COMPARATIVE ECOLOGY
OF
POLYTRICHUM COMMUNE HEDW. AND
POLYTRICHUM JUNIPERINUM HEDW.

by
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requirements for the degree of

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INTRODUCTION

While bryophytes have long been recognized as an important component of terrestrial primary succession (Cooper 1912), little is known of competitive processes within the bryophyte community (Watson 1974). Changes in corticolous species composition over the complex atmospheric gradient along tree trunks have been explained on the basis of adaptive differences in physiology (Hosokawa and Kubota 1957, Hosokawa and Odani 1957, Hosokawa _et al_. 1964). Enhanced substrate differences complicate the analysis of compositional change in terrestrial communities. A series of British studies, however, have documented changes in the prevailing growth form of the species in terrestrial bryophyte communities over environmental gradients in time and space (Gimingham and Robertson 1950, Birse and Gimingham 1955, Gimingham and Birse 1957, Birse 1957, 1958a, 1958b). Unfortunately, autecological species differences which could define such changes in the terrestrial community are largely unstudied.

With this purpose in mind, I have chosen to investigate the structural and physiological bases of the well-known transition from _Polytrichum juniperinum_ to _P. commune_ along a xeric to mesic environmental gradient. Both species are endohydrics (capable of internal water conduction (Buch 1947)), but each exhibits varying potential for internal and external water conduction relative to the local environment. For example, gametophytes of _P. commune_ grown under mesic conditions develop a lesser number of hydroids (internal water conducting cells) than gametophytes grown under xeric conditions (Hébant 1973).

Neither species exhibits extensive mixhydry (capacity for generalized absorption of surface water in an endohydric species (Buch 1947)). It is also unlikely that either species is capable of substantial direct uptake of atmospheric water vapor (Anderson and Bourdeau 1955, Lange 1969). The degree of mixhydry may vary with local environment as in the presence of thicker leaf cuticle in drier environments suggested by Sarafis (1971), but this possibility has not been thoroughly investigated.

The influence of growth form in moderating microenvironment is well established for members of the Polytrichaceae (Bayfield 1967, Gimingham 1967, Gimingham and Smith 1971), and Bazzaz _et_ _al_. (1970) observed adaptive physiological differences between forest and alpine populations of _P_. _juniperinum_. Thus, both morphological and physiological factors could be important in defining the environmental interrelationships of these two species.

Watson (1974) suggests that _P_. _juniperinum_ may be a generalist species which is outcompeted by a more specialist _P_. _commune_ in environmentally intermediate portions of potential habitat. In this study I have attempted to determine to what extent each species is limited by inherent inflexibility in physiology and morphology and alternatively, to what extent interspecific competition may influence relative success. In particular, I have studied possible morphological and physiological bases for xeric adaptation in P. juniperinum and have attempted to define how such adaptations affect its success relative to P. commune along a xeric to mesic environmental gradient.

METHODS AND MATERIALS

Site description

To simplify the problem I attempted to minimize substrate and macroclimatic differences by selecting nine sites of varied vascular plant cover along a single clay road-cut of northwestern exposure. The study area is located in the Driftless Area (Curtis 1959) of Wisconsin thirty-five miles west of Madison, Wisconsin. The surrounding hills are wooded and are part of the Southern Dry Forests described in Curtis (1959). Photographs of the sites may be found in Appendix II.

The sites are either open or closed. Open sites are shaded above by 12-20 m tall Quercus alba (site 7) and/or species of the section Q. Erythrobalanus (sites 5, 9B, and 10). Closed sites are shaded by high densities of 3-3.5 m tall trees and shrubs in addition to an upper tree canopy (sites 1, 6, 9A, and 11). The herbaceous species present are a mixture of roadside weedy species and species characteristic of the Southern Dry Forests (Curtis 1959). The overstory trees and shrubs present at each site are given in Table 1. A checklist of understory herbs, shrubs, and tree seedlings present at a frequency greater than two individuals for each site is given in Table 2.

The size of each site was determined as the amount of contiquous closed or open area not to exceed 16 m^2. Cover estimates, site size, and steepness of slope are given in Table 3.

Table 1: Overstory Species Present at Each Site*

Site	1	3	5	6	7	9A	9B	10	11
Canopy (< 4m) trees									
Betula sp.						X			
Carpinus caroliniana Walt.	X								
Quercus alba L.					X				X
Quercus section *Erythrobalanus*		X		X					X
Shrubs and small trees (> 4m)									
Betula sp.	X	X	X	X	X		X	X	X
Carpinus caroliniana Walt.		X		X					
Populus grandidentata Michx.				X					
Populus tremuloides Michx.		X	X	X	X		X	X	X
Ribes sp.	X								
Rubus sp.	X		X			X			
Salix sp.					X	X			X

*Nomenclature as in Gleason and Cronquist (1963)

Table 2: Understory Species Present at a Frequency > 2 at Each Site*

Site	1	3	5	6	7	9A	9B	10	11
Achillea Millefolium L.	X	X	X		X			X	
Adiantum pedatum L.	X								X
Antennaria sp.								X	
Aralia racemosa L.									X
Aster lateriflorus (L.) Britt.								X	
Aster sagittifolius Willd.	X			X	X			X	X
Aster sp.		X	X						
Athyrium Filix-femina (L.) Roth.	X					X			X
Eupatorium rugosum Houtt.									X
Fragaria sp.	X	X			X		X	X	
Goodyera sp.				X					
Heuchera sp.			X				X	X	
Onoclea sensibilus L.				X		X	X		
Oxalis sp.						X			
Parthenocissus sp.									X
Potentilla recta L.	X	X	X	X	X	X	X	X	
Prenanthes alba L.			X						
Prunella vulgaris L.	X								
Prunus serotina Ehrh.		X		X					
Quercus section Erythrobalanus					X				
Ribes sp.	X								X
Salix sp.			X						
Solidago ulmifolia Muhl.			X	X			X	X	X
Trifolium repens L.		X			X		X		
Trifolium sp.	X								
Viola spp.	X		X			X			

*Nomenclature as in Gleason and Cronquist (1963)

Table 3: Site Characteristics

Site	1	3	5	6	7	9A	9B	10	11
Bryophyte cover*	4	5	4	4	5	5	5	4	3
Slope**	3	3	4	4	3	1	2	2	5
Size of site (m^2)	15	5	11	10	4	3	3	4	3
Herbaceous stems (#/90cm^2)	15.2	17.0	18.0	11.9	19.9	19.4	31.3	41.0	24.4
Woody Stems (#/90cm^2)	.8	.3	.6	1.9	1.7	.8	2.3	3.1	2.7

* subjective estimate, 5=(100-90%), 4=(89-80%), 3=(79-70%), 2=(69-60%), 1=(59-50%)

**subjective estimate, 5=20°, 4=15°, 3=10°, 2= 5°, 1= 0°

Site environment

In order to index each site along a xeric-mesic environmental gradient, measurements of light, temperature, and relative humidity were made over the daylight course of a single, clear and sunny day (September 8, 1974).

These environmental data were not meant to represent a "typical day" but to serve as a means of quantifying the relative amount of environmental amelioration provided by the vascular canopy at each site.

Light was measured as photosynthetically active radiation (PhAR) using a Lambda Instruments LI-170 Quantum/Radiometer/Photometer equipped with a LI-190S Quantum Sensor calibrated to read in $\mu E m^{-2} s^{-1}$. Air temperature and relative humidity were read from a psychrometer (Bendix Model #566), and turf temperature was determined using four separate telethermometer probes (Yellow Springs Instruments) inserted into the turf.

It was necessary to use the same measuring devices at each site. In order to best approximate simultaneous measurements, only one location at each site was sampled. Sites were sampled from east to west (numerical order) along the roadcut. A total of thirty minutes was required to sample all nine sites once. Data represent an average of four readings within 0.5 m of a single location subjectively chosen as typical.

Determination of Synthetic Desiccation Stress Index (SDSI)

Experiments testing the effect of desiccation on bryophytes have shown that desiccation results in respiratory losses which are further enhanced as insolation levels increase (Hinshiri and Proctor 1971). For this reason both light and relative humidity data were used to index the potential desiccation stress at each site. The data were integrated for each site by planimetry using $0 \mu E m^{-2} s^{-1}$ and 100% relative humidity as the respective base lines. Sites were ranked in order of increasing PhAR and decreasing relative humidity. A composite rank was derived by adding the PhAR and relative humidity rankings such that each site was placed on a Synthetic Desiccation Stress Index (SDSI) with possible values between 2 and 18. Equal weighting of PhAR and relative humidity was chosen because there was no basis for determining more exact weightings.

Phytosociological data

In order to determine the frequency of *P. commune* and *P. juniperinum* on each site and the effect of each of these two species on the frequency of other bryophyte species, quadrat data were taken. An acrylic plastic ("Plexiglas") quadrat, 30 X 30 cm, was scored into 144 sectors and positioned at ten random locations within each site using a random numbers table. At each location the number of grid sections in which a species was present was recorded. Acrocarpous species were required to be "rooted" within a grid to be counted as present. Pleurocarpous species were simply present or absent. *Lycopodium clavatum* grew within the bryophyte stratum and was included in the species list. Higher vascular plants were recorded only as the number of herbaceous or woody stems present within the entire quadrat. Voucher specimens of the common bryophyte species were deposited in the University of Wisconsin-Madison Moss Herbarium.

The ten quadrats sampled at each site resulted in a standard error of the mean for each of the two major species of *Polytrichum* usually less than 10%, and always less than 15%, of their respective mean frequencies on the site.

Linear regressions of *P. commune* and *P. juniperinum* frequency were performed against the SDSI to determine the relationship of the two species to the SDSI. Frequency values were determined as the total number of occurrences in all ten quadrats for each species. The maximum frequency score possible was 1440.

Pearson's product-moment correlation coefficient (Steel and Torrie 1960) was calculated for *P. commune* and *P. juniperinum* with all other species which occurred at a frequency greater than 28 (2% maximum possible) within a single quadrat. The correlation was determined considering only those quadrats in which both species occurred. The results are thus useful in comparing the relative competitive effect of *P. commune* and *P. juniperinum* on the other species present (Edward Beals, pers. comm.).

Morphological data

Morphological data were taken to determine differences in growth form, rates of above-ground production, and rates of photosynthetic canopy loss over the gradient for each species.

Three sampling points were selected for each site using a random numbers table. A metal can with a 50 cm^2 base was used as a sample corer. Two contiquous samples for each species were taken at the area nearest to the random point which appeared to be relatively monospecific for that species. Thus, the data represent optimal performance for each species on each site. The two samples for each species were pooled for analysis. Samples were collected during the third week in August 1974, returned to Madison, stored air-dry in open paper bags at room temperature, and analyzed beginning in late September 1974. A total of forty-five samples were collected. P. commune could not be collected from sites 5 and 10, and P. juniperinum was virtually absent from site 9A. One sample was inadvertently left overnight in water during the sampling process. The gametophytes became uniformly brown and could not be analyzed. The remaining samples were analyzed such that any error as a result of differential storage time was distributed among rather than between sites.

For each sample the gametophytes were cut at soil-level and soaked in distilled water. This soaking process placed the leaves perpendicular relative to the stem and facilitated the separation of growth segments on the basis of leaf length. The stems are easily divided into successive annual growth segments on the basis of leaf length (Longton 1970). Leaves produced in late fall and winter are considerably shorter than those produced in mid-summer. Growth segments were separated by bissecting the region of shorter leaves.

Individuals were selected by blind choice and the following measurements made: total depth from apex to base of stem, depth of green tissue, length of each growth segment, and length of green tissue within each growth segment. Leaf length at the level of the first fully expanded leaves below the apex was also measured.

When possible, twenty-five functionally neuter stems were measured. If twenty-five stems were not present in the sample, all available neuter stems were measured. The number sampled ranged from fourteen to twenty-five. In each case the sample was such that the characters total depth, depth of green tissue, and leaf length showed a standard error of the mean less than 10% of the mean. Stem age classes were separated so that the dry weight of green versus brown tissue could be determined for each year's growth on zero-, one-, and two-year old stems. Sampling for dry weight data continued past those individuals measured for length relationships until as many stems as possible up to a maximum of fifteen for each age stem had been partitioned. The rest of the sample was then aged and divided into lots of green tissue, non-green tissue, and fertile stems for dry weight analysis. Stems were dried at 80-90°C for twenty-four hours and then weighed on a Mettler H10T balance.

Estimates of 1972, 1973, and 1974 production (to August) for each age class were made on an areal basis assuming solid uni-age cover as, e.g.:

$$\begin{array}{c}\text{1974}\\\text{above-ground production}\\\text{on 1973 stems}\end{array} = \frac{\begin{array}{c}\text{dry weight 1974 segments}\\\text{on 1973 stems}\end{array}}{\text{number of 1973 stems}} \times \frac{\begin{array}{c}\text{total \#}\\\text{stems}\end{array}}{\text{area}}$$

The Wilcoxan signed-rank test (Steel and Torrie 1960) was used to make interspecific comparisons of each character using all the sample points at which both species were collected.

The multivariate data were analyzed using program CANON (Kowal 1972) to perform canonical analysis (Seal 1964). The computer printout for CANON also included univariate intraspecific F-tests for each character over all samples as well as a multivariate test for dimensionality in canonical analysis (Seal 1964) using Rao's F approximation (Rao 1952). Canonical analysis was chosen because the observations were composed of several mutually correlated characters expressed in differing units of measurement. All characters were transformed to $\log_{10}$ before the analysis unless already expressed as a ratio, in which case an Arc-sin transformation was used. These transformations normalize the data distributions.

Physiological data

Sample material was collected from an open and closed site for each species in an effort to discover intraspecific physiological differences. Sites 5 and 11 were used for the collection of *P. juniperinum*; sites

3 and 6 for *P. commune*. Since the primary differences between sites were in PhAR and relative humidity, only the responses of net-photosynthesis to varied levels of PhAR and turf water content and of dark respiration to temperature were studied.

Samples were collected fresh daily, placed in an open, transparent plastic bag and returned to the laboratory. Material used in the afternoon was stored on the window sill at a constant laboratory temperature of 25°C in the same plastic bag. Specimens generally remained turgid throughout the day. The order of sites studied in morning versus afternoon experiments was varied so that in-lab storage variability was distributed among sites.

Samples were cut at soil level prior to experiments and tied into a secure clump with fine copper wire. The samples were then soaked in distilled water for a minimum of twenty minutes. This time interval assured full wetting. They were then shaken vigorously ten times to release excess moisture, weighed, and placed in the chamber. The gametophyte stems were held upright within the chamber by a sample holder. The holder did not restrict light interception and consisted of an inverted plastic bottle with a central opening cut in the base to hold the stems. An open, infrared gas analysis system as described in Eickmeier and Adams (1973) was used to determine carbon dioxide differentials on a Beckman Instruments gas analyzer Model 865, with two flow-through sample cells. Experimental conditions are given in Table 4.

