenic in others, may be responsible for low populations of the latter in areas where their ranges overlap or may even preclude such overlap (Kelsall and Prescott 1971; Broekhuizen and Kemmers 1976; Wheatley 1980; Riper et al. 1986).

Historical factors are biogeographic phenomena that have constrained the ability of species to disperse beyond their present ranges into continental areas that have suitable climates and habitats for the survival of a particular species. Because of biogeographic constraints such as mountain ranges, large bodies of water or different drainage systems, species using similar resources may not come into contact and therefore segregate resource use on a continental scale (e.g., Fausch and White 1981; Moyle 1986).

C. SUMMARY

The influence of patchy habitats on the coexistence of species can be examined at local, regional and continental spatial scales. Local and regional coexistence may result from habitat, resource or temporal heterogeneity or through fluctuations in relative competitive abilities in patches either because of the influence of dispersal variability on the numerical advantage of species in patches or environmental variability. Local coexistence will occur if one or more of these influences allow several species to establish and grow in the same patches whereas regional coexistence will occur either as a result of local coexistence or, if species are unable to coexist in the same patches, through their ability to occupy different patches in the same region. Continental coexistence may result from historical factors or differential sensitivity of species to environmental heterogeneity

between large geographic areas. Continental coexistence will occur because the ranges of species are restricted and therefore resources are spatially segregated.

D. REFERENCES

Abrams, P. 1983. The theory of limiting similarity. Annual Review of Ecology and Systematics 14:359-376.

Addicott, J. F., J. Aho, M. Antolin, D. Padilla, J. Richardson, and D. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340-346.

Andrewartha, H. G. and L. C. Birch. 1954. *The Distribution and Abundance of Animals.* The University of Chicago Press, Chicago, IL.

Atkinson, W. D., and B. Shorrocks. 1981. Competition on a divided and ephemeral resource: a simulation model. Journal of Animal Ecology 50:461-471.

Broekhuizen, S., and R. Kemmers. 1976. The stomach worm, *Graphidium strigosum* (Dujardin) Raillier and Henry, in the European hare, *Lepus europaeus* Pallas. *In* Z. Peilowski and S. Pucek eds. *Ecology and Management of European Hare Populations* pp. 157-171. Warsaw: Polish Hunting Association.

Caswell, H. 1978. Predator-mediated coexistence: a nonequilibrium model. American Naturalist 112:127-154.

Chesson, P. L. 1983. Coexistence of competitors in a stochastic environment: the storage effect. *In* H. I. Freedman and C. Strobeck, eds., *Population Biology,* pp. 188-198. Lecture Notes in Biomathematics no. 52. Springer-Verlag, Berlin, New York.

-----. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263-287.

-----. 1986. Environmental variation and the coexistence of species. *In* J. Diamond and T. Case eds., *Community Ecology*, pp. 240-256. Harper & Row, New York.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist 117:923-943.

Chesson, P. L., and T. J. Case. 1986. Overview: nonequilibrium community theories: chance, variability, history, and coexistence. *In* J. Diamond and T. Case eds., *Community Ecology*, pp. 229-239. Harper & Row, New York.

Comins, H. N., and I. R. Noble. 1985. Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. American Naturalist 126:706-723.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Denley, E. J., and A. J. Underwood. 1979. Experiments on factors influencing settlement, survival and growth of two species of barnacles in New South Wales. Journal of Experimental Marine Biology and Ecology 36:269-293.

Denno, R. F., and W. R. Cothran. 1975. Niche relationships of a guild of necrophagous flies. Annals of the Entomological Society of America 68:741-754.

Elton, C. 1949. Population interspersion: an essay on animal community patterns. Journal of Ecology 37:1-23.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for position in a Michigan stream. Canadian Journal of Fisheries and Aquatic Science 38:1220-1227.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52:107-145.

-----. 1985. Problems posed by sparse and patchily distributed species in

species-rich plant communities. *In* J. Diamond and T. Case eds., *Community Ecology,* pp. 207-228. Harper & Row; New York.

Hanski, I. 1976. Breeding experiments with carrion flies (Diptera) in natural conditions. Annales Entomologici Fennici 42:113-121.

-----. 1980. Spatial variation in the timing of the seasonal occurrence in coprophagous beetles. Oikos 34:311-321.

-----. 1981. Coexistence of competitors in patchy environments with and without predation. Oikos 37:306-312.

-----. 1983. Coexistence of competitors in patchy environment. Ecology 64:493-500.

Hanski, I., and S. Kuusela. 1980. The structure of carrion fly communities: differences in breeding seasons. Annales Zoologici Fennici 17:185-190.

Hanski, I., and E. Ranta. 1983. Coexistence in a patchy environment: three species of *Daphnia* in rock pools. Journal of Animal Ecology 52:263-279.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 33:1524-1550.

Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53:749-752.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist 95:137-145.

-----. 1975. Variations on a theme by Robert MacArthur. *In* M. L. Cody and J. M. Diamond, eds., *Ecology and Evolution of Communities* pp. 492-521. Harvard University Press, Cambridge, Mass.

Ives, A. 1988. Aggregation and the coexistence of competitors. Annales Zoologici Fennici 25:75-88.

Kareiva, P. 1986. Patchiness, dispersal, and species interactions: consequences for communities of herbivorous insects. *In* J. Diamond and T. Case eds., *Community Ecology*, pp. 192-206. Harper & Row, New York.

Kelsall, J. P., and W. Prescott. 1971. Moose and deer behaviour in snow in Fundy National Park, New Brunswick. Canadian Wildlife Service Report Series No. 15. Ottawa: Information Canada.

Koch, A. L. 1974. Coexistence resulting from an alternation of density independent and density dependent growth. Journal of Theoretical Biology 44:373-386.

Laurence, B. R. 1954. The larval inhabitants of cow pats. Journal of Animal Ecology 23:234-260.

Lawlor, L. R., and Maynard Smith. 1976. The coevolution and stability of competing species. American Naturalist 110:79-99.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J.

-----. 1979. Coexistence in a variable environment. American Naturalist 114:765-783.

MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. Proceedings of the National Academy of Science U.S.A. 51:1207-1210.

-----. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101:377-385.

Merritt R. W., and J. R. Anderson. 1977. The effects of different pasture and rangeland ecosystems on the annual dynamics of insects in cattle droppings. Hilgardia 45:31-71.

Moyle, P. B. 1986. Fish introductions into North America: patterns and ecological impact. *In* H. Mooney and J. Drake, (eds.), *Biological invasions of North America* Springer Verlag, N.Y. pp.22-43.

Nobel, P. S. 1980. Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. Ecology 61:1-7.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. Special Publications, Academy Natural Science, Philadelphia 12:245-270.

Rathcke, B. J. 1976. Competition and coexistence within a guild of herbivorous insects. Ecology 57:76-87.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. American Naturalist 111:337-359.

Shuter, B. J., J. A. MacLean, F. E. J. Fry and H. A. Regier. 1980. Stochastic simulation at temperature effects on first year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrica 38:196-218.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128-134.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. *In* S. T. A. Pickett and P. S. White eds., *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 101-152. Academic Press, Inc. Orlando, Florida.

Strong, D. R. 1982. Harmonious coexistence of hispine beetles in *Heliconia* in experimental and natural communities. Ecology 62:1039-1049.

-----. 1985. Density vagueness: abiding the variance in the demography of real populations. *In* J. Diamond and T. Case eds., *Community Ecology*, pp. 257-268. Harper & Row, New York.

van Riper, C., III, S. G. van Riper, M. L. Goff and M. Laird. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecological Monographs 56:327-344.

Volterra, F. 1926. Variations and fluctuations of the number of individuals in

animal species living together. J. Cons. Perm. Int. Ent. Mer. 3:3-51.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist 125:769-787.

Wheatley, B. P. 1980. Malaria as a possible selective factor in the speciation of macaques. Journal of Mammology 61:307-311.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. *In* S. T. A. Pickett and P. S. White eds., *The Ecology of Natural Disturbance and Patch Dynamics,* pp. 3-16. Academic Press, Inc. Orlando, Florida.

Wiens, J. A. 1977. On competition and variable environments. American Scientist 65:590-597.

Wiens, J. A., J. F. Addicott, T. J. Case and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. *In* J. Diamond and T. Case eds., *Community Ecology,* pp. 145-153. Harper & Row, New York.

II. LOCAL COEXISTENCE

A. INTRODUCTION

Patchiness is an important and inescapable feature of biological populations (Kareiva 1986). Patches are relatively small discrete units in space. Because patches can vary in size, location in the environment, internal homogeneity and discreteness (White and Pickett 1985) they can have a strong influence on the coexistence of species that use the same or similar resources (Elton 1949; Andrewartha and Birch 1954; Huffaker 1958; Hanski and Ranta 1983; Hanski 1987; Ives 1988). The influence of patchiness on coexistence can be examined at several spatial scales. The local scale is particularly important because it focuses on direct interactions among individuals on single habitat patches. Hence, observation at this scale can indicate a) the degree to which species compete for resources, b) how patch heterogeneity influences competitive coexistence, and c) potential mechanisms of coexistence operating at larger spatial scales.

I have studied species coexistence on divided resources in the mosses *Tetraplodon angustatus*, *T. mnioides*, *Splachnum ampullaceum* and *S. luteum* (F. Splachnaceae) which grow on droppings. Droppings are piles of feces, which can vary in size (10 cm^2 - 200 cm^2), composition (e.g., droppings of herbivores, omnivores, or carnivores) and location (e.g., in wet or dry habitats). Direct interactions within species of mosses (e.g., mating) and between species of mosses (e.g., competition for space) occur on individual droppings. There are two kinds of interaction between species of interest: those occurring on homogeneous patches (i.e., patches of similar size, composition and/or location in the environment) and those influenced by patch heterogeneity (i.e., patches differing in size, composition and/or location in the environment). Individuals of the same species on a single dropping will be referred to as a local population because only individuals growing together on a single dropping are able to mate with each other.

Local coexistence is potentially an important problem in communities of Splachnaceae because these mosses often coexist regionally and appear to be resource limited since they occupy all available space on droppings. Local coexistence may be promoted through mechanisms such as the differential influence of resource or habitat heterogeneity on establishment, growth and survival (MacArthur and Levins 1964, 1967; Lawlor and Maynard Smith 1976) or through variation between species in dominance in site establishment as a result of environmental fluctuations (Chesson and Warner 1981; Chesson 1983; Warner and Chesson 1985). These mechanisms will promote local coexistence if they allow several species to establish and grow in the same patches.

Among mosses, Splachnaceae are particularly amenable for studying mechanisms of coexistence since they grow quickly, occupying the entire surface of a dropping within 1-2 summers, and reproduce within 2-3 years. Therefore, interactions between species on patches can be examined over a reasonably short period of time. They have no known herbivores and no other mosses or vascular plants colonize these habitats as quickly, suggesting that interactions between species on patches are direct. Lastly, their sporophytes have brightly colored swollen apophyses (Figure II-1) and the sporophytes of each species have a strong characteristic odor (Pyysalo et al. 1978; Pyysalo et al. 1983) both of which are thought to attract flies that disperse the sticky spores to new droppings (Vitt 1981). Because the spores are dispersed by animals, it is easier to examine and compare spore dispersal in different species than it would be if spores were wind dispersed.

Life histories of the two genera differ. Each local population of *Tetraplodon* produces sporophytes for as many as five years, whereas each local population of *Splachnum* tends to produce sporophytes once. The genera also usually grow on different types of dung, related to the different habitats in which they grow. *Splachnum* are most frequently found on dung of herbivores

(primarily summer droppings of moose) [illegible] frequently in moist habitats within peatlands. *Tetraplodon* are most frequently found on dung of carnivores (wolf and coyote) and omnivores (bear), [illegible] occurs most frequently in dry habitats, on raised areas within peatlands or on the upland forest floor. However, all four species can grow on all three [illegible] types as long as the dung is in the appropriate habitat. These life history [illegible] suggest that mechanisms promoting coexistence among species within and between genera may differ.

Of the four species of Splachnaceae studied, all except *T. angustatus* produce mature sporophytes throughout the summer. *T. angustatus* produces sporophytes in the early spring, generally just after trees begin to leaf out. Sporophytes of populations of *T. mnioides*, *S. ampullaceum* or *S. luteum* on individual droppings mature synchronously. However, different local populations of these three species mature at different times throughout the summer within a region. This suggests that, with the exception of *T. angustatus*, all species likely have access to the same resources.

In this study, I first examine the frequency with which different species of Splachnaceae can co-occur on the same droppings. Secondly, I examine whether species compete for resources and whether their relative competitive abilities differ and are influenced by habitat and resource heterogeneity. Lastly, I discuss whether the degree of competitive asymmetry between species is consistent with their frequency of co-occurrence and whether it is necessary to consider mechanisms of coexistence at the regional scale in order to understand patterns of local coexistence.

Patterns of co-occurrence on droppings were studied by examining the frequency with which different species are found growing together on the same droppings in herbarium specimens. Intensity of competition for resources and the degree of competitive asymmetry between species on homogeneous resources were

examined by determining whether species produce more gametophytes when grown alone versus when grown with another species and whether species differ in relative gametophyte production when grown on moose dung in both laboratory and field studies. The influence of habitat and resource heterogeneity on the interactions between species were examined by determining the influence of dry and wet habitats on growth and on the chemical and nutrient composition of dung and by comparing the relative gametophyte production of species on moose and wolf dung.

B. METHODS

Local distribution patterns

Herbarium specimens of North American boreal and arctic species of *Splachnum* and *Tetraplodon*, including *T. angustatus*, *T. mnioides*, *S. ampullaceum*, and *S. luteum*, were examined to determine the frequency with which different species are found growing on the same droppings. See Chapter V for details of the species and the herbarium collections examined. The number of specimens in which each species grew alone and the number of specimens in which each combination of two or more species grew intermixed were tallied. Data were analyzed using G-tests of independence with Williams correction to determine whether species co-occurrence on droppings were more or less frequent than expected by chance (Sokal and Rohlf 1981).

I have assumed that the relative frequency of species and species combinations in the herbarium collections reflects their relative frequencies in the field. There is no evidence that intensity of collection varied geographically and there is no reason to suspect that mixed species combinations were collected any more or less frequently than single species populations (Chapter V).

Field Growth Experiment

A 10 (each species alone and all 2 species mixtures) x 2 (habitats) x 3 (densities of spores) factorial field experiment examining gametophyte production on moose dung was conducted to determine 1) the intensity of competition among species for resources, 2) whether species differ in their relative competitive abilities, and 3) if differences in competitive ability are influenced by heterogeneity among habitats. Because dung in both wet and dry treatments disappeared, there were too few replicates to examine possible effects of proportion of spores in each two species mixture. This experiment was conducted in an isolated peatland at Heatherdown, 80 km west of Edmonton, Alberta (53° 40' N, 114° 20' W). No natural populations of species of Splachnaceae were found in this peatland, therefore, dung set out in the field should not have been colonized by natural populations of Splachnaceae. The experiment used a randomized block design with five sites (blocks) consisting of a 'wet' low area and a 'dry' raised area (Table II-1). Within each block, dung of approximately the same size (20 cm^2) was placed one meter apart in a 5 x 40 rectangular array; the sequence of replicates was chosen randomly. Dung used in this experiment was gathered from captive moose kept in a common enclosure in the late winter of 1985, ensuring that droppings were uncolonized by Splachnaceae. Droppings of different moose were intermixed when gathered. Dung was inoculated with spores in the field in early June 1985.

For each species, the number of spores used to inoculate dung was determined by serially diluting a suspension of spores with water. Spores were first added to water creating the suspension. The number of spores/ml in the suspension was then estimated by taking the average of 10 estimates using a Petroff-Hausser bacteria counter. A portion of the suspension was then serially diluted until the solution contained the correct number of spores/ml. This suspension was placed into vials labeled with the species of spores in suspension

and the density of spores/ml.

Each patch of dung was examined in August of 1985, and in April, May and August of 1986. The area of dung covered by gametophytes and the relative abundance of species on each patch of dung were estimated by determining the species of gametophyte located under each intersection point on a 25 cm^2 grid divided into 1 cm^2 sections.

Two analyses of variance procedures were applied; both were of unbalanced design with fixed effects using rank transformed data (Conover and Iman 1981). Figures derived from these analyses show the median values for each treatment and the 75% quartile. In the first analysis, I determined whether species competed for space on dung by comparing the gametophyte production of each species when grown alone or in two species mixtures. In the second analysis, the interaction between species on dung was examined by comparing gametophyte production between species in each two species mixture.

Laboratory Growth Experiment

Relative growth rates and gametophyte production of the moss species on moose dung were examined in single and two-species mixtures under controlled laboratory conditions to determine whether species differ in their relative growth rates, intensity of competition for resources and relative competitive ability and if relative competitive ability is influence by moisture availability. In this experiment, moose dung collected as described previously was placed in 62 cm^2 petri dishes and inoculated with 50,000 spores of *T. angustatus*, *T. mnioides*, *S. ampullaceum* or *S. luteum*, or with 50,000 spores of each of two of those species. Five replicates of each treatment were then randomly assigned to a 'dry' and a 'wet' treatment. In the wet treatment petri dishes containing the dung were placed in plastic tubs and watered every three days. The petri dishes were always sitting in but not covered by water. The dry treatment was identical, except that every

two weeks no water was added for a one week interval. The one week interval without water caused the dung and the tubs to dry.

A repeated measures analysis of variance was used to examine differences in the relative growth rates of the mosses in both dry and wet treatments. Data were rank transformed and a one-way ANOVA was used to determine whether species competed for space on dung by comparing the relative gametophyte production of each species in the single species treatment with the relative gametophyte production of each species when grown in two-species mixtures. A one-was ANOVA using ranks is equivalent to a Kruskal-Wallace test (Conover and Iman 1981). A one-way ANOVA procedure using ranks was also used to examine the interaction between species on droppings by comparing the relative gametophyte production between species in each two-species mixture.

Growth on Carnivore Dung

The interactions between moss species on wolf dung were examined in a controlled laboratory experiment in 1985 and 1986 to determine the influence of resource heterogeneity (i.e., type of dung) on the relative gametophyte production between species. The design and analysis of this experiment was the same as in the laboratory experiment on herbivore dung with the exception that the dung used was collected from captive wolves fed a diet of white-tailed deer.

Chemical Composition of Dung

The influence of habitat heterogeneity on resource variability was studied by examining possible differences between the chemical composition of dung located in dry versus wet habitats. This experiment was conducted at Ft. Assiniboine by placing 5 patches of dung (collected as described previously) in a wet habitat and 5 patches of dung in an adjacent dry habitat in the spring of 1985. This dung was then left in the field for one year. In the spring of 1986, 2 samples

were taken from each patch and analyzed for Ca, Mg, Na, K, Al, Ti, Cu, Fe, Mn, Zn, P, S, total N and ash content. The concentrations of these chemicals were determined with an inductively coupled argon plasma spectrophotometer by Dr. Steve Zoltai at the Alberta Forestry Research Service. Concentrations of the various elements, total N and ash were compared between dung in dry and wet habitats using *t* tests.

C. RESULTS

Local Distribution Patterns

Examination of herbarium specimens revealed that *T. angustatus*, *T. mnioides*, *S. ampullaceum* and *S. luteum* did co-occur on the same droppings although they did so infrequently. The frequencies of co-occurrences between all pairs of species were lower than expected by chance and frequencies of co-occurrence between genera were lower than those within genera (Table II-2).

Field Experiment

1. Competition for Space

The results of the field experiment indicated that species competed for space (Table II-3). Significant species effects occurred as a result of each species producing more gametophytes, in both dry and wet habitats combined, when grown alone than when grown in mixture with another species (Figures II-2 - II-5).

Neither initial density of spores nor habitat had a consistent influence on comparisons of gametophyte production (Table II-3). Increasing density of spores resulted in an increase in gametophyte production only in comparisons of *S. luteum* growth alone versus its growth with other species (Figure II-5). Both *T. angustatus* (Figure II-2) and *T. mnioides* (Figure II-3) produced more

gametophytes in dry habitats than in wet habitats with the opposite true for *S. ampullaceum* (Figure II-4). There was no influence of habitat on *S. luteum* gametophyte production (Figure II-5).

Species by habitat or density interactions also did not have a consistent influence on comparisons of gametophyte production (Table II-3). Species by habitat interactions were significant for comparisons of gametophyte production between *T. angustatus* and *T. mnioides* growth alone versus their growth with *S. ampullaceum*, and *S. ampullaceum* growth alone versus its growth with *T. angustatus*. In the first two comparisons, *S. ampullaceum* gametophyte production was so low in dry habitats that its presence did not reduce the gametophyte production of either *Tetraplodon* species (Figures II-2 and II-3) and in the third comparison, *T. angustatus* growth was so low in wet habitats that its presence did not reduce the gametophyte production of *S. ampullaceum* (Figure II-4). Species by density interactions were significant for comparisons of gametophyte production between *T. angustatus* growth alone versus its growth with *S. ampullaceum* and *S. luteum* and *S. ampullaceum* growth alone versus their growth with *S. luteum*. In all cases density effects were stronger for species grown alone.

2. Competition Between Species

There was no consistent effect of species, habitat or initial density of spores on comparisons of gametophyte production between species grown in mixture (Table II-4). Species and habitat effects were significant only in the comparison of gametophyte production between *T. angustatus* and *T. mnioides*. In this comparison, species effects were significant because *T. mnioides* produced more gametophytes than *T. angustatus* in both dry and wet habitats and habitat effects were significant because species effects were greater in wet than in dry habitats (Figure II-6). There was no effect of density on gametophyte production between species in any of the two species mixtures.

All comparisons between species of different genera showed significant species by habitat interactions and none of the comparisons showed significant species by density interactions (Table II-4). In dry habitats, both species of *Tetraplodon* when grown in combination with either species of *Splachnum* produced more gametophytes (Figures II-7 - II-10). In wet habitats, the opposite was true: both species of *Splachnum* when grown in combination with either species of *Tetraplodon* produced more gametophytes (Figures II-7 - II-10). There was no significant interaction between habitat and species on interactions either between species of *Tetraplodon* (Figure II-6) or species of *Splachnum* (Figure II-11).

Laboratory Experiment: Growth on Moose Dung

1. Competition for Space

The results of the laboratory experiment indicated that species did compete for space on droppings (Table II-5). In all but two comparisons, gametophyte production between species grown alone was significantly greater than gametophyte production of species grown in mixture with another species (Table II-6). Exceptions were: dry treatment - *S. luteum* alone vs. *S. luteum* in mixture with *S. ampullaceum*; wet treatment - *S. ampullaceum* alone vs. *S. ampullaceum* in mixture with *T. mnioides*.

2. Competition Between Species

Laboratory results also indicated that relative growth rates differed under both dry and wet conditions (Table II-7) and these differences were expressed between species when grown in mixture (Table II-8). Both species of *Splachnum* grew more quickly than did the two species of *Tetraplodon* in the wet treatment (Figure II-13) with *S. luteum* growing relatively more quickly than all other species in the dry treatment (Figure II-12). In the dry and wet treatment, *S. luteum* produced significantly more gametophytes than all other species when grown with them. In the dry treatment, *T. mnioides* produced significantly more

gametophytes than *T. angustatus* whereas in the wet treatment these species did not differ in gametophyte production. There were no significant differences between the number of gametophytes produced between *S. ampullaceum* and any of the species with which it was grown in the dry treatment whereas in the wet treatment *S. ampullaceum* produced significantly more gametophyte than *T. angustatus* and *T. mnioides* when grown with these species. (Figures II-14 (Dry) and II-15 (Wet)).

Laboratory Experiment: Growth on Wolf Dung

In both wet and dry treatments comparing gametophyte production between species on wolf dung there were no clear patterns (Table II-9). All species produced apparently healthy gametophytes and there was no consistent pattern of differences of gametophyte production between species in either dry or wet treatments (Figures II-16 (Dry) and II-17 (Wet)).

Chemical Composition of Moose Dung in Dry and Wet Habitats

The chemical composition of moose dung differed between dry and wet habitats. The % total nitrogen, % ash and the concentrations of all elements examined, with the exception of aluminum and sulfur, were significantly greater (less of sodium) in moose dung located for one year in dry versus wet habitats (Table II-10).

D. DISCUSSION

Patterns of distribution and interaction between species of Splachnaceae at the local spatial scale indicated that different moss species co-occur infrequently on the same droppings. In the field and laboratory studies, species appeared to compete for some resource, possibly space, and the relative competitive abilities of species differed and were influenced by habitat. However, while the influence of

habitat on relative competitive ability may partially explain the infrequency of co-occurrences between species of different genera, this does not appear to be true for congeneric species since their relative competitive abilities were fairly symmetrical and they did not eliminate each other from dung. This infrequency of local coexistence, intensity of competition yet relative symmetry of competitive abilities suggests that patterns of local distribution and long-term coexistence likely result from mechanisms operating at larger spatial scales.

Because the distributions of species overlap throughout north temperate and boreal North America (Chapter V), low frequencies of co-occurrence in herbarium specimens are not a reflection of large scale spatial segregation between species. They more likely reflect either segregation at smaller spatial scales such as resource or habitat segregation or the influence of environmental or dispersal variability on the relative establishment ability and gametophyte production of different species.

Both field and laboratory growth experiments indicated that species compete for some resource, possibly space on dung, and they differ in relative gametophyte production. A species grown alone on dung produced more gametophytes than when grown in the presence of another species and neither the habitat in which dung was located, the initial density of spores, nor the interactions between factors appeared to influence this effect in a consistent manner. This suggests that all species can successfully establish and grow under both wet and dry conditions and a species will likely produce fewer gametophytes if spores of another species are also dispersed to the same fresh droppings. However, whereas species of different genera tended to eliminate each other from dung, congeneric species did not since they appeared to have relatively symmetrical competitive abilities.

The ability of species of different genera to eliminate each other from dung appeared to be strongly habitat dependent. In comparisons of gametophyte

production between species of different genera, there were significant species by habitat interactions. When species of different genera were grown together on the same droppings in dry habitats, both species of *Tetraplodon* produced more gametophytes and in many cases prohibited the growth of either species of *Splachnum* with the reverse being true in wet habitats. No such species by habitat interaction occurred in comparisons of gametophyte production between congeneric species. Also, neither initial density of spores nor interactions between density and other factors influenced interactions between any of the species. These results indicate that, of the factors I tested, the influence of habitat was the most important factor affecting gametophyte production between species of different genera.

It is not clear how habitat influences growth differences between species of the two genera. The results of the laboratory growth study indicated that species of *Splachnum* grew more quickly than species of *Tetraplodon*, and this appeared to be related to differences in the longevity of droppings in dry versus wet habitats. Droppings located in wet habitats were overgrown by the surrounding vegetation more quickly than were droppings located in dry habitats (2-3 years versus > 3 years) (Unpubl.). That species of *Splachnum* grew more quickly and thereby occupied space more quickly than species of *Tetraplodon* under wet conditions is, therefore, not surprising considering that they grow on a relatively more ephemeral resource. However, the growth advantage that species of *Tetraplodon* had over species of *Splachnum* in dry habitats in the field growth experiment was not evident under dry laboratory conditions. This difference suggests that laboratory conditions may not have duplicated field conditions in extent of dryness or in the degree to which habitat may affect resource variability through the differential influence of leaching or absorption on the chemistry of dung in dry versus wet habitats.

In the laboratory experiment, the chemistry of dung was unlikely to be influenced by leaching or absorption in either treatment since the system was closed and only water was added. However, under field conditions, dung left one year in dry habitats had more nutrients than dung left for one year in wet habitats. Conditions in wet habitats may increase rates of decomposition and leaching. The direct influence of differences in dung chemistry on growth was not examined; however, bryophytes generally are very sensitive to the chemical composition of the substrates on which they grow (Brown 1982).

The habitat in which a dropping is located may, therefore, partially explain how local coexistence can occur between species of different genera. Droppings in dry and wet habitats should provided relatively exclusive sites from which species of the two genera may both be able to establish on droppings located in intermediate habitats. A similar process appears to be important in promoting local coexistence, for example, in carrion fly communities (Hanski 1976), dung fly communities (Merritt and Anderson 1977), and rocky intertidal communities (Denley and Underwood 1979). In these communities, the species composition of patches at the extremes of environmental gradients differ whereas the species composition of patches in intermediate habitats overlap.

However, this scenario is inconsistent for observed frequencies of local coexistence between species of different genera. On the one hand, there is no reason to expect that fewer droppings occur in intermediate habitats than in either dry or wet habitats and therefore there should be numerous droppings that are suitable for the establishment and growth of species of both genera. Yet, on the other hand, species of the two genera rarely co-occur on the same droppings. This suggests that habitat alone cannot explain the local distribution of species but rather the influence of resource heterogeneity (i.e., type of dung), the influence of environmental variability on local establishment and growth or mechanisms operating at larger spatial scales such as habitat restricted dispersal of

spores (Chapter III) may influence frequencies of co-occurrence.

The influence of dung of herbivores versus dung of carnivores on the the local establishment and growth of species and therefore on the local distribution of species of different genera is, however, unclear. In the field, I have observed that species of *Tetraplodon* tend to grow more frequently on droppings of carnivores and species of *Splachnum* tend to grow more frequently on droppings of herbivores. If local coexistence is influenced by the type of dung such that different types of dung accentuate differences in relative competitive ability and therefore the probability of local competitive exclusion, then this may help to explain the infrequency of local co-occurrence between species of different genera. However, judging by gametophyte production and appearance of gametophytes in the laboratory growth experiment on wolf dung, it appeared that wolf dung was as suitable a resource as moose dung for all species of Splachnaceae. This difference between field and laboratory observations may be a reflection of the habitats in which herbivores and carnivores spend much of their time, smaller droppings of carnivores being scarcer in wet habitats because they are more rapidly overgrown than the larger droppings of herbivores or as discussed previously, laboratory conditions may not have duplicated field conditions.

There is also an inconsistency between expected and observed frequencies of local coexistence among congeneric species. Although congeneric species differed in their relative gametophyte production and this difference appeared to reflect differences in their growth rates, their competitive abilities were relatively symmetrical in both dry and wet habitats and as a consequence they did not eliminate each other from dung. Therefore, their expected frequency of co-occurrence on droppings should be high. They, however, co-occur infrequently. Again, this suggests that either the influence of environmental variability on local establishment and growth or mechanisms operating at larger spatial scales such as dispersal variability influence frequencies of co-occurrence.

The possibility that local patterns of distribution may have been influenced by environmental variability resulting in different species being dominant in site establishment under different combinations of environmental condition has not been examined in this study. This process may cause strong recruitment for different species at different times and allow several species to establish either on the same or on different patches (Chesson and Warner 1981; Chesson 1983; Warner and Chesson 1985). If environmental variation causes large fluctuations in the relative competitive abilities of species in patches, local competitive exclusion may occur and as a result local coexistence should be infrequent. However, smaller fluctuations in relative competitive ability may permit local coexistence by allowing several species to establish and grow in the same patches. The relationship between environmental and recruitment variation in promoting species coexistence has been established, for example, in fish communities (Sale 1977), forest trees (Comins and Noble 1985; and long lived perennial herbs (Grubb 1985).

The species examined in this study are widely distributed across North America (Chapter IV); suggesting that they can establish and grow under a wide variety of environmental conditions. However, despite this apparent tolerance, local environmental factors such as moisture have been shown to influence the relative establishment and growth of different species. Also, the difference between field and laboratory growth results suggest that relative establishment and growth ability may depend critically on environmental conditions. To what extent local variation in environmental variables such as moisture, temperature, sunlight or dung chemistry influences establishment, relative growth abilities and local coexistence of species of Splachnaceae on droppings requires further study.

Summary

Overall the local interactions between species of Splachnaceae and the influence of habitat and resource heterogeneity on those interactions do not appear

to explain patterns of local distribution. First, although different species of Splachnaceae can coexist locally, they appear to do so infrequently. Second, species appeared to compete intensely for resources and their relative competitive abilities differed and were influenced by habitat and, possibly resource heterogeneity. Third, the degree of competitive asymmetry between species of different genera was strongly influenced by habitat and may be large enough to explain the infrequency of local coexistence between species of different genera in dry and wet habitats. However, overall, there is an inconsistency between expected and observed frequencies of local coexistence between species of different genera because local coexistence should occur frequently on droppings in intermediate habitats. Fourth, since the relative competitive abilities of congeneric species were fairly symmetrical in both dry and wet habitats and as a consequence they did not exclude each other from dung, their frequency of local coexistence appears to be lower than expected. This infrequency of local coexistence, intensity of competition yet relative symmetry of competitive abilities suggests that patterns of local distribution and long-term coexistence likely result from mechanisms operating at larger spatial scales.

Table II-1. Experimental design of field growth experiment in which 10 species treatments were each replicated at 3 density treatments in both dry and wet habitat treatments.