Table 4: Conditions Observed During Infrared Gas Analysis Experiments

Response Type	Flow-rate (l/min)	Initial Wet Weight (g)	Consecutive Treatment Levels	
			Temperature ($^{\circ}$C)	PhAR (μE$m^{-2}s^{-1}$)
Net-photosynthesis to light	2.5	40	20*	21, 83, 138, 244, 415, 613, 818, 1061
Dark respiration to temperature	3.0	35	5, 12.5, 20, 27.5, 35	Darkness
Net-photosynthesis to drying	2.5	15	20*	818**

* Previous experiments indicated a temperature optimum for net-photosynthesis near 20°C for both species.

**Light saturation for both species

The sample was allowed to equilibrate dark respiration at the beginning of light response and dark respiration response experiments. This process generally took about one hour. Although the incoming chamber air was first passed through a water column, the gametophytes still continually lost water. The initial sample wet weights were well above published saturation levels for P. commune (300% dry weight, Anderson and Bourdeau 1955) and the equilibration period did not bring the gametophytes to below saturation. The final RWC* in these experiments was never below 60%. To minimize drying a consistent ten-minute treatment response was considered sufficient equilibration. Thus, the experiments were able to take place at water contents slightly above and below that at which maximum photosynthesis occurred in the drying response experiments.

Air was not hydrated before entering the chamber during the drying response experiments. The sample was suspended within the chamber on a balance pan attached to a torsion balance below the chamber. Sample weight was taken every ten minutes for the first hour, and at twenty-minute intervals thereafter until the sample had reached approximately 20-25% RWC*.

All samples were dried at 80-90°C for twenty-four hours to determine sample dry weight.

$$\text{*RWC = Relative Water Content} = \frac{\text{(Current weight)-(Dry weight)}}{\text{(Wet weight)-(Dry weight)}} \times 100\%$$

as in Barrs (1968) except wet-weight replaces saturated weight

Analysis of variance, one-way classification (Steel and Torrie 1960), was used to test for differences among and between species with respect to initial sample wet weight.

The results of the drying experiments were graphed as RWC and time versus absolute and per-cent maximum net-photosynthesis respectively. Values for net-photosynthesis were interpolated from the graph of each experiment at intervals of two RWC units using line connections between observed points. Means were determined by averaging interpolated values.

RESULTS

Site environment

The results of indexing each site along a synthetic desiccation stress index (SDSI) are presented in Table 5. The environmental data used to calculate the SDSI are given in Appendix I.

Phytosociological data

The quadrat data are summarized in Table 6. Sites are arranged in order of increasing PhAR rank.

Linear regressions of *P. commune* and *P. juniperinum* frequency (rows 1 and 2 in Table 6) made against the SDSI are shown in Figures 1 and 2.

The correlation (Pearson's "r") of *P. commune* and *P. juniperinum* with the nine other species showing greater than 2% frequency is given in Table 7.

Morphological data

A description of the results of the Wilcoxan's signed rank test (Steel and Torrie 1960) in testing for interspecific differences between *P. commune* and *P. juniperinum* is presented in Table 8.

Means of the age-class data for each species are shown as age-class distributions in Figure 3.

The graphical results of a canonical analysis of each species on those sites for which data were available for both species is presented in Figures 4 and 5. The results of the intraspecific univariate

Table 5: Calculation of Synthetic Desiccation Stress Index (SDSI)

Site	Relative Humidity Rank	Light Rank	Composite Rank
1	6.0	1.0	7.0
3	9.0	5.5	14.5
5	7.0	9.0	16.0
6	4.0	4.0	8.0
7	4.0	7.5	11.5
9A	2.0	2.0	4.0
9B	1.0	5.5	6.5
10	4.0	7.5	11.5
11	8.0	3.0	11.0

Table 6: Total Species Frequency in Ten Quadrats

Species	9A	1	11	3	6	9B	7	10	5
Polytrichum commune Hedw.*	1356	867	343	1157	1257	1277	1035	180	17
Polytrichum juniperinum Hedw.	25	531	1038	909	310	348	886	891	1144
Amblystegium sp.	5	0	0	0	0	0	0	0	0
Atrichum spp.	5	489	612	125	46	61	458	494	673
Aulacomnion palustre (Hedw.) Schwaegr.	4	34	10	23	0	0	0	0	0
Ceratodon purpureus (Hedw.) Brid.	2	0	4	0	0	1	8	114	21
Costate Hypnaceae	0	191	200	23	7	34	0	105	0
Ecostate Hypnaceae	0	0	0	0	0	0	0	13	0
Lichens	0	0	0	0	0	0	70	37	2
Lophocolea sp.	7	27	183	189	141	10	83	3	0
Lycopodium clavatum L.**	0	0	0	0	0	37	0	2	0
Marchantia sp.	0	0	0	0	0	1	0	0	0
Mnium cuspidatum Hedw.	11	85	292	94	6	12	1	0	0
Pleurozium schreberi (Brid.) Mitt.	0	0	0	0	0	0	2	0	0
Polytrichum piliferum Hedw.	0	0	0	0	0	0	18	0	0

* Nomenclature, Crum (1973); ** Nomenclature, Gleason and Cronquist (1963)

Figure 1 -- Linear regression of the frequency of *P. commune* versus the Synthetic Desiccation Stress Index (SDSI).

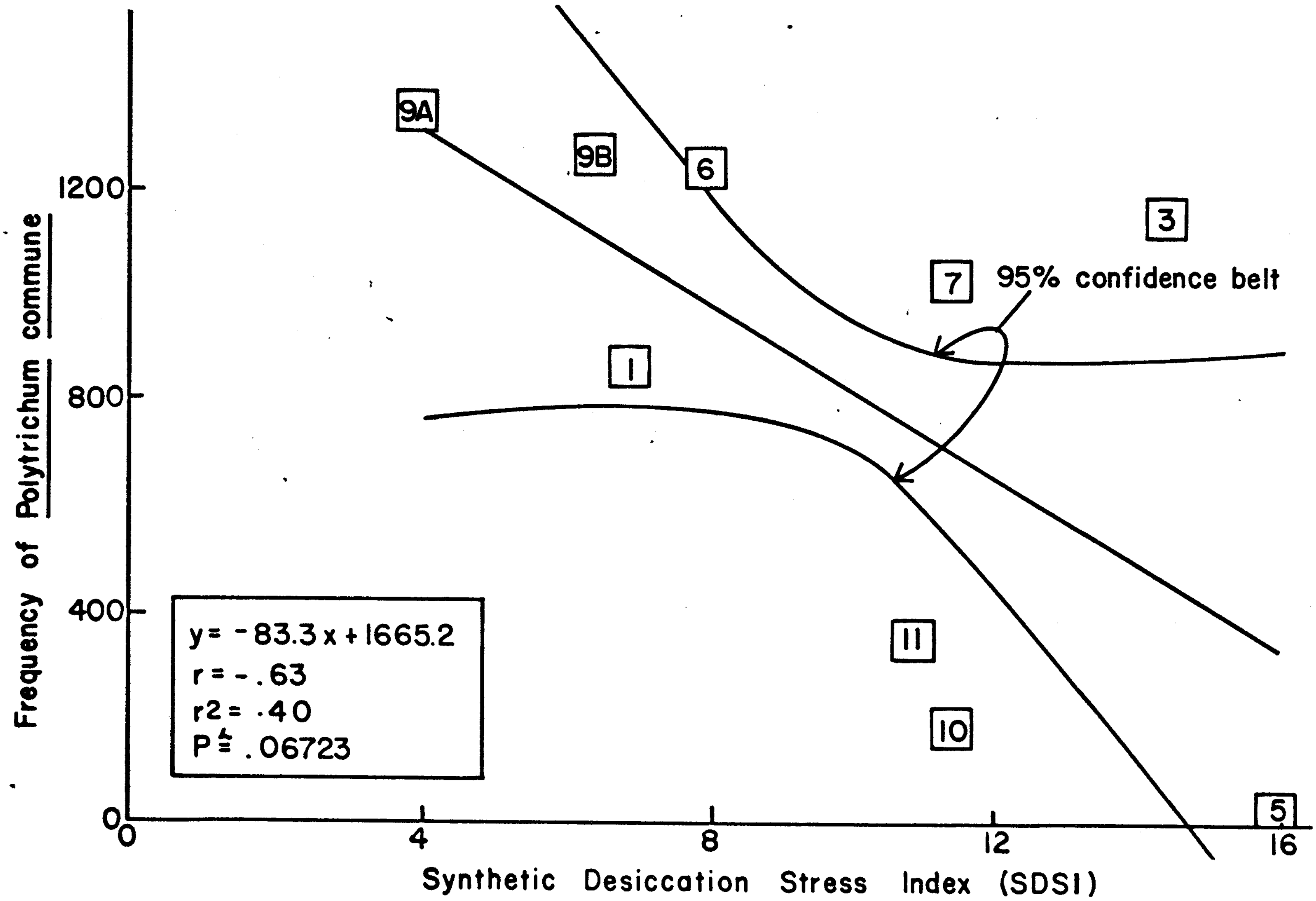

Frequency of Polytrichum commune
1200
800
400
0
0
4
8
12
16
Synthetic Desiccation Stress Index (SDSI)
9A
9B
6
3
7
95% confidence belt
1
11
10
5
y= -83.3 x + 1665.2
r = -.63
r2 = .40
P ≤ .06723

Figure 2 -- Linear regression of the frequency of _P_. _juniperinum_ versus the Synthetic Desiccation Stress Index (SDSI).

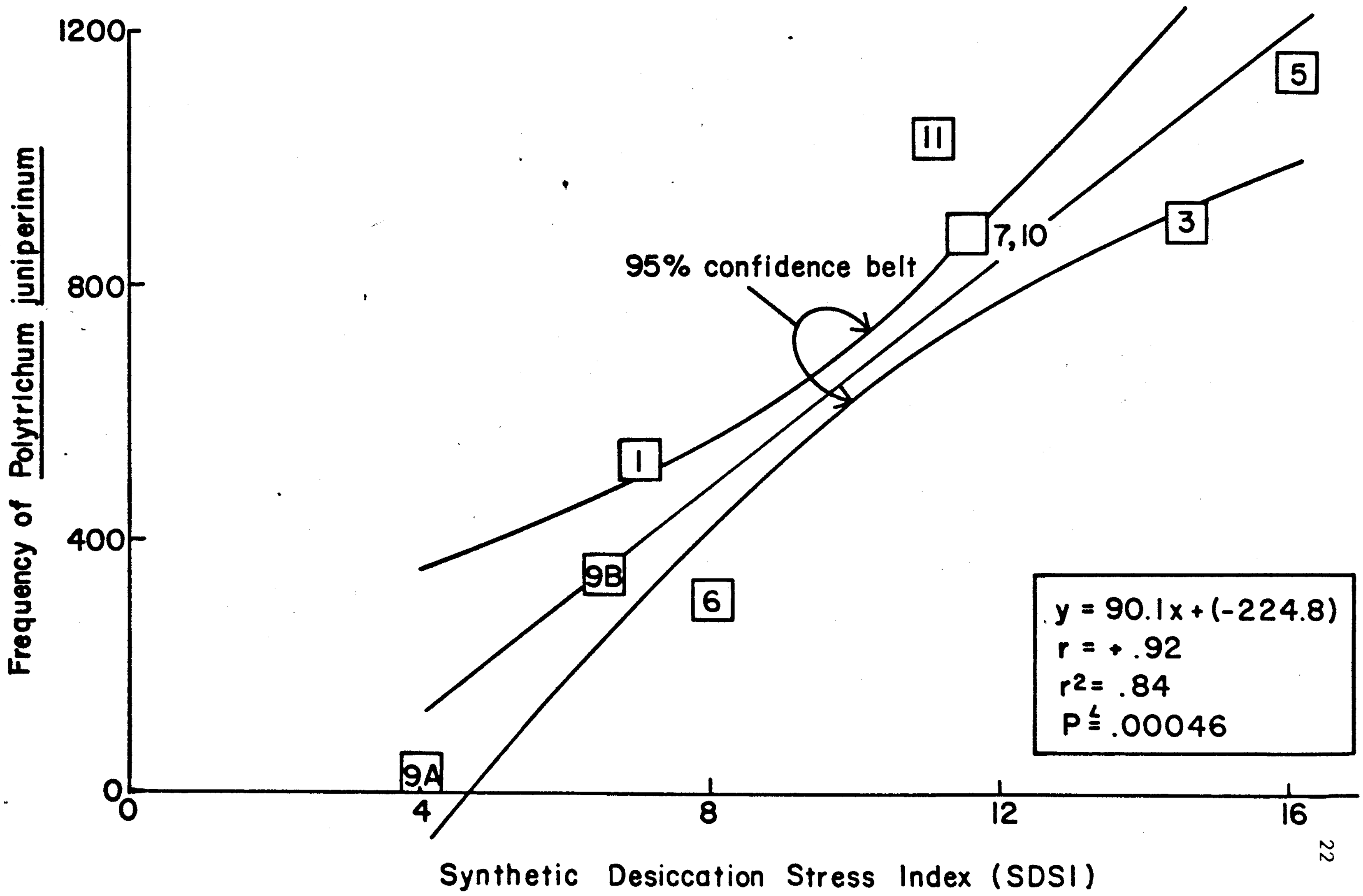

1200
800
400
0
0
4
8
12
16
Frequency of Polytrichum juniperinum
Synthetic Desiccation Stress Index (SDSI)
95% confidence belt
11
5
7,10
3
1
9B
6
9A
y = 90.1x + (-224.8)
r = + .92
r2 = .84
P ≦ .00046

Table 7: Pearson's Correlation of P. commune and P. juniperinum with species showing greater than 2% total possible frequency using only those quadrats in which both of the species being correlated are present.