Species	Density of Spores	Habitat
T. angustatus alone	100,000	Dry
T. mnioides alone	10,000	Wet
S. ampullaceum alone	1,000	
S. luteum alone		
T. angustatus + *T. mnioides*		
T. angustatus + *S. ampullaceum*		
T. angustatus + *S. luteum*		
T. mnioides + *S. ampullaceum*		
T. mnioides + *S. luteum*		
S. ampullaceum + *S. luteum*		

Table II-2 Number of herbaria specimens of *T. angustatus*, *T. mnioides*, *S. ampullaceum*, *S. luteum* alone and in mixture examined. The percentage of each species found growing in each species combination is also presented. For example, of 741 specimens of *T. angustatus* 6.75 % were growing in combination with *T. mnioides* and of 2,221 specimens of *T. mnioides* 2.25 % were growing in combination with *T. angustatus*. The probability that the number of specimens having species growing together in each species combination was fewer than expected by chance has been estimated using G-tests of independence with Williams correction.

Splachnaceae Species	Number of Specimens	% of Specimens Growing in the Given Species Combination	G-test Probability
T. angustatus	741		
T. mnioides	2,221		
S. ampullaceum	401		
S. luteum	201		
T. angustatus + *T. mnioides*	50	6.75 + 2.25	*
T. angustatus + *S. ampullaceum*	-	-	*
T. angustatus + *S. luteum*	-	-	*
T. mnioides + *S. ampullaceum*	1	0.05 + 0.25	*
T. mnioides + *S. luteum*	1	0.50 + 0.25	*
S. ampullaceum + *S. luteum*	5	1.25 + 2.49	*

* $P < .001$.

Table II-3. ANOVA results comparing gametophyte production of *T. angustatus*, *T.mnioides*, *S. ampullaceum* and *S. luteum* alone versus their gametophyte production when grown with each other (Species effects) at three different densities in dry and wet habitats on moose dung in the field growth experiment.

		T. angustatus	*T. mnioides*	*S. ampullaceum*	*S. luteum*
T. angustatus alone	Species		***	***	**
	Density		**	NS	NS
	Habitat		*	***	*
	Species x Habitat		NS	**	NS
	Species x Density		NS	*	*
T. mnioides alone	Species	*		***	*
	Density	*		NS	NS
	Habitat	NS		***	*
	Species x Habitat	NS		***	NS
	Species x Density	NS		NS	NS
S. ampullaceum alone	Species	***	**		***
	Density	NS	NS		NS
	Habitat	***	***		*
	Species x Habitat	*	NS		NS
	Species x Density	NS	NS		*

	Species	**	***	**
	Density	***	**	*
S. luteum	Habitat	NS	NS	NS
alone	Species x Habitat	NS	NS	NS
	Species x Density	NS	NS	NS

* P < .05, ** P < .01, *** P < .001, NS = not significant.

Table II-4. ANOVA results comparing gametophyte production between *T. angustatus*, *T.mnioides*, *S. ampullaceum* and *S. luteum* when grown in two species mixtures (Species effects) at three different densities in dry and wet habitats on moose dung in the field growth experiment.

		T. mnioides	*S. ampullaceum*	*S. luteum*
	Species	**	NS	NS
	Density	NS	NS	NS
T. angustatus	Habitat	*	NS	NS
	Species x Habitat	NS	***	*
	Species x Density	NS	NS	NS
	Species		NS	NS
	Density		NS	NS
T. mnioides	Habitat		NS	NS
	Species x Habitat		***	**
	Species x Density		NS	NS
	Species			NS
	Density			NS
S. ampullaceum	Habitat			NS
	Species x Habitat			NS
	Species x Density			NS

* P < .05, ** P < .01, *** P < .001, NS = not significant.

Table II-5. ANOVA results comparing gametophyte production of *T. angustatus*, *T. mnioides*, *S. ampullaceum* and *S. luteum* alone versus their gametophyte production when grown with each other on moose dung in the laboratory growth experiment.

	T. angustatus		*T. mnioides*		*S. ampullaceum*		*S. luteum*	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
T. angustatus alone			***	**	***	**	**	**
mnioides alone	**	***			**	**	***	***
S. ampullaceum alone	**	*	**	NS			***	***
S. luteum alone	***	***	***	**	NS	***		

* P < .05, ** P < .01, *** P < .001, NS = not significant.

Table II-6 Comparison of area of growth of *T. angustatus*, *T. mnioides*, *S. ampullaceum*, *S. luteum* alone and when in mixture with each other in both dry and wet treatment of the laboratory growth experiment.

Species	With:	Cover as a % of Cover When Alone		Probability	
		Dry	Wet	Dry	Wet
T. angustatus	*T. mnioides*	8	58	***	**
	S. ampullaceum	39	4	***	***
	S. luteum	11	0	**	***
T. mnioides	*T. angustatus*	92	62	**	***
	S. ampullaceum	51	0	**	***
	S. luteum	20	3	***	***
S. ampullaceum	*T. angustatus*	61	96	**	*
	T. mnioides	34	100	**	NS
	S. luteum	0	26	***	***
S. luteum	*T. angustatus*	89	100	**	NS
	T. mnioides	80	97	***	*
	S. ampullaceum	80	74	NS	*

* P < .05, ** P < .01, *** P < .001, NS = not significant.

Table II-7. Repeated measures analysis of variance comparing the area occupied by gametophyte in single species dry and wet treatments in the laboratory growth experiment. The upper part of each ANOVA table contains the test for the grand mean and a test of the equality of means between species. The lower part of each table contains a test of the change in area covered by gametophyte for each species (R), and the equality of means between the species (RG).

Source	Degrees of Freedom	Sum of Squares	Mean Square	F value	Probability
A) Dry					
Mean	1	99,220.8	99,220.8	709.7	***
Species	3	6,871.3	2,290.4	16.4	***
Error	15	2,097.1	139.8		
R	3	44,385.4	14,795.1	231.2	***
RG	9	5,410.2	601.1	9.4	***
Error	45	2,888.0	64.0		
B) Wet					
Mean	1	122,786.2	122,786.2	596.1	***
Species	3	8,034.2	2,678.1	13.0	***
Error	16	3,295.8	206.0		
R	3	32,447.0	10,815.7	96.3	***
RG	9	2,659.4	295.5	2.6	***
Error	48	5,389.0	112.3		

*** $P < .001$.

Table II-8. ANOVA results comparing gametophyte production between *T. angustatus*, *T.mnioides*, *S. ampullaceum* and *S. luteum* when grown in two species mixtures with each other on moose dung in the laboratory growth experiment.

	T. mnioides		*S. ampullaceum*		*S. luteum*	
	Dry	Wet	Dry	Wet	Dry	Wet
T. angustatus	**	NS	NS	***	***	***
T. mnioides			NS	***	**	**
S. ampullaceum					*	**

* P < .05, ** P < .01, *** P < .001, NS = not significant.

Table II-9. ANOVA results comparing gametophyte production between *T. angustatus*, *T.mnioides*, *S. ampullaceum* and *S. luteum* when grown in two species mixtures with each other on wolf dung in the laboratory growth experiment.

	T. mnioides		*S. ampullaceum*		*S. luteum*	
	Dry	Wet	Dry	Wet	Dry	Wet
T. angustatus	NS	**	NS	NS	***	NS
T. mnioides			**	*	NS	***
S. ampullaceum					NS	*

* P < .05, ** P < .01, *** P < .001, NS = not significant.

Table II-10. Comparison of Chemical composition of dung in dry and wet habitats. Results are mg/kg of material.

Element/Compound	Dry Habitat: Mean	Dry Habitat: Standard Error	Wet Habitat: Mean	Wet Habitat: Standard Error	t	Probability
Total Nitrogen (%)	3.48	0.02	2.56	0.04	18.85	***
Ash (%)	16.67	0.37	12.15	0.57	6.66	***
Aluminum	664.80	14.58	646.28	9.73	1.06	NS
Calcium	25861.84	519.32	16315.39	1210.64	7.25	***
Copper	4.50	0.06	4.26	0.09	2.20	*
Iron	1357.24	23.74	1196.25	40.25	3.44	**
Magnesium	5215.62	179.97	1442.37	186.38	14.56	***
Manganese	259.05	4.92	188.28	20.54	3.35	**
Phosphorus	11453.49	257.52	4772.90	492.17	12.03	***
Potassium	1234.32	20.01	550.20	46.44	13.53	***
Sodium	85.05	3.65	95.31	3.21	-2.11	*
Sulfur	1585.84	30.67	1572.42	50.46	0.23	NS
Titanium	11.19	0.28	9.82	0.29	3.39	**
Zinc	392.27	7.35	357.50	5.89	3.69	**

* $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

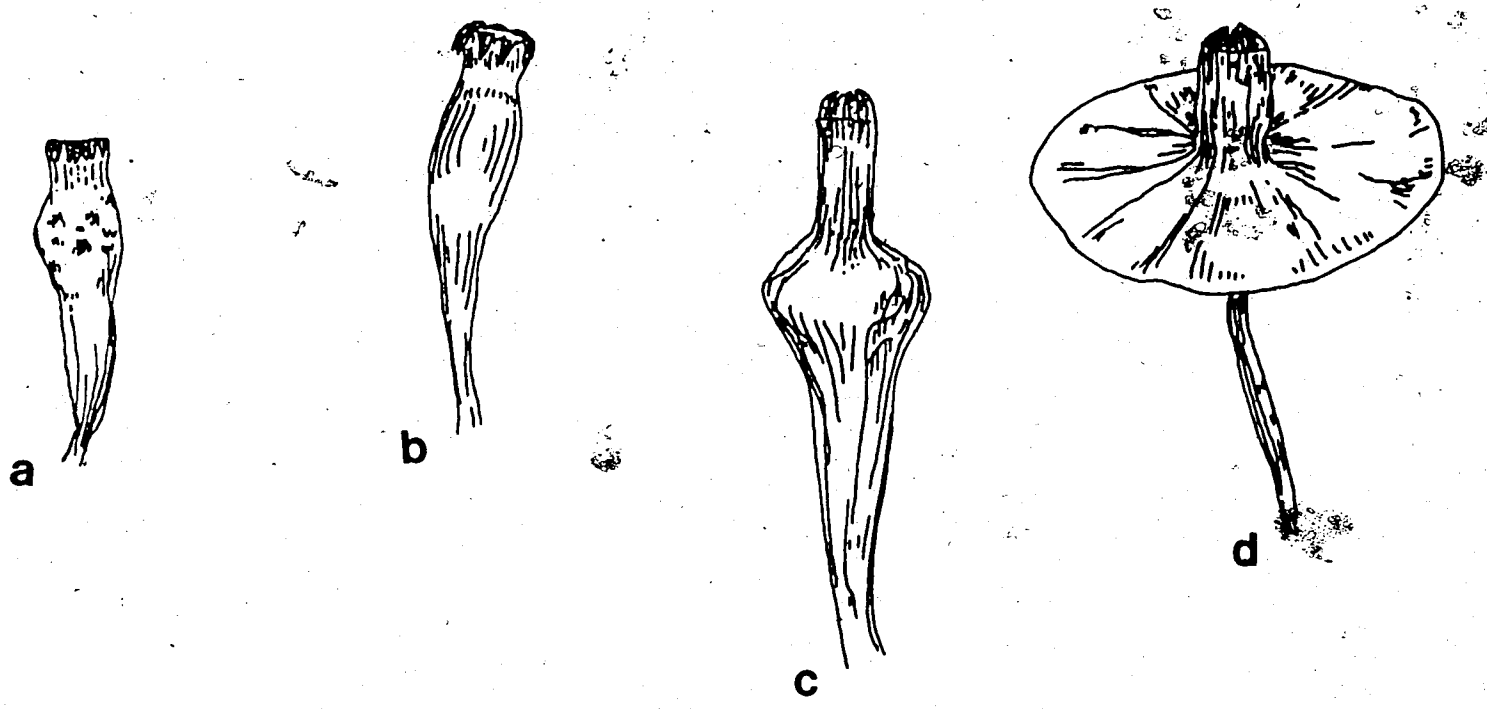

Figure II-1. Morphology of the apophysis of a) *T. angustatus* (x 17), b) *T. mniοides* (x 19), c) *S. ampullaceum* (x16), and d) *S. luteum* (x15).

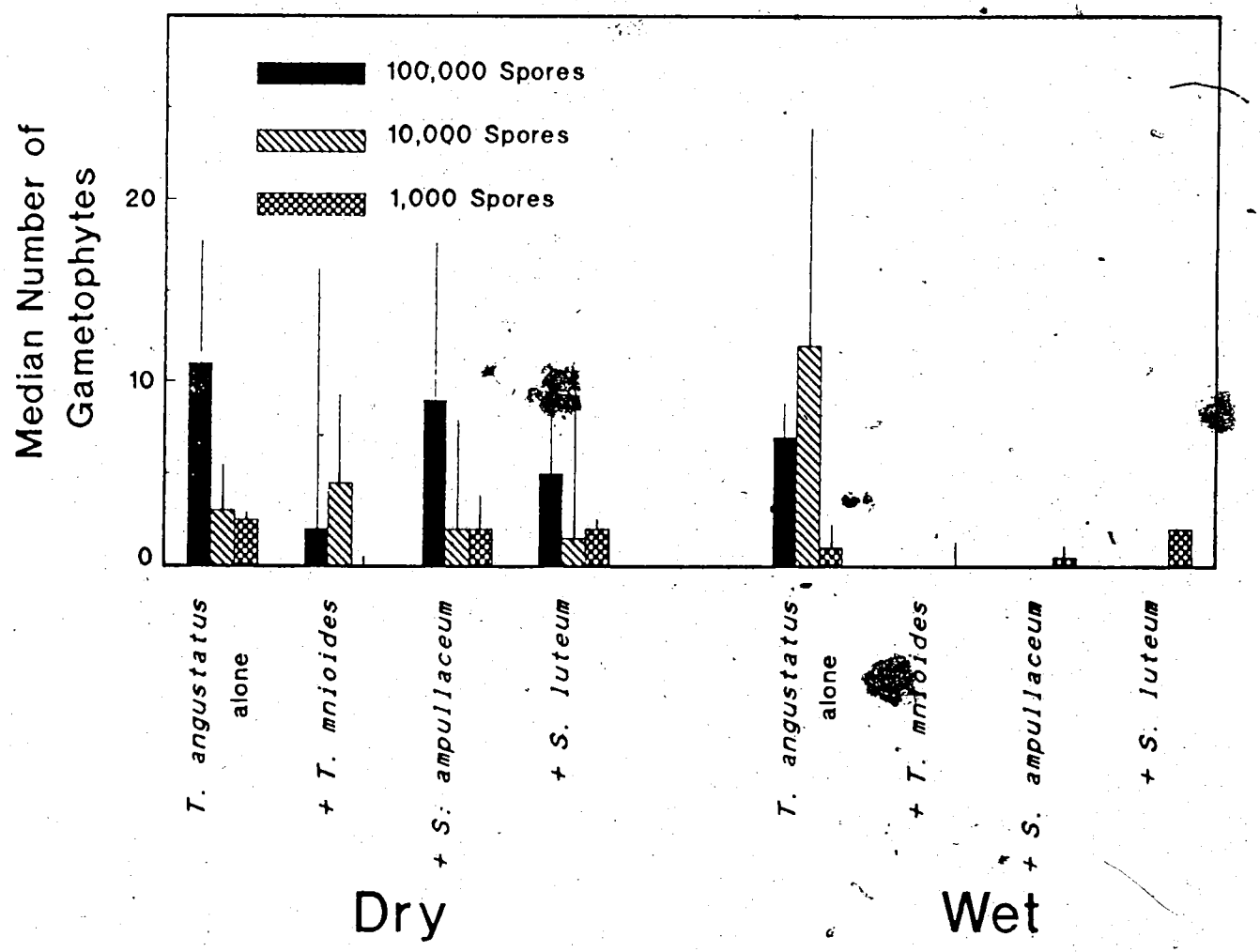

Figure II-2. Median gametophyte production in dry and wet habitats in the field growth experiment of *T. angustatus* alone and *T. angustatus* in mixure with *T. mnioides*, *S. ampullaceum* and *S. luteum*.

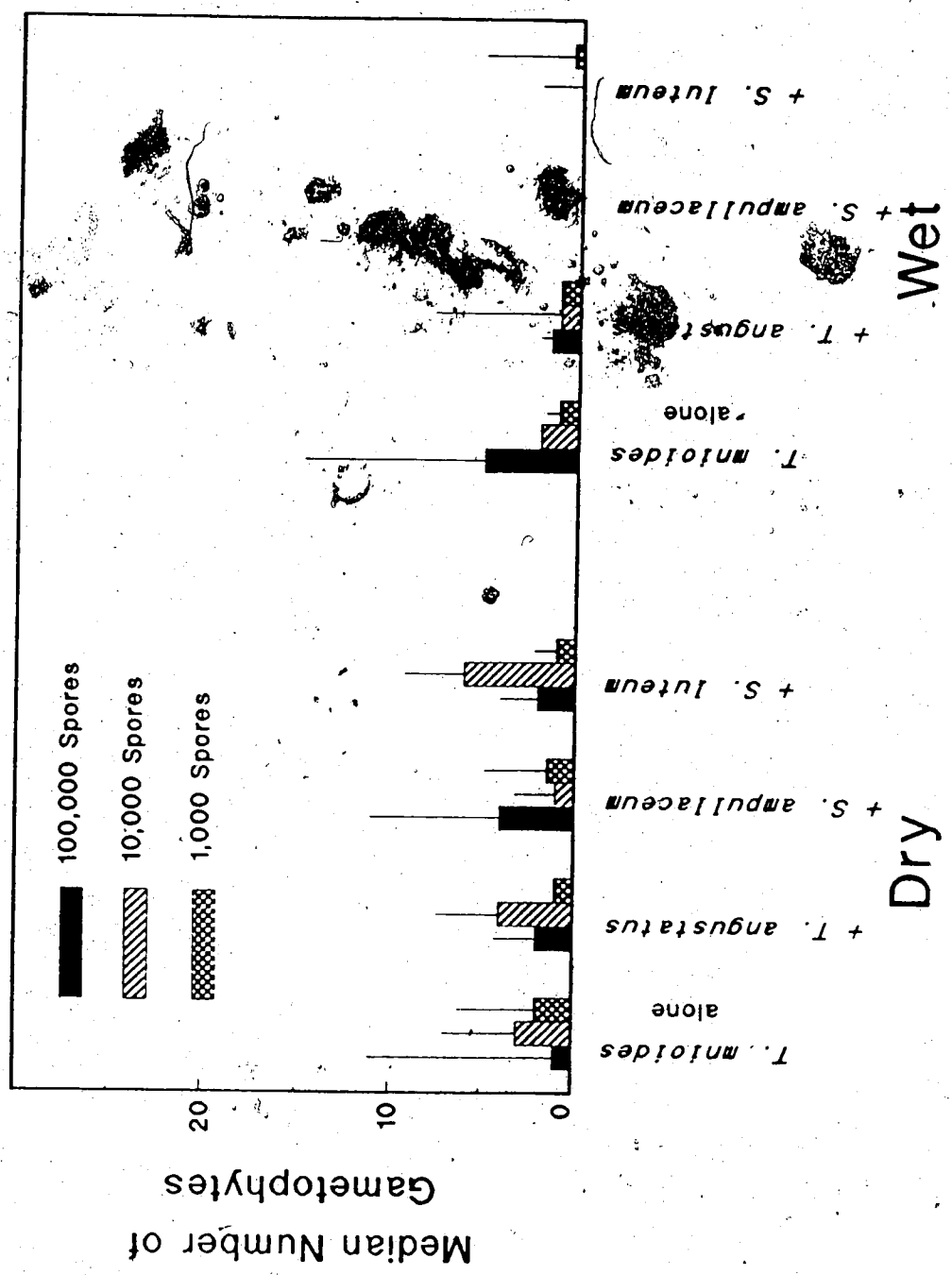

Figure II-3. Median gametophyte production in dry and wet habitats in the field growth experiment of *T. mnioides* alone and *T. mnioides* in mixture with *T. angustatus*, *S. ampullaceum* and *S. luteum*.

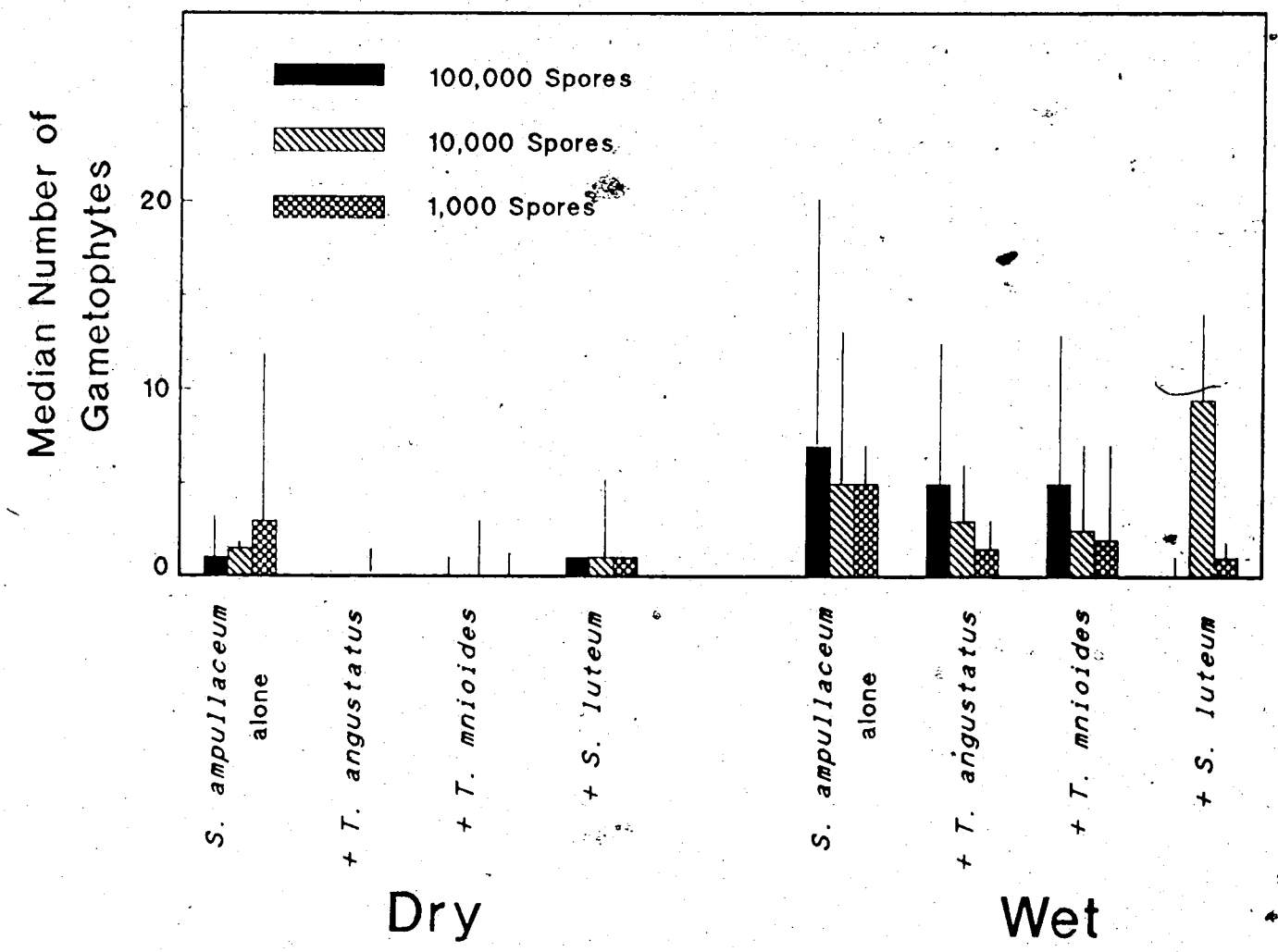

Figure II-4. Median gametophyte production in dry and wet habitats in the field growth experiment of *S. ampullaceum* alone and *S. ampullaceum* in mixture with *T. angustatus*, *T. mnioides* and *S. luteum*.

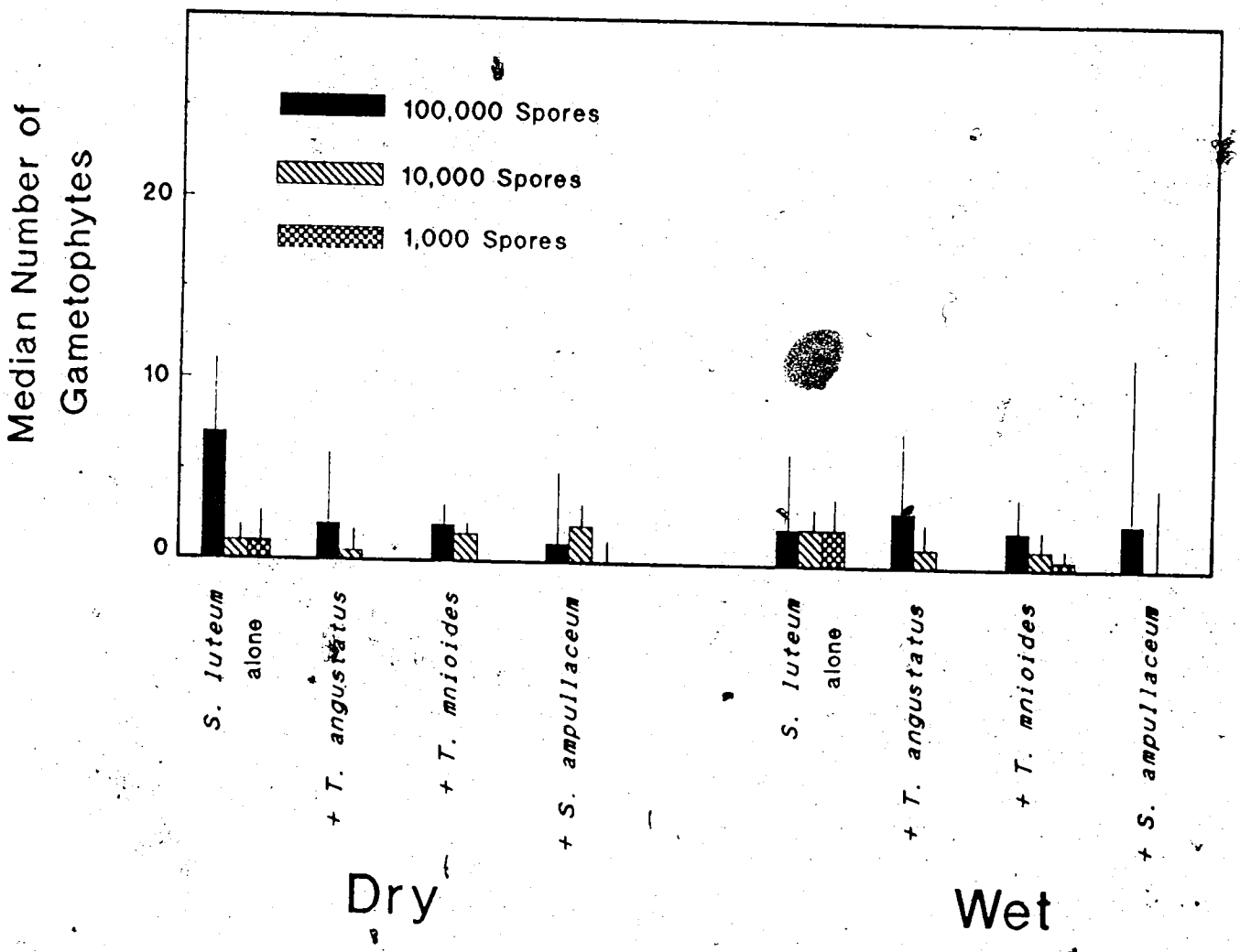

Figure II-5. Median gametophyte production in dry and wet habitats in the field growth experiment of *S. luteum* alone and *S. luteum* in mixture with *T. angustatus*, *T. mnioides* and *S. ampullaceum*.

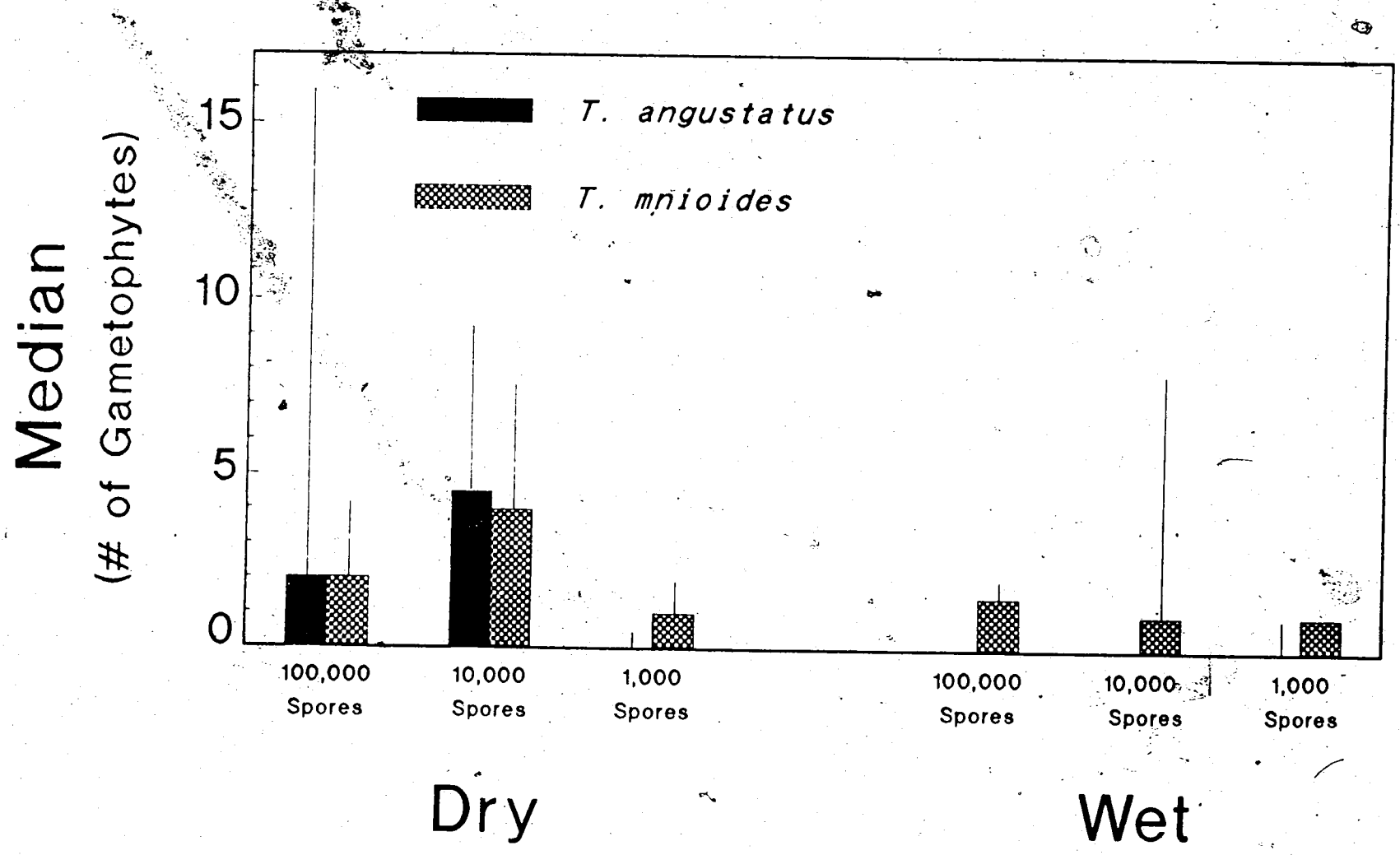

Figure II-6. Median gametophyte production in dry and wet habitats in the field growth experiment of two species mixtures of *T. angustatus* and *T. mnioides*.

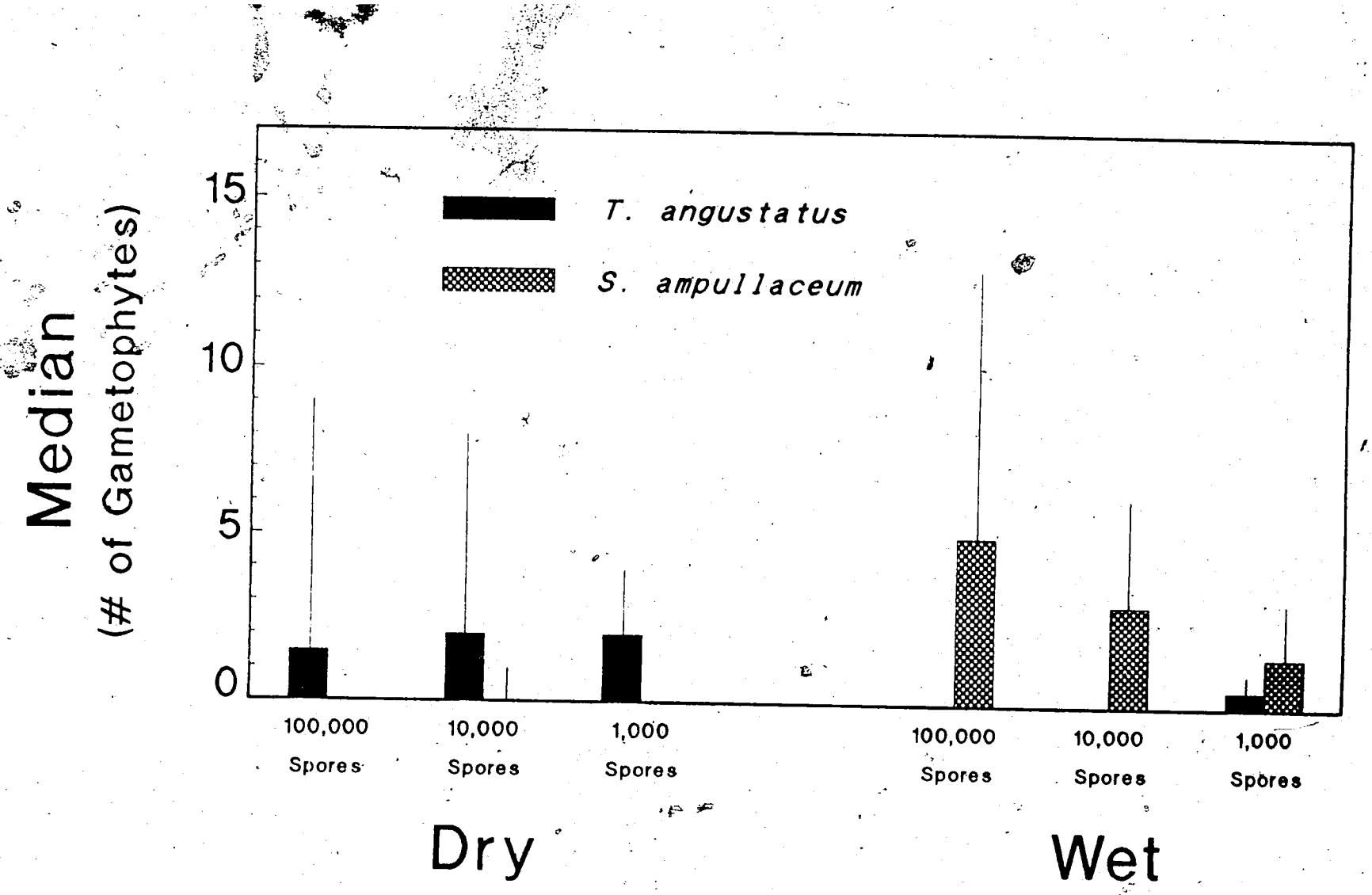

Figure II-7. Median gametophyte production in dry and wet habitats in the field growth experiment of two species mixtures of *T. angustatus* and *S. ampullaceum*.

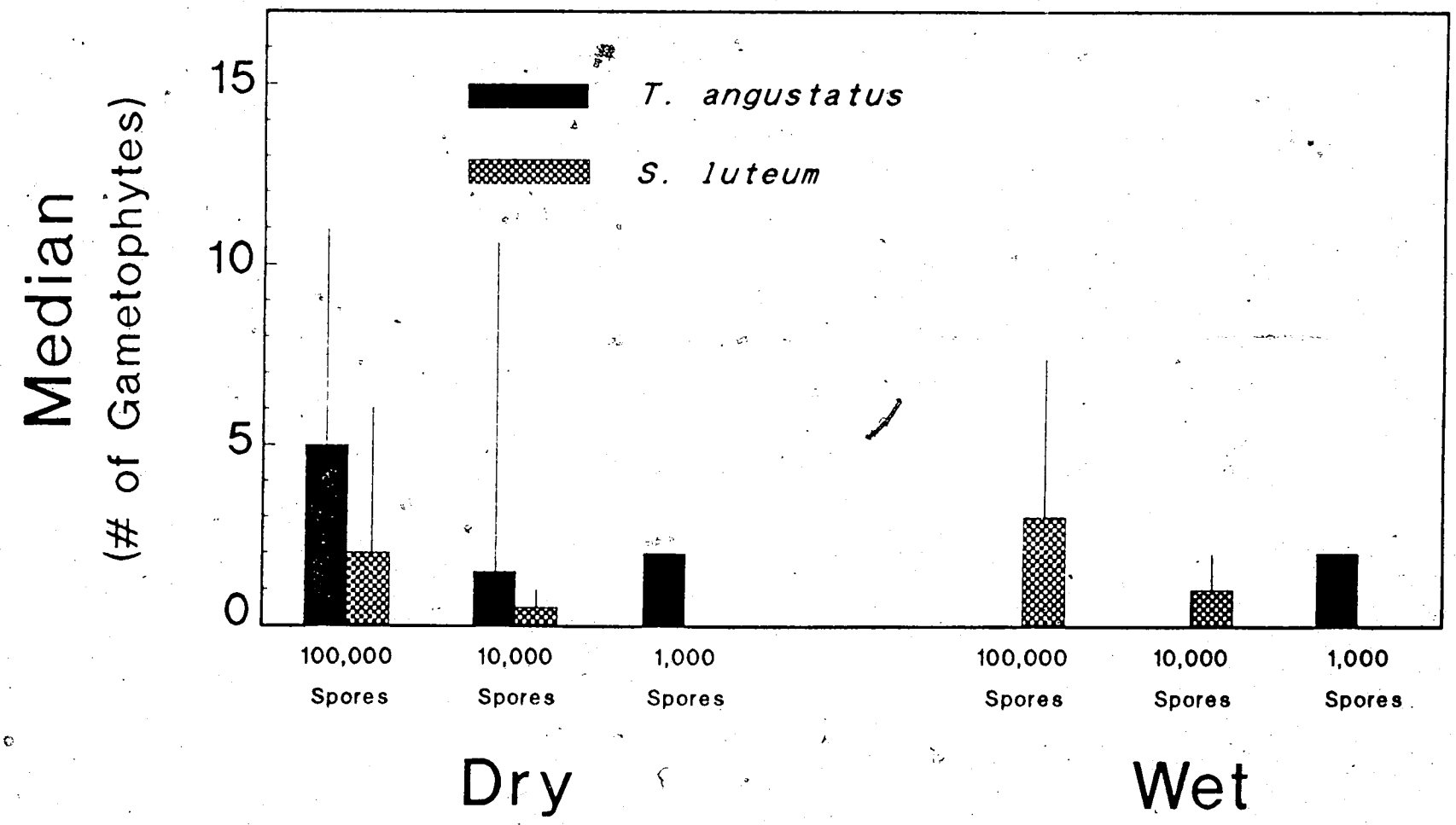

Figure II-8. Median gametophyte production in dry and wet habitats in the field growth experiment of two species mixtures of *T. angustatus* and *S. luteum*

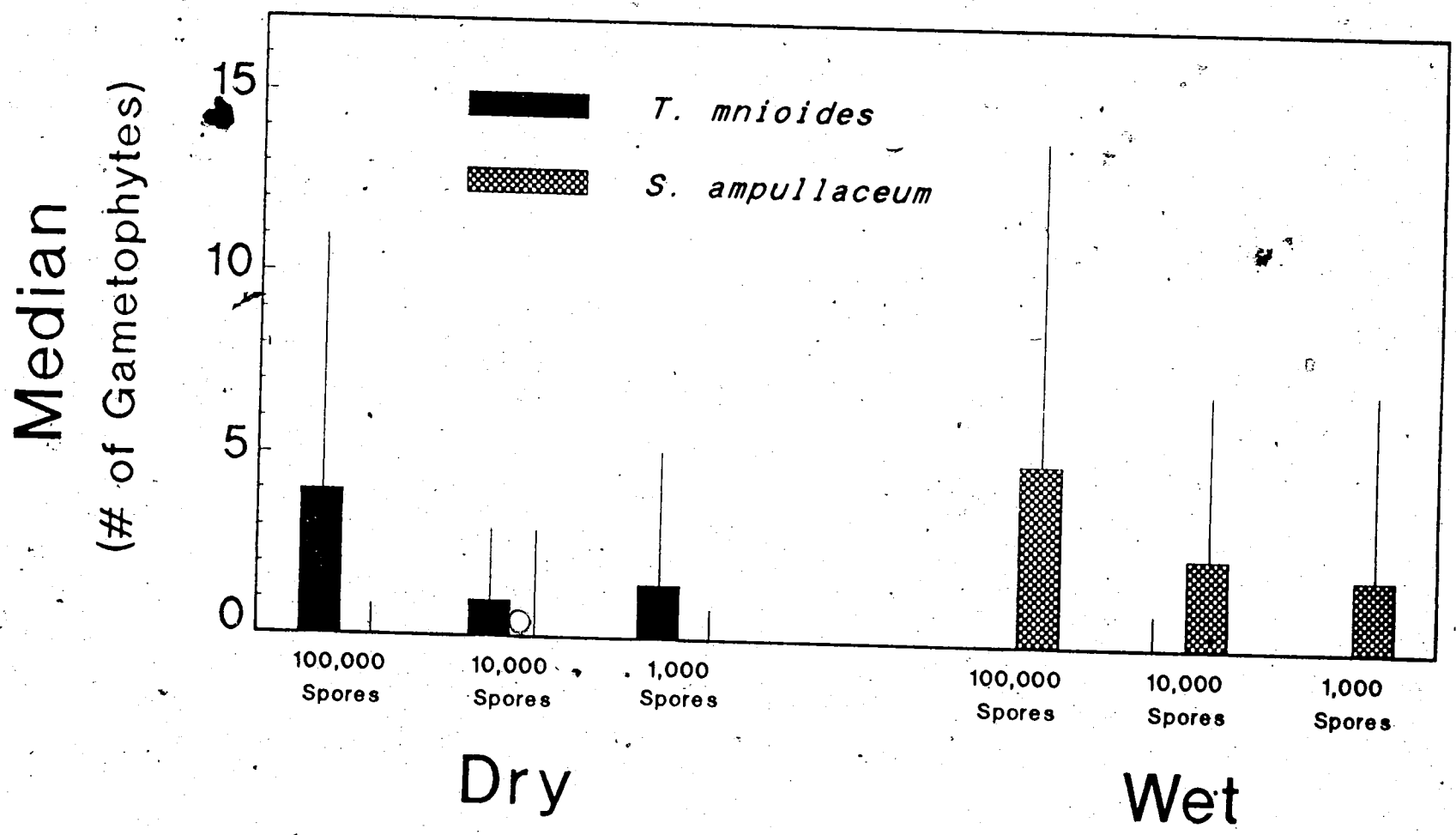

Figure II-9. Median gametophyte production in dry and wet habitats in the field growth experiment of two species mixtures of *T. mnioides* and *S. ampullaceum*.

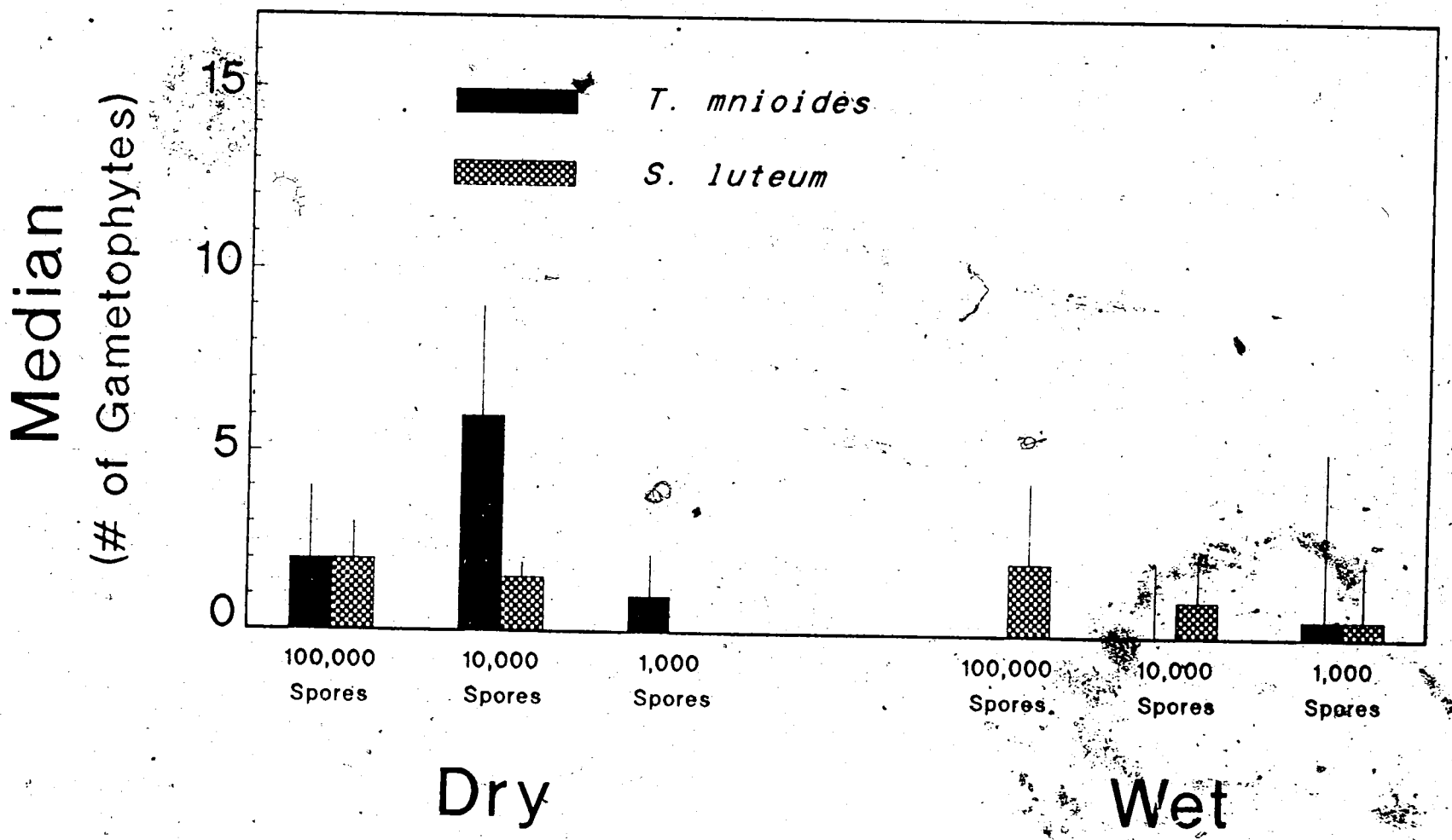

Figure II-10. Median gametophyte production in dry and wet habitats in the field growth experiment of two species mixtures of *T. mnioides* and *S. luteum*.

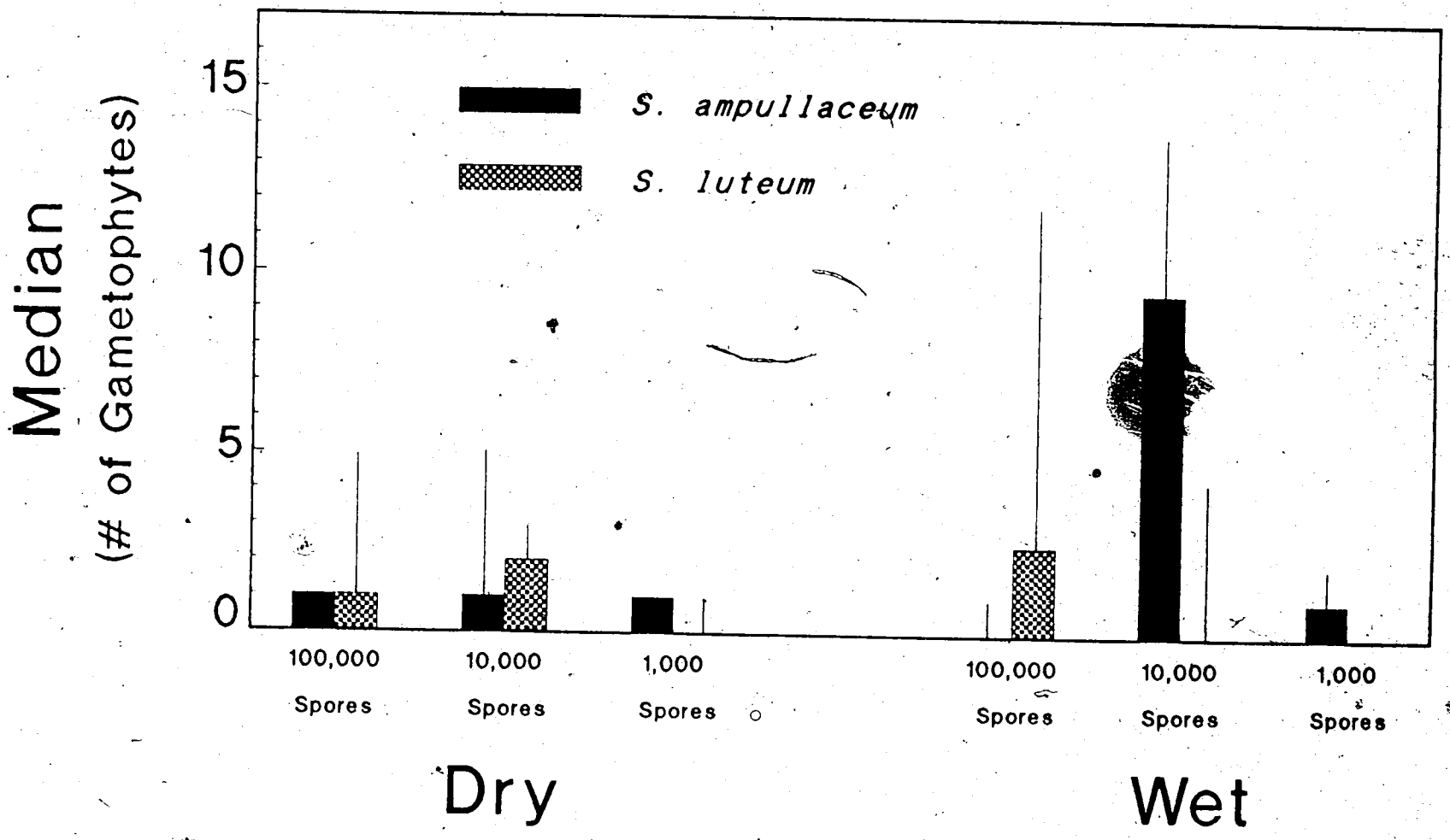

Figure II-11. Median gametophyte production in dry and wet habitats in the field growth experiment of two species mixtures of *S. ampullaceum* and *S. luteum*.

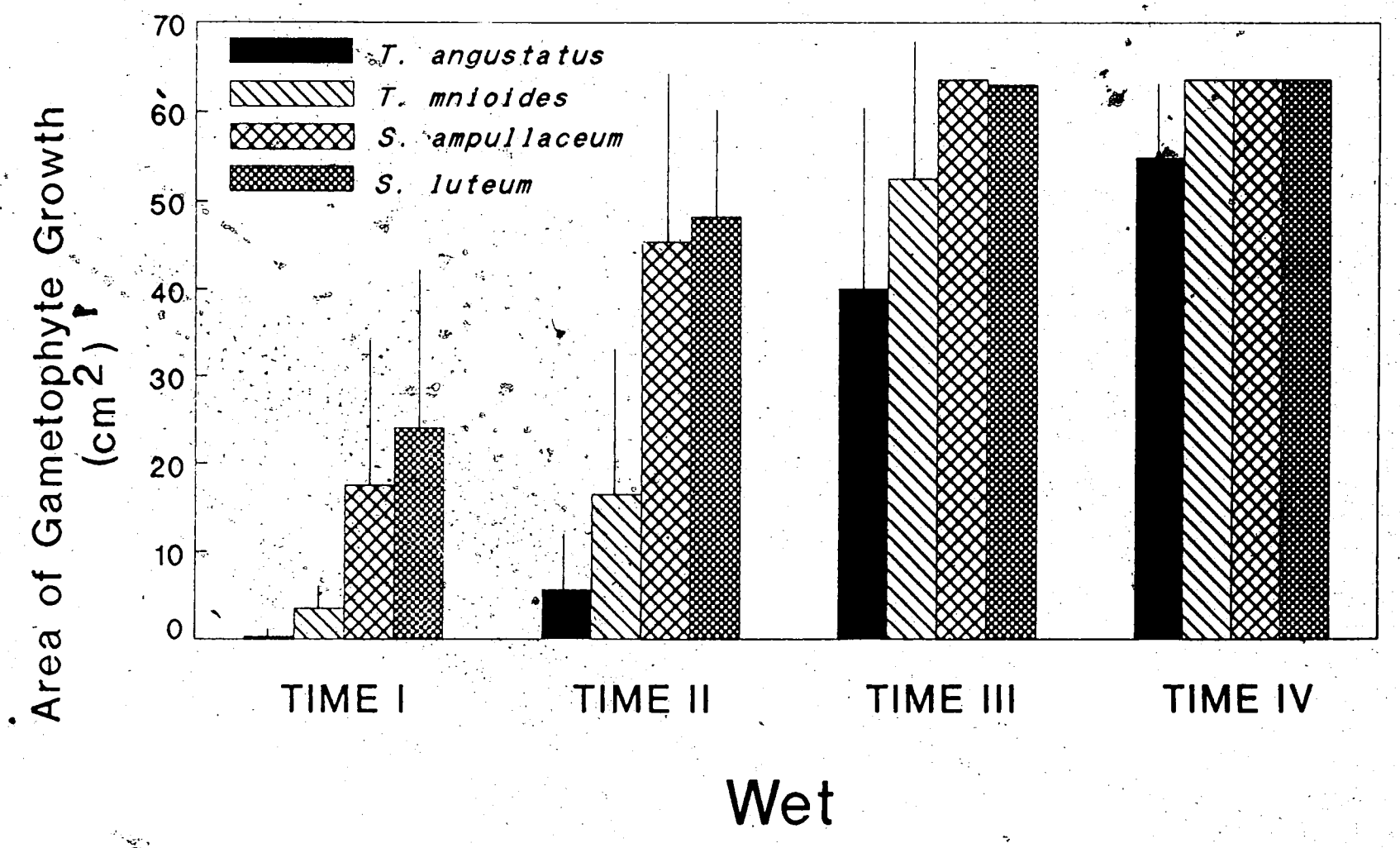

Figure II-12. Area covered by gametophyte growth in the wet treatment of the laboratory growth experiment on moose dung. Standard error bars are given.

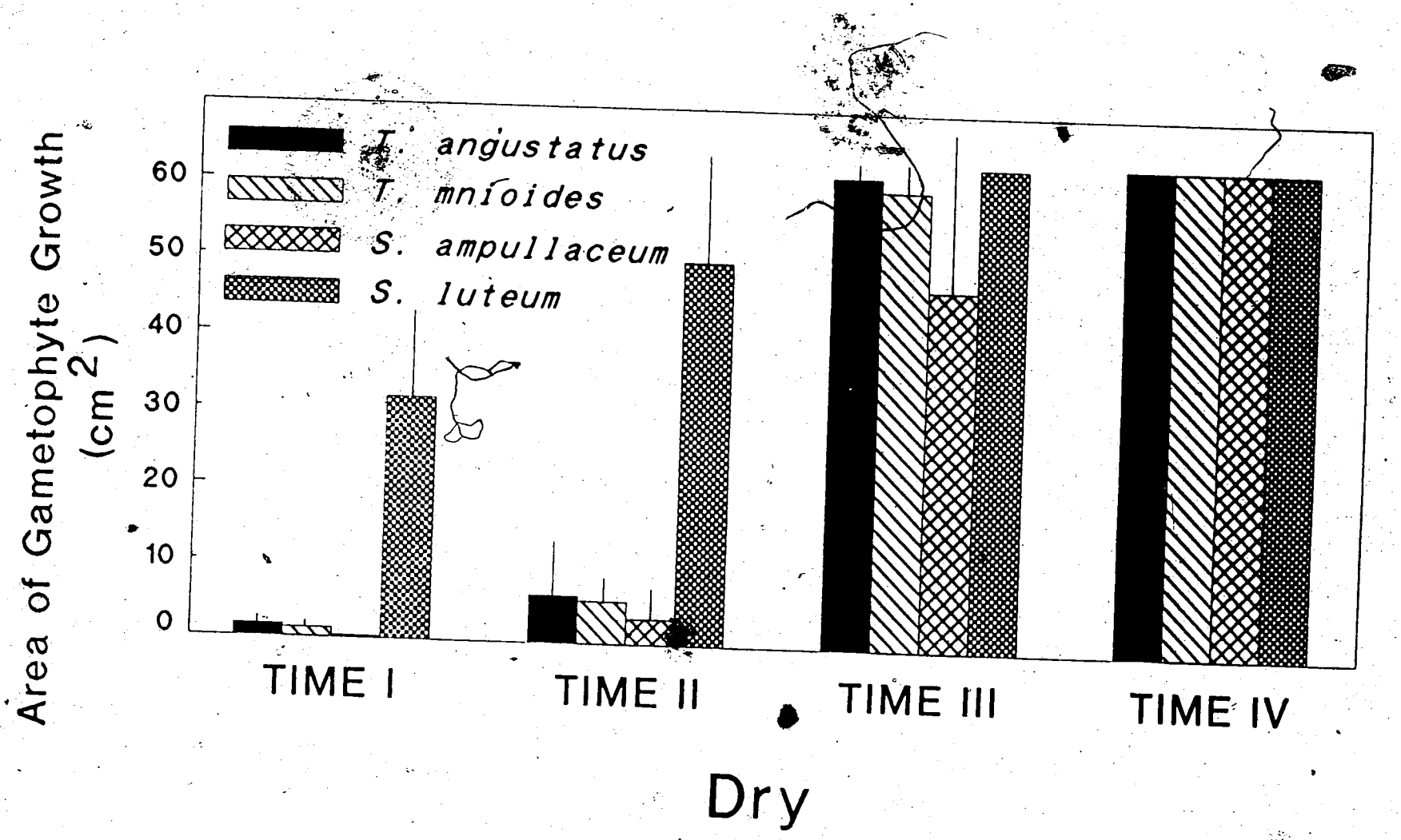

Figure II-13. Area covered by gametophyte growth in the dry treatment of the laboratory growth experiment on moose dung. Standard error bars are given.

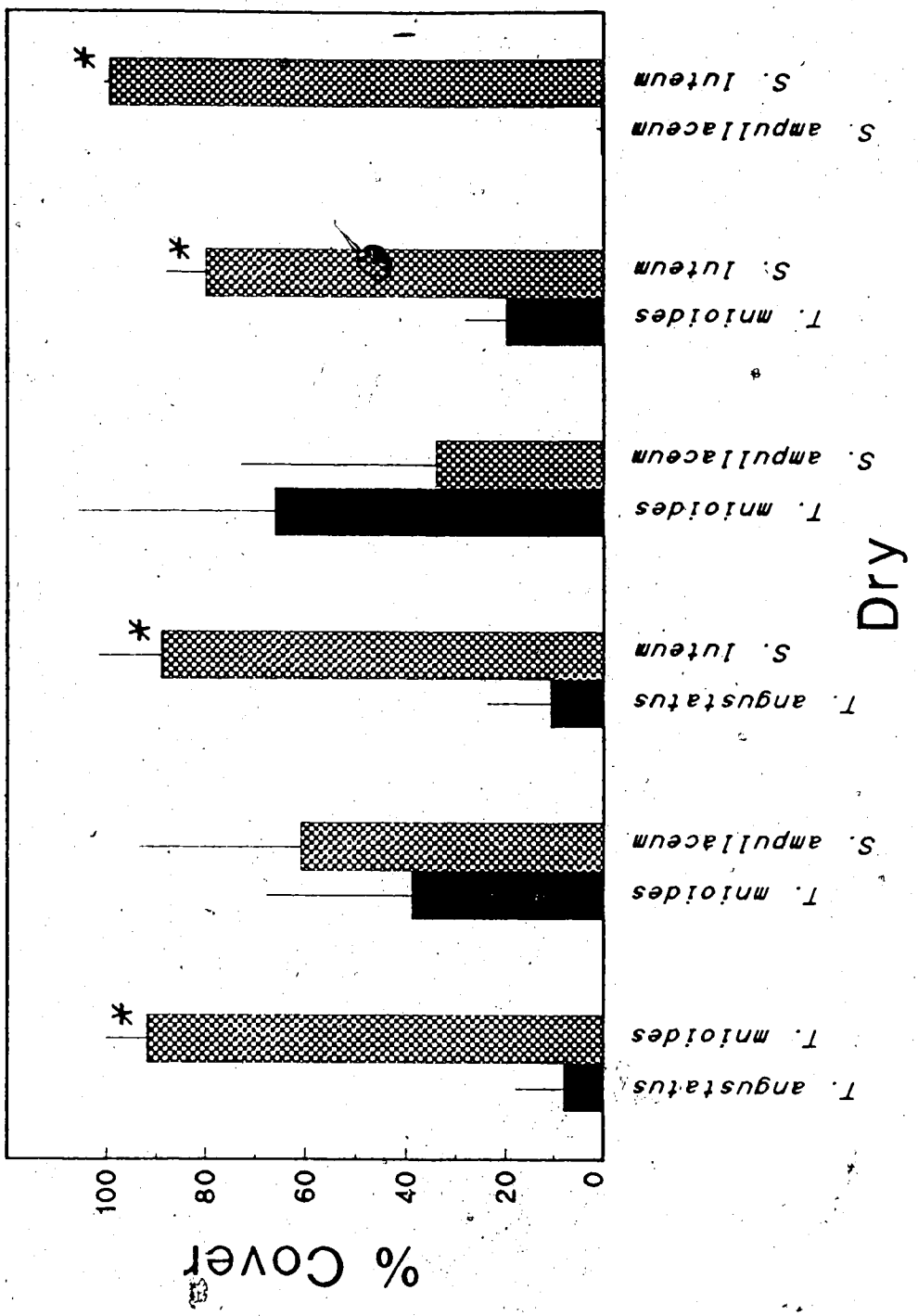

Figure II-14. Percent cover of each species in two species mixtures in the dry treatment of the laboratory growth experiment on Moose dung comparing all two species combinations. Standard error bars are given.

* = P < .05 that there are no significant differences in the number of gametophytes produced.

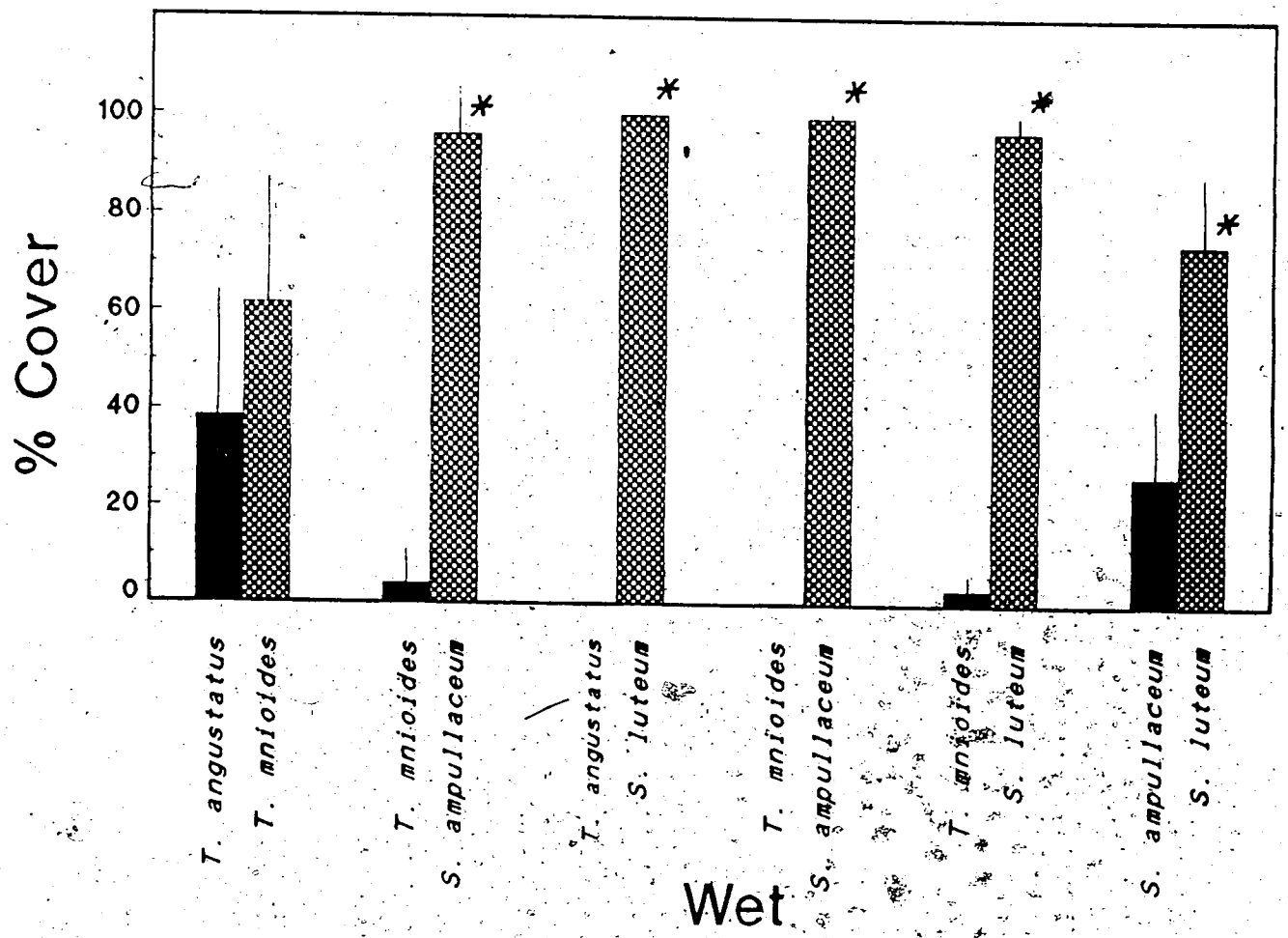

Figure II-15. Percent cover of each species in the two species mixtures in the wet treatment of the laboratory growth experiment on moose dung comparing all two species combinations. Standard error bars are given.