Species	P. commune	P. juniperinum
P. commune	+1.000	- .510
P. juniperinum	- .510	+1.000
Mnium cuspidatum	- .440	+ .470
Aulacomnion palustre	- .350	- .400
Ceratodon purpureus	- .750	+ .260
Lophocolea sp.	- .240	+ .310
Lichens	+ .130	- .410
Lycopodium clavatum	+ .470	+ .200
Costate Hypnaceae	- .630	+ .180
Atrichum spp.	- .550	+ .220

Table 8: Results of Wilcoxan's Signed Rank Test with P. commune and P. juniperinum paired by collection point within a site

Category	Abbreviation	Determined as:	Units	Result	Significance
Overall size:					
Turf depth	TD	Height/Stem	cm	PC > PJ	.02
Leaf length	LL	Leaf length	mm	PC > PJ	.01
Weight of gametophyte	DWPS	Dry wt./stem	mg/stem	PC > PJ	.01
Turf density:					
Turf density	DEN	Stems/area	stems/dm^2	PJ > PC	.01
Photosynthetic canopy:					
Photosynthetic canopy depth	DG	$\frac{\text{Length green}}{\text{stem}}$	cm	PC > PJ	.01
Photosynthetic canopy/stem		$\frac{\text{Green dry wt}}{\text{stem}}$	mg/stem	PC > PJ	.01
Total photosynthetic canopy	GDWA	$\frac{\text{Green dry wt}}{\text{area}}$	g/dm^2	PJ > PC	.01
1974 photosynthetic canopy	74G	$\frac{\text{1974 Green dry wt}}{\text{area}}$	g/dm^2	N.S.	N.S.
1973 photosynthetic canopy	73G	$\frac{\text{1973 Green dry wt}}{\text{area}}$	g/dm^2	PJ > PC	.01
% ps. canopy as '74 tissue	74G/TG	$\frac{\text{1974 Green dry wt}}{\text{Total Green d.w.}}$	%	PC > PJ	.01
Ps. canopy conservation	73G/T73	$\frac{\text{Length '73 Green}}{\text{Total Length '73}}$	%	PJ > PC	.01
Above-ground production:					
1974 on 1974 stems	NP 74(74)	See Methods	g/m^2	PJ > PC	.01
1974 on 1973 and 1972 stems	NP 74(73), NP 74(72)	"	"	N.S.	N.S.
1973 on 1972 stems	NP 73(72)	"	"	PJ > PC	.05
Standing crop	DWA	Dry wt/area	"	PJ > PC	.01
Ratio NP 74(73)/NP 74(74)	NP 74(73)/NP 74(74)	NP 74(73)/NP 74(74)		PC > PJ	.01

Figure 3 -- Means of the age-class data for _P_. _commune_ and _P_. _juniperinum_ on each site where the species occurs.

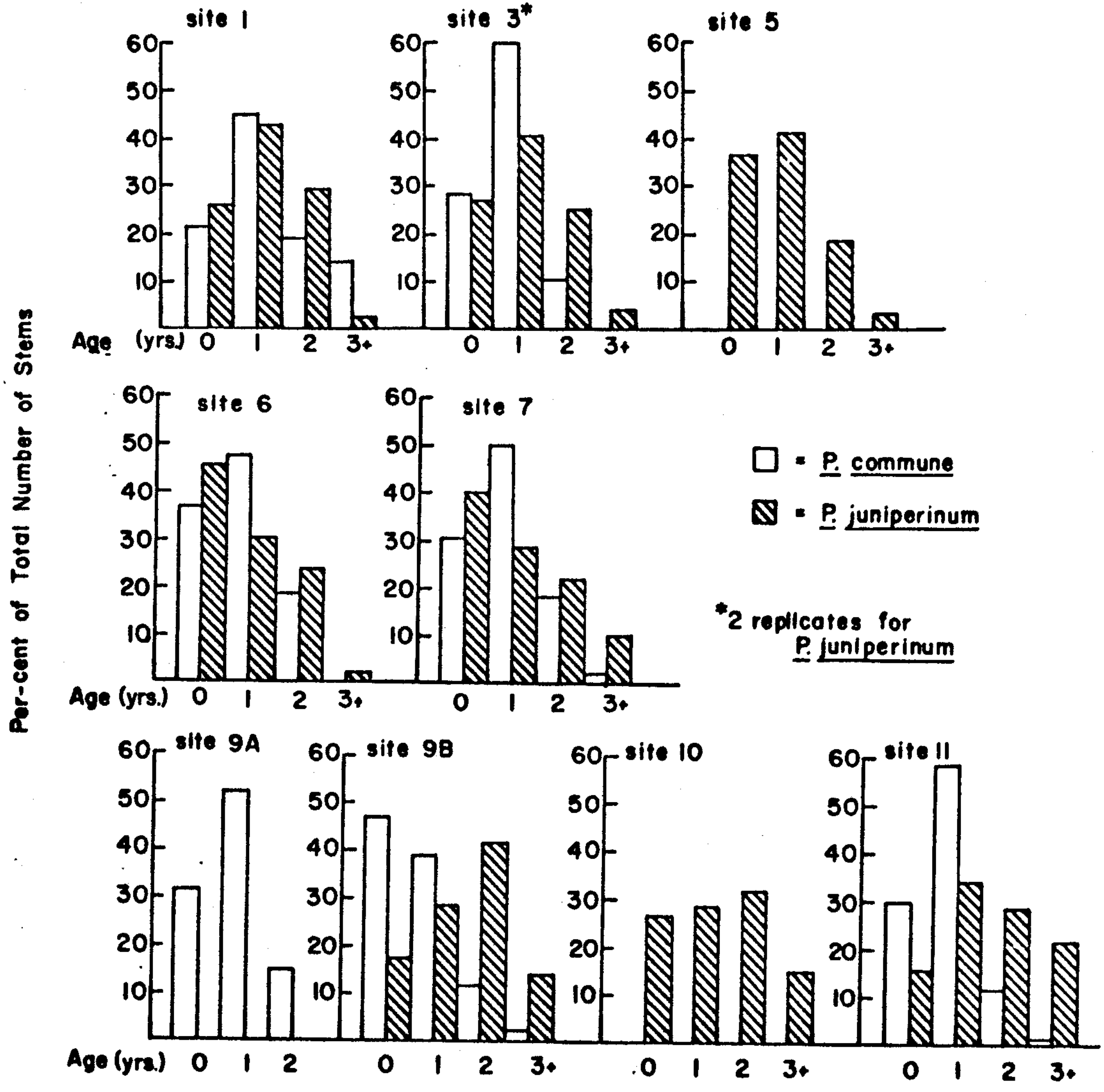

site 1
site 3*
site 5
site 6
site 7
site 9A
site 9B
site 10
site 11
60
50
40
30
20
10
Age (yrs.) 0 1 2 3+
Per-cent of Total Number of Stems
□ = P. commune
▨ = P. juniperinum
*2 replicates for P. juniperinum

Figure 4 -- Canonical analysis of *P. commune* morphology. Each symbol represents an individual sample. Each population (site) is represented by a different symbol and is composed of three individuals. The population (site) mean serves as the center for a 95% confidence circle whose radius is determined following the method described in Kowal *et al.* (1975).

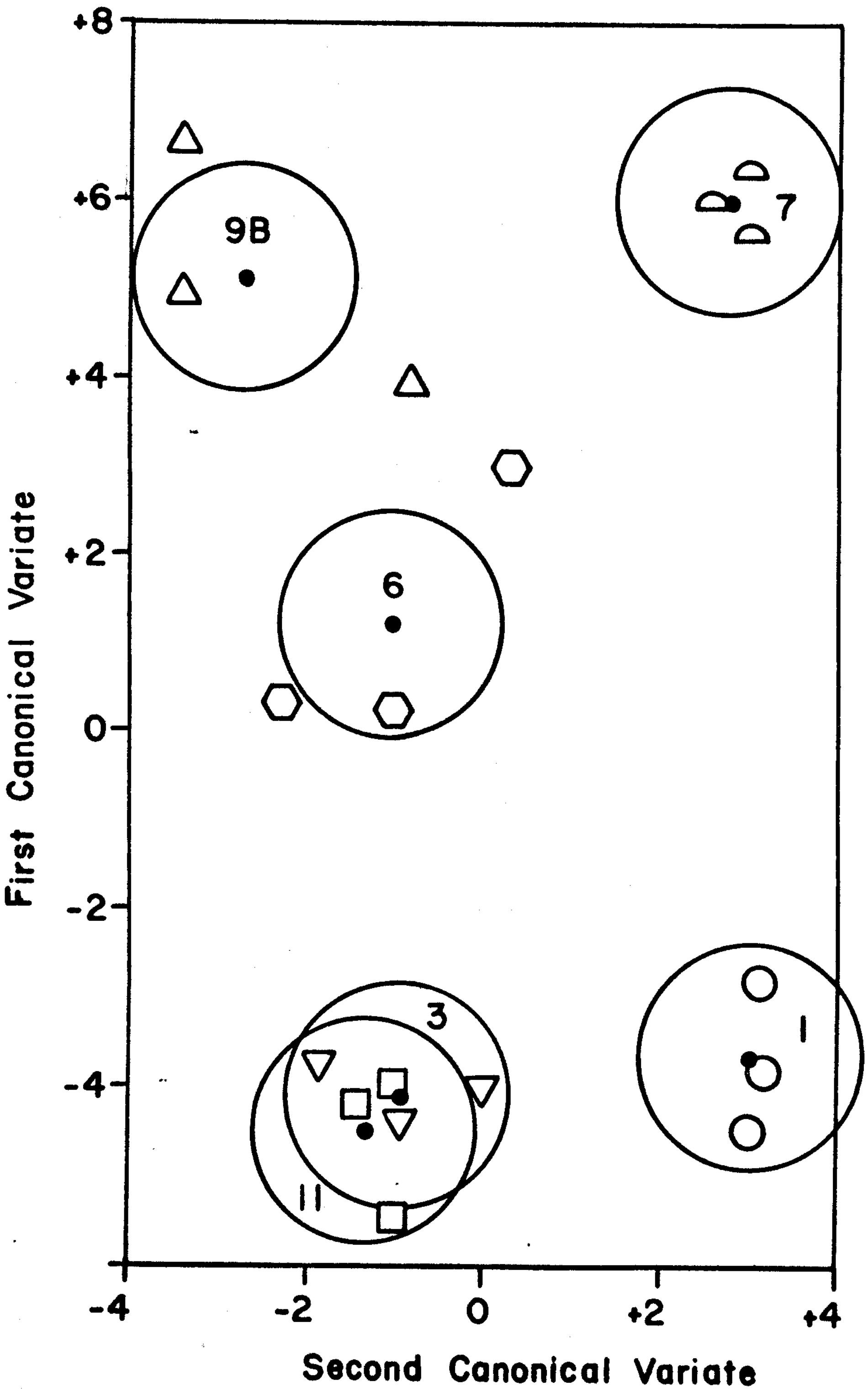
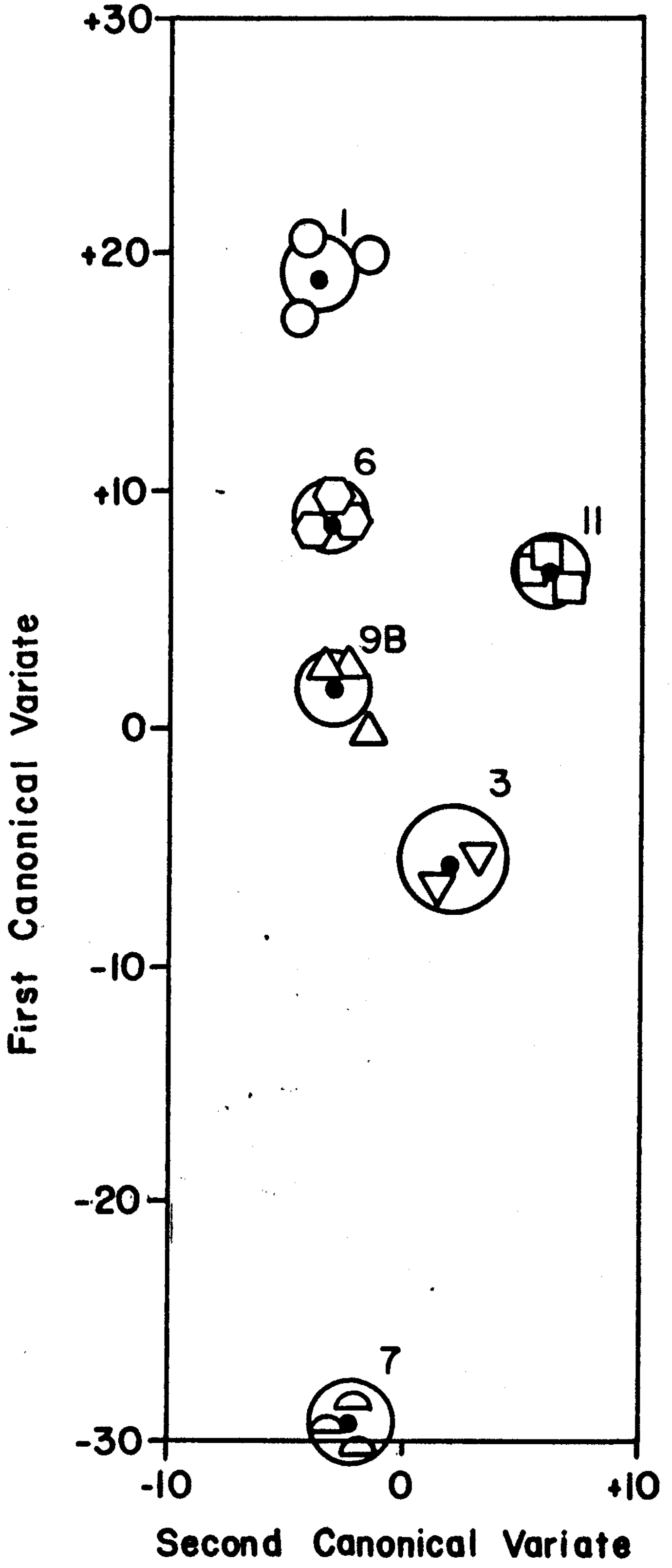

+8
+6
+4
+2
0
-2
-4
-4
-2
0
+2
+4
First Canonical Variate
Second Canonical Variate
9B
7
6
3
11
1

Figure 5 -- Canonical analysis of P. juniperinum morphology. Each symbol represents an individual sample. Each population (site) is represented by a different symbol and is composed of three (two, site 3) individuals. The population (site) mean serves as the center for a 95% confidence circle whose radius is determined following the method described in Kowal et al. (1975).


+30
+20
+10
0
-10
-20
-30
-10
0
+10
1
6
11
9B
3
7
First Canonical Variate
Second Canonical Variate

F-tests and the test for dimensionality in canonical analysis using Rao's F approximation (Rao 1952) are given in Table 9. Tables 10 and 11 present the sites ordered as they appear on the first canonical variate with the closed sites at the left. The means of the data used in the canonical analyses are given in order of the decreasing relative importance of the character in determining the first canonical variate. The relative importance of characters was determined by comparing the absolute values of the coefficients of the latent vector for each canonical variate standardized such that the error variance of each character is equal to one (Kowal 1972). These tables permit visual inspection of the direction of the variation in each character along the length of the first canonical variate. The data for the sites on which data were available for only one of the species are placed in the table in the order in which an intraspecific canonical analysis for all sites placed them on the first canonical variate in relation to the other sites.

Physiological data

The results are presented graphically in Figures 6-9. Table 12 gives the results of the analysis of variance of the initial wet weight data.

Table 9: Results of Intraspecific Univariate F-tests and the Test for Dimensionality in Canonical Analysis

Test	*P. commune*	*P. juniperinum*
Test for dimensionality in canonical analysis (Seal 1964) (using Rao's F approx. (Rao 1952))		
first canonical variate	P=.368	P=.016
second canonical variate	P=.823	P=.276
Univariate Intraspecific F-tests		
significant at 1% level (in decreasing order of significance)	LL	DEN LL DG
significant at 5% level (in decreasing order of significance)	NP 74(73)	DWPS GDWPS NP 74(73)

Table 10: Means of Three Replicates of Morphological Data for *P. commune*

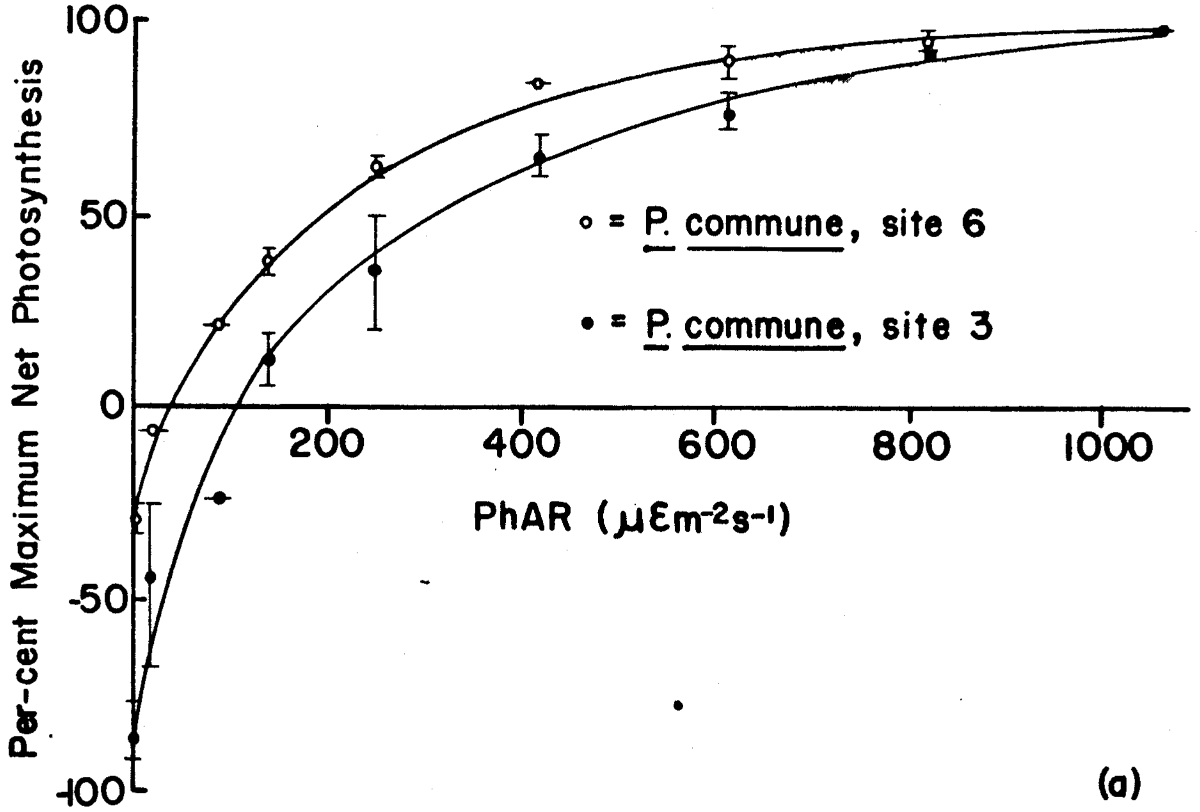
Site #	9A	11	3	1	6	9B	7
Mean on 1st. canonical variate		-4.6	-4.0	-3.7	+1.2	+5.2	+6.0
Characters in order of decreasing relative importance in determining the first canonical variate:							
LL (mm)	8.9	9.1	8.7	8.8	8.5	7.6	7.0
73G/T73 (%)	13.0	11.0	11.0	18.0	7.0	13.0	8.0
GDWPS (mg/stem)	14.1	16.3	13.8	10.0	12.7	7.8	9.1
TD (cm)	12.4	9.3	8.8	9.3	11.4	8.2	8.3
DEN (stems/dm^2)	84.0	62.0	91.0	58.0	72.0	84.0	63.0
NP 74(74) (g/m^2)	173.0	101.0	114.0	61.0	135.0	151.0	88.0
74G/TG (%)	88.0	88.0	92.0	82.0	92.0	92.0	93.0
NP 74(73) (g/m^2)	159.0	110.0	125.0	72.0	132.0	146.0	86.0
DWPS (mg/stem)	30.7	29.5	28.4	27.2	29.6	26.7	25.7
DG (cm)	3.6	3.3	3.2	2.9	3.9	2.7	2.6
Other characters not used in the canonical analysis:							
NP 74(73)/NP 74(74)	.92	1.12	1.24	1.25	.98	1.05	1.01
GDWA (g/m^2)	153.0	119.0	134.0	94.0	109.0	103.0	85.0
DWA (g/m^2)	258.0	183.0	258.0	158.0	214.0	224.0	162.0

Table 11: Means of Three* Replicates of Morphological Data for *P. juniperinum*

Site #	1	6	11	9B	3	7	10**	5**
Mean on lst. canonical variate	+19.2	+9.2	+6.6	+1.7	-6.8	-29.7		
Characters in order of decreasing relative importance in determining the lst. canonical variate:								
TD (cm)	7.9	7.8	8.4	8.6	7.8	5.1	4.4	2.6
GDWPS (mg/stem)	7.2	7.6	2.7	2.8	2.4	3.9	6.9	4.6
DEN (stems/dm^2)	111.0	128.0	80.0	141.0	260.0	202.0	166.0	184.0
LL (mm)	6.2	6.3	6.7	4.6	5.5	5.0	2.8	3.0
NP 74(73) (g/m^2)	80.0	114.0	170.0	99.0	169.0	132.0	80.0	62.0
73G/T73 (%)	30.0	39.0	25.0	10.0	20.0	15.0	38.0	41.0
NP 74(74) (g/m^2)	111.0	126.0	180.0	147.0	222.0	185.0	114.0	116.0
74G/TG (%)	71.0	75.0	80.0	88.0	86.0	91.0	69.0	69.0
DG (cm)	2.8	3.4	2.9	2.2	2.7	1.9	1.8	1.3
DWPS (mg/stem)	19.5	17.4	25.3	22.7	15.4	14.5	15.5	8.9
Other characters not used in the canonical analysis:								
NP 74(73)/NP 74(74)	.61	.90	.99	.67	.76	.72	.66	.55
GDWA (g/m^2)	110.0	127.0	175.0	105.0	139.0	128.0	116.0	81.0
DWA (g/m^2)	218.0	224.0	497.0	328.0	393.0	289.0	270.0	158.0

*two replicates on site 3; ** predominantly fertile turf

Figure 6 -- Response of net-photosynthesis to light. Bars represent range of two (three, site 5) replicates for each site. (a) *P. commune* (b) *P. juniperinum*.


100
50
0
-50
-100
Per-cent Maximum Net Photosynthesis
200
400
600
800
1000
PhAR (μEm-2s-1)
○ = P. commune, site 6
● = P. commune, site 3
(a)

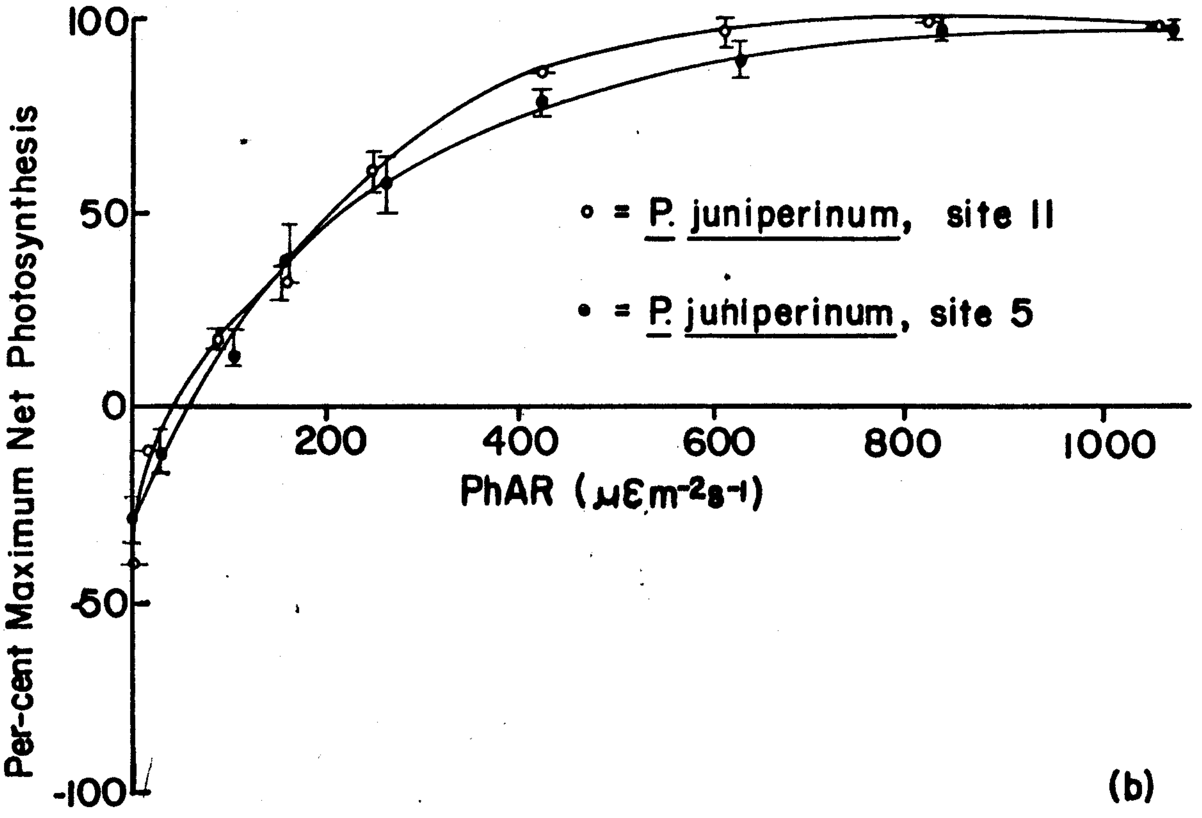

100
50
0
-50
-100
Per-cent Maximum Net Photosynthesis
200
400
600
800
1000
PhAR (μEm-2s-1)
○ = P. juniperinum, site 11
● = P. juniperinum, site 5
(b)

Figure 7 -- Response of dark respiration to temperature. Bars represent the 95% confidence interval about the mean of 4 replicates for each species.