* = $P < .05$ that there are no significant differences in the number of gametophytes produced.

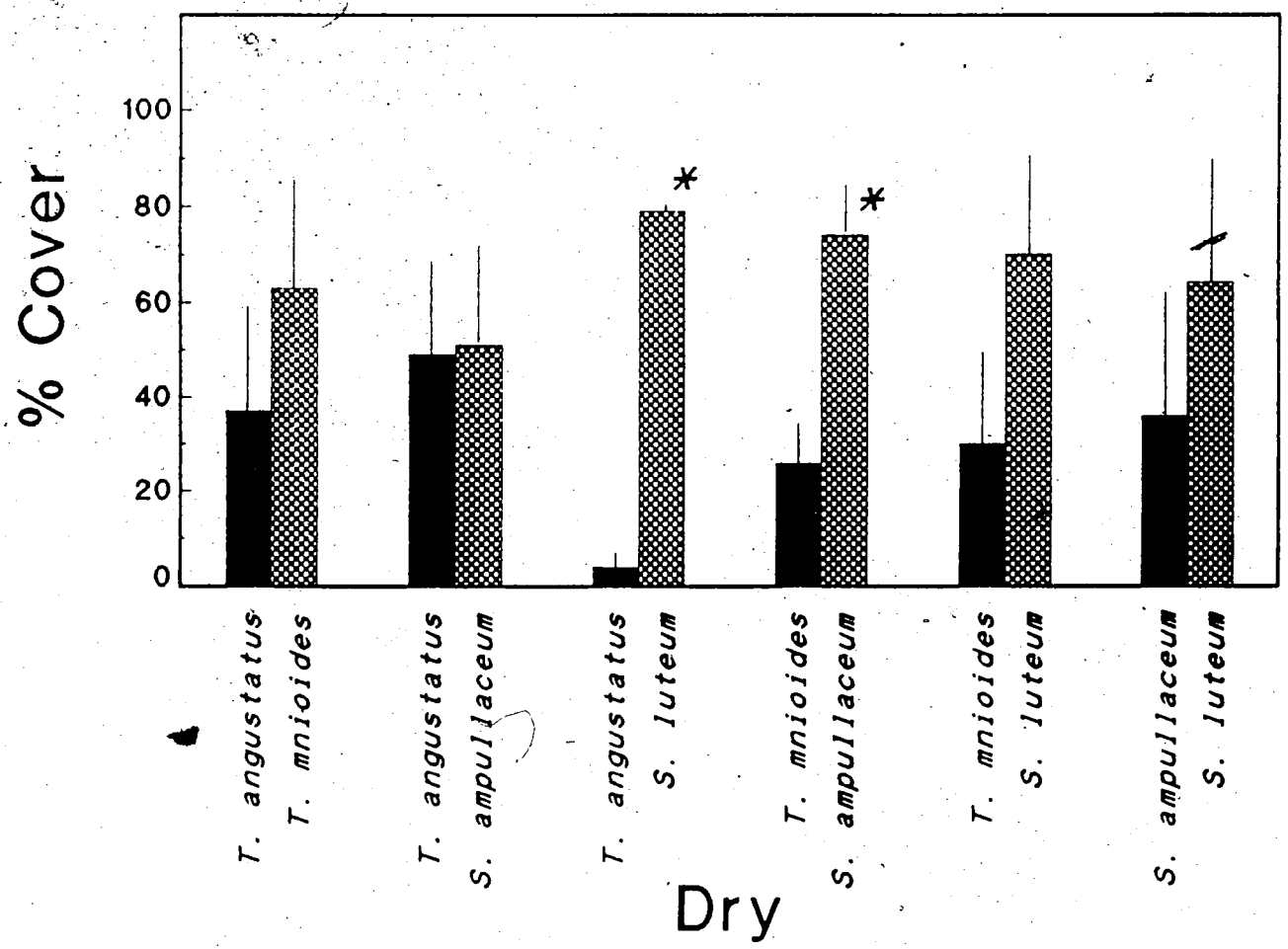

Figure II-16. Percent cover of each species in the two species mixtures in the dry treatment of the laboratory growth experiment on wolf dung comparing all two species combinations. Standard error bars are given. * = $P < .05$ that there are no significant differences in the number of gametophytes produced.

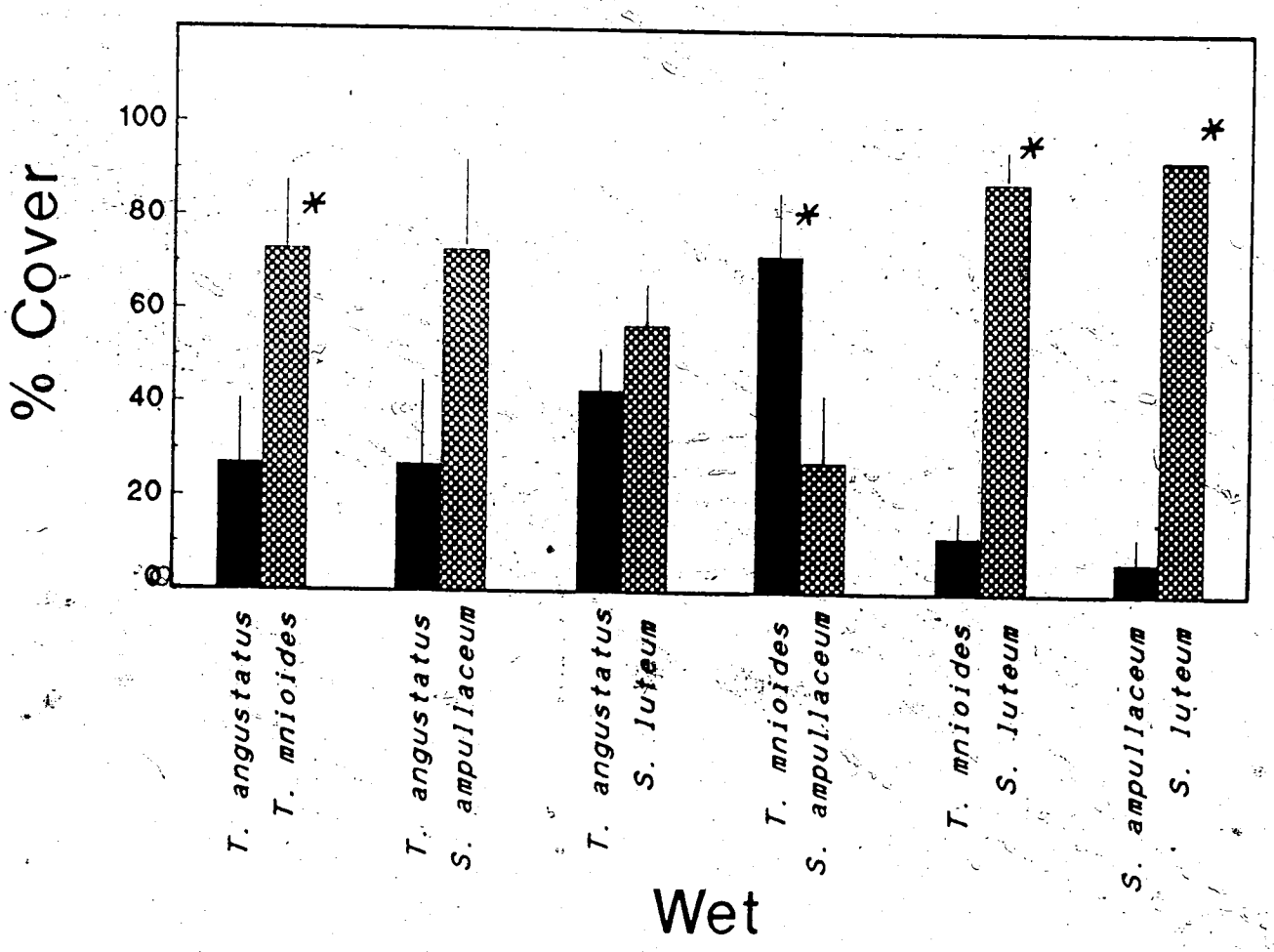

Figure II-17. Percent cover of each species in the two species mixtures in the dry treatment of the laboratory growth experiment on wolf dung comparing all two species combinations. Standard error bars are given. * = $P < .05$ that there are no significant differences in the number of gametophytes produced.

E. REFERENCES

Andrewartha, H. G. and L. C. Birch. 1954. *The Distribution and Abundance of animals.* The University of Chicago Press, Chicago, IL.

Brown, D. H. 1982. Mineral Nutrition. in *Bryophyte Ecology* ed. A. J. E. Smith. Chapman and Hall, New York.

Chesson, P. L. 1983. Coexistence of competitors in a stochastic environment: the storage effect. *In* H. I. Freedman and C. Strobeck, eds., *Population Biology,* pp. 188-198. Lecture Notes in Biomathematics no. 52. Springer-Verlag, Berlin, New York.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist 117:923-943.

Comins, H. N., and I. R. Noble. 1985. Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. American Naturalist 126:706-723.

Conover, W. J., and R. C. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. The American Statistician 35:124-129.

Denley, E. J., and A. J. Underwood. 1979. Experiments on factors influencing settlement, survival and growth of two species of barnacles in New South Wales. Journal of Experimental Marine Biology and Ecology 36:269-293.

Elton, C. 1949. Population interspersion: an essay on animal community patterns. Journal of Ecology 37:1-23.

Grubb, P. J. 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. *In* J. Diamond and T. Case eds., *Community Ecology,* pp. 207-228. Harper & Row, New York.

Hanski, I. 1976. Breeding experiments with carrion flies (Diptera) in natural conditions. Annales Entomologici Fennici 42:113-121.

Hanski, I. 1987. Carrion fly community dynamics: patchiness, seasonality and

coexistence. Ecological Entomology 12:257-266.

Hanski, I., and E. Ranta. 1983. Coexistence in a patchy environment: three species of *Daphnia* in rock pools. Journal of Animal Ecology 52:263-279.

Kareiva, P. 1986. Patchiness, dispersal, and species interactions: consequences for communities of herbivorous insects. *In* J. Diamond and T. Case eds., *Community Ecology,* pp. 192-206. Harper & Row, New York.

Ives, A. 1988. Aggregation and the coexistence of competitors. Annales Zoologici Fennici 25:75-88.

Lawlor, L. R., and Maynard Smith. 1976. The coevolution and stability of competing species. American Naturalist 110:79-99.

MacArthur, R. H., and Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. Proceedings of the National Academy of Science U.S.A. 51:1207-1210.

-----. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101:377-385.

Merritt R. W., and J. R. Anderson. 1977. The effects of different pasture and rangeland ecosystems on the annual dynamics of insects in cattle droppings. Hilgardia 45:31-71.

Pyysalo, H., A. Koponen and T. Koponen. 1978. Studies on entomophily in Splachnaceae (Musci). I. volatile compounds in the sporophyte. Annales Botanici Fennici 15:293-296.

-----. 1983. Studies on entomophily in Splachnaceae (Musci). II. volatile compounds in the hypophysis. Annales Botanici Fennici 20:335-338.

Sokal, R. R., and J. F. Rohlf. 1981. Biometry. W. H. Freeman and Company, San Franscisco.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. American Naturalist 111:337-359.

Vitt, D. H. 1981. Adaptive modes of the moss sporophyte. The Bryologist

84:166-186.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist 125:769-787.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. *In* P. S. White and S. T. A. Pickett eds., *The Ecology of Natural Disturbance and Patch Dynamics,* pp. 3-9. Academic Press, Orlando, Florida.

III. REGIONAL COEXISTENCE

A. INTRODUCTION

Patchiness is an important feature of biological populations and it can have an strong influence on the coexistence of species that use the same or similar resources (Elton 1949; Andrewartha and Birch 1954; Hanski and Ranta 1983; Hanski 1987; Ives 1988). The influence of patchiness on coexistence can be examined at several spatial scales, of which the regional scale is important because it focuses on interactions between species across several adjacent patches in an area defined by the dispersal ranges of the species being examined. Observation at this scale can indicate the degree to which dispersal variation between patches together with variation in species interactions on patches influences competitive coexistence.

I have studied species coexistence on divided resources by examining the mosses *Tetraplodon angustatus, T. mnioides, Splachnum ampullaceum* and *S. luteum* (F. Splachnaceae). These mosses grow on the droppings of large mammals and have their spores dispersed to droppings by flies (Diptera). Their coexistence can be examined at the local, regional and continental spatial scales. In this chapter, I will examine the coexistence of Splachnaceae at the regional spatial scale, represented by the mosses on adjacent droppings in an area roughly defined by their dispersal ranges.

The regional scale is represented by areas of 1-2 ha and is a function of population density and the mobility of flies that transport spores of Splachnaceae. This is the area from which spores of different local populations of Splachnaceae (Chapter 2) are likely able to disperse to the same fresh dropping.

Regional coexistence is an important problem in communities of Splachnaceae because these mosses use similar patchy resources, appear to be resource limited since they occupy the entire surface of droppings, appear to

occupy all suitable droppings, and species frequently co-occur regionally by growing on the same and on different droppings (Chapter II). These mosses are also particularly amenable for studying mechanisms of coexistence since the species are restricted to a well defined resource, grow relatively quickly, have direct interactions on patches and have quantifyable dispersal abilities (Chapter II).

The regional coexistence of Splachnaceae may be promoted by mechanisms including habitat and resource heterogeneity (MacArthur and Levins 1964, 1967; Lawlor and Maynard Smith 1976), seasonal variation (Hanski and Kuusela 1980; Paine 1977; Sousa 1985), and variation in relative competitive ability through time and space (Chesson 1985; Comins and Noble 1985). Competitive success may fluctuate because of dispersal variability that affects the numerical advantage of species in patches or environmental variability. Dispersal variation may promote coexistence through processes such as priority effects (Slatkin 1974; Hanski 1983), the independent propagation of propagules (Atkinson and Shorrocks 1981; Hanski 1981) or [illegible] between local competitive and dispersal ability (Skellam 1951; Hutchinson 1959; Hanski and Ranta 1983). Environmental variation may promote coexistence by causing strong recruitment for different species at different times and thereby allowing several species to establish in patches in the same region (Chesson and Warner 1981; Chesson 1983; Warner and Chesson 1985).

In this study, I consider patterns of regional coexistence in communities of Splachnaceae by examining the influence of spatial and temporal heterogeneity on coexistence and by investigating whether an inverse relationship between dispersal and competitive ability exists. The roles of priority effects and environmental fluctuations on coexistence are also discussed.

The influence of spatial heterogeneity on coexistence was studied by examining distribution patterns within regions. The influence of temporal heterogeneity on coexistence was examined by determining whether a temporal separation in sporophyte maturation between species of *Tetraplodon* results in

resource segregation.

The relationship between competitive and dispersal abilities was investigated by comparing the competitive relationships between species (Chapter II) with their relative spore dispersal abilities. Relative spore dispersal ability was examined in two trapping experiments, each conducted over a two year period. To examine relative spore dispersal ability, I first determined the degree of specificity between fly species and species of Splachnaceae and secondly, I compared the spore dispersal abilities of the faunas associated with the different moss species.

The degree of specificity between fly species and moss species was examined in both trapping experiments by first determining whether different species attracted similar fly faunas. Secondly, since flies were trapped on different moss species on different dates in both trapping experiments, I then determined whether the faunal differences between moss species resulted from temporal changes in the fly faunas or specificity between moss species and fly species. I did this by examining the degree of temporal and yearly variation in the fly faunas attracted to dung and to species of Splachnaceae by comparing the results of the two trapping experiments.

The spore dispersal abilities of the fly faunas associated with different species of Splachnaceae were compared in the second trapping experiment by determining: 1) which species of flies carried spores; 2) whether spore-carrying fly species were equally attracted to dung in dry and wet habitats; 3) the number of spores carried by individual spore-carrying flies; and, 4) what species of spores were carried on individual flies.

B. METHODS

Regional Distribution Patterns

The influence of spatial heterogeneity on the distribution of species within a region was examined during the summers of 1983, 1985 and 1986 by extensively surveying their distribution in an area of approximately 3 ha near the town of Ft. Assiniboine, Alberta (54° 18' N 114° 50' W). This was done by systematically searching upland forests and wetlands for populations of Splachnaceae. When local populations were found, the percent cover of species was recorded. To characterize habitat, the vegetation in a 25 cm^2 area adjacent to each dropping was noted.

The influence of regional habitat heterogeneity on the distribution of species was examined using Detrended Correspondence Analysis (DECORANA). DECORANA is an ordination technique based on reciprocal averaging, in which the arching phenomenon on the second ordination axis is mathematically eliminated (Gauch 1982). The data were first ordinated to summarize community patterns. In the ordination, samples of four plant communities were compared: the plant species in a 25 cm^2 area surrounding local populations of *T. angustatus*, *T. mnioides*, *S. ampullaceum* and *S. luteum*. For *T. angustatus*, *T. mnioides* and *S. ampullaceum*, 25 randomly chosen samples were used whereas for *S. luteum*, there were only 10 local populations and all 10 samples were used in the ordination. If the plant species surrounding local populations of species of Splachnaceae were similar (i.e., the species grew on droppings in similar habitats), then the samples should cluster together in ordination space. If the vegetation was different (i.e., the species grew in different habitats), then the samples of each should cluster separately. The community patterns were then compared with a moisture gradient in order to examine the influence of moisture availability on the ordination results.

Temporal Division of Resources

The influence of temporal heterogeneity (i.e., seasonal heterogeneity) on resource segregation and coexistence of species of *Tetraplodon* was examined in a field experiment conducted in the summer of 1985. This experiment determined whether seasonal differences in the timing of sporophyte maturation between *T. angustatus* and *T. mnioides* resulted in their temporal segregation on dung in dry habitats. At a site 20km from Ft. Assiniboine where both *T. angustatus* and *T. mnioides* were equally abundant, fresh moose dung was placed into the field in May, when *T. angustatus* sporophytes were mature, and in June, when most *T. mnioides* sporophytes were mature. Five transects of five piles of dung per transect were placed at five different locations (> 25 m apart) at the study site in May and again in June. The May and June transects were placed parallel to each other 30 cm apart. All transects were left in the field through the summer. In September, all dung was placed in one laboratory growth chamber to hasten gametophyte growth. In May 1986, the relative abundance of species on each pile of dung was determined.

Patterns of co-occurrence of *T. angustatus* and *T. mnioides* on natural droppings were also examined at this site and in herbarium specimens collected from across North America (See Chapter V for details regarding the herbarium specimens used). The number of specimens in which each species of *Tetraplodon* grew alone and the number of specimens in which the two species grew together was tallied. Data were analyzed using G-tests of independence with Williams correction to determine whether species co-occurred on droppings more or less frequently than expected by chance (Sokal and Rohlf 1981).

Dispersal of Spores

In order to determine the degree of specificity between fly and moss species, I examined whether the fly faunas attracted to each moss species differed

in two trappings experiments and I compared the results of these experiments to determine the importance of temporal variability versus specificity on the faunal differences. In the first trapping experiment, flies were trapped on 15, 14, 14 and 14 populations of *T. angustatus, T. mnioides, S. ampullaceum* and *S. luteum*, respectively at the Ft. Assiniboine site, on five fresh piles of dung and in ten randomly placed traps in both dry and wet habitats. The dung used was a mixture of droppings collected from captive moose fed the same diet (Chapter 2). Trapping lasted 9 days in early/mid May 1984 on *T. angustatus*, 12 days in late June/early July 1984 on *T. mnioides*, 10 days in early August 1985 on *S. ampullaceum* and 10 days in mid July 1985 on *S. luteum*. Total trapping time ranged from 4 to 7 hours a day depending on the weather. The traps were made of 1 liter clear plastic pop bottles cut in half with the upper half inverted and inserted into the lower half. A nylon mesh funnel was placed into the spout of the bottle to enhance the capture of flies and to prevent trapped flies from escaping. These traps were elevated above the Splachnaceae, dung and ground cover with short metal stakes.

In the second trapping experiment, the relative spore dispersal abilities of the fly faunas associated with different moss species were also examined by determining the species of flies carrying spores and the number and species of spores carried by spore-carrying flies. In this experiment, flies were trapped on *T. angustatus* for 8 days (38 hrs) in mid May 1986, *T. mnioides* for 8 days (35 hrs) in late June/early July 1986, *S. ampullaceum* for 5 days (24 hrs) in late July 1986 and *S. luteum* for 3 days (18 hrs) in early August 1987 at the same study site as in the first trapping experiment. Flies were trapped on two mature local populations of each of the four moss species. On each date, fresh moose dung, collected as previously described, was placed 5-10 m from each moss population in both dry and wet habitats and left in the field for three days. Flies were trapped on dung all three days. Trapping on dung and Splachnaceae

was conducted at 15-minute intervals by two people. At each interval, each person trapped flies on either a Splachnaceae population or on dung in a dry or or a wet habitat, rotating trapping effort throughout the day. Total trapping time ranged from 4 to 7 hours a day depending on the weather. When dung was three days old it was collected, put into sealed containers and within a week was returned to Edmonton, where it was placed into a controlled environmental chamber to later determine which species of moss grew on the dung.

During trapping intervals, flies were captured in nets and killed with CO^2 (so as not to kill spores of Splachnaceae). Flies were then sorted into plastic vials. If many flies were trapped during one interval, then several flies of the same species were placed into each vial. During the evening following trapping, flies were examined individually under a dissecting microscope to determine if they were carrying spores.

If spores were found on a fly, the fly was returned to its vial and set aside. Within 24 hours of capture, the number of spores carried was estimated by adding .250 ml of water to the vial, shaking the vial for 30 seconds and then using a Petroff-Hausser bacteria counter to estimate the number of spores in the solution. The fly was then removed, pinned and labeled. Five spore counts were made from the solution in each vial. The remaining solution was kept cool and within one week returned to Edmonton and used to inoculate individual samples of moose dung placed in 5 cm plastic planters and grown in an environmental chamber in order to determine which species of spores a particular fly was carrying.

If no spores were found, the flies were pinned and labeled. A random sample of these flies were treated in the same manner as those flies carrying spores to determine whether they did in fact carry spores.

Pinned flies were sorted by family and morpho-species. Of all the flies captured, 70% were named to species, and 85% of those captured on Splachnaceae were named to species. Families represented by few individuals that were rarely associated with Splachnaceae were generally not identified further. All initial fly species identifications were made by Graham Griffiths (Dept. Entomology, Univ. of Alberta) with the exception of the Scatophagidae which were identified by William Vockeroth (Canadian National Museum).

Cluster analysis (TWINSPAN) was used to compare the faunas associated with the different moss species and the fly faunas associated with dung in dry and wet habitats. TWINSPAN is a polythetic divisive classification technique that emphasizes indicator species, and the production of an arranged matrix. In a TWINSPAN analysis, the data are first ordinated by reciprocal averaging. Those species that characterize t[illegible]ocal averaging axis extremes are then emphasized in order to polarize the s[illegible]es, and the samples are divided into two clusters by breaking the ordination axis near its middle. The sample division is refined by a reclassification using species with maximum value for indicating the poles of the ordination axis. The division process is then repeated on the two sample subsets to give four clusters, and so on, until each cluster has no more than a chosen minimum number of members (Gauch 1982).

For both trapping experiments, all fly species were included in the TWINSPAN analysis. Since few flies were trapped in the control traps in the first trapping experiment, they were not considered in the analyses. In the first trapping experiment, all replicates of all samples (species of Splachnaceae, dung in dry and dung in wet habitats) are used in the analyses. In the second trapping experiment, trapping dates were used as sample replicates; because trapping intervals were short (3 to 12 days) there should have been little influence of time on the fly faunas.

The results of the TWINSPAN analyses are presented as dendrograms of the sample hierarchies. The TWINSPAN analysis deliberately arranges the two clusters at each node so that the most similar samples fall together in the dendrogram's sample sequences (Gauch 1982). Therefore, in the dendrograms presented, samples with the most similar fly faunas are closest together in the dendrogram. This is reflected in the sequence of divisions such that the higher-level divisions separate samples with fly faunas that are relatively more dissimilar than are samples separated in subsequent divisions.

C. RESULTS

Patterns of Distribution

Habitat heterogeneity has a strong influence on the regional distribution of species. In central Alberta, the distributions of *Tetraplodon* and *Splachnum* varied with moisture level. DECORANA analysis indicated that species of *Tetraplodon* were found in drier habitats and species of *Splachnum* were found in wetter habitats (Figure III-1). In dry habitats where *Tetraplodon* grow, lichens (*Cladonia* spp.), feather mosses (*Pleurozium schreberi and Hylocomnium splendens*), and litter predominated. In wet habitats where *Splachnum* grow, brown mosses (*Tomenthypnum nitens, Drepanocladus aduncus*, and *D. revolvens*) and sphagnum mosses (*Sphagnum angustafolium* and *S. wornstorfii*) predominated. There were no apparent habitat differences in the distributions of congeneric species (Figure III-1).

Temporal Division of Resources

The temporal separation of sporophyte maturation between species of *Tetraplodon* appeared to result in a seasonal segregation of resources. In the ANOVA results examining differences in seasonal colonization of dung by *T.*

angustatus and *T. mnioides*, there was a significant interaction between date and species ($F = 14.4$; $p < 0.001$, $df = 1$). Dung placed into the field in May, when *T. angustatus* sporophytes matured, was colonized exclusively by *T. angustatus* whereas dung placed into the field in June, when *T. mnioides* sporophytes matured, was mainly colonized by *T. mnioides* (Figure III-2).

Patterns of distribution of *T. angustatus* and *T. mnioides* within this same region also suggested that they grow on different droppings. Although both species grow in the same habitats, they were often found on different droppings in the vicinity of Ft. Assiniboine and throughout North America they were also infrequently found growing on the same droppings (Table III-1).

Comparison of Flies Trapped on Splachnaceae

In the first trapping experiment, 2,721 flies from 34 families (Appendix III-1) and in the second trapping experiment, 4,252 flies from 23 families (Appendix III-2) were trapped on the four species of Splachnaceae and dung in dry and wet habitats. In the first and second trapping experiments, 81% and 85%, respectively, of the flies have been identified to species. Overall, over 70% of the flies associated with the mosses were members of the families Anthomyiidae, Calliphoridae, Fanniidae, Muscidae and Scatophagidae. All individuals in these families have been identified to species.

In both the first (Figure III-3) and second (Figure III-4) trapping experiments, each species of Splachnaceae attracted relatively different faunas of flies. These could be separated into: 1) those taxa attracted to *T. mnioides*, *S. ampullaceum* and *S. luteum*; and, 2) those taxa attracted to *T. angustatus*. This division may have represented a seasonal difference in the faunas and in the first trapping experiment, it was the most distinct division whereas in the second trapping experiment it was the least distinct division. The first group could be further subdivided into a *T. mnioides* and *S. luteum* fauna and a *S. ampullaceum*

fauna.

Temporal Variation in the Fly Faunas

A comparison of the fly faunas attracted to dung between the two trapping experiments indicated that the faunas differed both between and within each trapping experiment, suggesting that the dung fly faunas differed between and within years. Because temporal variation in the dung fly faunas was a reflection of their having been trapped on dung in dry and wet habitats at the same time as they were trapped on each moss species, dung is referred to as being 'associated with' a particular species of Splachnaceae. The combined faunas of both trapping experiments divided into two groups: 1) Those attracted to dung associated with *T. angustatus* in the second trapping experiment; and 2) those attracted to all other dung (Figure III-5). The second group could be divided into two subgroups separating the fly faunas in the two trapping experiments. This division may have reflected either the influence of trapping design or variation between years in the fly faunas. Within both subgroups, the fly faunas attracted to dung associated with the different species grouped together.

In contrast, faunal differences between moss species appeared to result more from specificity between moss and fly species than from the influence of temporal variation in the dung fly fauna, suggesting that although dung fly faunas differed considerably between and within years, each species of Splachnaceae attracted a distinct and relatively consistent fly fauna. The fly faunas attracted to each species of Splachnaceae were similar in the two trapping experiments (Figure III-6). When fly faunas of both trapping experiments were combined, they divided into the same two groupings and the first grouping could be subdivided into the same two subgroups as the faunas the trapping experiments considered separately (Figure III-6). The second grouping could be further divided into two subgroups: a *T. angustatus* division and a small division containing several *T. mnioides*

samples from the first trapping experiment. Overall, however, there was little influence of either trapping design or temporal variation on the fly faunas attracted to each species of Splachnaceae.

Spore-Carrying Flies

1. Flies Trapped on *T. angustatus*

On *T. angustatus* and associated dung in dry and wet habitats, 1,007 flies from 28 taxa were captured. One species, *Scatophaga furcata*, accounted for 75% of flies captured. Most flies (93.7%) were trapped on dung (43.4% in dry habitats and 50.3% in wet habitats). Few of these (0.6%) were carrying spores (0.4% of those trapped on dung in dry habitats and 0.2% of those trapped on dung in wet habitats). Of the 6.25% of flies trapped on *T. angustatus*, many (60.3%) carried spores.

Spore-carrying flies trapped on *T. angustatus* and associated dung belonged to 10 Dipteran taxa. Individuals of three species, *Helina cothurnata*, *Eudasyphora cyanocolor* and *S. furcata* comprised 76% of the flies captured carrying spores. Two of these species, *E. cyanocolor* and *Helina cothurnata* had the most individuals carrying spores and on average, these individuals carried the greatest number of spores (Table III-2). Of those species of flies in which five or more individuals carried spores and more than 20 individuals were also trapped on dung, most individuals carrying spores were associated with dung in dry habitats (Figure III-7).

Overall, flies attracted to *T. angustatus* and associated dung carried 51,118 spores/hour. Flies that were relatively rare carried the greatest number of spores. *E. cyanocolor* and *Helina cothurnata*, representing 3.67% and 1.69%, respectively, of the flies trapped on *T. angustatus*, carried 79% of the spores. The most frequently trapped fly, *S. furcata*, carried few spores (11.0%).

2. Flies Trapped on *T. mnioides*

On *T. mnioides* and associated dung in dry and wet habitats, 1,605 flies from 82 taxa were captured. No species accounted for more than 25% of flies captured. Most flies (74.1%) were trapped on dung (54.9% in dry habitats and and 19.2% in wet habitats). Few of these (0.8%) were carrying spores (0.5% of those trapped on dung in dry habitats and 0.3% of those trapped on dung in wet habitats). Of the 26% of flies trapped on *T. mnioides*, 16.5% carried spores.

Spore-carrying flies trapped on *T. mnioides* and associated dung belonged to 18 Dipteran taxa. Individuals of five species, *Calliphora vomitoria*, *E. cyanocolor*, *Phormia terrae-novae*, *Cynomyopsis cadaverina* and *Hydrotae meteorica* comprised 63% of flies captured carrying spores and together they carried 75% of spores. Three of these species, *C. vomitoria*, *E. cyanocolor* and *C. cadaverina*, as well as *Phormia regina*, carried on average the most spores. Few individuals of the two most common species captured, *Fannia spathiophora* and *Hydrotae meteorica*, carried spores (Table III-3). Of those fly species in which five or more individuals carried spores and more than 20 individuals were also trapped on dung, most individuals carrying spores were associated with dung in dry habitats (Figure III-7). Overall, flies attracted to *T. mnioides* and associated dung carried 53,423 spores/hour.

3. Flies Trapped on *S. ampullaceum*

On *S. ampullaceum* and associated dung in dry and wet habitats, 757 flies from 49 taxa were captured. One species, *Pegoplata patellans* accounted for 27.3% of the flies captured. Most flies (89.4%) were trapped on dung (22.5% in dry habitats and 66.9% in wet habitats). Few of these (4.7%) were carrying spores (1.3% of those trapped on dung in dry habitats and 3.4% of those trapped on dung in wet habitats). Of the 10.7% of flies trapped on *S. ampullaceum*, 38.8% were carrying spores.

Spore-carrying flies trapped on *S. ampullaceum* and associated dung belonged to 16 Dipteran taxa. Of the individuals captured carrying spores, 40%

were *Pegoplata patellans*, the most frequently captured fly species. Four other species had 5 or more individuals that carried spores, *S. furcata, Mydaea* sp. 1, *Scatophaga suilla* and *Hebecnema nigricolor*. These four species together with *P. patellans* accounted for 72.3% of the flies which carried spores and together they carried 65.8% of the spores (Table III-4). Of those fly species in which five or more individuals carried spores and more than 20 individuals were also trapped on dung most were associated with dung in wet habitats (Figure III-8). Overall, flies attracted to *S. ampullaceum* and associated dung carried 80,625 spores/hour.

4. Flies Trapped on *S. luteum*

On *S. luteum* and associated dung in dry and wet habitats, 883 flies from 46 taxa were captured. No species accounted for more than 25% of the flies captured. Most flies (58.9%) were trapped on dung (23.3% in dry habitats and 35.6% in wet habitats). Few of these (2.1%) were carrying spores (0.8% of those trapped on dung in dry habitats and 1.3% of those trapped on dung in wet habitats). Of the 41.1% of flies trapped on *S. lutem*, 16.0% were carrying spores.

Spore-carrying flies trapped on *S. luteum* and associated dung belonged to 15 taxa. Individuals of three species, *Phormia regina*, *Ravinia* sp. 1, and *C. vomitoria* comprised 65.2% of the flies carrying spores and together they carried 65.5% of the spores (Table III-5). The first and third most common flies captured, *Ravinia* sp. 1 and *P. regina* respectively, had the most individuals carrying spores and carried the most spores overall. Of those fly species in which five or more individuals carried spores and more than 20 individuals were also trapped on dung, none showed a strong habitat preference (Figure III-8). Overall, flies attracted to *S. luteum* and associated dung carried 50,694 spores/hour.

5. Summary

In summary, more flies were attracted to dung than to any species of Splachnaceae and few of these flies appeared to be carrying spores. Most spores were carried by individuals of species attracted to the mosses; however, few species of flies carried most of the spores. Flies trapped on *T. angustatus*, *T. mnioides* and their associated dung carried approximately the same number of spores/hour. These flies were predominately attracted to dung in dry habitats. Therefore, the two species of *Tetraplodon* do not appear to differ in dispersal ability. Flies trapped on *S. ampullaceum* and associated dung carried more spores/hour than flies trapped on *S. luteum* and associated dung. Spore-carrying flies attracted to *S. ampullaceum* and associated dung were primarily attracted to dung in wet habitats whereas spore-carrying flies attracted to *S. luteum* and associated dung did not show a habitat preference. Therefore, *S. ampullaceum* appears to have more of its spores dispersed to dung in wet habitats, the habitat in which species of *Splachnum* commonly grow, than does *S. luteum*.

Species of Spores Carried by Spore-Carrying Flies

Gametophyte growth almost always occurred on dung inoculated with the rinsings of flies on which spores were visible under the dissecting microscope. Most of these species of Splachnaceae were the same species as the treatment in which the flies had been caught. However, the rinsings from 6.3% of the flies trapped on *T. angustatus* and associated dung, and 46.7% of the rinsings from flies trapped on *T. mnioides* and associated dung, also produced *S. luteum*, and 4.3% of the rinsings from flies trapped on *T. mnioides* and associated dung also produced *S. ampullaceum* (Table III-6).

86% of dung inoculated with the rinsings of the control flies, those on which no spores were visible under the dissecting microscope, also produced Splachnaceae. As in the flies on which spores were visible, the species of Splachnaceae growing on the dung was mostly (83.8%) the same species as one

on which the flies had been caught (Table III-6). However, on 29% of the rinsings from flies trapped on *T. angustatus*, *T. mnioides* and associated dung the surface of the dung remained partly uncovered by gametophyte after one year. 96% of the rinsings from flies trapped on *S. ampullaceum* and associated dung produced strong growth of *S. ampullaceum*.

D. DISCUSSION

This study has identified habitat heterogeneity, temporal variability (seasonal variability) and tradeoffs between relative competitive and dispersal ability as mechanisms that may act to promote the coexistence of species of Splachnaceae on a regional spatial scale. Habitat heterogeneity appears to be important in promoting the regional coexistence between species of the two genera whereas temporal heterogeneity and a tradeoff between relative competitive and dispersal ability may be important in promoting regional coexistence between species of *Tetraplodon* and *Splachnum* respectively. Each of these mechanisms may be important because the patchy distribution of droppings in both space and time may provide both a measure of heterogeneity by which different species can segregate resources and colonization opportunities for species through which dispersal and environmental variability can act to give different species advantages in different patches at different times.

Patterns of regional distribution suggest that differences between dry and wet habitats influence the relative establishment and growth of the two genera. Habitat analysis has shown that *Tetraplodon* grow in habitats characterized by xeric plant species whereas *Splachnum* grow in habitats characterized by more mesic plant species. This may be due to species of different genera having different tolerances to moisture availability and variation in the chemical composition of dung as caused by differential leaching or absorption (Chapter II), or to habitat-restricted spore dispersal.

Habitat-restricted spore dispersal may influence regional coexistence because the dispersal of spores of *Tetraplodon* mainly to dry habitats may reinforce the habitat differences existing between the two genera. Dispersal of these spores primarily to dry habitats may result in their density being greater than that of spores of *Splachnum* whereas the reverse may be true in wet habitats. This, compounded with the growth advantage species of *Tetraplodon* have in dry habitats, may further enhance habitat segregation between the two genera and hence promote their regional coexistence.

Habitat differences do not, however, appear to promote the regional coexistence of congeneric species. Habitat analysis suggested that congeneric species grow on droppings located in similar habitats. Moreover, in field growth experiments, there were no interactions between habitat and species when species of the same genera were grown together; suggesting that relative growth rates of congeneric species are not habitat-dependent (Chapter II). Neither were habitat-related dispersal differences found between species of *Tetraplodon*. However, they were found between species of *Splachnum* since flies carrying spores of *S. ampullaceum* were more prevalent in wet habitats. It does not appear, however, that this dispersal difference between species of *Splachnum* influences the habitats in which the two species are found growing. These results suggest that other mechanisms of coexistence such as the influence of temporal (Paine 1977; Hanski and Kuusela 1980), dispersal (Slatkin 1974; Hanski 1983; Hutchinson 1975; Hanski and Ranta 1983) or environmental variation (Chesson and Warner 1981; Chesson 1983; Warner and Chesson 1985) may promote the regional coexistence of congeneric species.

Because experimental results indicated that seasonal difference in sporophyte maturation between *T. angustatus* and *T. mnioides* also resulted in a seasonal segregation of resources, temporal variation (i.e., seasonal variation) appears to be an important mechanism promoting their regional coexistence. Dung placed into

the field in spring, when sporophytes of *T. angustatus* matured, was only colonized by *T. angustatus* whereas dung placed into the field during the summer, when sporophytes of *T. mnioides* matured, was primarily colonized by *T. mnioides*. Furthermore, analysis of distribution patterns in central Alberta have shown that in regions in which both species are common, they infrequently grew on the same droppings. Since there was no evidence that species of *Tetraplodon* are segregating resources on the basis of habitat or dung type (e.g., dung of carnivores versus dung of herbivores) (Chapter II), these results likely occurred because spore-carrying flies visit primarily fresh droppings and therefore the spores of each species should be dispersed mainly to droppings that are fresh when their sporophytes mature.

The importance of a tradeoff between relative competitive and dispersal ability as a mechanism promoting regional coexistence (Skellam 1951; Hutchinson 1975; Hanski and Ranta 1983) should be a function of the consistency with which each species of Splachnaceae attracts a specific fauna of flies since dispersal ability is a function of the faunas that each species attracts. Comparison of the faunas attracted to dung associated with *T. angustatus* (which matures in the spring) with the faunas attracted to dung associated with the remaining species (which mature in the summer) indicated that the fly faunas differed seasonally. Also, comparison of the faunas attracted to dung associated with the summer maturing species (on which flies were trapped at different times during the summer) indicated that the faunas varied within a season. This faunal variation between and within seasons suggests that the differences in the fly faunas attracted to each of the species of Splachnaceae may be a reflection of temporal changes in the the faunas rather than a reflection of specificity between species of Splachnaceae and species of flies.

However, comparison of the faunas attracted to dung and each species of Splachnaceae between years indicated that despite strong differences between years

in the faunas attracted to dung, differences between the faunas attracted to each species of Splachnaceae were neither as evident nor as strong. This suggests that differences between faunas attracted to different species of Splachnaceae are not a total reflection of variation within or between years but also represent variation in the degree to which different species of Splachnaceae attract different species of flies. This specificity between species of Splachnaceae and flies may result from the differences between moss species in sporophyte morphology, color and odor (Pyysalo et al. 1978; Vitt 1981; Pyysalo et al. 1983). The influence of these factors on specificity is a problem requiring further study. Further work on this system, however, should also recognize the influence of seasonal variation in the faunas and collect data from different species of mosses both at the same time and over longer periods of time to allow the question of specificity to be more clearly distinguished from seasonal availability.

The specificity between species of Splachnaceae and species of flies suggests that dispersal differences and therefore tradeoffs between relative competitive and dispersal abilities between species of Splachnaceae should be relatively constant over time. Therefore, the tradeoff between relative competitive and dispersal ability that appears to exist between *S. ampullaceum* and *S. luteum* in central Alberta may be an important mechanism promoting their coexistence. This tradeoff exists because *S. ampullaceum* appeared to have more of its spores dispersed to dung in wet habitats since more of its spores were carried by flies per hour and more of these spore-carrying flies were associated with droppings in wet habitats than was the case for *S. luteum*. Also, laboratory growth experiments have shown that *S. ampullaceum* is a weaker competitor than *S. luteum* (Chapter

The dispersal superiority that *S. ampullaceum* appeared to have over *S. luteum* may have resulted from the close association between *S. ampullaceum* and the fly *Pegoplata patellans*. This species of fly was more closely associated with *S. ampullaceum* than other fly species were with either *S. ampullaceum* or *S.*

luteum. In both trapping experiments, most of the flies attracted to *S. ampullaceum* were *P. patellans*, and in the second trapping experiment most spores of *S. ampullaceum* were carried by *P. patellans*. Most individuals of *P. patellans* carrying spores were trapped on dung, 71% in wet habitats. None of the species of flies carrying large numbers of *S. luteum* spores were so closely associated with dung in wet habitats.

Unlike the two species of *Splachnum*, there did not appear to be a tradeoff between relative dispersal and competitive ability between *T. angustatus* and *T. mnioides*. For both species of *Tetraplodon*, the average number of spores carried on flies per hour were similar and these spore-carrying flies were most closely associated with dung in dry habitats. Therefore, there was no evidence that the weaker competitor *T. angustatus* (Chapter II), had a dispersal advantage over the superior competitor, *T. mnioides*.

Priority effects (initial abundances determine which species survive in a patch) (Slatkin 1974; Hanski 1983) and environmental variation resulting in different species being dominant in site establishment under different combinations of environmental conditions (Chesson and Warner 1981; Chesson 1983; Warner and Chesson 1985) are two potentially important mechanisms of regional coexistence in patchy environments that I have not examined directly in this study. For priority effects to be an important mechanism promoting the regional coexistence of Splachnaceae, spores must be dispersed to droppings independent of the age of the dropping, and priority of access to droppings must give species a competitive advantage. This does not appear to be the case since results of the trapping study indicated that few flies visited dung older than two days, suggesting that most spores reach droppings within a one- or two-day period. Such small differences in arrival time should have no impact on the relative growth advantages of different species since sporulation and growth occur over a longer period of time (Webster 1978). Environmental fluctuations, however, may be an

important mechanism promoting regional coexistence since field and laboratory growth experiments have suggested that relative establishment and growth ability may depend on environmental conditions (Chapter II). This could promote regional coexistence because different species may then be able to establish and grow on either the same or on different droppings in the same region as environmental conditions fluctuate. The influence of environmental fluctuations as a mechanism promoting local (Chapter II) and regional coexistence is an important problem requiring further study.

Summary

Three mechanisms have been identified that may promote the coexistence of Splachnaceae on a regional spatial scale; habitat heterogeneity, temporal variability (seasonal variability) and a tradeoff between relative competitive and dispersal ability. Each of these mechanisms of coexistence may be important because the patchiness of droppings in both both space and time provides both a a measure of heterogeneity by which different species can segregate resources and colonization opportunities for species through which dispersal and environmental variability can act to give different species advantages in different patches at different times.

Habitat heterogeneity appears to promote coexistence between the two genera since habitat analysis has shown that droppings located in habitats characterized by relatively xeric vegetation was primarily occupied by *Tetraplodon* whereas dung in habitats characterized by relatively mesic vegetation were primarily occupied by *Splachnum*. This difference may be a result of differences in relative growth ability between genera in dry and wet habitats (Chapter II) and the association of spore-carrying flies of *Tetraplodon* primarily with dung in dry habitats.

Temporal (seasonal) differences in sporophyte maturation may promote the regional coexistence of *T. angustatus* and *T. mnioides* because *T. angustatus* primarily colonized dung in spring, when its sporophytes mature whereas *T.*

mnioides primarily colonized dung in early summer when its sporophytes mature. This seasonal segregation of dung likely results from spore-carrying flies being most attracted to fresh dung.

Because the faunas attracted to each species of Splachnaceae differ and appear to be relatively constant over time, both dispersal differences and tradeoffs between competitive and dispersal ability may also be relatively constant over time. Therefore, the tradeoff between competitive and dispersal ability that was shown to exist between *S. ampullaceum* and *S. luteum* may be an important mechanism promoting their regional coexistence.

Table III-1. Number of droppings on which *T. angustatus*, *T. mnioides* and both *T. angustatus* and *T. mnioides* were found growing. Specimens from Ft. Assiniboine are from an area in which both species are found growing and herbarium specimens include specimens from throughout North America. The G-test probability with Williams correction has been calculated to determine whether the number of specimens having both species growing together was fewer than expected by chance.

	T. angustatus only	*T. mnioides* only	*T. angustatus* and *T. mnioides*	G-test Probability
Ft. Assiniboine	26	13	10	*
Herbaria Specimens	741	2,221	50	***

* $P < .05$, *** $P < .001$.

Table III-2. Spore-carrying fly species captured on *T. angustatus* in the second trapping experiment.

Fly Species	Number with Spores	x Number of Spores/Fly	Std. Error	Total Number of Spores Carried
Eudasyphora cyanocolor	13	74,039	99,997	962,500
Helina cothurnata	11	52,273	39,456	575,000
Scatophaga furcata	8	26,563	27,187	212,500
Sepsis spp.	3	5,833	3,818	17,500
Eutrichota cylindrica	1	27,500	-	27,500
Morellia podagrica	1	25,000	-	25,000
Phormia terrae-novae	2	16,250	5,303	32,500
Cynomyopsis cadaverina	1	80,000	-	80,000
Lasiomma sp. 2	1	5,000	-	5,000
Pegoplata nigriscutellata	1	5,000	-	5,000

Table III-3. Spore carrying fly species captured on *T. mnioides* in the second trapping experiment.

Fly Species	Number with Spores	x Number of Spores/Fly	Std. Error	Total Number of Spores Carried
Calliphora vomitoria	11	45,909	50,389	505,000
Eudasyphora cyanocolor	10	29,000	16,716	290,000
Phormia terrae-novae	9	20,000	19,843	180,000
Cynomyopsis cadaverina	7	30,000	26,926	210,000
Hydrotae meteorica	7	17,500	7,773	122,500
Phormia regina	4	41,875	49,681	167,500
Muscina assimilis	4	20,625	8,260	82,500
Lucilia sp. 1	4	23,125	13,444	92,500
Fannia spathiophora	3	24,167	35,385	72,500
Ravinia sp. 1	2	6,250	1,768	12,500
Pegohylomyia sp. 1	2	13,750	12,374	27,500
Myospila meditabunda	1	7,500	-	7,500
Helina sp. 2	1	27,500	-	27,500
Tricops sp. 2	1	10,000	-	10,000
Helina cothurnata	1	10,000	-	10,000
Polietes orichalceoides	1	15,000	-	15,000
Sarcophaga sp. 1	1	25,000	-	25,000
F. Sciomyzidae	1	12,500	-	12,500

Table III-4. Spore-carrying fly species captured on *S. ampullaceum* in the second trapping experiment.

Fly Species	Number with Spores	x Number of Spores/Fly	Std. Error	Total Number of Spores Carried
Pegoplata patellans	26	23,173	19,436	602,500
Scatophaga furcata	6	32,500	22,528	195,000
Mydaea sp. 1	5	25,500	23,345	127,500
Scatophaga suilla	5	29,000	22,542	145,000
Hebecnema nigricolor	5	40,500	47,677	202,500
Hydrotae militarus	3	45,000	64,952	135,000
Phaonia curvipes	2	15,000	14,142	30,000
Calliphora vomitoria	3	28,750	12,374	57,500
Thricops sp. 3	2	10,000	10,607	20,000
Polietes orichalceoides	2	68,750	19,445	137,500
F. Sphenoceridae	1	25,000	-	25,000
Eudasyphora cyanocolor	1	50,000	-	50,000
F. Tachinidae	1	7,500	-	7,500
Sarcophaga sp. 2	1	12,500	-	12,500
Scatophaga stercoraria	1	105,000	-	105,000
Hydrotae unispinosa	1	7,500	-	7,500

Table III-5. Spore-carrying fly species captured on *S. luteum* in the second trapping experiment.

Fly Species	Number with Spores	x Number of Spores/Fly	Std. Error	Total Number of Spores Carried
Phormia regina	18	14,583	13,807	262,500
Ravinia sp. 1	16	11,875	9,197	190,000
Calliphora vomitoria	9	16,111	20,771	145,000
Myospila meditabunda	5	3,500	2,236	17,500
Pegoplata patellans	4	15,625	12,645	62,500
Pegoplata nigriscutellata	2	6,250	1,768	12,500
Eudasyphora cyanocolor	2	23,750	30,052	47,500
Hydrotae scambus	2	3,750	1,767.8	7,500
Hylemyza partita	2	6,250	1,768	12,500
Craspedochaeta sp. 1	1	12,500	-	12,500
Phormia sp. 3	1	2,500	-	2,500
Sp. 6	1	100,000	-	100,000
Morellia podagrica	1	7,500	-	7,500
Hydrotae meteorica	1	2,500	-	2,500
Hydrotae sp. 3	1	30,000	-	30,000

Table III-6. Growth of Splachnaceae from spore rinsings of flies with visible spores and from control flies. The numbers following the '/' are cases in which there was little growth.

Treatment	*T. angustatus*	*T. mnioides*	*S. ampullaceum*	*S. luteum*	No Growth	Total
T. angustatus	36			1	2	40
Dry Dung	3			2		3
Wet Dung	4				1	5
T.angustatus (Control)						
Dry Dung (Control)	9/7			3	7	18
Wet Dung (Control)	11/3			5	4	18
T. mnioides	1	78	3	39		82
Dry Dung		2	1	2		4
Wet Dung		6		2		6
T. mnioides (Control)		6/3		1		6
Dry Dung (Control)		8/2	1			9
Wet Dung (Control)		6/4	5	2		14
S. ampullaceum			39/4			39
Dry Dung			22/4			22
Wet Dung			9			9
S. ampullaceum (Control)			8/2			8
Dry Dung (Control)			19	1		19
Wet Dung (Control)			19			19

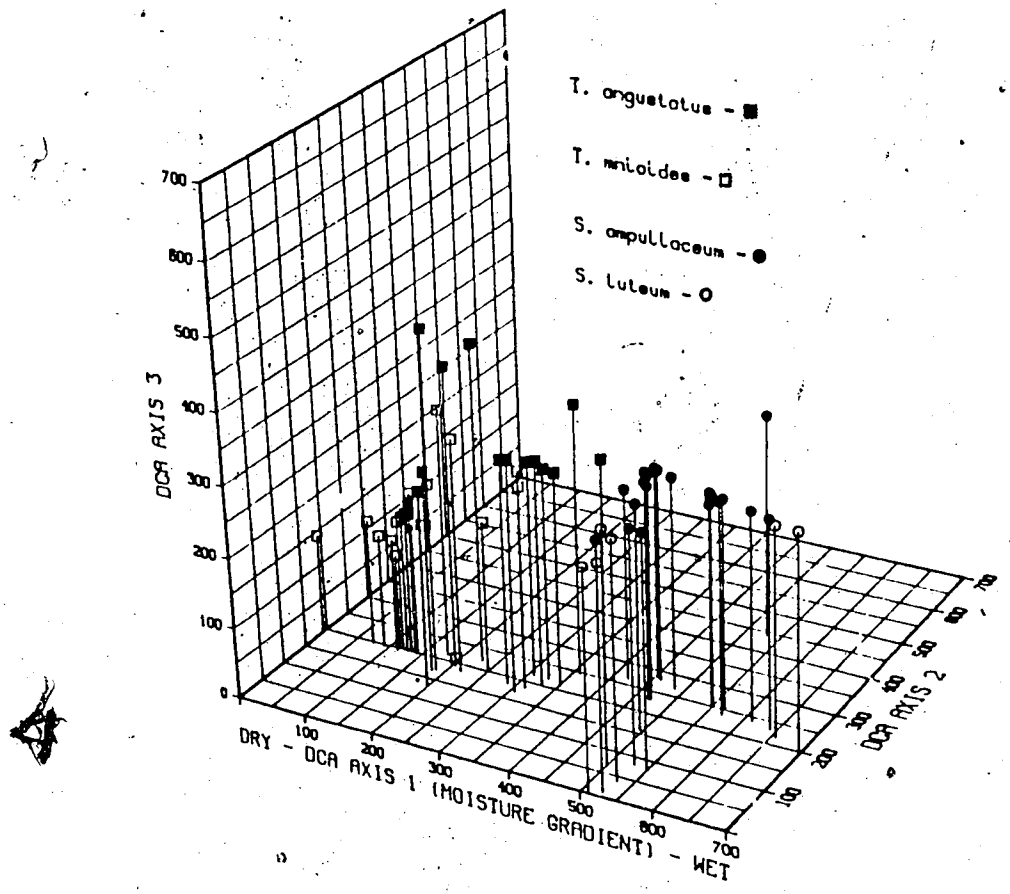

Figure III-1. Ordination results examining the relationship between habitat variation within regions and the location of *T. angustatus*, *T. mrioides*, *S. ampullaceum* and *S. luteum* populations within regions. A moisture gradient is represented by the first DCA axis.

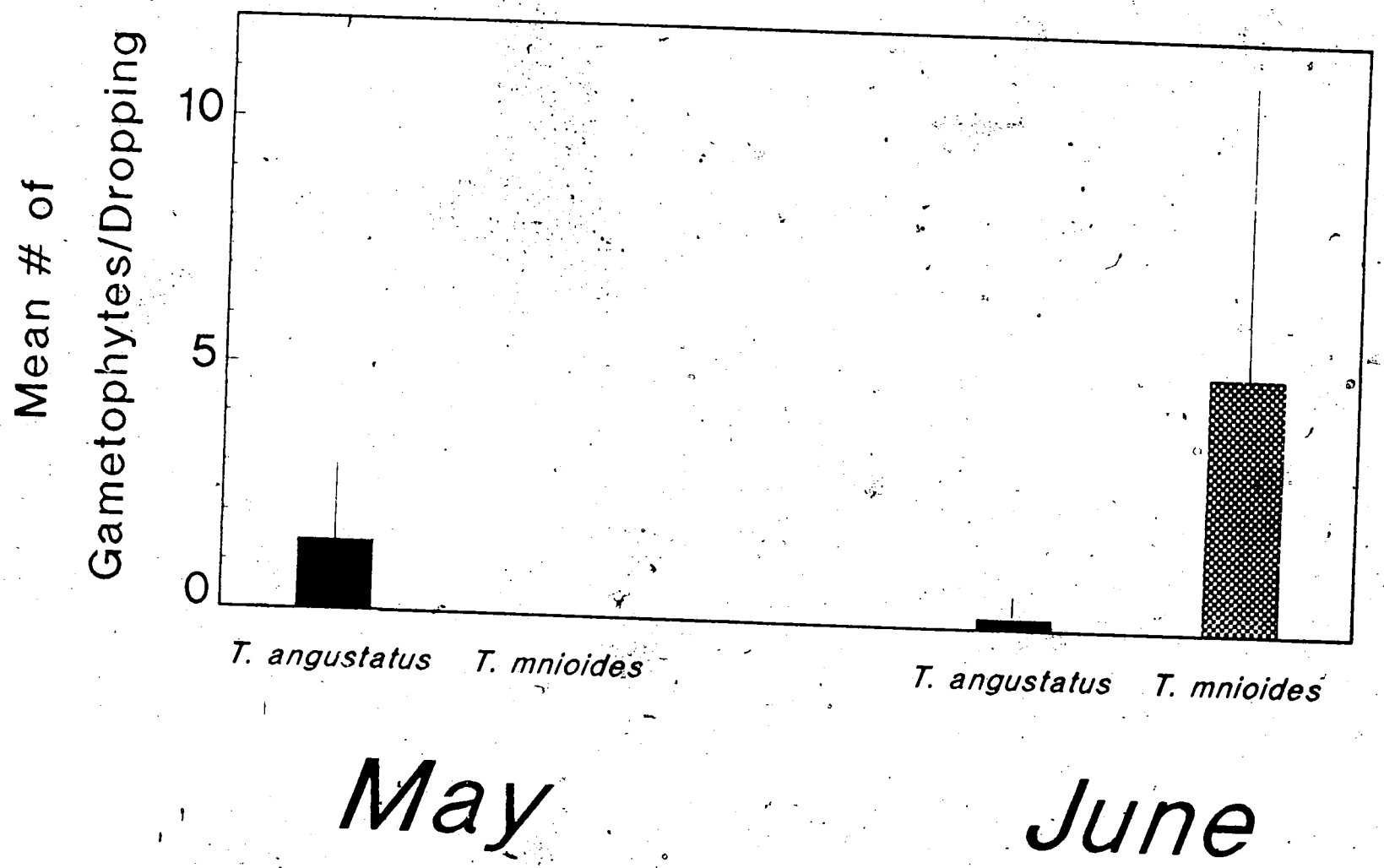

Figure III-2. The growth of *T. angustatus* and *T. mnioides* on droppings placed into the field in May (when *T. angustatus* sporophytes mature) and mid June (when *T. mnioides* sporophytes mature).

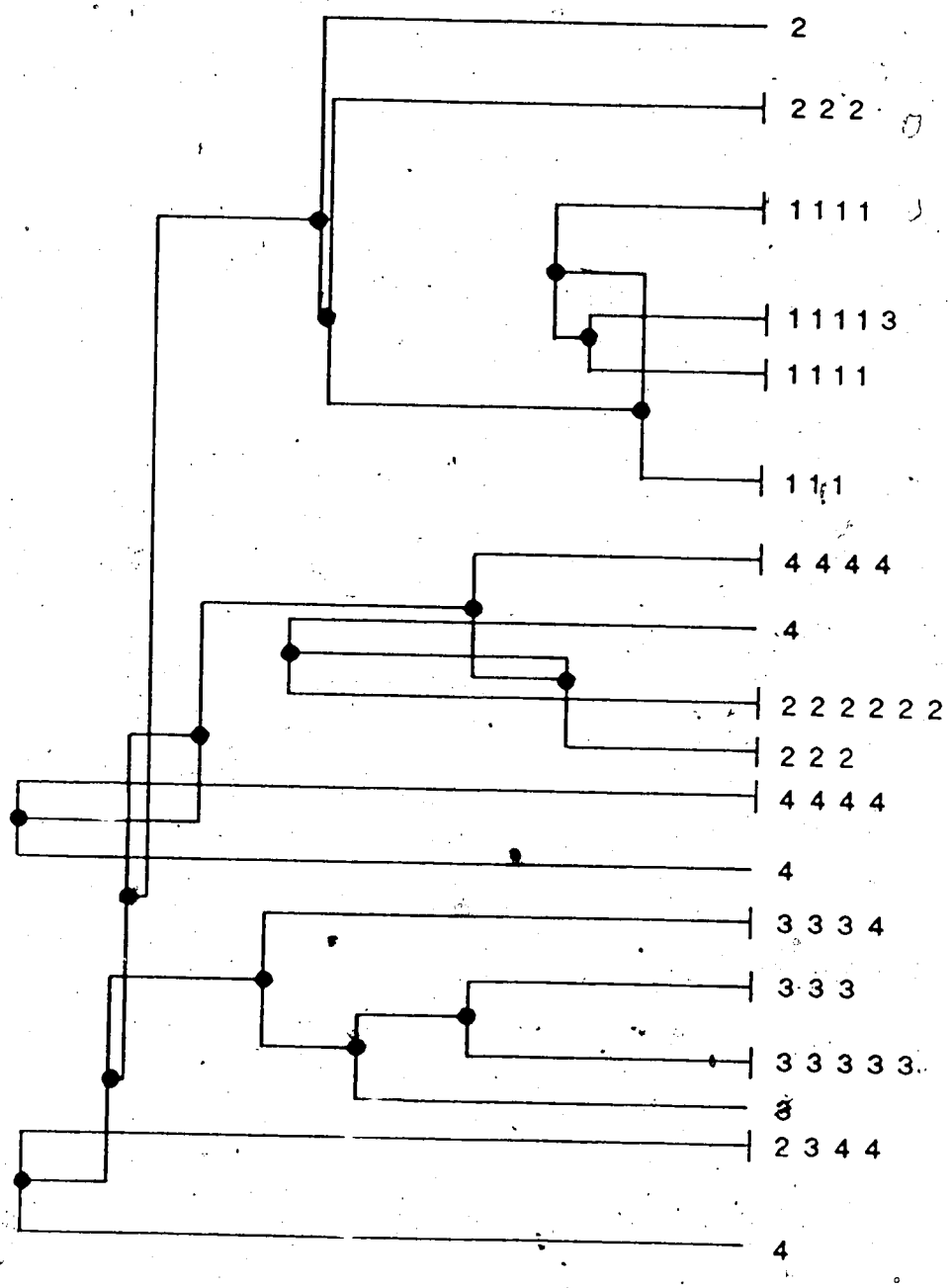

Figure III-3. Dendrogram derived from the TWINSPAN analysis comparing the fly faunas associated with T. angustatus (1), T. minoides (2), S. ampullaceum (3) and S. luteum (4) in the first transplant experiment.