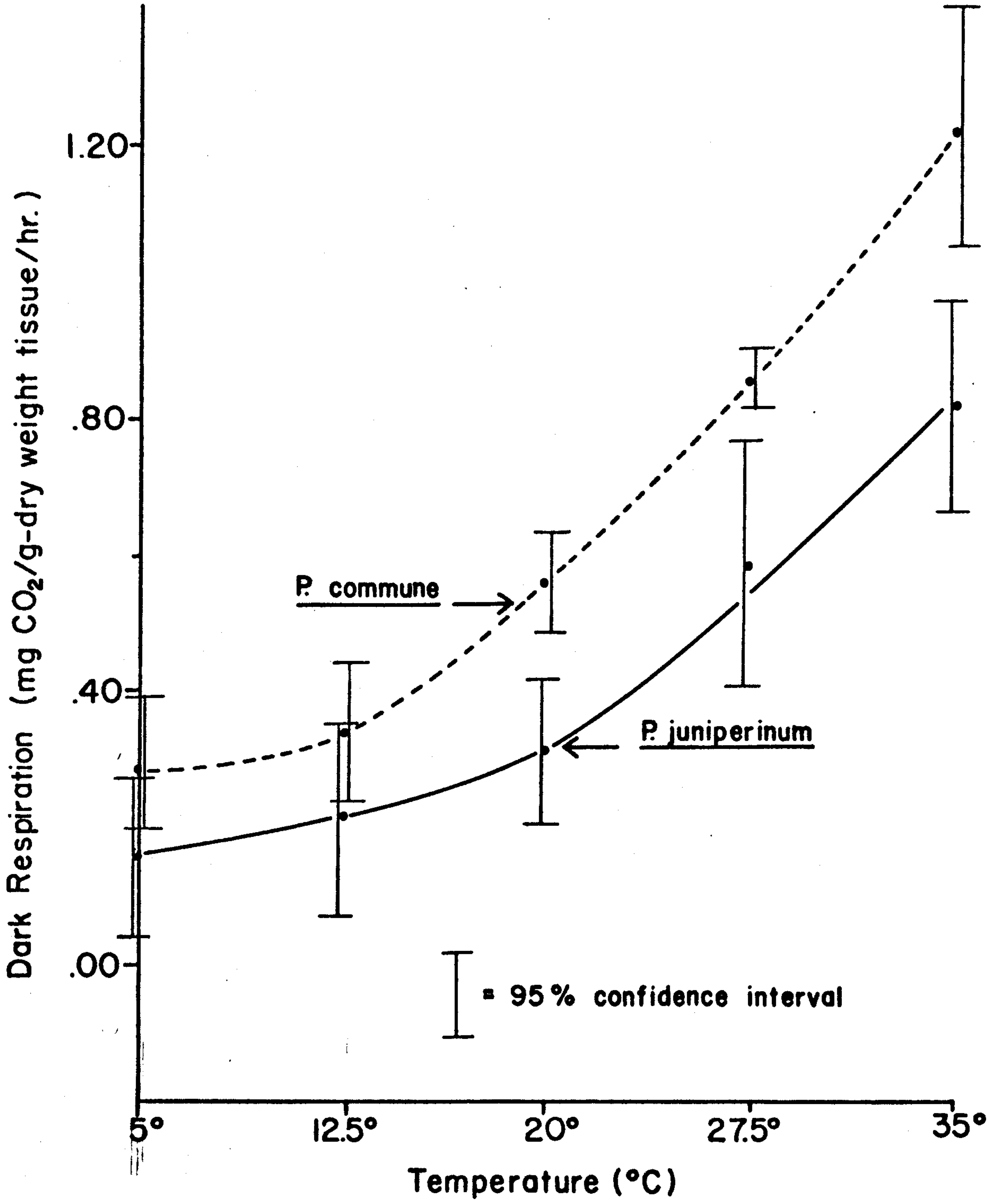
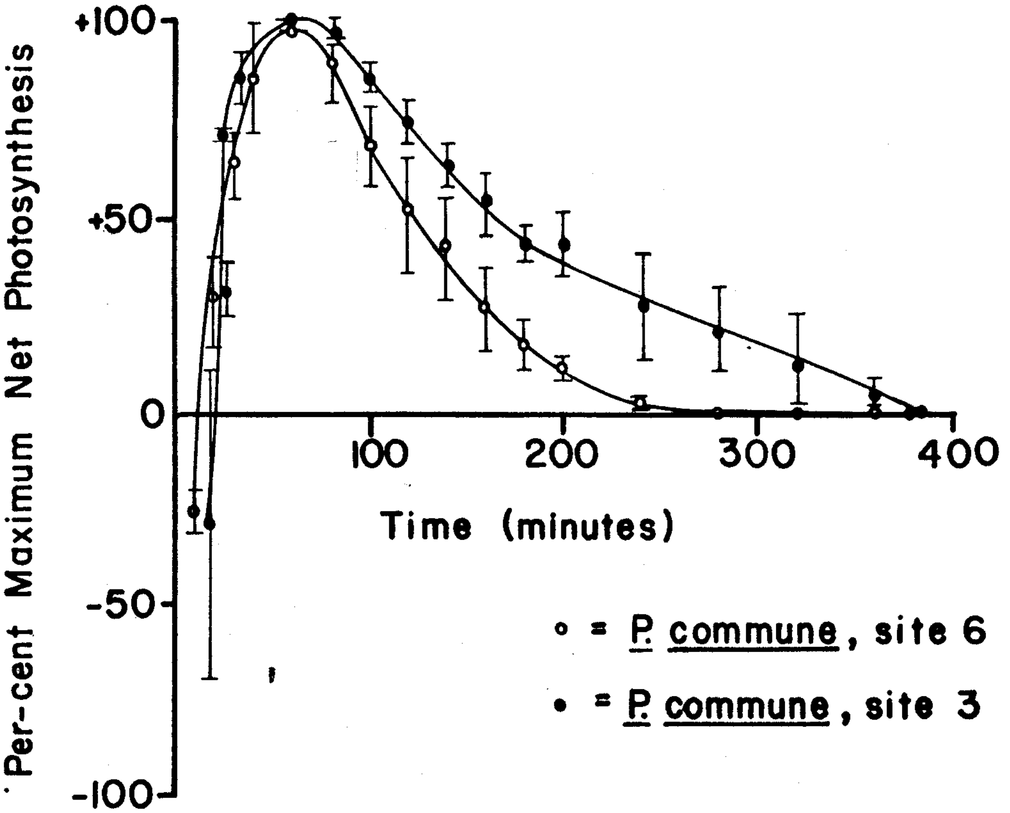
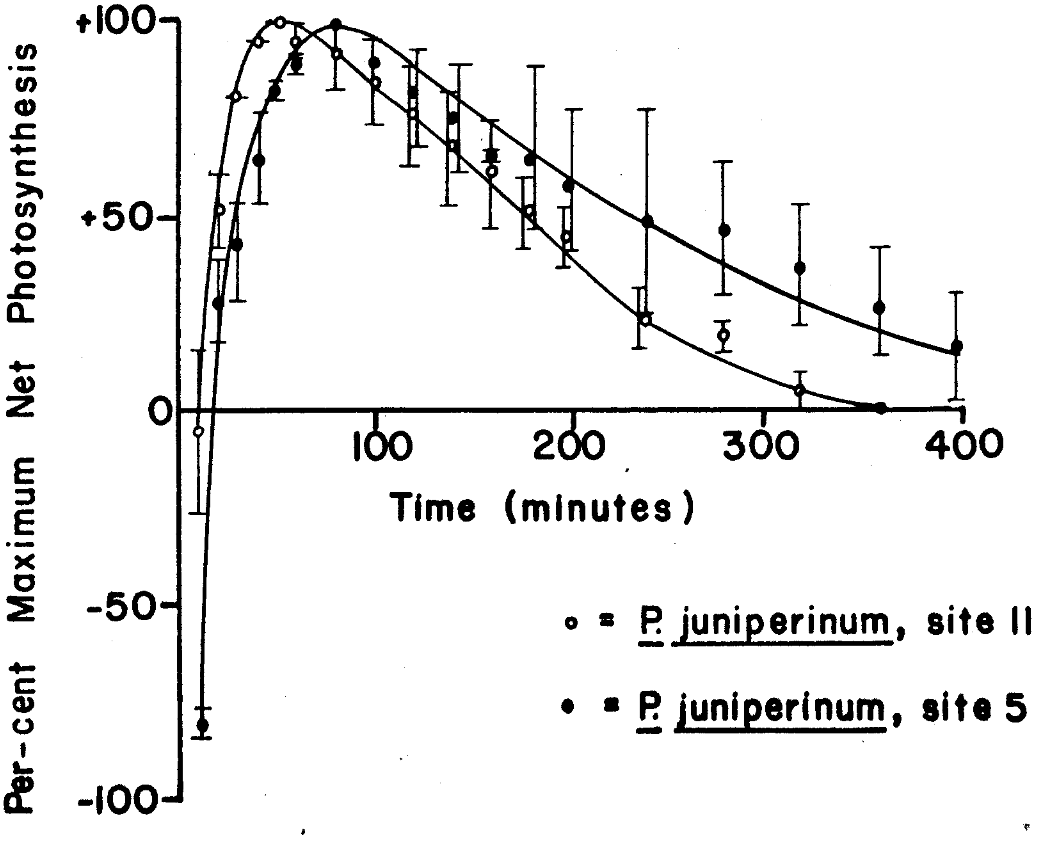

Dark Respiration (mg CO2/g-dry weight tissue/hr.)
1.20
.80
.40
.00
P. commune
P. juniperinum
= 95% confidence interval
5°
12.5°
20°
27.5°
35°
Temperature (°C)

Figure 8 -- Response of net-photosynthesis to length of drying period following re-hydration. Bars represent range of two replicates for each site. (a) *P. commune* (b) *P. juniperinum*

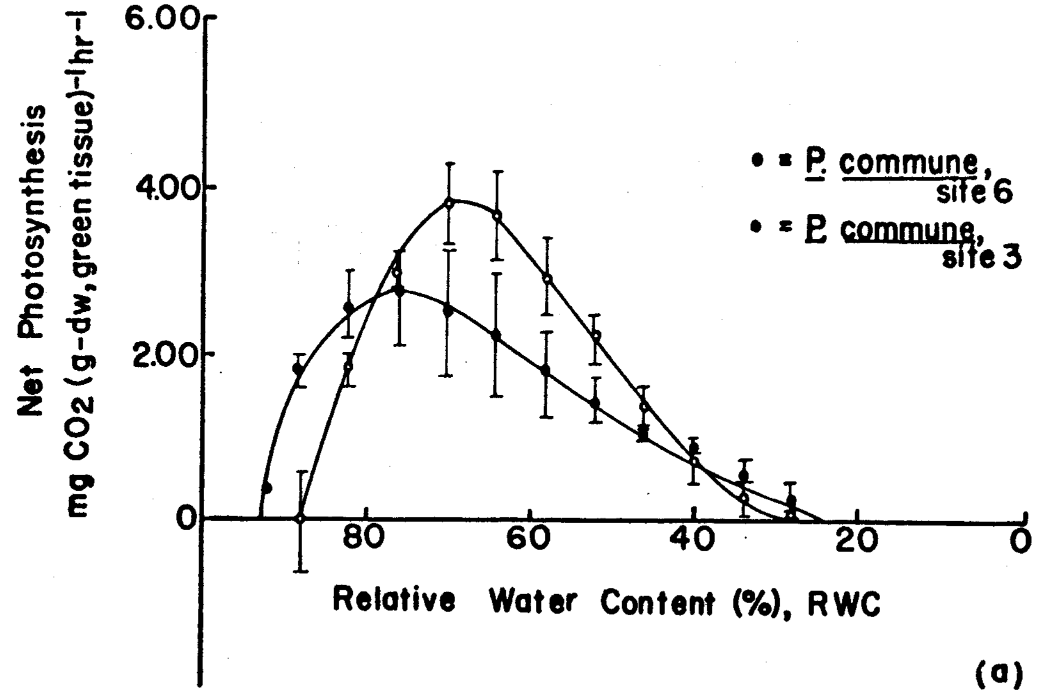

+100
+50
0
-50
-100
Per-cent Maximum Net Photosynthesis
100
200
300
400
Time (minutes)
○ = P. commune, site 6
● = P. commune, site 3

(a)


+100
+50
0
-50
-100
Per-cent Maximum Net Photosynthesis
100
200
300
400
Time (minutes)
○ = P. juniperinum, site 11
● = P. juniperinum, site 5

(b)

Figure 9 -- Relationship of net-photosynthesis to relative water content. Bars represent range of two replicates for each site. (a) P. *commune* (b) P. *juniperinum*.


Net Photosynthesis
mg CO2 (g-dw, green tissue)-1hr-1
6.00
4.00
2.00
0
80
60
40
20
0
Relative Water Content (%), RWC
• = P. commune, site 6
• = P. commune, site 3
(a)

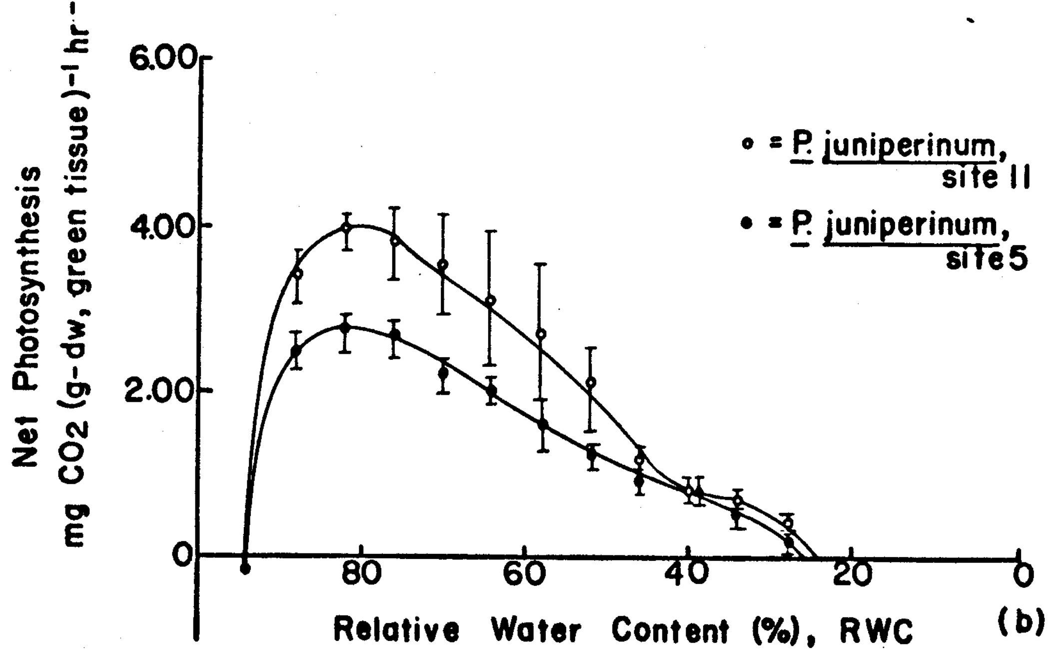

Net Photosynthesis
mg CO2 (g-dw, green tissue)-1 hr-1
6.00
4.00
2.00
0
80
60
40
20
0
Relative Water Content (%), RWC
○ = P. juniperinum, site 11
• = P. juniperinum, site 5
(b)

Table 12: Results of Analysis of Variance of Initial Wet Weight Data (one-way classification, Steel and Torrie 1960)

Means of initial wet weight data:

	$\bar{x}$	n
P. commune, site 3 (PC 3)	556% DW*	12
P. commune, site 6 (PC 6)	499% DW	10
P. juniperinum, site 5 (PJ 5)	531% DW	8
P. juniperinum, site 11 (PJ 11)	544% DW	8

Comparisons of means: F-tests and significance levels

	F	Significance Level
PC 3 vs. PC 6	8.10	1%
PJ 5 vs. PJ 11	4.04	N.S.
PC 3 vs. PJ (5,11)	1.86	N.S.
PC 6 vs. PJ (5,11)	5.71	5%

---

* DW=dry weight

DISCUSSION

Comparative Habitat

The linear regressions of *P. commune* and *P. juniperinum* frequency on the synthetic desiccation stress index (SDSI), Figures 1 and 2, indicate that differences in the SDSI account for a greater proportion of the variation in frequency of *P. juniperinum* than of *P. commune*. The frequency of *P. commune* is better explained on the basis of the SDSI on sheltered sites (SDSI < 10) than on exposed sites (SDSI > 10). The exposed sites which have a higher than expected frequency of *P. commune* (sites 3 and 7) differ from sites 5, 10, and 11 in having higher potential soil water holding capacity. Sites 5 and 10 have the largest amounts of gravel while site 11 has the steepest topography.

If differences in soil water holding capacity explain the deviations from the regression line for *P. commune* on exposed sites, *P. commune* is likely to be more dependent upon substrate water than is *P. juniperinum*. At low SDSI values, evapotranspiration may be lessened diminishing the effect of soil moisture. Thus, level sites such as 1 and 6 all exhibit a strong relationship to the SDSI.

The gradually increasing frequency of *P. juniperinum* relative to *P. commune* as the SDSI increases strongly suggests that *P. juniperinum* has a greater degree of desiccation resistance than does *P. commune*. *P. commune* is a successful competitor under low desiccation stress. Greater levels of substrate moisture on higher SDSI sites decrease the effective desiccation stress and serve to enhance the relative success of *P. commune*.

Evidence of Relative Field Desiccation Rates of *P. commune* and *P. juniperinum*

Several of the interspecific differences observed between *P. commune* and *P. juniperinum* (Table 8) indicate greater field desiccation in *P. commune*.

Numerous studies have found that desiccation in bryophytes results in the browning of previously green tissue (Fukushima 1968, Hinshiri and Proctor 1971), that this loss of photosynthetic canopy is enhanced as light levels increase (Tallis 1959, Willis 1964, Hinshiri and Proctor 1971), and that recovery from desiccation or freezing is slowed under higher levels of illumination (Hinshiri and Proctor 1971, Kallio and Heinonen 1973). The greater degree of conservation of photosynthetic canopy in *P. juniperinum* (Table 8) thus suggests less desiccation damage in this species relative to *P. commune*.

P. juniperinum also exhibits a lower ratio of 1974 growth on 1973 gametophytes relative to 1974 growth on 1974 gametophytes (NP 74(73)/NP 74(74), Table 8). This could result from a real decrease in production with gametophyte age in *P. juniperinum* or from increased translocation of assimilates. Bayfield (1967) found that in *P. commune* substantial amounts of photosynthate were being translocated and that vertical extension above-ground increased when stored reserves were removed. The increased vertical growth in *P. commune* relative to

P. juniperinum may indicate a greater rate of depletion of stored reserves in P. commune possibly as a result of greater relative desiccation stress in this species.

The predominantly greater proportion of older (1972 and earlier) gametophytes in P. juniperinum turf (Figure 3) may indicate a longer history of P. juniperinum on these sites, but also may reflect greater relative longevity in this species. A higher survival rate in P. juniperinum would be another indication of greater resistance to desiccation in this species relative to P. commune.

These field observations support the existence of a higher rate of desiccation damage in P. commune relative to P. juniperinum over the entire range of environment sampled.

Possible Physiological and Morphological Bases for Greater Desiccation Resistance in P. juniperinum

The greater desiccation resistance observed in P. juniperinum could result from structure which minimizes water loss and/or physiological tolerance of desiccation.

Several authors (Bazzaz et al. 1970, Longton 1970, Smith 1971) have suggested that the inflexed, achlorophyllous leaf margins enclosing the photosynthetic lamellae in P. juniperinum and its allies serve to increase the relative humidity and temperature of the air surrounding the lamellae. They propose that this increases the effective growing season. The negative effects of similarly increased lamellar temperatures during summer months in P. juniperinum could be offset by its lower dark respiration rates (Figure 7). The actual effect of the leaf margins in _P_. _juniperinum_ upon lamellar environment, however, has not yet been rigorously tested.

The advantages of compact growth form in increasing turf water retention are well documented both for _P_. _commune_ (Bayfield 1967, 1973), for other members of the genus (Gimingham 1967, Gimingham and Smith 1971), and for a variety of other species (Tagawa 1961, Gimingham 1967, Gimingham and Smith 1971, Hebrard 1974). The lower profile and greater density of _P_. _juniperinum_ turf should act to increase water cachement, and to decrease the water loss rate. In addition, the shorter _P_. _juniperinum_ gametophytes (especially those on sites 5 and 10) will have a greater capacity for external water conduction since the transport distance is shorter (Anderson and Bourdeau 1955). Secondly, the greater density of this turf should increase the period of external transport by maintaining higher internal turf relative humidity throughout the course of the drying period. My experiments were not designed to test the effect of growth form on water retention. Laboratory and field experiments studying the time course of water loss both from external surfaces and as a result of decreasing tissue water potentials at various levels within the turf would be of great value in determining the precise effects of denser growth forms on turf water balance.

Another possible benefit of the more compact growth form of _P_. _juniperinum_ is to shield the photosynthetic canopy from high levels of insolation. Since _P_. _juniperinum_ shows no evidence of specialization into sun and shade populations on these sites (Figure 6), this species appears to retain the capacity for efficient use of low light levels on sunny sites. Thus higher densities on sunny sites may not have a great effect on the overall level of net-photosynthesis.

The higher densities in P. juniperinum probably result from a higher rate of new stem production and a greater average longevity of gametophytes (p. 39). Both Bayfield (1967) and Collins and Oechel (1974) have documented the movement of available reserve photosynthate from adult into new branch shoots via an underground stem system in P. commune. Since there is reason to believe that P. juniperinum maintains a higher level of reserve photosynthate than does P. commune (p. 39), P. juniperinum could attain a higher rate of new stem production. This may account for the significantly higher turf densities in P. juniperinum.

The lower dark respiration rates in P. juniperinum coupled with similar overall rates of net-photosynthesis in the two species (Figure 9) should act to increase daily carbon balance and may also decrease the carbon compensation period following desiccation. The length of this period is a function of the changing ratio of gross photosynthesis to respiration following rehydration (McKay 1935, Stafelt 1938, Ensgraber 1954, Willis 1964, Lee and Stewart 1971, Proctor 1972, Kallio and Heinonen 1973, Bewley and Thorpe 1974).

The effect of drying on net-photosynthesis is similar for both species when the open (3,5) sites are compared with the closed sites (6,11). The turf samples from the open sites appear to maintain net-photosynthesis over a longer time interval following wetting (Figure 8) relative to the closed site samples. In addition, samples from the open sites attain lower initial followed by less rapidly declining rates of net-photosynthesis as drying proceeds (Figure 9).

The higher rates of net-photosynthesis observed for the samples from sites 6 and 11 probably reflect the lower rate of oxidation degradation of chlorophyll often observed in samples from shady sites (Tallis 1959, Willis 1964, Hinshiri and Proctor 1971).

While the differences observed in Figure 8 for P. juniperinum are probably a result of slower chamber drying of the much shorter turf from site 5, the differences observed in P. commune are at least in part physiological since the relation between RWC and net-photosynthesis differs between the two sites (Figure 9). Net-photosynthesis in the turf from site 6 is impaired at high water contents, while the turf from site 3 exhibits a significantly higher initial wet weight (Table 12) and achieves maximum net-photosynthesis at higher water contents.

The formation of "wet" and "dry" races in bryophytes appears to be related to both the nature of the precipitation and to the drying stress of the local environment (Lee and Stewart 1971). In the Polytrichaeae low mixhydry and saturation weight relative to co-occuring pleurocarpous species are the rule (Gimingham 1967, Gimingham and Smith 1971, Hebrard 1974), but in regions where precipitation is heavy but infrequent and where the drying stresses are severe, higher saturation weights also occur in the Polytrichaceae (Bayfield 1967). Thus, Bayfield (1967) found that *P. gracile*, an inhabitant of rubble heaps, attained a saturation weight of 550% dry weight relative to *P. commune* at 300% dry weight. The significantly higher wet weight on site 3 for *P. commune* relative to site 6 indicates a similar intraspecific difference on these sites.

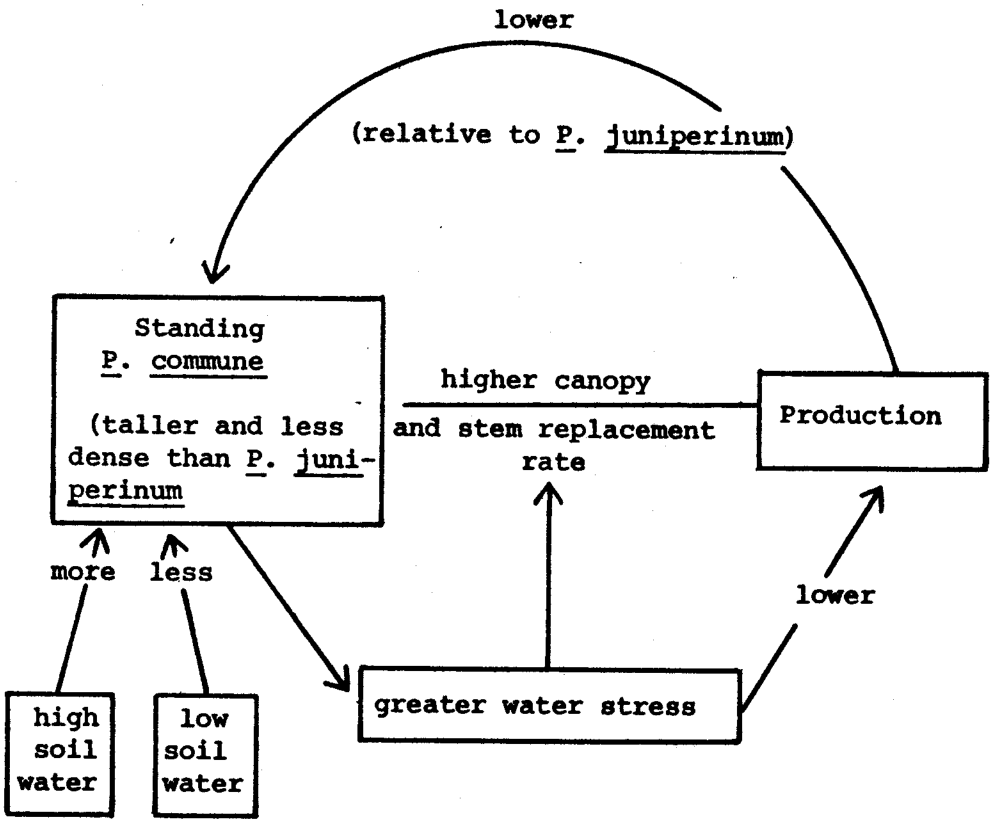
In bryophytes species which have high saturation weights usually also have more permeable surface tissues (Buch 1947). It thus seems likely that the *P. commune* on site 6 exhibits less mixhydry than the *P. commune* on site 3. If all of the exposed sites in this study result in the formation of "wet (high wet weight) populations" of *P. commune*, increased evapotranspiration may result unless growth form sufficiently moderates water loss. This could help to explain the varied behavior of *P. commune* at high SDSI values.

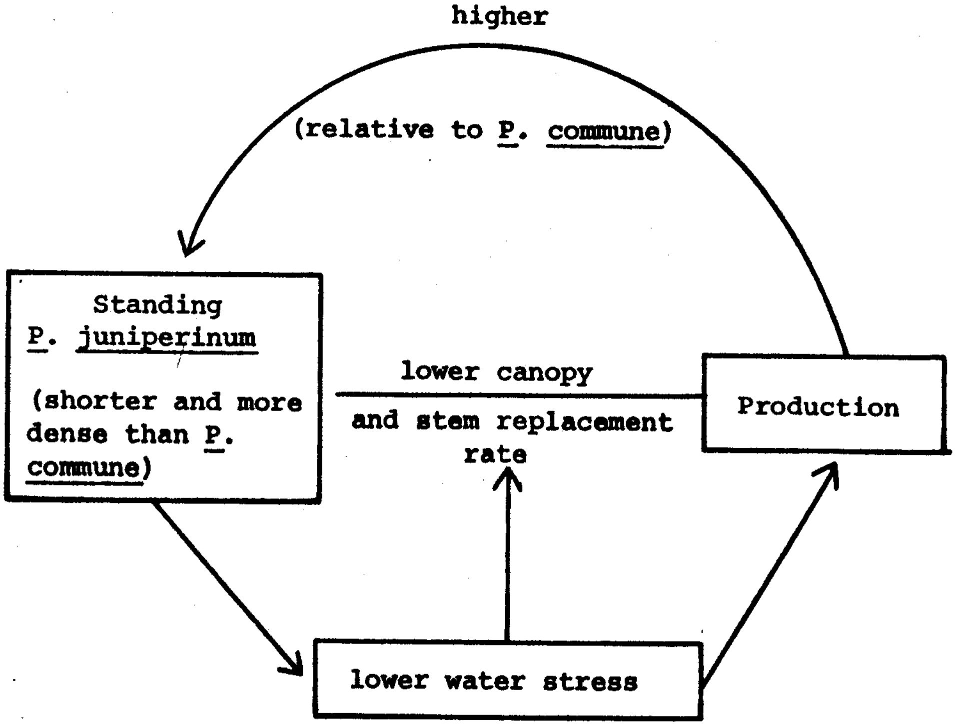
These observations on growth form and physiology, summarized in Figure 10, suggest that the basis for greater desiccation resistance in *P. juniperinum* is a combination of drought evasion (growth form moderation of water loss) and potential drought tolerance resulting from the lower dark respirationrates in this species.

Interactions of *P. commune* and *P. juniperinum* on Mesic Sites

P. commune exhibits no evidence of greater physiological adaptation towards sites of low SDSI than does *P. juniperinum*. The success of the latter species on site 11 is evidence of its capacity to succeed at low light levels. The lower respiration rates and water retention advantages of growth form in *P. juniperinum* should serve to increase the relative success of this species throughout the xeric-mesic gradient.

Figure 10 -- Schematic of species relationships on high SDSI sites.


lower
(relative to P. juniperinum)
Standing P. commune
(taller and less dense than P. juniperinum
higher canopy and stem replacement rate
Production
more
less
lower
high soil water
low soil water
greater water stress


higher
(relative to P. commune)
Standing P. juniperinum
(shorter and more dense than P. commune)
lower canopy and stem replacement rate
Production
lower water stress

The outstanding characteristic of *P. commune* is the massive size of its gametophytes relative to those of *P. juniperinum*. This greater weight and height of *P. commune* shoots makes this species more susceptible to collapse in the lower regions of the turf resulting in prostrate and spreading lower stems (Figure 13). The process is a part of the cycle of growth, collapse, and re-growth of *P. commune* tussocks described by Bayfield (1967). When collapse occurs, effective turf depth is reduced and a highly interdigitated meshwork of gametophytes is created below the surface of the still upright photosynthetic canopy. This structure could easily inhibit the growth of other species by absorbing considerable amounts of rainfall and light above the soil surface. It thus seemed likely that *P. commune* was structurally outcompeting *P. juniperinum* on low SDSI sites.

Support for this hypothesis is found in Table 7. None of the bryophytes is positively correlated with *P. commune*. The strongest negative correlations with *P. commune* occur for species in which the adult form remains within 5 cm of the soil surface (*Ceratodon purpureus*, costate Hypnaceae, and *Atrichum* spp.). The growth form of *Atrichum*, a genus closely related to *Polytrichum*, is the nearest analogue present to young gametophytes of *Polytrichum*. Young shoots of *P. commune* would be supplied with translocated assimilates from older shoots until they reached the upper regions of the turf. Similar translocation could occur in *P. juniperinum* as long as sufficient photosynthate was available.