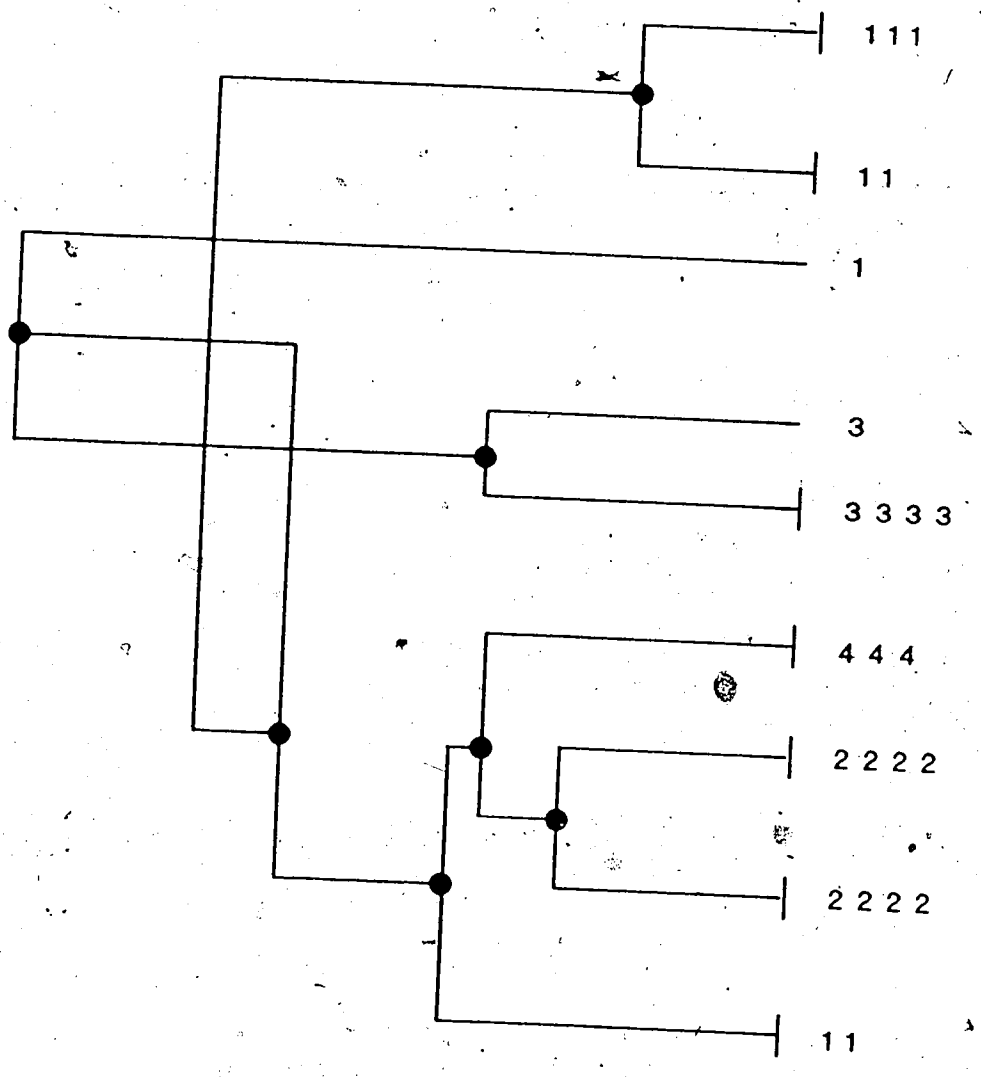

Figure III-4. Dendrogram derived from the TWINSPAN analysis comparing the fly faunas associated with *T. angustatus* (1), *T. minoides* (2), *S. ampullaceum* (3) and *S. luteum* (4) in the second trapping experiment.

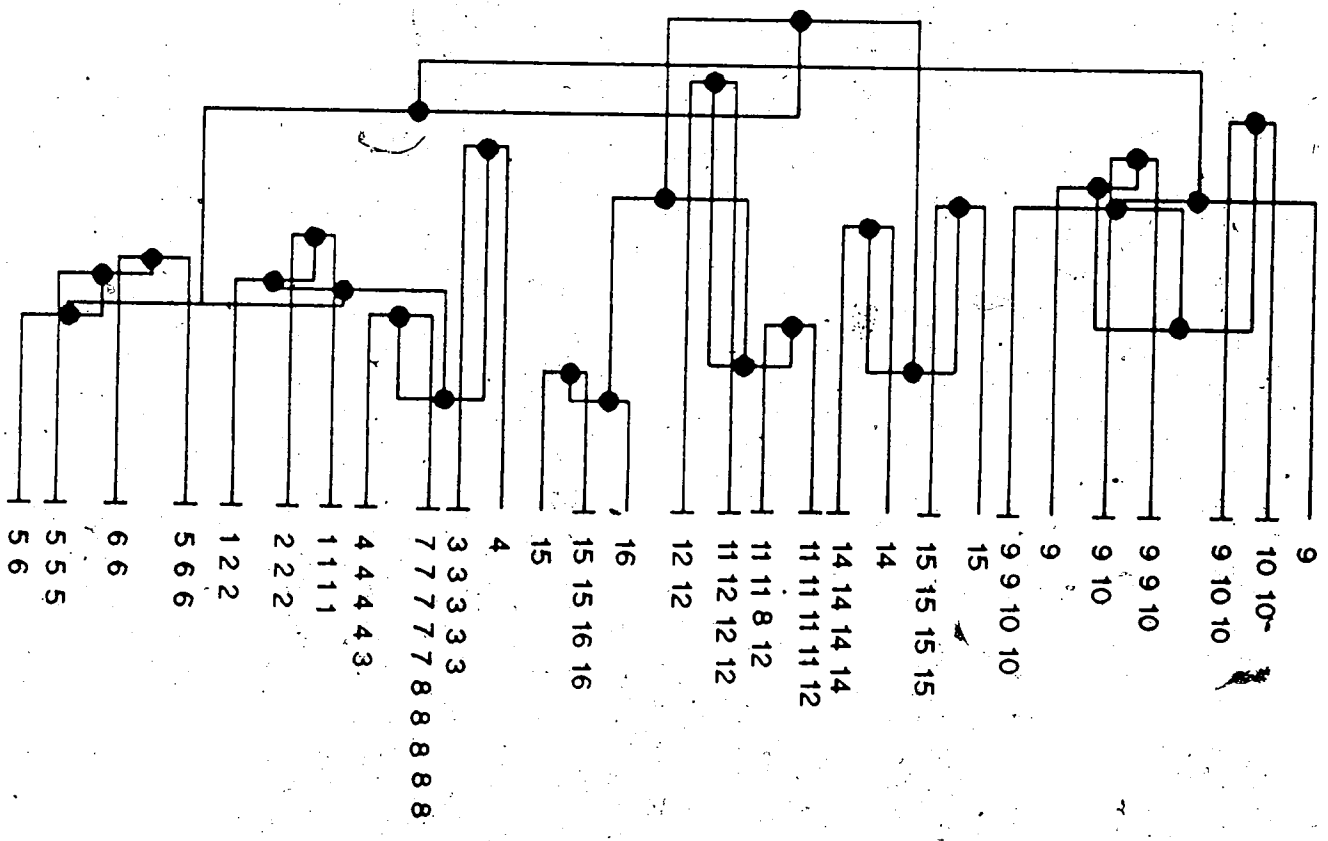

Figure III-5. Dendrogram derived from the TWINSPAN analysis comparing the fly faunas attracted to droppings associated with *T. angustatus* (dry=1,wet=2), *T. mnioides* (dry=3, wet=4), *S. ampullaceum* (dry=5, wet=6) and *S. luteum* (dry=7, wet=8) in the first trapping experiment and of the fly faunas attracted to droppings associated with *T. angustatus* (dry=9,wet=10), *T. mnioides* (dry=11, wet=12), *S. ampullaceum* (dry=13, wet=14) and *S. luteum* (dry=15, wet=16) in the second trapping experiment.

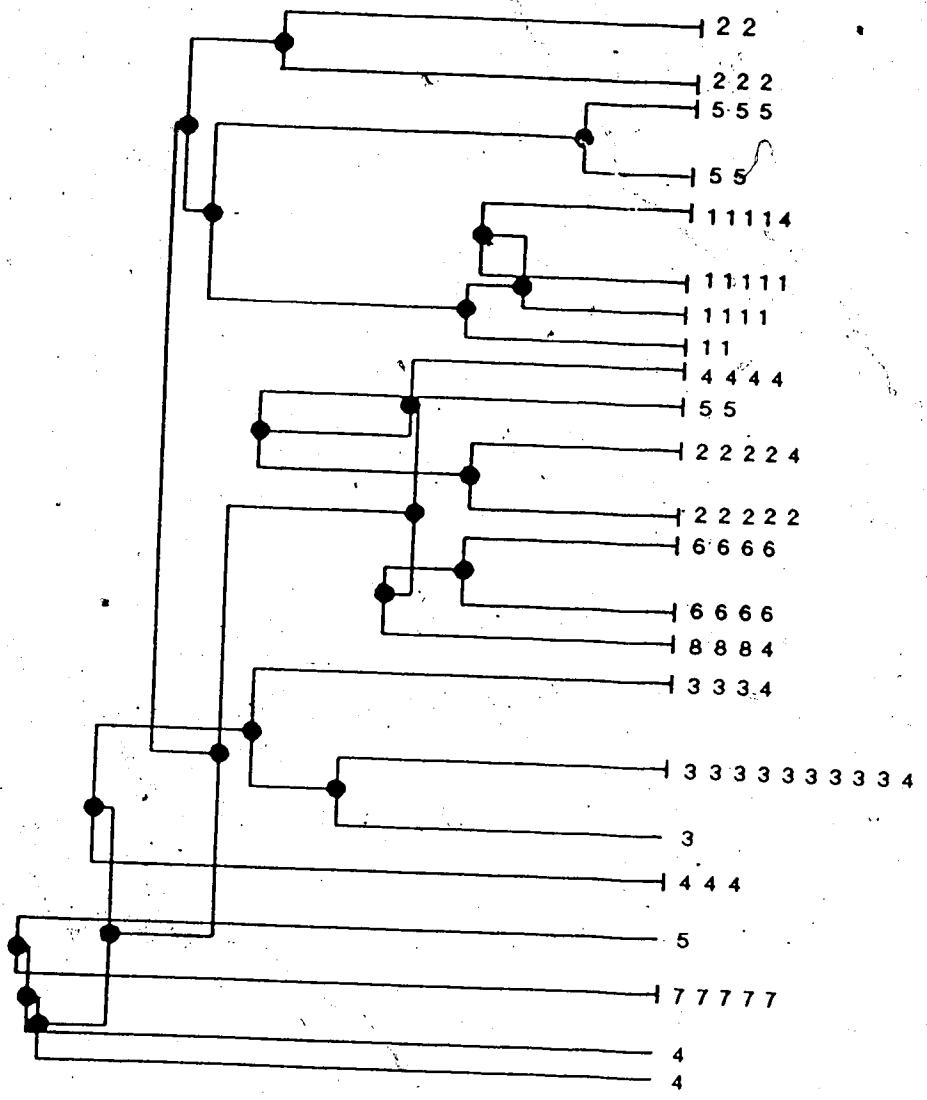

Figure III-6. Dendrogram derived from the TWINSPAN analysis comparing the fly faunas associated with *T. angustatus* (1), *T. mnioides* (2), *S. ampullaceum* (3), and *S. luteum* (4) in the first trapping experiment and the fly faunas associated with *T. angustatus* (5), *T. mnioides* (6), *S. ampullaceum* (7) and *S. luteum* (8) in the second trapping experiment.

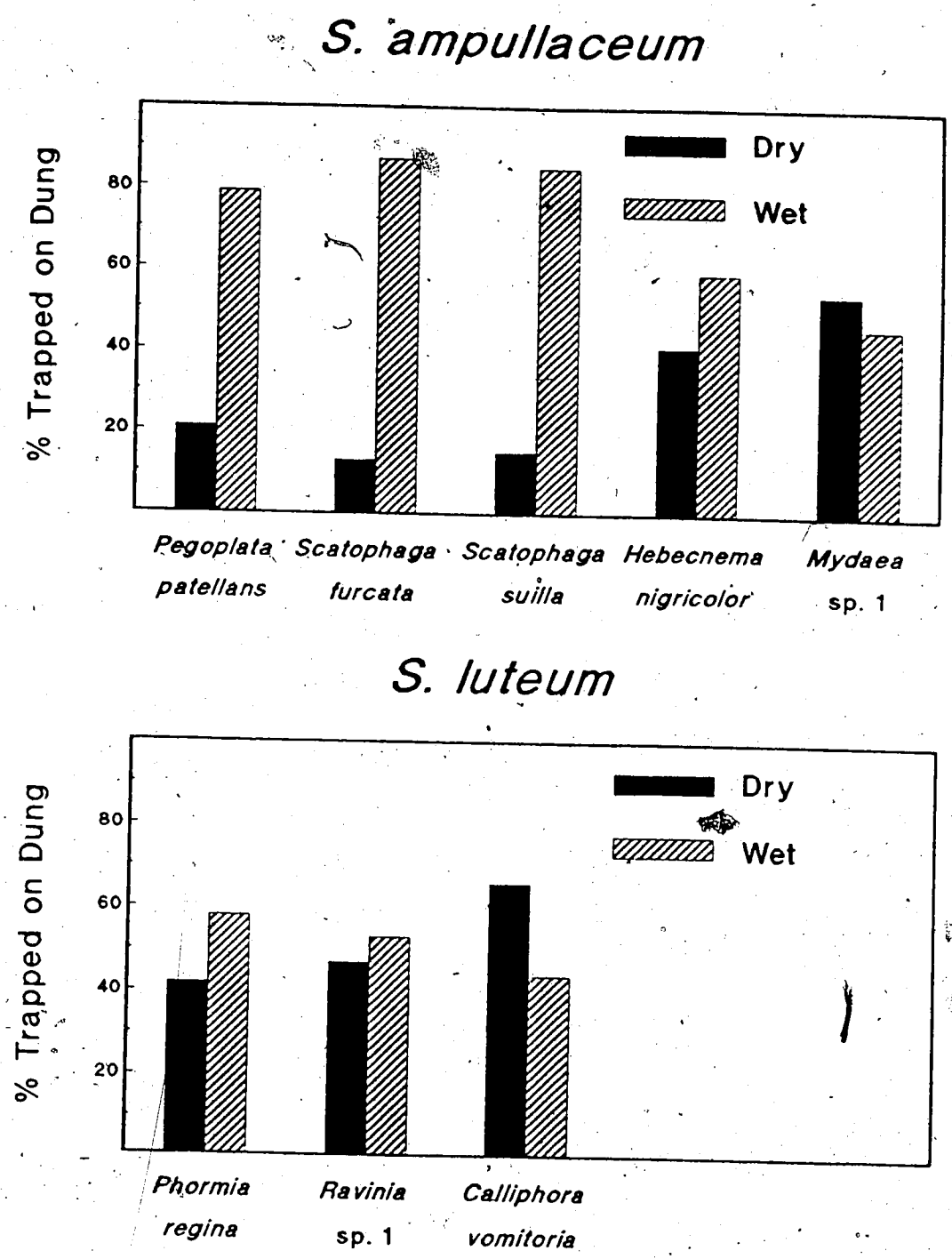

Figure III-7. The percent of each spore-carrying fly species trapped on dung in dry and wet habitats associated with *S. ampullaceum* and *S. luteum*. Only fly species in which more than 5 individuals carried spores and more than 20 individuals were trapped on dung are considered.

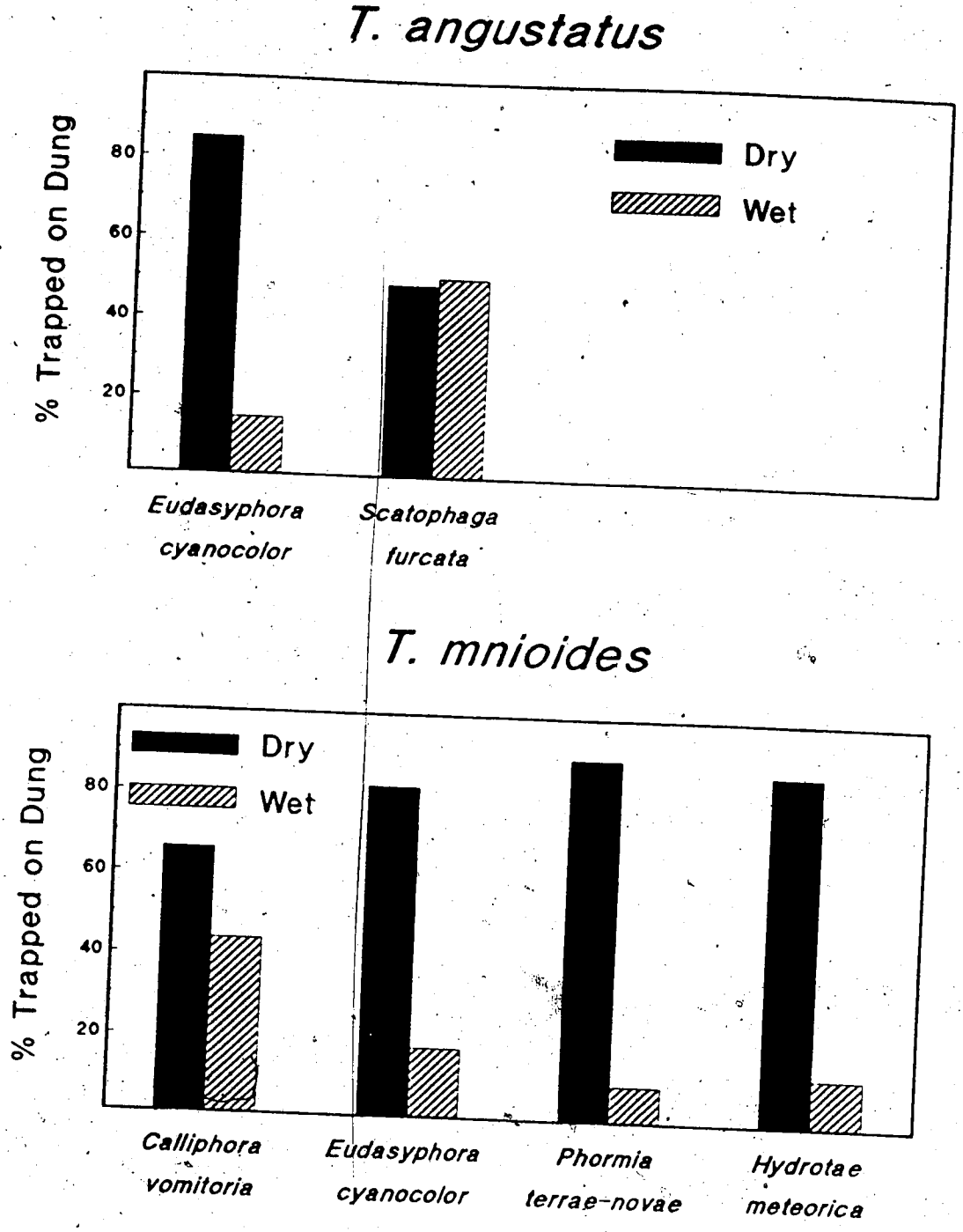

Figure III-8. The percent of each spore-carrying fly species trapped on dung in dry and wet habitats associated with *T. angustatus* and *T. mnioides*. Only fly species in which more than 5 individuals carried spores and more than 20 individuals were trapped on dung are considered.

E. REFERENCES

Andrewartha, H.G. and L. C. Birch. 1954. The Distribution and Abundance of Animals. The University of Chicago Press, Chicago, IL.

Atkinson, W.D. and Shorrocks. 1981. Competition on a divided and ephemeral resource: a simulation model. Journal of Animal Ecology 50:461-471.

Chesson, P. L. 1983. Coexistence of competitors in a stochastic environment: the storage effect. *In* H. I. Freedman and C. Strobeck, eds., *Population Biology,* pp. 188-198. Lecture Notes in Biomathematics no. 52. Springer-Verlag, Berlin, New York.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263-287.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist 117:923-943.

Commins, H.N., and I. R. Noble. 1985. Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. American Naturalist 126:706-723.

Elton, C. 1949. Population interspersion: an essay on animal community patterns. Journal of Ecology 37:1-23.

Hanski, I. 1981. Coexistence of competitors in patchy environment with and without predation. Oikos 37:306-312.

Hanski, I. 1983. Coexistence of competitors in patchy environment. Ecology 64:493-500.

Hanski, I. 1987. Carrion fly community dynamics: patchiness, seasonality and coexistence. Ecological Entomology 12:257-266.

Hanski, I., and S. Kuusela. 1980. The structure of carrion fly communities: differences in breeding seasons. Annales Zoologici Fennici 17:185-190.

Hanski, I., and E. Ranta. 1983. Coexistence in a patchy environment: three

species of *Daphnia* in rock pools. Journal of Animal Ecology 52:263-279.

Hutchinson, G.E. 1975. Variations on a theme by Robert MacArthur. *Ecology and Evolution of Communities* (Ed. by M.L. Cody & J. M. Diamond) pp. 492-541. Belknap, Harvard University Press, Cambridge, Massachusetts.

Ives, A. 1988. Aggregation and the coexistence of competitors. Annales Zoologici Fennici 25:75-88.

MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. Proceedings of the National Academy of Science U.S.A. 51:1207-1210.

-----. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101:377-385.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. Special Publications, Academy Natural Science, Philadelphia 12:245-270.

Pyysalo, H., A. Koponen and T. Koponen. 1978. Studies on entomophily in Splachnaceae (Musci). I. volatile compounds in the sporophyte. Annales Botanici Fennici 15:293-296.

Pyysalo, H., A. Koponen and T. Koponen. 1978. Studies on entomophily in Splachnaceae (Musci). II. volatile compounds in the hypophysis. Annales Botanici Fennici 20:335-338.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrica 38:196-218.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128-134.

Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman and Company, San Francisco.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. *In* S. T. A. Pickett and P. S. White eds., *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 101-152. Academic Press, Inc. Orlando,

Florida.

Vitt, D. H. 1981. Adaptive modes of the moss sporophyte. The Bryologist 84:166-186.

Webster, H. 1974. Studies of the Splachnaceae (Musci) and their mineral nutrition. Ph.D. dissertation, University of Tennessee, Knoxville.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist 125:769-787.

Appendix III-1. Fly species captured on Splachnaceae and associated dung and in control traps in the first trapping experiment.

Fly Species	*T. angustatus*	Dry Dung	Wet Dung	*T. mnioides*	Dry Dung	Wet dung	*S. ampullaceum*	Dry Dung	Wet dung	*S. luteum*	Dry Dung	Wet Dung	Controls
F. Acartophthalmidae													
F. Anthomyiidae								1	1		7	1	
Acrostilpa latipennis													
Alliopsis angustifrons													
Anthomyia mimitica	4									1			1
Anthomyia occulifera	9	4											
Botanophila appendicula											3	1	1
Calythea bidentata										1			
Chirosia hirtipes												1	
Delia sp. 1.													2
Delia sp. 2					1								
Delia platura					1					1			
Delia nigricaudata				4		3				3		1	1
Egle concomitaus	2	1	4	8	4	1		1		1	1		
Eutrichota lusescens			1										
Hydrophoria sp. 1										1			
Hylomyza partita	4	30	20	10	39	24	8	20	22	1	23	19	
Lasiomma sp. 1	4			2									
Lasiomma sp. 2			1					1					
Lasiomma atricauda			1	1	1	1					3	10	
Lasiomma vegoguttatum				1	1	4					2	2	
Leucophora sp.1				1									
Pegoplata infirma					1								
Pegoplata juvenalis												2	

Pegoplata patellans					3	1	33		7		14	2			
Pegoplata nigroscutellata	37	2	5	7	2	3			4	2	9	2	7		
Parapegomya socculata	1			3	1	1					1				
F. Calliphoridae															
Calliphora terrae-novae				2							1				
Cynomyopsis cadaverina				8		2		1				3			
Lucillia illustris				8					1		1				
Phormia regina				70		2					1	1			
Phormia terrae-novae				17	1	1			1			1			
F. Canidae															
Meoneura spp.		14	14	34	6	5		5	2	2	28	30			
F. Cecidomyidae													1		
F. Chironomidae		1				1	4			2	4		9		
F. Chloropidae		5	4	3		1	9	2	1	7	2	3	16		
F. Culicidae				1	1										
F. Dolichopodidae		1			1	8			1	2	1	2	10		
F. Drosophilidae		1	1												
F. Ephydridae			1				1		1				1		
F. Fanniidae															
Fannia brevicauda								2	11						
Fannia spathiophora	1			27	7	4				9	4	34	1		
F. Heliomyzidae	1			18											
F. Heteromyidae															
F. Hybotidae			2	1	5			2			6	1	2		
F. Lauxaniidae											3		2		
F. Milichiidae											1				
F. Muscidae															
Alloeostylus diaphanus				1	11	1		1			1		1		
Azelia sp.1		1	1		1						6	3			

Coenosia sp.1						1				1			
Coenosia sp.3											1		
Coenosia sp.4				1									
Eudasyphora cyanocolor		9	13	34	150	36		3	3	3	131	50	
Helina cothurnata	9	2	6			1				2	1	3	
Helina sp.1				4			1			2	3	5	1
Helina sp.2										5	1	1	
Helina sp.4										2			
Helina sp.5			2							1			
Hydrotae cristata				5									
Hydrotae militarus				3			1		1	2	1	2	
Hydrotae sp.2				1		2					1		1
Hydrotae sp.3						2				2			
Hypodermoides solitarius					1						2	1	
Graphomyia maculata						15			2	1	1	14	
Gymnodia sp.1													1
Lasiops sp.1				4	7					9	12	6	
Lasiops sp.3					1						1	1	
Lasiops sp.4						1					2		
Lasiops sp,5											1		
Limnophora sp.1										3			
Morellia podagrica					8	3	2		4	4	5	9	
Muscina assimilis			1	11	6	10			4	1	3	10	
Myospita meditabunda		11	22	5	20	52		9	12	2	20	50	
Mydaea sp.1	1				4	2	2	1		4	21	23	1
Mydaea sp.2				5	2				3	1	3		
Mydaea sp.4											1		
Mydaea sp.5					1	1		1		2	3	2	
Orthellia caesarium		1	1			2			1		1	1	

Phaonia curvipes					1	1	1	1	3		3	3				
Phaonia sp.1				2	2		4	1			8	6	2			
Phaonia sp.2											1	1				
Phaonia sp.3												1				
Pseudophaonia griseocaerulea			2		2			2								
Pseudophaonia orichalceoidies			1								6					
Pseudocoenesia sp.1												2				
Schoenomyza sp.1													3			
Spilogona sp.1			7					1				2				
Spilogona sp.2										1	2					
F. Mycetiphilidae				1	1						1	4				
F. Phoridae	25	1	5	4							1	1	9			
F. Piophilidae								4			7	9				
F. Psychodidae												1	1			
F. Rhagionidae											1					
F. Sarcophagiadae																
Ravinia sp.1				2	7	10		1		2	5	12	1			
Sarcophaga sp.1		4	4	3						1	1	3				
Sarcophaga sp.2													1			
F. Scatophagidae																
Scatophaga furcata		4	59			1				1	1	2	1			
Scatophaga suilla								1								
F. Sciaridae	1	2	1				7	1	1		2	3	4			
F. Sciomyzidae	1	1	1	2		2	2		1	4			14			
F. Sepsidae																
Sepsis spp.		6	9	52	4	24	4	2	7	1	28	18				
F. Sphenoceridae	2	4		4	2	1	4	18	15	1	2	2				
F. Stratiomyidae																
Sargus sp.1					23	2	4	63	89		14	2	1			

F. Syrphidae		1	1			1	7	3	2
F. Tabanidae									1
F. Tachinidae				2	1	2	3	6	3
Tephrochlamys sp.1	1								
F. Tipulidae								1	

Appendix III-2. Fly species trapped on each Splachnaceae species and associated dung in the second trapping experiment. In cases where flies were trapped carrying spores, the number following the '/' is the number of individuals of that particular fly species carrying spores.

Fly Species	*T. angustatus*	Dry Dung	Wet Dung	*T. mnioides*	Dry Dung	Wet dung	*S. ampullaceum*	Dry Dung	Wet dung	*S. luteum*	Dry Dung	Wet Dung
F. Acartophthalmidae						2		1	4			
F. Anthomyiidae												
Acrostilpa atricauda						2						
Acrostilpa latipennis						1						
Alleostylus diaphanus					5							
Alliopsis sylvestris									1			
Craspodechaeta sp.1					1					1/1		
Delia augusta						1						
Delia florilega				1								
Delia platura					2	1	5	4	24	2	1	1
Delia sp.2		2			1					1		
Eutrichota labradorensis				1								
Hylomyza partita		1	2		18	4		3	9	6	20	13
Lasiomma sp. 1	1	1										
Lasiomma sp. 2	1/1	1										
Lasiomma sp. 3	1				1				1	2	1	1
Hebecnema nigricolor					1		3	7	10/1			
Hebecnema umbricata									1			
Hebecnema vespertina		2	15					1				
Lyperisiops alcis									1			
Paregle cinerella					3	2						
Parapegomya occulata					1							1
Pegohylomya sp.2				5/3	10	1		2	2			
Pegoplata patellans					9	4	18/11	40/5	159/12	16/4	1	

Pegoplata nigroscutellata	1/1			2	18	4					3/2	3	3
Thricops sp. 1				1	17	2							
Thricops sp. 2					4	4							
Thricops sp. 3					4	1	1	4	12				
Thricops sp. 4						1							
F. Calliphoridae													
Calliphora vicina						1			1				
Calliphora vomitoria				17/12	20/1	11	2/2	14/1	16/1	16/1	16/1	5	
Cynomyopsis cadaverina	2/1	1		9/7		1					2		
Eucalliphora liliaceae				1	2				3				
Lucilia sp. 1				4		1							
Lucilia sp. 2				1						1			
Eutrichota cylindrica	1/1												
Phormia regina				8/4	1	1			5	72/17	13	15/1	
Phormia terrae-novae	2/2	2		21/7	187/2	20				11	1	7/1	
Phormia sp. 3										6/1		3	
F. Chironomidae			1										
F. Chloropidae		1	1										
F. Dolichopodidae													
F. Drosophilidae	1		17							2			
F. Eupidae			1						6				
F. Fanniidae													
Fannia brevicauda		1		3	1		8/1	3	41	46	5	25	
Fannia fuscula	1												
Fannia pallidoventris						2							
Fannia spathiophora				229/3	87	34				5	2	2	
Fannia sp. 1					2/2								
Fannia sp. 2								1					
Fannia sp. 3								3				2	

Fannia sp. 4							1	14	1			6	
Fannia sp. 5												1	
Fannia sp. 6												1	
Fannia sp. 7											1		
Fannia sp. 8												1	
Fannia sp. 9		14	21	1									
F. Heliomyzidae		1		1	2			8	5				
F. Hybotidae		1											
F. Muscidae													
Azelia sp.1									4				
Azelia sp.2									1				
Coenosia sp.1		1	3				2		5				
Eudasyphora cyanocolor	10/10	23/3	4	16/9	59	13/1		11/1	7	5/2	4	5	
Helina cothurnata	16/11		1	1/1	2								
Helina sp. 1				1	2	3			1/1				
Helina sp. 2				2/1	3							1	
Helina sp. 4						2							
Helina sp. 6					1						1		
Hydrotae meteorica				42/9	161	24		4	2	19/1	15	17	
Hydrotae militarus				14	23	25	3/3	1	1	5	3	2	
Hydrotae scambus				14	23	25				41/3	10	19	
Hydrotae unispinosa				2	8	4	3/3			1			
Hydrotae sp. 2					3								
Hydrotae sp.3				2	1	1				1		1	
Hypodermoides solitarus					7	3		2	5				
Graphomyia maculata				1	10	11				1		1	
Gymnodia sp. 1			1										
Limnophora sp. 1				1						2		1	
Limnophora sp. 2				1									

Limnophora sp. 3															
Morellia podagrica	1/1												1		
Muscina assimilis			3	49	7			3	6	3/1	5	6			
Myospita meditabunda		3	3/-	9	11/1				5						
Mydaea sp.1			1	14	21				4	13/4	8	21/1			
Mydaea sp.2			3	38	14	10/4		33/1	28/2	2	2	2			
Orthellia caesarium				4	4										
Phaonia curvipes												1			
Phaonia sp.2				1	2	2/1		1/1	3						
Phaonia sp.3				1							2				
Schoenomyza sp.1						1									
Spilogona sp.1					5										
Spilogona sp.2			1			2			4						
F. Phoridae				1											
F. Sarcophagidae		2	2	3	1										
Ravinia sp.1															
Ravinia sp.2			3/2	7	1				3	47/13	69/1	79/2			
Sarcophaga sp.1										1	2				
Sarcophaga sp.2			1/1									1			
Sarcophaga sp.3						1/1									
Sarcophaga sp.4											1				
F. Scatophagidae												1			
Megapthalmoides utixcota						1									
Scatophaga furcata	18/8	360/1	374/2	5	3	10/4		11	62/3						
Scatophaga stercoraria						1		1	2						
Scatophaga suilla			1		1	7/4		44	70/1						
F. Sciaridae	1	1	3		1										
F. Sciomyzidae	1		1	2/1	1				1						
F. Sepsidae															

Sepsis spp.	7/3	34	85	4	36	50			2	24	17	64
F. Simulidae				3	2	6			1			
F. Sphenoceridae		1	8	1	5	1	1/1	3	4			
F. Stratiomyidae												
Sargus sp.1						1				1	1	6
F. Syrphidae					2	1						
F. Tachinidae			1				1			6	2	

IV. REGIONAL COEXISTENCE AND SPORE AGGREGATION: A SIMULATION STUDY

A. INTRODUCTION

Habitat division or patchiness can influence communities of interacting species (Elton 1949; Andrewartha and Birch 1954; Huffaker 1958; Kareiva 1986). The influence of environmental patchiness on ecological communities has been examined primarily with mathematical models (e.g., Slatkin 1974; Levin 1974; Atkinson and Shorrocks 1981; Hanski 1981; Ives and May 1985; Commins and Hassell 1987). Few studies, however, have examined the significance of these models by extending them to examine the dynamics of particular systems (e.g., Kareiva 1986; Ives 1988). Here I extend Atkinson and Shorrocks' (1981) model simulating the influence of the independent intraspecific aggregation of individuals in a patchy environment on competitive coexistence to examine the coexistence of the mosses *Splachnum ampullaceum* and *S. luteum* (F. Splachnaceae) on a regional spatial scale. These mosses grow on the dung of large mammals and have spores that are dispersed to dung by flies (Diptera). I have simulated coexistence in this community because the spatial and temporal scales at which this problem must be examined are extensive and preclude the use of experimental studies. Also, since plants almost always exhibit clumped spatial dispersions (Kershaw 1973), the extension and modification of Atkinson and Shorrocks' (1981) model to plant communities contributes to our understanding of the role of aggregation promoting coexistence.