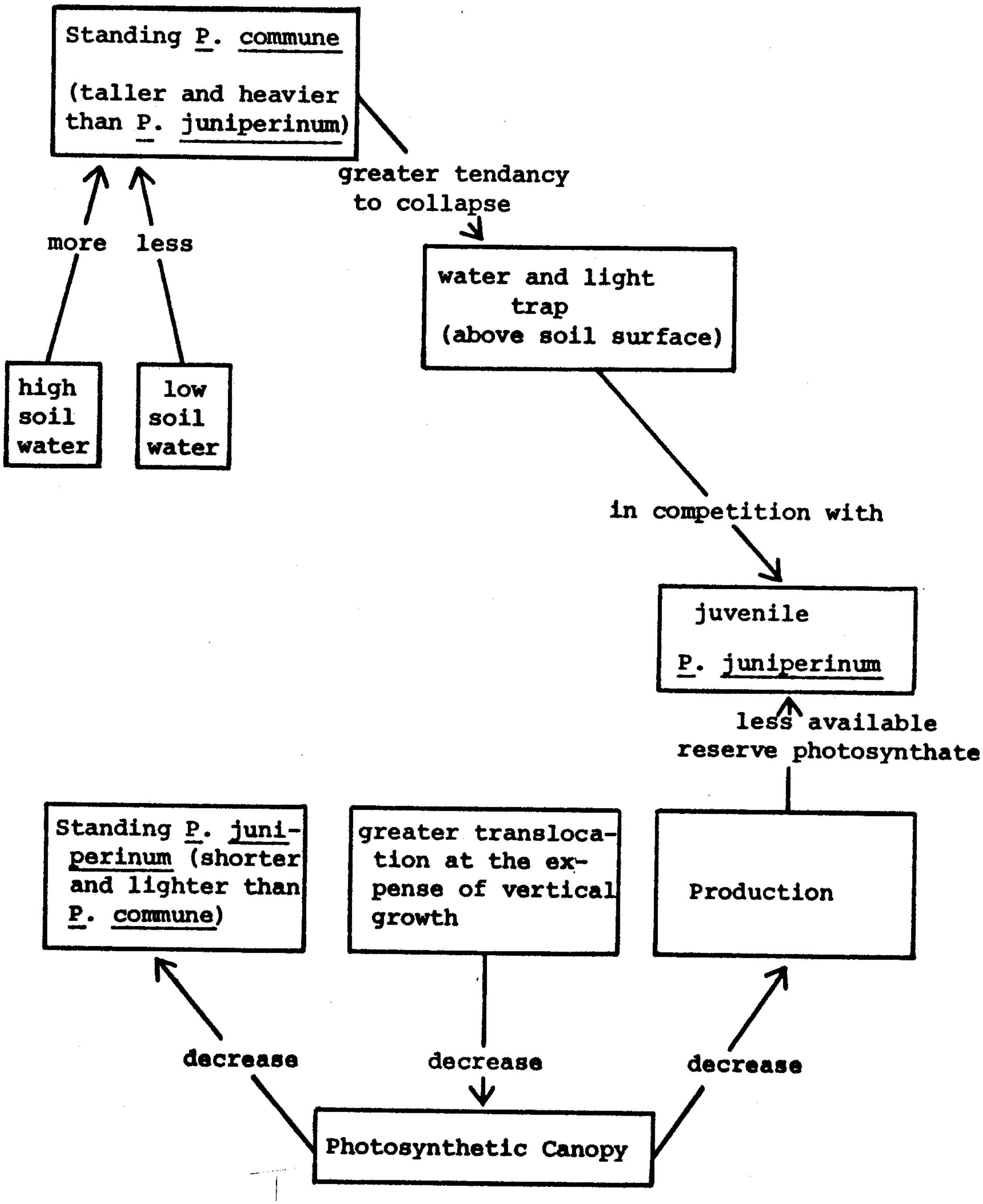
Figure 11 -- Photograph of P. commune on site 9B showing "sprawled" nature of turf.

The actual effect of well-established P. commune on P. juniperinum is indicated by the morphological data from site 9B. The above-ground production of P. juniperinum on this site is lower than it is on site 11 despite the lower density, lower light, and higher SDSI on site 11 (Table 11). Comparing the ratio of NP 74(73)/NP 74(74) on the two sites, greater translocation is evident on site 9B at the expense of above-ground growth. In turn, the reduction in vertical growth greatly decreases the amount of photosynthetic canopy (GDW/area, Table 11) which in turn decreases the photosynthate available for translocation. In this way P. commune could gradually outcompete P. juniperinum. This view of the interactions between P. commune and P. juniperinum on mesic sites is summarized in Figure 12.

Relationship of this Study to the General Biology of P. commune and P. juniperinum

Very little is known of the general biology of P. juniperinum. The species represents a taxonomic complex which occupy an extensive range of environments (Smith 1971) from alpine meadows to fairly dry scrub oak forests on sandy soils (Bazzaz et al. 1970). P. commune also occupies a wide range of habitats and exhibits morphological variation from "short loose swards" (2-5 cm high, short internodes, 1-2 mm leaf length) on insolated, exposed clay-type soils to "tall loose swards" (to 30 cm high, long internodes, 15 mm leaf length) on the moist, rich soils of forest floors (Sarafis 1971). P. juniperinum is generally considered to be the more xeric of the two species (Crum 1973).

Figure 12 -- Schematic of species relationships on high SDSI sites.


Standing P. commune
(taller and heavier than P. juniperinum)
greater tendancy to collapse
more
less
high soil water
low soil water
water and light trap (above soil surface)
in competition with
juvenile P. juniperinum
less available reserve photosynthate
Standing P. juniperinum (shorter and lighter than P. commune)
greater translocation at the expense of vertical growth
Production
decrease
decrease
decrease
Photosynthetic Canopy

The recent study of Watson (1974) represents an unprecedented attempt at comparative bryophyte ecology. She was able to define the habitat of P. commune, P. juniperinum, and P. piliferum in a two-dimensional space defined by light and soil pH. Light was estimated by assessing the degree of vascular plant cover. Soil pH was highly correlated with soil texture. She found that P. commune occupied regions of low light and moderate pH relative to P. juniperinum while that species exhibited a bi-modal distribution over higher and lower pH regions of higher light. The P. juniperinum which occupied low pH soils of high water holding capacity, however, appears to have been predominantly of alpine origin and factors other than soil moisture could be responsible for the absence of P. commune in these habitats. Unfortunately, none of Watson's study sites are similar to the sites studied here. Direct comparisons are not valid, but her general suggestion that P. commune could be a specialist species which outcompetes the generalist species P. juniperinum in habitats favorable to P. commune is substantiated by these results.

P. commune shows evidence of a specialized physiology in its potential differentiation into sun-, shade-populations (Figure 6), and wet- and dry-populations (Figure 9, Table 12). P. juniperinum appears to exhibit a consistent physiology over the gradient (Figures 6 and 9).

The lack of substantial morphological variation in P. commune similar to that observed in P. juniperinum over the gradient is puzzling in the light of Sarafis' (1971) results described above.

The growth form variation she noted in P. commune appeared to be plastic and controlled by a combination of ambient light intensity and water availability (Sarafis 1971). This raises the possibility that the genotype(s) found on these sites is not as plastic as the European and Australian plants studied by Sarafis (1971). What appears to be inherent inflexibility in P. commune on these sites does not appear to be true for the species as a whole.

Similarly, while P. juniperinum may maintain a consistent physiology on these sites, Bazzaz et al. (1970) found evidence of physiological differentiation in this species between alpine and forest populations. Unfortunately they did not determine whether the variation was phenotypic or genotypic.

The relative importance of competition versus environment in defining the vegetation studied here has been explored. P. commune appears to be unable to tolerate the more xeric sites while P. juniperinum is outcompeted on the more mesic sites. General mechanisms for these two processes have been suggested (Figures 10 and 12). Further work might be profitably concentrated in three specific areas: 1) further verification of the intraspecific differences in physiology suggested for P. commune, 2) a comparison of the carbohydrate and water use strategies in each species grown under varied environmental conditions (pattern of translocation, internal versus external water conduction, degree of mixhydry etc.), and 3) investigation of the effect of adult turf of one species on spore germination and juvenile establishment of the other species.

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APPENDIX I

Environmental Measurements -- September 8, 1974

Site	1	3	5	6	7	9A	9B	10	11
Time: 8:20 a.m.-8:57 a.m.									
PhAR ($m^{-2}s^{-1}$) (± s)	21 (±2.6)	45 (±7.1)	110 (±4.5)	46 (±7.5)	85 (±4.1)	20 (±3.8)	63 (± .8)	75 (±3.7)	39 (±2.9)
Relative Humidity (%) (± s)	96 (±3.0)	94 (±0.0)	96 (±3.0)	99 (±3.0)	96 (±3.0)	99 (±3.0)	99 (±3.0)	96 (±3.0)	100 (±0.0)
Air Temperature (°C) (± s)	15.6 (± .13)	15.5 (± .10)	15.4 (± .05)	15.7 (± .15)	15.9 (± .13)	15.7 (± .08)	15.7 (± .10)	15.4 (± .13)	15.7 (± .05)
Turf Temperature (°C) (± s)	15.4 (± .35)	15.0 (± .00)	15.4 (± .52)	15.7 (± .36)	15.0 (± .08)	15.1 (± .10)	15.3 (± .36)	15.7 (± .33)	16.1 (± .70)
Time: 10:00 a.m.-10:25 a.m.									
PhAR (± s)	35 (±2.6)	69 (±3.0)	172 (±3.3)	66 (±0.6)	115 (±2.1)	29 (±1.5)	75 (±3.9)	121 (±6.4)	41 (±3.0)
Relative Humidity (± s)	99 (±2.5)	96 (±2.5)	95 (±0.0)	93 (±2.9)	95 (±0.0)	95 (±0.0)	95 (±0.0)	96 (±2.5)	93 (±2.9)
Air Temperature (± s)	18.4 (± .13)	18.8 (± .05)	19.0 (± .15)	19.2 (± .24)	19.0 (± .06)	18.8 (± .10)	18.9 (± .06)	19.3 (± .22)	19.3 (± .13)
Turf Temperature (± s)	18.8 (± .24)	20.2 (± .36)	19.5 (± .45)	18.4 (± .34)	18.7 (± .48)	18.4 (± .17)	17.9 (± .33)	18.2 (± .68)	18.2 (± .29)

(cont'd)

Site	1	3	5	6	7	9A	9B	10	11
Time: 12:00-12:28 p.m.									
PhAR (± s)	41 (±3.4)	73 (±2.8)	169 (±6.9)	71 (±7.3)	116 (±2.5)	37 (±4.8)	75 (±3.2)	141 (±10.1)	44 (±3.1)
Relative Humidity (± s)	85 (±2.0)	84 (±2.3)	83 (±4.0)	88 (±4.5)	85 (±2.0)	93 (±2.3)	93 (±2.3)	83 (±2.0)	82 (±3.3)
Air Temperature (± s)	22.9 (± .55)	22.7 (± .17)	22.4 (± .45)	22.0 (± .17)	22.3 (± .26)	22.2 (± .35)	22.0 (± .24)	22.8 (± .10)	22.5 (± .37)
Turf Temperature (± s)	22.3 (± .35)	22.8 (± .26)	21.5 (±1.08)	21.8 (± .65)	21.9 (± .75)	22.0 (± .75)	22.4 (± .85)	20.7 (± .66)	21.2 (±1.33)
Time: 2:00-2:28 p.m.									
PhAR (± s)	44 (±8.7)	76 (±4.9)	200 (±0.0)	84 (±12.5)	169 (±3.5)	49 (±21.2)	94 (±5.6)	196 (±14.9)	65 (±2.4)
Relative Humidity (± s)	83 (±1.9)	80 (±2.3)	86 (±0.0)	84 (±2.3)	86 (±2.4)	87 (±0.6)	87 (±2.5)	86 (±2.5)	79 (±3.8)
Air Temperature (± s)	24.1 (± .67)	24.1 (± .22)	23.7 (± .10)	24.1 (± .22)	24.2 (± .10)	24.3 (± .28)	23.9 (± .10)	24.4 (± .00)	24.5 (± .15)
Turf Temperature (± s)	25.7 (± .99)	24.1 (± .85)	23.8 (± .90)	23.8 (± .79)	24.6 (± .80)	23.7 (± .76)	24.6 (± .43)	24.7 (± .38)	23.4 (± .68)

(cont'd)

Site	1	3	5	6	7	9A	9B	10	11
Time 4:00-4:30 p.m.									
PhAR (± s)	46 (±5.3)	82 (±4.7)	169 (±8.3)	68 (±5.9)	151 (±4.9)	84 (±42.8)	100 (±7.0)	183 (±9.2)	72 (±6.3)
Relative Humidity (± s)	77 (±3.6)	71 (±3.4)	79 (±5.2)	85 (±2.0)	86 (±0.0)	81 (±2.0)	86 (±0.5)	84 (±2.3)	77 (±2.0)
Air Temperature (± s)	24.9 (± .95)	24.8 (± .31)	25.0 (± .17)	23.7 (± .53)	23.9 (± .14)	23.9 (± .39)	23.7 (± .48)	23.7 (± .30)	24.1 (± .32)
Turf Temperature (± s)	25.1 (± .29)	24.0 (± .64)	24.2 (± .47)	24.4 (± .48)	24.8 (±1.18)	23.7 (± .48)	22.5 (± .39)	23.1 (±1.21)	24.1 (± .79)
Time 6:00-6:24 p.m.									
PhAR (± s)	65 (±27.0)	162 (±70.4)	142 (±9.3)	105 (±48.5)	118 (±17.1)	46 (±10.3)	80 (±8.6)	153 (±10.6)	48 (±13.9)
Relative Humidity (± s)	79 (±2.5)	81 (±2.0)	81 (±2.0)	80 (±2.3)	80 (±2.3)	81 (±2.0)	81 (±2.0)	82 (±0.0)	84 (±2.3)
Air Temperature (± s)	23.5 (± .44)	23.4 (± .13)	23.3 (± .47)	23.4 (± .39)	24.2 (± .42)	23.5 (± .53)	23.8 (± .49)	23.5 (± .19)	23.7 (± .12)
Turf Temperature (± s)	24.3 (± .43)	24.5 (± .67)	23.3 (± .79)	23.4 (± .67)	23.9 (± .74)	24.1 (±1.08)	23.6 (± .60)	24.0 (± .70)	26.7 (±1.19)