Atkinson and Shorrocks (1981) simulated the outcome of competition between two insect species that use patchy and ephemeral resources (e.g., fruit, fungi, carrion or dung). Their model suggested two processes that can prolong coexistence: increasing dividedness of resources, and increasing aggregation of the competitors. In this model, each of the two competitors had discrete,

non-overlapping generations (with the two species being temporally synchronized), and patches persisted for one generation. Insect larvae competed within a patch, so that the number of adults produced per patch was a non-linear function of the number of eggs oviposited. If resources were increasingly divided (i.e., patches became smaller but total resource abundance remained constant) or if insect eggs were independently aggregated on patches, then coexistence was prolonged.

Atkinson and Shorrocks (1981) assumed 'contest' competition, where the density effects tend to scale roughly linearly with the number of competitors. However, Ives and May (1985) found Atkinson and Shorrocks' (1981) results to be largely unaffected whether 'scramble' and/or 'contest' competition was assumed. Ives and May (1985) concluded that, if resources existing in patches are discrete and ephemeral, intraspecific aggregation in a patchy environment can, by itself, facilitate competitive coexistence.

Study System

Splachnum ampullaceum and *S. luteum* coexist throughout much of north temperate and boreal North America on a regional spatial scale. The regional scale involves areas of approximately 1-2 ha. This is the area from which spores of different local *Splachnum* populations are likely to disperse to the same fresh dropping. Coexistence at this scale is a function of factors such as population density and the mobility of flies that transport the spores of Splachnaceae.

These mosses are relatively fast growing, occupying the entire surface of a dropping within one or two summers, and reproducing within two or three years. No other mosses or vascular plants colonize these habitats as quickly as *S. ampullaceum* and *S. luteum* and the mosses have no herbivores. The two species differ in sporophyte morphology, but they are found growing on the same types of droppings (mainly moose, *Alces alces*) in the same types of habitats (Chapter III). Further details about the biology of the system can be found in Chapter

II.

There are several reasons why the spores of different species do not aggregate independently of each other on droppings. First, droppings attract flies for a short period of time (1-2 days) (Chapter II). Therefore, the time that droppings are likely to be colonized by spores is very short. Second, there is little synchrony in spore production either within or between *S. ampullaceum* and *S. luteum*. Therefore, how many spores of each species are dispersed to fresh droppings is likely to depend on how many mature populations of each *Splachnum* species are in close proximity to that dropping. As a result, even in regions where both *S. ampullaceum* and *S. luteum* are found growing, the spores of each species may become aggregated on different droppings.

B. THE MODEL

In central Alberta, where I have studied the coexistence of Splachnaceae, *S. ampullaceum* and *S. luteum* are primarily restricted to peatlands and peatlands are relatively discrete in space being separated from one another by upland forest. I have therefore simulated the regional aggregation of *S. ampullaceum* and *S. luteum* both within a single region (one peatland) and within an area encompassing three discrete regions (peatlands) with limited spore dispersal between them (Figure IV-1).

Within a region, the spores of *S. ampullaceum* and *S. luteum* were distributed independently of each other on n droppings of the same size, according to a randomly-generated negative binomial distribution (Hastings and Peacock 1974). The aggregation parameter (k) used to generate the negative binomial distribution was set at 0.5 (no aggregation) and 0.01 (moderate aggregation). The number of new droppings (n) available per year was set at either 5, 10, 25, 75 or allowed to vary randomly between 0 and 25 or 0 and 75. A generation delay of three years was imposed, such that no colonized

dropping produced propagules until two more sets of *n* droppings received spores. Occupied droppings ceased to exist after the mosses on them have reproduced. Spores were distributed on the first three sets of *n* droppings according to the reproductive output of either *S. ampullaceum* or *S. luteum* on droppings that they occupied completely. Spores were distributed on further sets of *n* droppings as a function of the relative number of spores produced by each *Splachnum* species in the simulation.

The competition equations used to determine the reproductive output of each species in each patch were variations of the Ricker equations:

$$S_1(t) = \lambda_1 S_1(t-3) e^{-\beta S_1(t-3) - \alpha_{12} S_2(t-3)}$$

$$S_2(t) = \lambda_2 S_2(t-3) e^{-\beta S_2(t-3) - \alpha_{21} S_1(t-3)}$$

where S_1 and S_2 are the reproductive output of *S. ampullaceum* and *S. luteum* respectively per patch at time t, β and α are the intra- and interspecific competition coefficients, and λ_1 and λ_2 are the intrinsic rates of increase of *S. ampullaceum* and *S. luteum* respectively.

λ_1 and λ_2 were calculated by determining, from field observations, the average density of female gametophytes per dropping, assuming a 1:1 sex ratio of gametophytes on droppings (*S. ampullaceum* = 422.25/cm², and *S. luteum* = 318/cm²), and estimating the mean number of spores produced per sporophyte (*S. ampullaceum* = 1,020,000; *S. luteum* = 5,810,000). Based upon these estimates, λ_2 (*S. luteum*: 104,199,910 spores/dropping) was greater than λ_1 (*S. ampullaceum*: 68,438,709 spores/dropping).

Two values of α_{12} and α_{21} were estimated for each species. The first values were based on the results of a field growth study in which *S. ampullaceum* and *S. luteum* were found not to differ in relative competitive ability when grown together on droppings at different densities and relative proportions (Chapter II).

α_{12} and α_{21} were, therefore, each set at 0. Therefore, using this first estimate for α_{12} and α_{21}, *S. luteum* has an advantage over *S. ampullaceum* because of a fecundity advantage despite having no competitive advantage. The second values of α_{12}(=-0.7841) and α_{21} (=1.3078) were derived from the results of a laboratory study in which *S. luteum* had a competitive advantage over *S. ampullaceum* when they were grown under homogeneous conditions at equal spore densities (Chapter II). Therefore, using this second estimate for α_{12} and α_{21}, *S. luteum* has an advantage over *S. ampullaceum* because of both a fecundity and a competitive advantage. Both sets of values were used since they likely represent the range of relative competitive abilities between the two species.

In order to better represent competition in Splachnaceae, the Ricker equations were modified. The terms:

$$S_1(t-3)e^{-\beta S_1(t-3)}$$

$$S_2(t-3)e^{-\beta S_2(t-3)}$$

were dropped from the original equation because in the Splachnaceae system these terms will always equal 1, since intraspecific competition, although intense, will have no effect on the total reproductive output of a species on a dropping. A dropping colonized by 1,000 spores of either *S. ampullaceum* or *S. luteum* will be covered by essentially the same number of gametophytes as one colonized by 1,000,000 spores of the same species, and therefore will produce essentially the same number of sporophytes and spores.

This equation was further modified by incorporating the terms:

$$\frac{S_1(t-3)}{S_2(t-3)+S_1(t-3)}e^{\alpha_{12}\frac{S_2(t-3)}{S_1(t-3)+S_2(t-3)}}$$

$$\frac{S_2(t-3)}{S_1(t-3)+S_2(t-3)}e^{\alpha_{21}\frac{S_1(t-3)}{S_2(t-3)+S_1(t-3)}}$$

into the competition equations. This was done because the output of spores from a dropping is not related to the density of spores colonizing that dropping, but rather is assumed to be a function of the relative proportion of spores of different species that colonize. Therefore, the competition equations used in this study were as follows:

$$S_1(t) = \lambda_1 \frac{S_1(t-3)}{S_2(t-3)+S_1(t-3)} e^{\alpha_{12}\frac{S_2(t-3)}{S_1(t-3)+S_2(t-3)}}$$

$$S_2(t) = \lambda_2 \frac{S_2(t-3)}{S_1(t-3)+S_2(t-3)} e^{\alpha_{21}\frac{S_1(t-3)}{S_2(t-3)+S_1(t-3)}}$$

The number of *S. ampullaceum* and *S. luteum* spores produced on all three-year-old droppings are summed and then distributed according to a randomly generated negative binomial distribution on n fresh droppings. This process continues until one of the species becomes extinct, and is repeated ten times for each combination of parameter values. The mean and standard deviations of the period of time to extinction of the 10 runs are presented in the results. The relative influence of each parameter and the influence of interactions between parameters on period of time to extinction were analyzed using ANOVA, with competitive asymmetry, number of droppings and degree of aggregation as categorical variables.

The second model considered the dynamics of *S. ampullaceum* and *S. luteum* on droppings in an area encompassing three peatlands assuming limited spore dispersal between the peatlands. The same combinations of parameter values used in the previous model were also used in this model, with the exception that the number of droppings per peatland did not exceed 25. A dispersal parameter that determines the percentage of spores dispersed among the peatlands was added to this model. It was set at either 0%, 1% or 5% of total spore

production per species per peatland. Each peatland potentially received spores dispersed from the other two peatlands. The dispersal values have been arbitrarily chosen since there are no data detailing the vagility of the fly species involved in the long distance dispersal of spores, the length of time spores remain on each species of fly, or the efficiency with which spores are transferred to dung by different species of flies. The relative influence of each parameter and the influence of interactions between parameters on period of time to extinction were analyzed using ANOVA, with competitive asymmetry, number of droppings and degree of aggregation and amount of dispersal as categorical variables.

C. RESULTS

In the one-peatland model all the factors examined (competitive asymmetry, aggregation and patch number) significantly increased the period of time to extinction (Table IV-1). The interaction between competition and aggregation was also significant (Table IV-1) because the influence of aggregation on time to extinction was greater with than without symmetrical competitive ability (Figure IV-2).

Given symmetrical competitive abilities, the moderate aggregation of spores on droppings increased the period of time to extinction by 1/3 over no aggregation of spores (Figure IV-2). As the number of droppings in a peatland is increased, the period of time to extinction also increased. Periods of coexistence of over 15 generations were achieved as the number of droppings added annually to a peatland approached 25 (Figure IV-2). Random fluctuations in the number of droppings between 0 - 25 resulted in a time to extinction similar to that obtained when the number of droppings added each year were held constant at 25 (Figure IV-2). Finally, random fluctuations in the number of droppings between 0 - 75 resulted in a time to extinction approximately twice as long as did fluctuations between 0 - 25 (Figure IV-2).

With the exception of random fluctuation between 0 - 25 and 0 - 75, the influence of competitive asymmetry on all combinations of these factors was to decrease the period of time to extinction by 2-3 generations (6-9 years). In simulations in which the number of droppings fluctuated between 0-25 and 0-75 droppings, the period of time to extinction was reduced by approximately half (Figure IV-2).

In the three-peatland model all the factors examined (competitive asymmetry, aggregation, patch number and dispersal) significantly increased the period of time to extinction (Table IV-2). The interaction between competition and aggregation, competition and patch number and aggregation and patch number were also significant (Table IV-2) because the influence of each of these factors together on time to extinction was greater than the influence of each factor alone (Figure IV-3).

The degree to which these three factors influenced the time to extinction in the three-peatland model with competitive equality differed little from the results obtained for dynamics within a single peatland (Figure IV-3). The period of time to extinction in the three-peatland model without dispersal between peatlands (Figure IV-3) was similar to the single peatland model (Figure IV-2), with the exception of there being a longer period of time to extinction at 10 and 25 droppings per peatland. Also, a comparison of no dispersal of spores between adjacent peatlands, 1%, and 5% indicated that spore dispersal at the levels examined increased the period of time to extinction, but generally by less than 2 generations (6 years). The influence of competitive asymmetry on all combinations of these factors was to decrease the period of time to extinction by approximately 50%. (Figure IV-3).

The period of time to extinction in a single peatland where numbers of droppings fluctuated between 0 and 75 (Figure IV-2) was 5-10 generations greater than the period of time to extinction in the three-peatland model (Figure IV-3)

at 25 droppings per peatland (75 total) under all parameter values for clumping and dispersal. Therefore, the inclusion of spatial division among peatlands appeared to have had less of an influence on the period of time to extinction, at the parameter values examined, than did the total number of droppings available for colonization.

D. DISCUSSION

Splachnum ampullaceum and *S. luteum* use the same resources and coexist regionally throughout much of north temperate and boreal North America. Simulation results suggested that the dividedness of droppings and the independent intraspecific aggregation of spores on droppings promote coexistence of these species. Increasing numbers of new colonization sites (droppings) available each year increased the period of time to extinction from 2-10 generations for all combinations of parameter values examined. The independent intraspecific aggregation of spores on droppings increased the period of time to extinction between *S. ampullaceum* and *S. luteum* by approximately 1/3 (2-6 generations) for all combinations of parameter values examined.

Unlike the simulation model of Atkinson and Shorrocks (1981), in which resource levels were held constant and an increase in patch number consequently decreased patch size, in the present study, increasing patch number was equivalent to increasing resource abundance. This increase in resource abundance increases the period of time to extinction between *S. ampullaceum* and *S. luteum*.

A comparison between the single peatland and the three-peatland model also suggested that resource abundance was an important in increasing time to extinction between species. This is because there was little difference between times to extinction in a three-peatland model with or without dispersal of spores between adjacent peatlands, and a single peatland model in which the number of droppings either equaled or fluctuated within the same range of values as the

total number of droppings in the three-peatland model. However, the possible influence of long-distance dispersal as a factor promoting competitive coexistence remains unclear. For example, an inverse relationship between long-distance dispersal ability and competitive ability should promote coexistence (Hutchinson 1975; Hanski and Ranta 1983). More data is required about the relative long distance dispersal abilities of the flies dispersing spores of *S. ampullaceum* and *S. luteum* before conclusions can be drawn concerning the influence of the spatial division between peatlands on moss coexistence.

The abundance of droppings in central Alberta in fact fluctuates considerably between years. For example, in a region of approximately 2 ha in central Alberta I located 300 droppings occupied by either *S. ampullaceum* or *S. luteum* in 1983, whereas in 1985, I located only 20 occupied droppings. This difference between years was a direct result of resource fluctuations since, with the exception of very fresh droppings, all droppings in this area were occupied by either one or both species of *Splachnum*. The number of droppings fluctuate because moose, the main source of droppings in central Alberta, undergo large population fluctuations (Blyth and Hudson 1987). Therefore, simulations in which the number of droppings per year fluctuated between 0 and 75 were those that most realisticly model the natural situation. Significantly, since more extreme fluctuations appear to be even more appropriate, realistic estimates of times to extinction should likely be much longer than those obtained from the current simulations.

Aggregation also clearly increased the period of time to extinction, as predicted by Atkinson and Shorrocks (1981). The actual degree of spore aggregation in *S. ampullaceum* and *S. luteum* is unknown. However, with knowledge of the relative abundance of the two species in a region, it should be possible to quantify the degree of aggregation in each species. Trapping experiments show that flies can be captured on droppings and the species of

spores carried can be determined (Chapter III).

The degree to which species aggregate can be influenced by changes in the density of species (Taylor et al. 1978). Atkinson and Shorrocks (1981) suggested that density increases resulting in decreased aggregation were destabilizing. I have not examined this possibility in the *Splachnum* system. It is likely that increasing densities of *S. ampullaceum* and *S. luteum* will result in decreased aggregation because of the greater probability that a fresh dropping will be near mature populations of both species. It is not known whether *Splachnum* densities are ever high enough to influence the degree to which spores become aggregated on droppings. However, because *Splachnum* are easily grown in the field, it should be possible to manipulate field densities and determine the degree to which density influences the aggregation of spores on droppings.

The parameter values used in the simulations to measure the relative competitive abilities of *S. ampullaceum* and *S. luteum* represent the range of probable values as derived from field and laboratory studies. Overall, it appears that *S. luteum* has a competitive advantage over *S. ampullaceum* because of both a fecundity and a growth advantage. However, it is unclear what values within this range are most appropriate for the growth advantage (α) and to what degree fluctuating environmental conditions (e.g., the amount of rainfall) may influence this advantage. Under certain sets of conditions the relative competitive abilities of the two species could even be reversed (Chapter II). This is important because environmental fluctuations that could cause this can themselves promote competitive coexistence (Chesson 1985). For this reason, the influence of environmental variation on the relative competitive abilities and coexistence of *Splachnum* requires further study.

The influence of differential dispersal ability on the coexistence of *S. ampullaceum* and *S. luteum* has not been examined in this study. The results of fly trapping suggest that *S. ampullaceum* has more of its spores dispersed to

droppings than does *S. luteum* (Chapter 3). This difference in relative dispersal ability should, in effect, decrease the influence of fecundity and growth differences between the species and thereby increase the period of time to extinction. Also, the inverse relationship between relative dispersal and competitive ability that appears to exist between *S. ampullaceum* and *S. luteum* may itself be a mechanism promoting regional coexistence (Chapter 3).

Summary

The mosses *S. ampullaceum* and *S. luteum* grow primarily on droppings and have spores that are dispersed to droppings by flies. Despite using the same resources, these mosses coexist throughout much of north temperate and boreal North America. Results of a simulation study indicated that the independent aggregation of spores on droppings and the availability for colonization, at least periodically, of large numbers of droppings may be important factors promoting the regional coexistence of *S. ampullaceum* and *S. luteum* both within a single peatland and within several adjacent peatlands. Further experimental work is necessary in order to determine to what degree spores become aggregated on droppings, the influence of population density on the degree of aggregation, the relative long-distance dispersal ability and the influence of environmental variation on the relative competitive abilities of *S. ampullaceum* and *S. luteum*.

Table IV-1 ANOVA examining the influence of competitive asymmetry, degree of aggregation and patch number on the period of time to extinction in the one-peatland model.

Source	Degrees of Freedom	Sum of Squares	Mean Square	F value	Probability
Model	11	7,692.4	699.3	44.3	***
Competition	1	2,448.0	-	245.9	***
Aggregation	1	3,876.0	-	29.9	***
Competition *Aggregation	1	472.0	-	27.5	***
Patch Number	2	866.8	-	27.5	***
Competition *Patch Number	2	1.3	-	0.04	NS
Aggregation*Patch Number	2	19.3	-	0.61	NS
Comp*Aggre*Patch Num	2	8.9	-	0.28	NS
Error	108	1,702.0	15.8		
Total	119	9,394.4			

*** P < .001, NS = not significant.

Table IV-2 ANOVA examining the influence of competitive asymmetry, degree of aggregation, patch number and dispersal on the period of time to extinction in the three-peatland model.

Source	Degrees of Freedom	Sum of Squares	Mean Square	F value	Probability
Model	35	127,470.2	3,642.0	60.5	***
Competition	1	58,293.2	-	968.9	***
Aggregation	1	36,824.7	-	612.0	***
Competition *Aggregation	1	9,620.3	-	159.9	***
Patch Number	2	15,107.9	-	125.5	***
Competition *Patch Number	2	3,192.6	-	26.5	***
Aggregation*Patch Number	2	1,183.1	-	9.8	***
Comp*Aggre*Patch Num	2	243.2	-	2.0	NS
Dispersal	2	1,591.8	-	13.2	***
Competition *Dispersal	2	250.0	-	2.1	NS
Aggregation*Dispersal	2	147.0	-	1.2	NS
Comp*Aggre*Disper	2	12.17	-	0.1	NS
Patch Number*Dispersal	2	493.9	-	2.0	NS
Comp*Patch Num*Disper	2	207.9	-	0.9	NS
Aggre*Patch Num*Disper	2	102.1	-	0.4	NS
Comp*Aggre*Patch Num*Disper	2	200.0	-	0.8	NS
Error	108	19,495.5	60.2		
Total	119	146,965.7			

*** P < .001, NS = not significant.

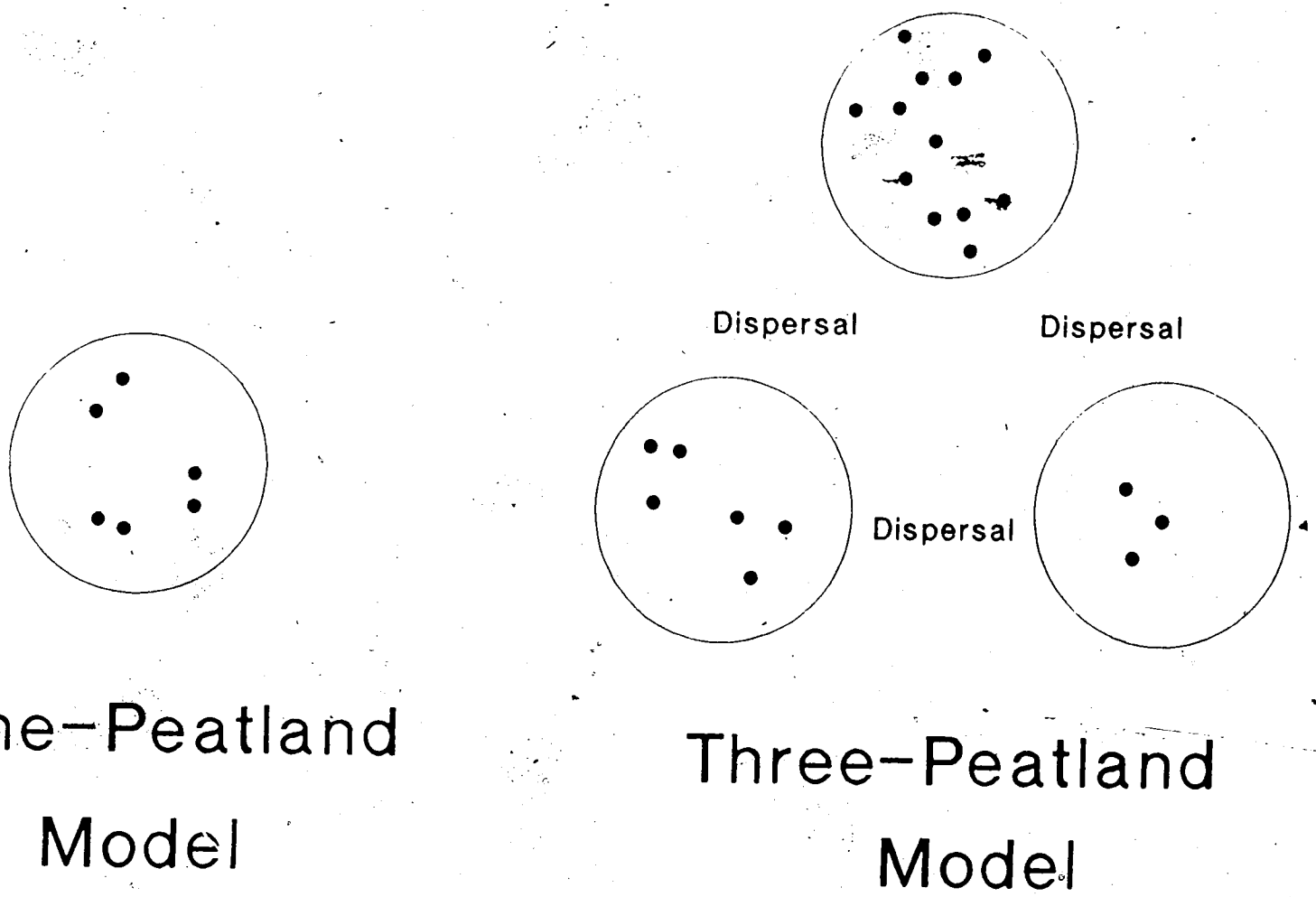

Figure IV-1. Diagramatic representation of the single-peatland and three-peatland models.

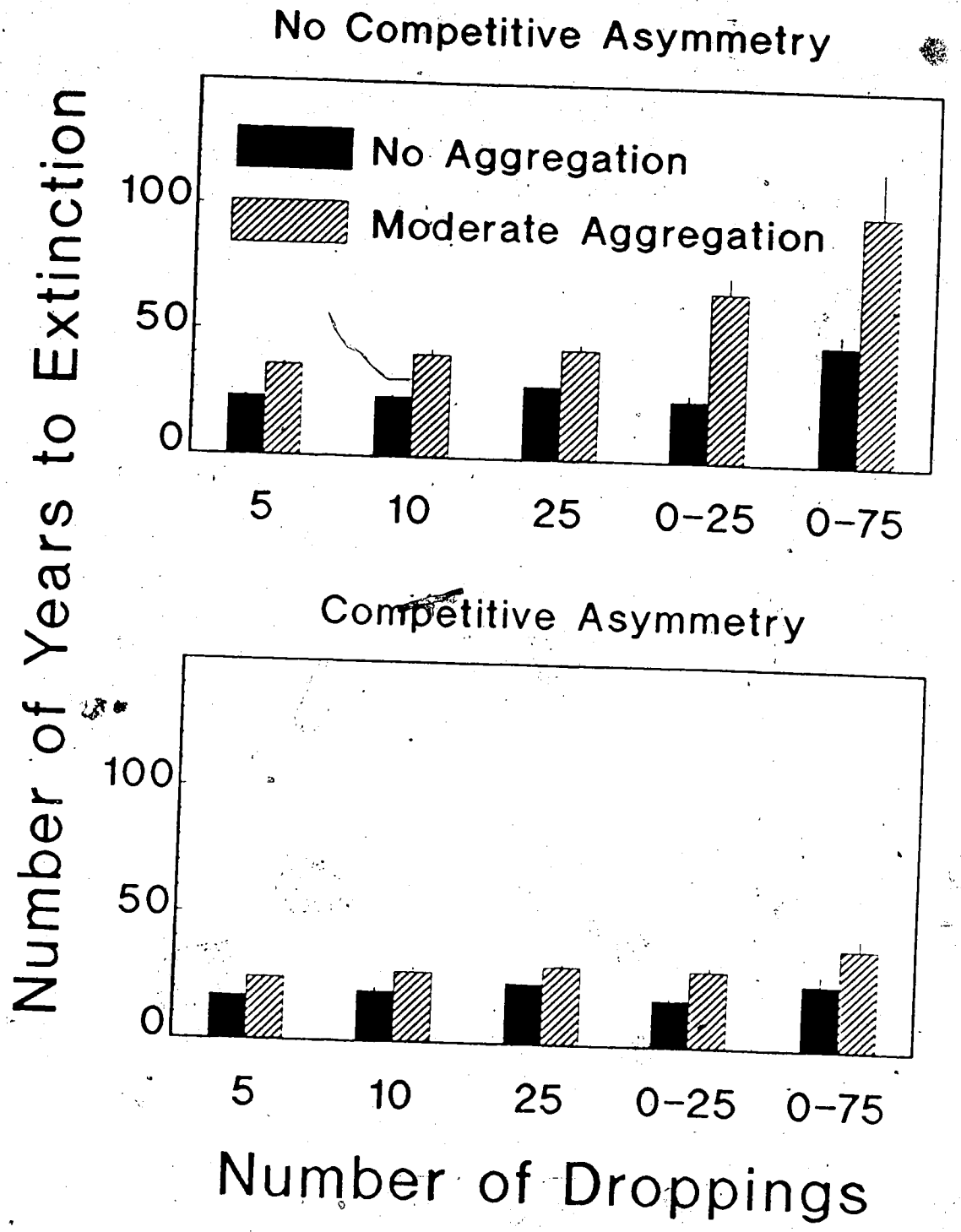

Figure IV-2. The period of time to extinction in the one-peatland model with 5,10, 25 and random (0-25 and 0-72) numbers of new droppings added each year with and without competitive asymmetry.

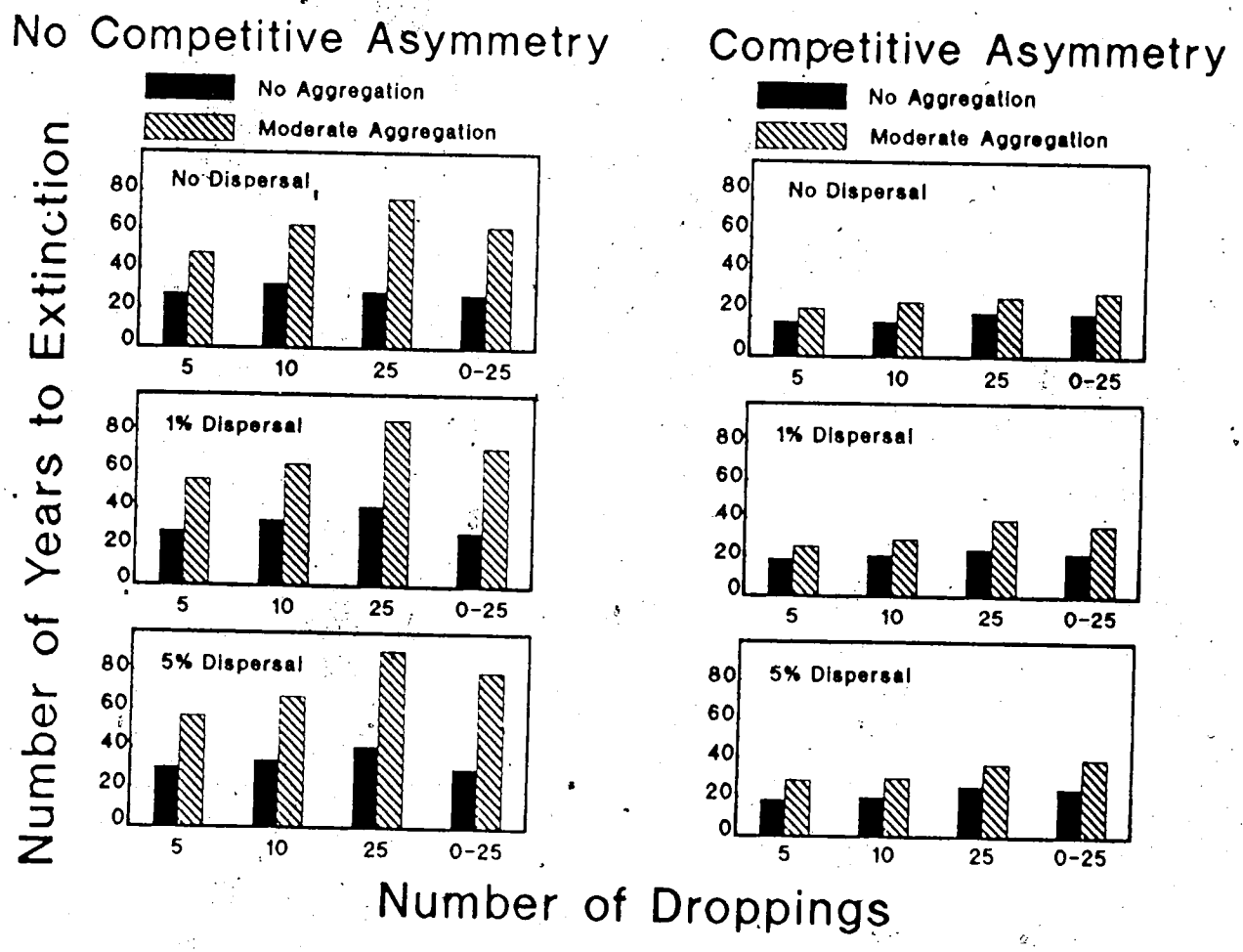

Figure IV-3. The period of time to extinction between *S. ampullaceum* and *S. luteum* in the three-peatland model with 5, 10, 25 and random (0-25) numbers of new droppings added each year with and without competitive asymmetry and with 0, 1 and 5% dispersal of spores.

E. REFERENCES

Andrewartha, H. G., and L. C. Birch. 1954. *The Distribution and Abundance of Animals*. The University of Chicago Press, Chicago, IL.

Atkinson, W. D., and B. Shorrocks. 1981. Competition on a divided and ephemeral resource: a simulation model. Journal of Animal Ecology 50:461-471.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263-287.

Commins, J. N., and M. P. Hassell. 1987. The dynamics of predation and competition in patchy environments. Theoretical Population Biology 31:393-421.

Elton, C. 1949. Population interspersion: an essay on animal community patterns. Journal of Ecology 37:1-23.

Hanski, I. 1981. Coexistence of competitors in patchy environment with and without predation. Oikos 37:306-312.

Hanski, I. and E. Ranta. 1983. Coexistence in a patchy environment: three species of *Daphnia* in rock pools. Journal of Animal Ecology 52:263-279.

Hastings, N. A. J., and J. B. Peacock. 1974. *Statistical Distributions*. Butterworths, London.

Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53:749-752.

Huffaker, C.B. 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.

Hutchinson, G. E. 1951. Copepodology for an ornithologist. Ecology 32:571-577.

-----. 1975. Variations on a theme by Robert MacArthur. *In* M. L. Cody and J. M. Diamond, eds., *Ecology and Evolution of Communities*, pp. 492-521. Harvard University Press, Cambridge, Mass.

Ives, A. R. 1988. Aggregation and the coexistence of competitors. Annales

Zoologici Fennici 25:75-88.

Ives, A. R., and R. M. May. 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. Journal of Theoretical Biology 115:65-92.

Kareiva, P. 1986. Patchiness, dispersal and species interactions: consequences for communities of herbivorous insects. *In* J. Diamond and T. Case eds., *Community Ecology*, pp. 192-206. Harper and Row, New York.

Kershaw, K. A. 1973. *Quantitative and Dynamic Plant Ecology*, 2nd ed. Edward Arnold, London.

Levin, S. A. 1974. Dispersion and population interactions. American Naturalist 108:207-228.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128-134.

Taylor, L. R., Woiwod, I. P. and J. N. Perry. 1978. The density-dependence of spatial behaviour and the rarity of randomness. Journal of Animal Ecology 47:383-406.

V. CONTINENTAL DISTRIBUTION PATTERNS

A. ABSTRACT

Splachnum ampullaceum, S. luteum, S. rubrum, S. sphaericum and *S. vasculosum* and *Tetraplodon angustatus, T. mnioides* and *T. urceolatus* are widely distributed from the east to the west coast of northern North America. However, the north-south distributions and the relative abundances of the species are not uniform across this range. *Splachnum* species differ as to whether they are most abundant in eastern *(S. ampullaceum)* or western North America *(S. luteum* and *S. sphaericum*) and in their north-south distribution (*S.vasculosum* in arctic regions, *S. luteum* in boreal and arctic regions and *S. rubrum* in boreal regions. *Tetraplodon* species differ in their north-south distributions (*T. urceolatus* in arctic regions, *T. mnioides* in arctic and boreal regions and *T. angustatus* in boreal regions) but are uniform in east-west distribution. *Tetraplodon* species are more frequent than *Splachnum* species and of *Splachnum* species the most frequent are those with the least modified sporophytes. In those specimens where two or more Splachnaceae species occur intermixed, only the species combination of *S. luteum* and *S. sphaericum* was frequent.

B. INTRODUCTION

The Splachnaceae have a worldwide distribution; however, the individual genera and species are more restricted in distribution. The genera *Aplodon, Splachnum, Tetraplodon, Voitia* and *Tayloria* subgenera *Tayloria* and *Cyrtodon* are concentrated in the Northern Hemisphere; *Brachymitrion, Moseniella* and *Tayloria* subgenus *Orthodon* in the tropical zones; and *Tayloria* subgenera *Eremodon* and *Pseudotetraplodon* in the Southern Hemisphere. In this paper the North American distributions of 5 species in the genus *Splachnum* and 3 species in the genus *Tetraplodon* are determined. All of these species are circumboreal in distribution.

In addition, I examined the relative abundances of the species and the frequency with which different species, both within and between genera, have been found growing together on the same microsites.

All species of the genera *Splachnum* and *Tetraplodon* are unique in that they grow on organic substrates, primarily dung, and have their spores dispersed to these substrates by Dipterans (Koponen & Koponen 1977; Cameron & Wyatt 1986; Marino 1988). These mosses have several unique adaptations promoting the dispersal of spores by Dipterans. These include the brightly colored and enlarged hypophysis, its characteristic odors (Pyysalo et al. 1978; Pyysalo et al. 1983), the elongate setae, sticky spores and the shrinkage of the capsule wall so that spores are pushed out of the capsule in a single sticky mass (Vitt 1981).

The local distribution and life history strategies of *Splachnum* and *Tetraplodon* differ. Species of the genus *Tetraplodon*, at least those of the boreal forest, are found growing primarily in dry habitats on raised areas within peatlands or on the upland forest floor; Northern Hemisphere species in the genus *Splachnum* occur primarily in moister habitats within peatlands. Associated with these habitat differences are differences in life-history strategies. Individual populations of *Tetraplodon* species produce sporophytes for as many as five years, whereas single populations of *Splachnum* species generally produce sporophytes only once. In all probability, this is related to the persistence of dung patches in these two general habitat types. In wet habitats, dung patches (patches of *Splachnum*) are overgrown by the surrounding bryophyte vegetation in two to three years and largely depleted of nutrients after one year. In dry habitats, dung patches (patches of *Tetraplodon*) are overgrown very slowly (> 3 years) or not at all and retain significant nutrients for more than one year (Marino 1988).

C. MATERIALS AND METHODS

The North American distributions of *Splachnum ampullaceum* Hedw., *S. luteum* Hedw., *S. rubrum* Hedw., *S. sphaericum* Hedw. and *S. vasculosum* Hedw., and *Tetraplodon angustatus* (Hedw.) BSG, *T. mnioides* (Hedw.) BSG and *T. urceolatus* (Hedw.) BSG were determined from herbarium specimens obtained from the University of Alaska (ALA), the University of Alberta (ALTA), the University of Copenhagen (C) (excluding material from Greenland), the National Herbarium of Canada (CANM), the University of Cincinnati (CINC), the University of Colorada (COLO), Duke University (DUKE), The Field Museum of Natural History (F), the Farlow Herbarium, Harvard University (FH), the University of Helsinki (H), the University of Iowa (IA), the University of Michigan (MICH), the University of Minnesota (MIN), the Missouri Botanical Garden Herbarium (MO), the University of Montreal (MT), the Memorial University of Newfoundland (NFLD), the New York Botanical Garden (NY), the Pennsylavania State University (PAC), the Swedish Museum of Natural History (S), The University of Laval (QFA), the University of Sherbrooke (SFS), the University of Tennessee (TENN), the University of Toronto (TRTC), the University of British Columbia (UBC), the United States National Herbarium (US), the University of Wisconsin (WIS), and the University of Washington (WTU). No varietal distinctions were made in determining the distributions of the Splachnaceae species. Therefore, *Splachnum vasculosum* Hedw. var. *vasculosum* and var. *heterophyllum* (Hook.) Brassard were both included in the distribution map of *S. vasculosum*. *Splachnum melanocaulon* (Wahlenb.) Schwaegr. appears to be a distinct species (Persson 1963) and he reported material from one locality in central Alaska. A second specimen is present in ALTA .Kluane Lake area, Yukon Territory Vitt # 6183. These are the only two specimens which I am aware of from North America and the species will not be treated further in this paper.

Taxonomic difficulties are present between *T. mnioides* and *T. urceolatus*. Whereas I consider *T. urceolatus* to be recognizable at the specific rank, there are some specimens that are difficult to determine., I have used the following characters to differentiate these taxa: *T. mnioides* - leaves flaccid, elongate twisted apices, setae green, generally > 2 cm in length; *T. urceolatus* - leaves firm, concave, stiff rounded apices, setae yellow, generally ≤ 2 cm in length; and, *T. mnioides* approaching *T. urceolatus* - leaves firm, concave, slightly twisted, apices rounded, setae green, < 2 cm in length.

All herbaria specimens used for the maps were examined and annotated by the author, the number of specimens of each species tallied and individual species distributions plotted. In specimens with more than one species growing intermixed, the number of specimens of each species combination was tallied and the distributions of each species combination plotted. It is assumed that the relative frequency of species and species combinations in the herbarium collections reflect the same relative frequencies of the species and species combinations in the field. There is no evidence that intensity of collection of Splachnaceae varied from the east to the west coast of North America and there is no reason to suspect that mixed species combinations would be collected any more or less frequently than single species populations.

D. RESULTS

All *Splachnum* species examined are distributed in boreal and montane regions of North America from the east to the west coast. The abundance of the different species is not, however, uniform across the continent. *Splachnum ampullaceum* is most abundant in the Appalachian Mountains from West Virginia into New England, the Canadian Maritime Provinces, Newfoundland, Quebec and Ontario (Figure V-1). *Splachnum luteum* is most abundant in Alaska, Yukon, western Northwest Territories, northern British Columbia and central and northern

Alberta (Figure V-1). *Splachnum sphaericum*, although also most abundant in western North America, differs from *S. luteum* by being very common in the southern Canadian Rocky Mountains (Figure V-1). *Splachnum rubrum* is evenly distributed throughout the boreal forests of North America (Figure V-1). The distribution of *S. vasculosum* is also even across the North American continent; however, it is mainly restricted to the Rocky Mountains, northern boreal and arctic regions (Figure V-2).

Two of the *Tetraplodon* species examined are more evenly distributed from east to west in North America than are the *Splachnum* species; however, the north-south distribution of these *Tetraplodon* species differ. *Tetraplodon angustatus* is primarily restricted to the boreal forests of North America, with relatively few specimens having been collected north of tree line (Figure V-2). The distribution of *T. mnioides* ranges across both boreal and arctic regions of North America (Figure V-2). The third species, *T. urceolatus*, is found primarily in western North America north of tree line and at high elevations in the Canadian Rocky Mountains (Figure V-2). Those specimens identified as '*T. mnioides* approaching *T. urceolatus*' are found in areas where the ranges of *T. mnioides* and *T. urceolatus* overlap (Figure V-3).

The total number of specimens of the different species found in herbaria differs markedly. *Tetraplodon angustatus* and especially *T. mnioides* are by far better represented than the other North American Splachnaceae species examined (741 and 2,221 specimens respectively). The ranking of abundance of *Splachnum* species from most to least abundant is: *S. sphaericum* (552), *S. ampullaceum* (401), *S. vasculosum* (296), *S. luteum* (201), and *S. rubrum* (71).

The species combination of *S. luteum* and *S. sphaericum* was the only one frequently encountered in the herbarium collections (Table V-1). Co-occurrence of these two species is restricted to northwestern North America (Figure V-10).

E. DISCUSSION

All *Splachnum* and *Tetraplodon* species examined are distributed across northern North America from the Atlantic to the Pacific coast. However, the relative abundances of the different species are not uniform across this wide range. *Splachnum* species differ as to being most abundant in eastern (*S. ampullaceum*) or western North America (*S. luteum* and *S. sphaericum*) and in their north-south distributions (*S. vasculosum* in arctic regions, *S. luteum* in boreal and arctic regions and *S. rubrum* in boreal regions). *Tetraplodon* species differ in their north-south distributions (*T. urceolatus* in arctic regions, *T. mnioides* in arctic and boreal regions and *T. angustatus* in boreal regions) but are uniform in abundance from east to west.

Possible explanations of the variation in the regional abundance of *Splachnum* species across their distributional range include: 1) restricted centers of refuge during the most recent North American glaciation; 2) variation in the abundance of suitable local habitats; 3) substrate specificity; and, 4) differences in dispersal mechanisms. During the most recent glacial advance, different *Splachnum* species may have become isolated in separate refugia. Present day distribution patterns suggest that *S. ampullaceum* may have been confined to ice free areas of southeastern North America or in coastal eastern refugia, whereas *S. sphaericum* and *S. luteum* may have been confined to ice free areas of northwestern North America. The more even east-west southern distribution of *S. rubrum* and northern distribution of *S. vasculosum* suggests that these two species may not have been confined to refugia in one geographic area. An alternative explanation for this variation in regional abundance is that the local habitats and/or the type of droppings in and on which different *Splachnum* species are found are not uniformly distributed across northern North America. There is, however, no evidence within genera that suggests that the different *Splachnum* or *Tetraplodon* species are confined to particular local habitats. All *Splachnum* species

have, for example, been collected from peatland types as diverse as rich fens to bogs. There is also no evidence that the different Splachnaceae species are restricted to growing on different types of organic substrates. *Tetraplodon angustatus, T. mnioides, S. ampullaceum* and *S. luteum* have all been found growing on carnivore (coyote), omnivore (bear) and herbivore (moose) dung in central Alberta (Marino 1988) and in laboratory experiments examining growth of these species on moose and wolf dung, all species grew well on both dung types (Chapter II). Differences in regional abundance of *S. ampullaceum, S. luteum* and *S. sphaericum* may also have been influenced by dispersal. The more frequent occurrences near the center of the ranges are due to local, short distance dispersal events, while the more scattered localities at the edge of the ranges are the result of less frequent long distance dispersal events.

The more uniform east-west North American distribution of *Tetraplodon* as compared to *Splachnum* species may be a result of or a combination of: 1) a more rapid post-glacial recolonization rate relative to *Splachnum* species, 2) a relatively widespread glacial refugial distribution in North America, and 3) a uniform east-west distribution of suitable local habitats. The dung in dry habitats that *Tetraplodon* species colonize persists longer and is therefore a more stable resource relative to the dung in wet habitats that is colonized by *Splachnum* species. This, coupled with the the repeated sporophyte production over several years of *Tetraplodon* species growing on a dropping compared to the single episode of sporophyte production in *Splachnum* species growing on a dropping, should promote the relatively rapid dispersal of *Tetraplodon* into uncolonized geographical areas. *Tetraplodon* species may not have been confined to geographically restricted glacial refugia, therefore their movement into ice-free areas of North America may have been essentially uniform across the continent. *Tetraplodon* species tend to be found in drier habitats than *Splachnum* species but within this broad range none of the species, within either genus, appears to be

confined to particular local habitats. Therefore, it is unlikely that the 'dry' habitat types in which *Tetraplodon* species are found are more evenly distributed east to west across northern North America than are the 'wet' habitat types in which *Splachnum* species are found.

Tetraplodon species are, as expected, more abundant than any of the *Splachnum* species. This is likely because dung in dry habitats on which *Tetraplodon* species grow generally persists longer and is therefore a more stable resource than is dung in wet habitats on which *Splachnum* species grow. *Tetraplodon* species therefore, should be more common than *Splachnum* species.

The greater abundance of *T. mnioides* compared to *T. angustatus* can be explained by the greater distributional range of *T. mnioides* and its longer season of sporophyte production. In a given local area, *T. angustatus* populations produce mature sporophytes only in early spring, generally just after the trees begin to leaf out. Different patches of *T. mnioides* in a given local area produce mature sporophytes throughout much of the summer. Marino (1988) has found in Alberta that *T. angustatus* primarily grows on fresh dung which becomes available in the early spring whereas fresh dung which became available during the summer was colonized primarily by *T. mnioides*. *Tetraplodon mnioides* therefore, has more time to colonize dung patches and has more dung patches available to colonize.

Splachnum species with the most elaborate sporophytes (*S. luteum* and *S. rubrum*) are less abundant than those species with less elaborate sporophytes (*S. sphaericum*, *S. ampullaceum* and *S. vasculosum*). *Splachnum rubrum* in particular appears to be uncommon despite a distribution which is as wide as those of the other *Splachnum* species. Since there is no evidence of habitat differentiation within the genus, alternative explanations such as relative dispersal and competitive abilities may be important in determining the local abundance of the different *Splachnum* species.

Many species were collected growing together; however, with the exception of *S. luteum* and *S. sphaericum*, none of these species combinations occurred frequently. The *S. luteum* and *S. sphaericum* species combination may occur frequently because both species are most abundant over essentially the same geographic region. The high degree of regional and local (dung patch) overlap between these two species raises the problem of how they can coexist using the same resources. Marino (1988) has examined a number of mechanisms that may promote the coexistence of Splachnaceae species on dung in Alberta.

Examination of specimens and the distributions of *T. mnioides* and *T. urceolatus* suggests that the status of *T. urceolatus* should be examined more closely. In most cases the morphological distinction between *T. mnioides* and *T. urceolatus* is clear. There is however, a small number of specimens which are ambiguous. The distributions of *T. mnioides* and *T. urceolatus* overlap in the Canadian Rockies, northern boreal, and arctic regions. Along the zone of overlap, populations are present that need further study. However, the overall parapatric ranges of the two taxa and the general morphological distinctness when sympatric suggest distinct ancestry. With additional study, the intermediate populations may fit into a modified concept of one of the species, especially if quantification of additional characters is included.

In summary, the relative abundances of several Splachnaceae species are not uniform across their wide distributional range in North America. *Tetraplodon* species are more abundant than *Splachnum* species; and of *Splachnum* species the most abundant are those with the least elaborate sporophytes. Of the specimens with two or more Splachnaceae species intermixed, only the combination of *S. luteum* and *S. sphaericum* is common.

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Table V-1 Number of herbaria specimens of in which two or more species of Splachnaceae were growing intermixed, and the percent of all specimens of each specie found growing in the given species combination. For example, of 741 specimens of *T. angustatus* 6.75 % were growing in combination with *T. mnioides* and of 2,221 specimens of *T. mnioides* 2.25 % were growing in combination with *T. angustatus*.

Splachnaceae Species	Number of Specimens	% of Specimens Growing in the Given Species Combination
S. ampullaceum + *S. sphaericum*	13	3.24 + 2.35
S. ampullaceum + *S. rubrum*	2	0.50 + 2.80
S. ampullaceum + *S. luteum*	5	1.25 + 2.49
S. rubrum + *S. luteum*	13	18.3 + 6.47
S. sphaericum + *S rubrum*	3	0.54 + 4.23
S sphaericum + *S. luteum*	127	23.0 + 60.0
T. angustatus + *T. mnioides*	50	6.75 + 2.25
T. mnioides+ *S. ampullaceum*	1	0.05 + 0.25
T. mnioides+ *S. sphaericum*	5	0.22 + 0.90
T. mnioides+ *S. luteum*	1	0.05 + 0.50
S. ampullaceum + *S. rubrum* + *S. luteum*	1	0.25 + 1.41 + 0.54
S. luteum + *S. rubrum* + *S. sphaericum*	3	1.49 + 4.23 + 0.54

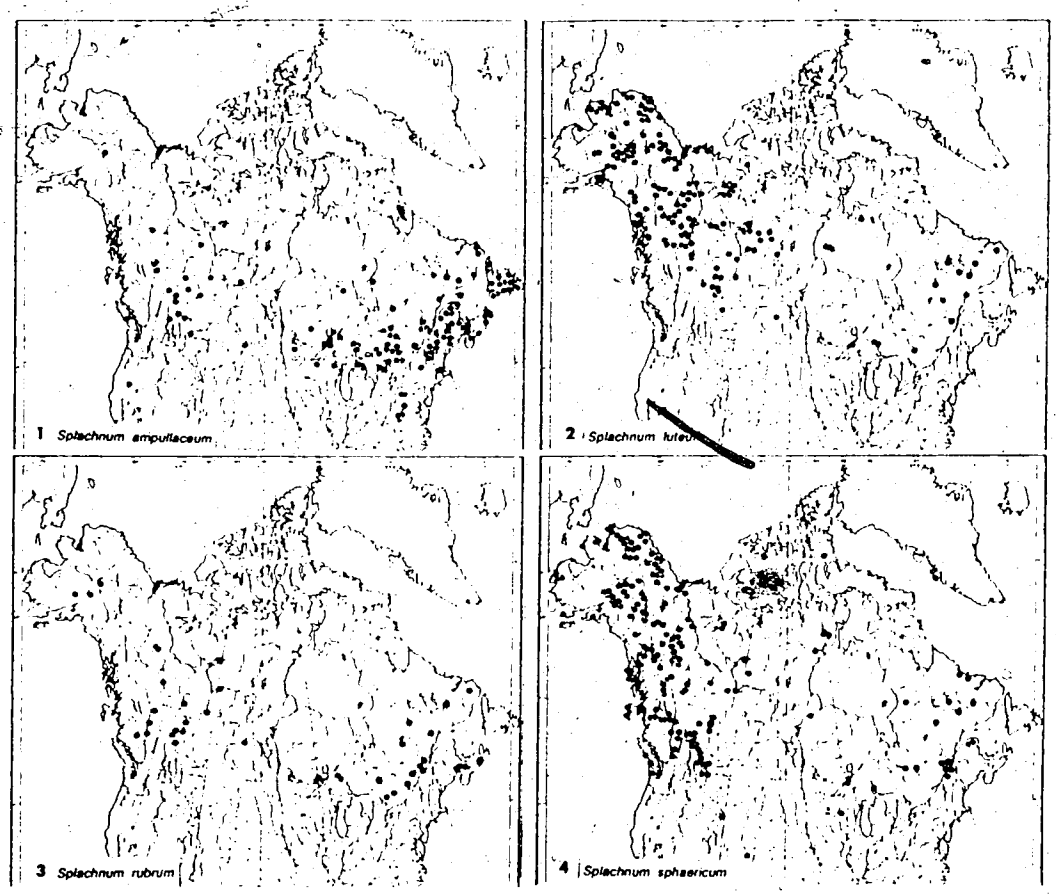

Figure V-1. North American distributions of: 1. *Splachnum ampullaceum*; 2. *Splachnum luteum*; 3. *Splachnum rubrum* and, 4. *Splachnum sphaericum*.

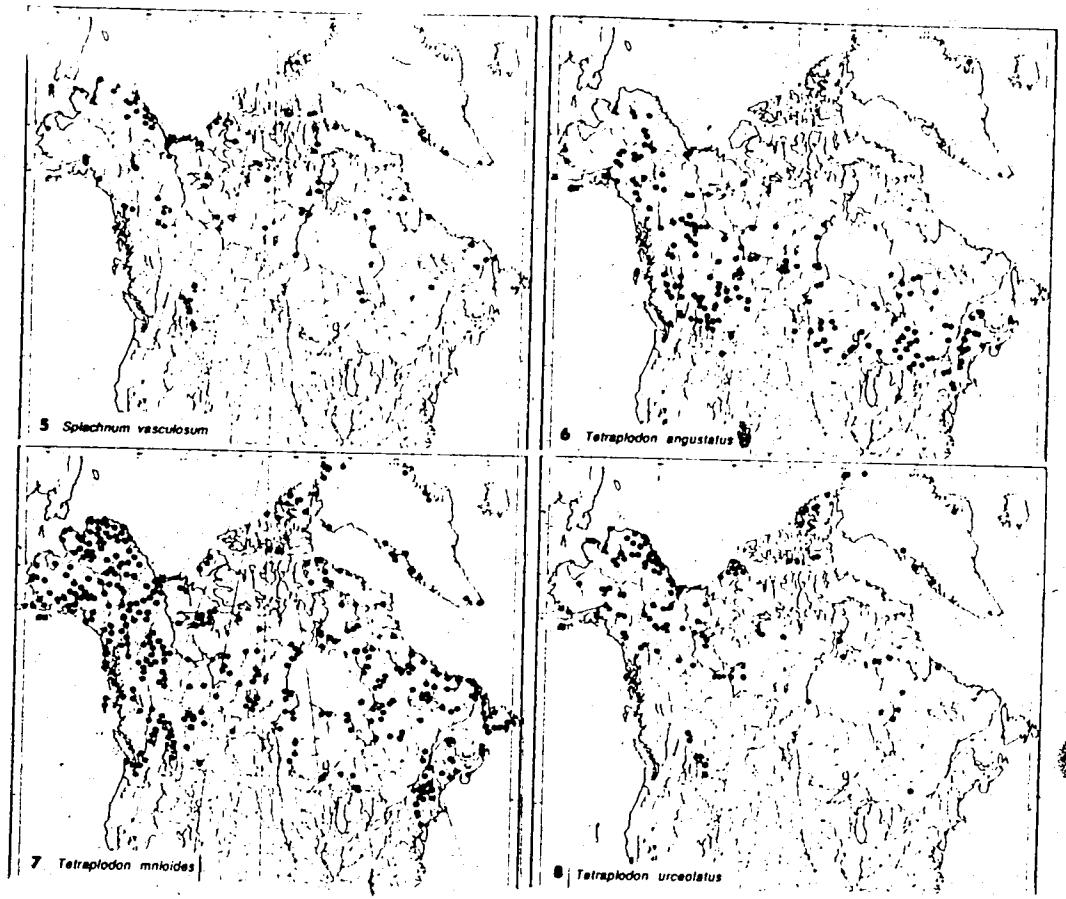

Figure V-2. North American distributions of: 5. *Splachnum vasculosum*, including var. *vasculosum* and var. *heterophyllum*; 6. *Tetraplodon angustatus*; 7. *Tetraplodon mnioides*; 8. *Tetraplodon urceolatus*.

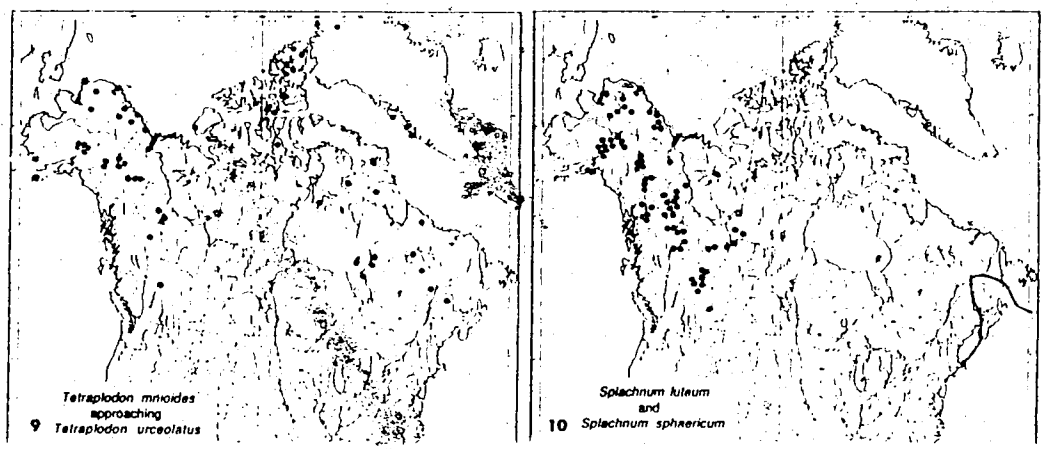

Figure V-3. North American distributions of: 9. *Tetraplodon mnioides* approaching *Tetraplodon urceolatus;* and, 10. intermixed populations of *Splachnum luteum* and *Splachnum sphaericum.*

F. LITERATURE CITED

Cameron, R. G. & R. Wyatt. 1986. Substrate restriction in entomophilous Splachnaceae: role of spore dispersal. The Bryologist 89: 279-284.

Koponen, A. & T. Koponen. 1977. Evidence of entomophily in Splachnaceae (Bryophyta). Bryophytorum Bibliotheca 13: 569-577.

Marino, P. C. 1988. Habitat division and species coexistence: a case study of mosses in the family Splachnaceae. Annales Zoologici Fennici 25: 89-98.

Persson, H. 1963. Brypohytes of Alaska and Yukon Territory collected by Hansford T. Shacklette. The Bryologist 66: 1-26.

Pyysalo, H., A. Koponen & T. Koponen. 1978. Studies on entomophily in Splachnaceae (Musci). I. volatile compounds in the sporophyte. Annales Botanici Fennici 15: 293-296.

Pyysalo, H., A. Koponen & T. Koponen. 1983. Studies on entomophily in Splachnaceae (Musci). II. volatile compounds in the hypophysis. Annales Botanici Fennici 20: 335-338.

Vitt, D. H. 1981. Adaptive modes of the moss sporophyte. The Bryologist 84: 166-186.

VI. GENERAL DISCUSSION

The influence of patchiness on the coexistence of species must be examined at several scales of observation. As the area of each scale differs, the ecological processes being examined, the time scale appropriate to those processes, and an organism's activity or influence during that time period will also differ. Thus, no single choice of scale allows a complete understanding of coexistence (Wiens et al. 1986; Addicott et al. 1987).

I have studied the coexistence of the mosses *Tetraplodon angustatus, T. mnioides, Splachnum ampullaceum* and *S. luteum* at the local, regional and continental spatial scales. These mosses use similar patchy resources. In this chapter, I will briefly review patterns and mechanisms of coexistence at each spatial scale and suggest that habitat patchiness influences the interactions between species and that mechanisms of coexistence are best understood from the perspective of several scales of observation.

Overall patterns of distribution indicate that species of Splachnaceae seldom coexist locally on the same droppings (Chapter II) but do coexist at both the regional and continental scales across much of north temperate and boreal North America (Chapter V). Local interactions between species are influenced by dryness of habitat, however, their influence does not appear to explain completely the infrequency of local coexistence (Chapter II). This suggests that local distributions must result from processes operating at larger spatial scales. Infrequent local coexistence also suggests that regional coexistence must be a result of processes operating at the regional spatial scale rather than simply being a consequence of local coexistence. Three mechanisms have been identified that may promote coexistence regionally; habitat heterogeneity, temporal (seasonal variation) and dispersal variability (Chapters III and IV). Continental coexistence of species is a consequence of processes operating at the regional spatial scale. Therefore, patterns of geographic distribution of these mosses appear to result primarily from the

influence of regional heterogeneity on local interactions, or from processes operating at a regional spatial scale. However, the relative importance of these processes differ both between and and within genera.

Coexistence between species of different genera appeared to result from both the influence of regional heterogeneity on local interactions and from regional processes. The influence of habitat heterogeneity on local interactions appeared to have a significant influence on competitive asymmetry between species of different genera such that species of *Tetraplodon* often eliminated species of *Splachnum* from dung in dry habitats with the reverse being true in wet habitats (Chapter 2). As a consequence, species of different genera may coexist regionally through the spatial segregation of resources. On a regional scale, limited spore dispersal may accentuate the spatial segregation of resources since spore-carrying flies attracted to *Tetraplodon* species were more closely associated with dung in dry than in wet habitats and therefore species of *Tetraplodon* may also have a numerical advantage on dung in dry habitats (Chapter 3).

The influence of regional habitat heterogeneity on local interactions did not appear to be an important mechanism promoting the coexistence of congeneric species, rather coexistence between congeneric species may result from regional processes such as temporal (seasonal) heterogeneity and dispersal variability. However, the processes that appear to promote the regional coexistence of congeneric species differ between the two genera. Temporal heterogeneity appeared to be the most important factor promoting coexistence between species of *Tetraplodon*. Seasonal differences in sporophyte maturation between species of *Tetraplodon* appeared to result in a seasonal segregation of resources such that *T. angustatus* primarily colonized dung in spring, when its sporophytes mature and *T. mnioides* primarily colonized dung in early summer when its sporophytes mature (Chapter 3). Dispersal variability appeared to be the most important factor promoting the coexistence between species of *Splachnum*. Dispersal variability may

promote coexistence between species of *Splachnum* through the influence of tradeoffs between competitive and dispersal ability (Chapter 3) and through the independent aggregation of spores on dung (Chapter 4).

These mechanisms appear to promote the coexistence of Splachnaceae because of the patchy distribution of droppings in space and time. The distribution of droppings in space has a strong influence on the local interactions and regional distributions of species of different genera and the distribution of droppings in time appeared to have a strong influence on the local distribution of species of *Tetraplodon*. Also, mechanisms of coexistence such as tradeoffs between competitive and dispersal ability and the independent aggregation of spores on different droppings depend on the presence of new patches being made available in both space and time. Patchiness in space and time, therefore, provides both a measure of heterogeneity by which different species can segregate resources and colonization opportunities for species through which dispersal and environmental variability can act to give different species advantages in different patches at different times.

The results of this study also suggest that coexistence among Splachnaceae is a consequence of numerous processes, few of which can be fully understood from the perspective of only one spatial scale. Local interactions between species of different genera, for example, can only be understood from the perspective of regional habitat heterogeneity and the understanding that spores have limited dispersal regionally may be necessary to explain the regional and local distributions of species of different genera. Also, it was necessary to first understand the local interactions between species of *Splachnum* in order to identify that a tradeoff between competitive and dispersal ability exists. Coexistence in communities of Splachnaceae can only be understood, therefore, from the perspective of several scales of observation.

In conclusion, this study has shown that habitat patchiness influences the coexistence of Splachnaceae and that the processes promoting coexistence are best understood from the perspective of several scales of observation. Therefore, since habitat patchiness is an essential component of most communities (Kareiva 1986) it follows that community interactions will in general be influenced by the spatial and temporal heterogeneity associated with patchiness. This further suggests, that patterns of community structure will also in general be best understood from the perspective of several scales of observation since a single choice of scale will not provide a complete understanding of the processes promoting those patterns.

A. REFERENCES

Addicott, J. F., J. Aho, M. Antolin, D. Padilla, J. Richardson, and D. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340-346.

Kareiva, P. 1986. Patchiness, dispersal, and species interactions: consequences for communities of herbivorous insects. *In* J. Diamond and T. Case eds., *Community Ecology*, pp. 192-206. Harper & Row, New York.

Wiens, J. A., J. F. Addicott, T. J. Case and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. *In* J. Diamond and T. Case eds., *Community Ecology*, pp. 145-153. Harper & Row, New York.