APPENDIX II

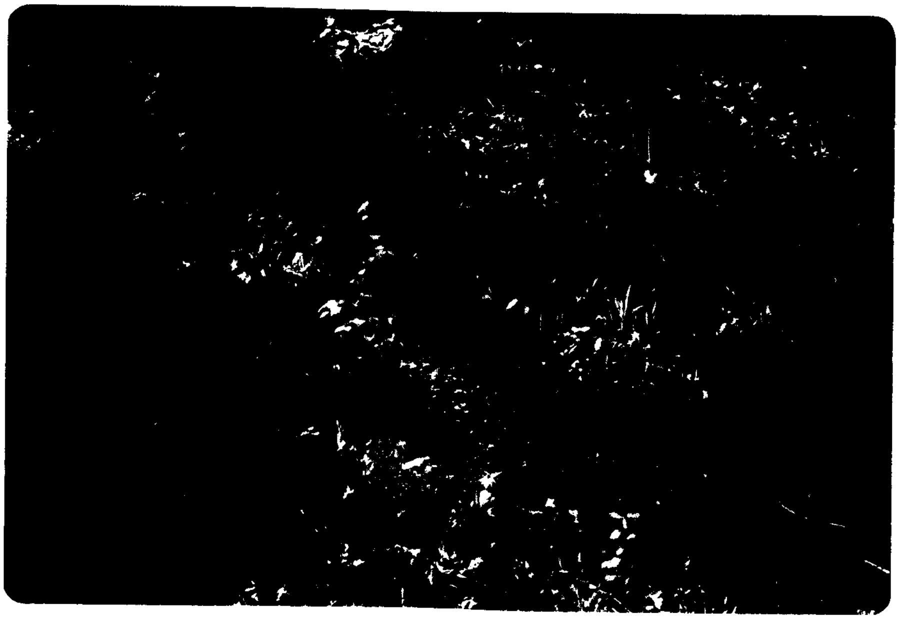
OVERVIEW OF EACH SITE

SITE 1

OVERVIEW OF EACH SITE

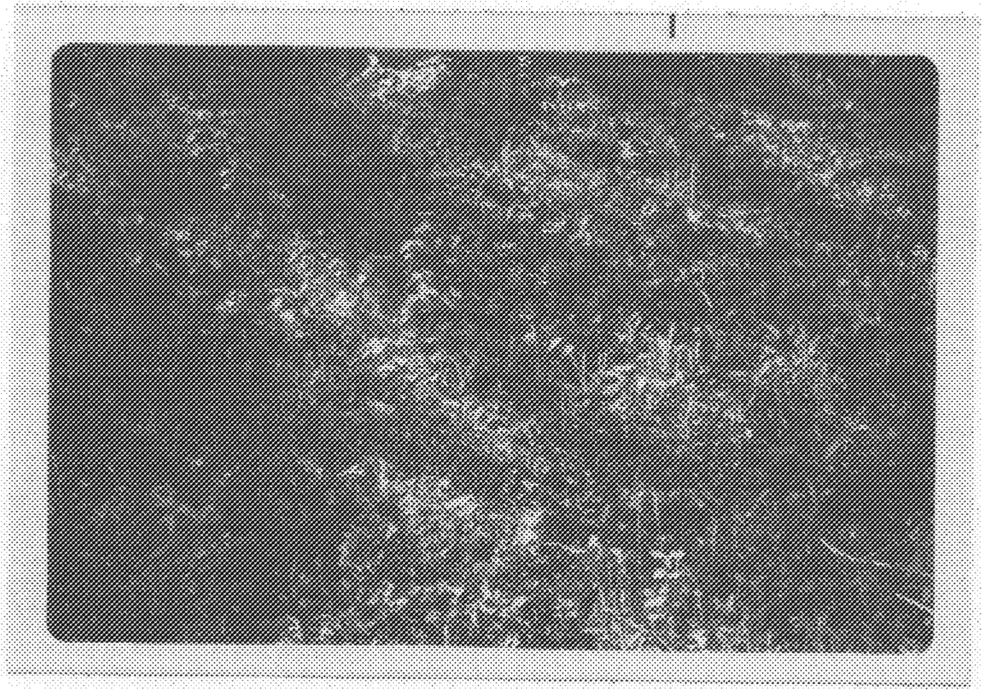
SITE 1

SITE 3



SITE 5

SITE 3



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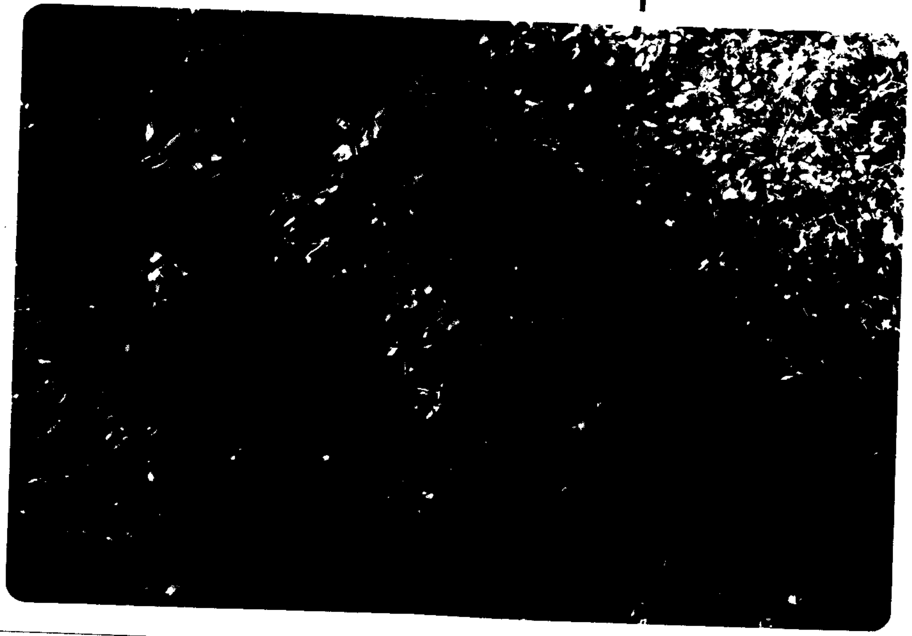

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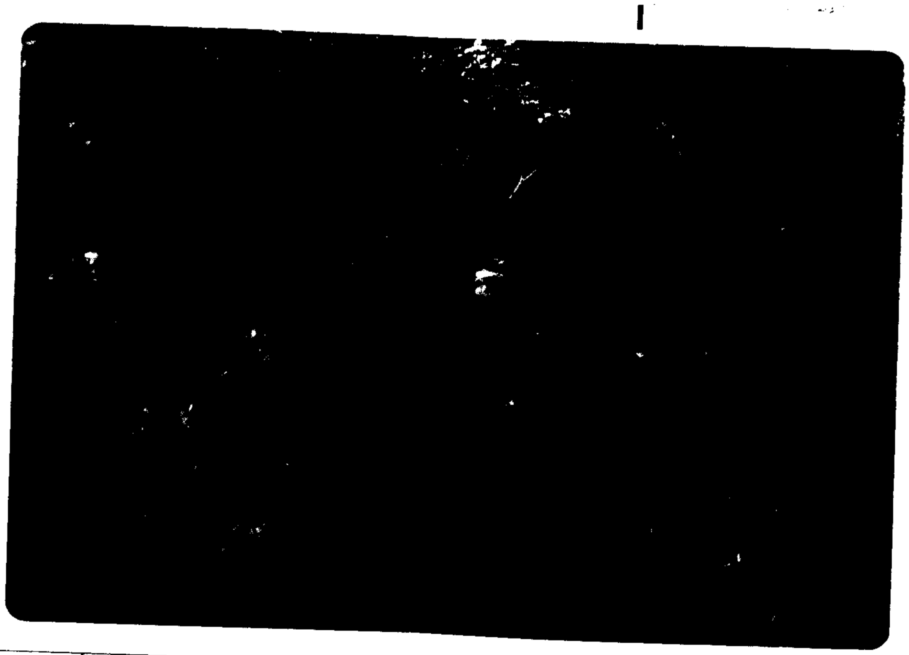
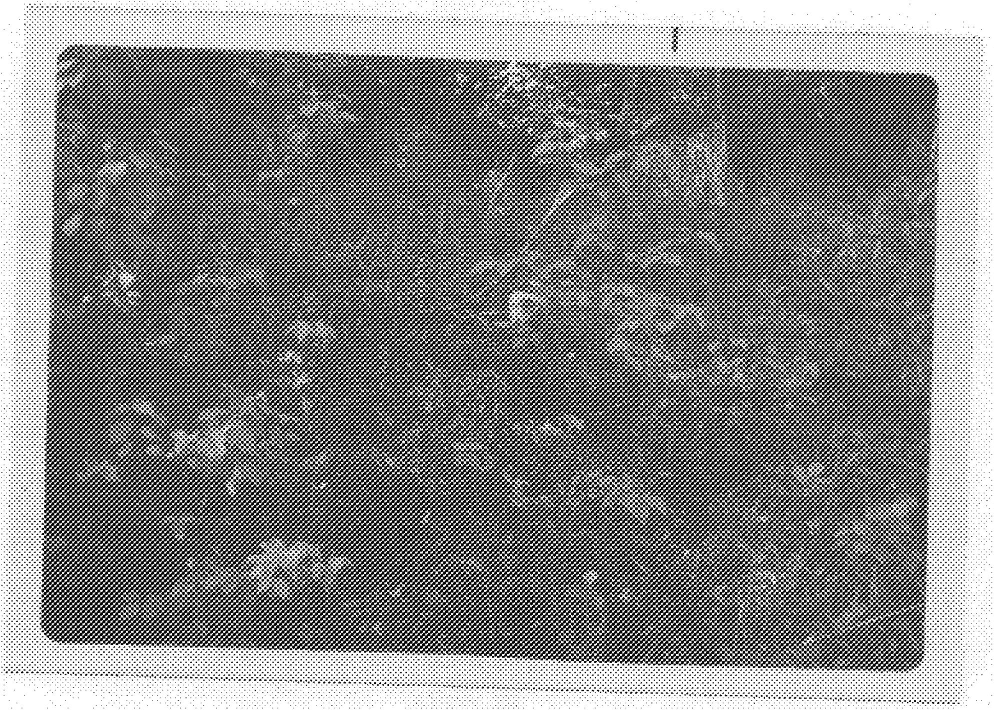


SITE 7

SITE 6



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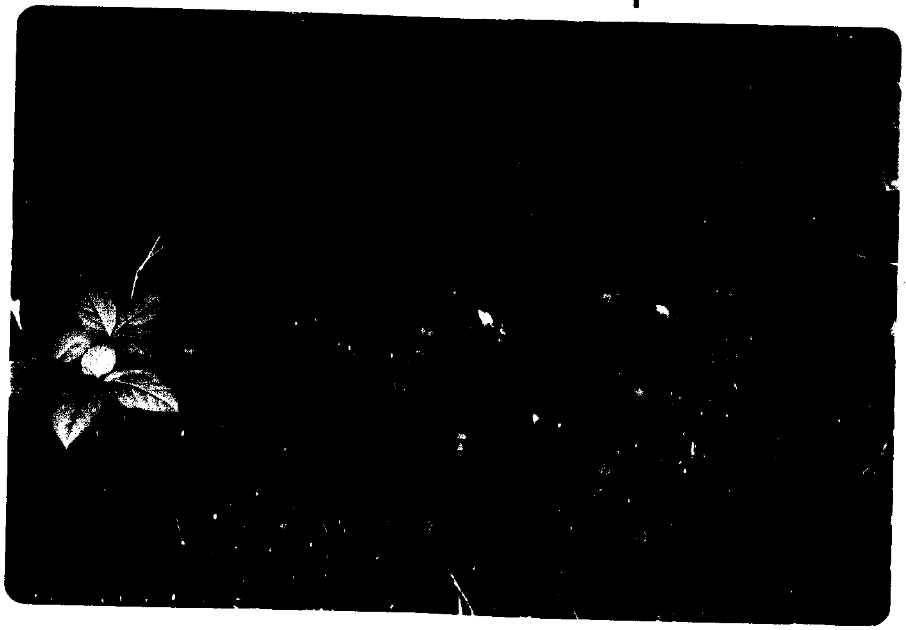

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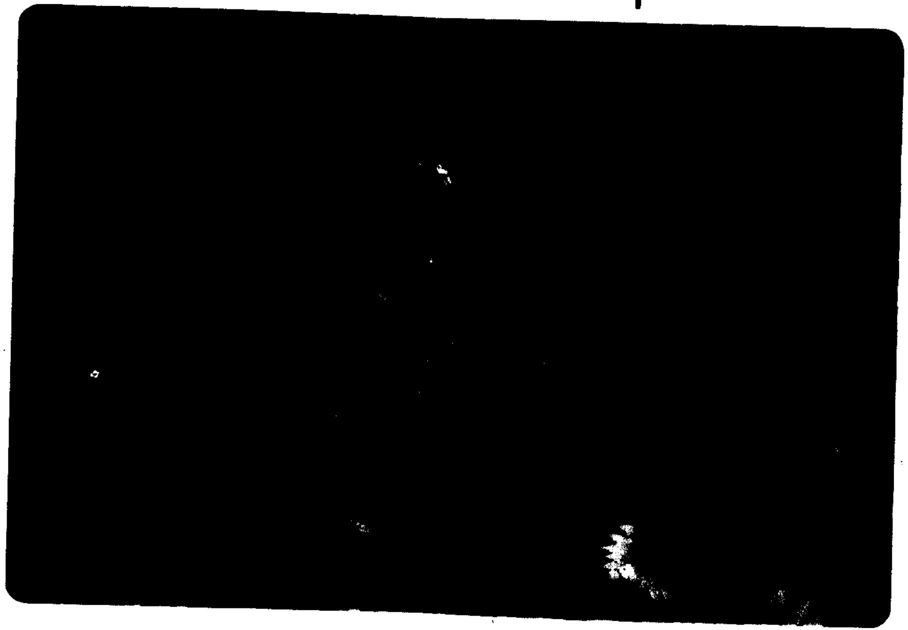
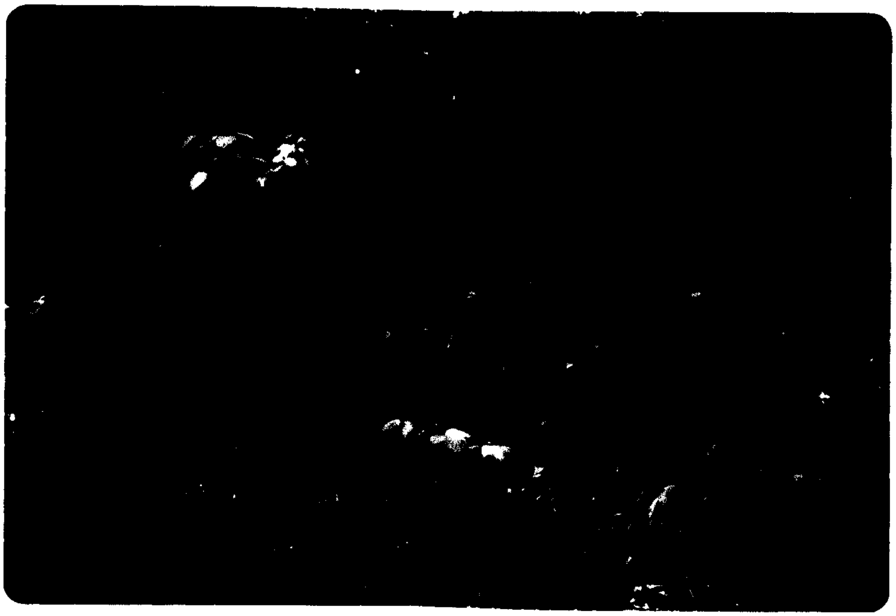


SITE 9B

SITE 9A

SITE 9B



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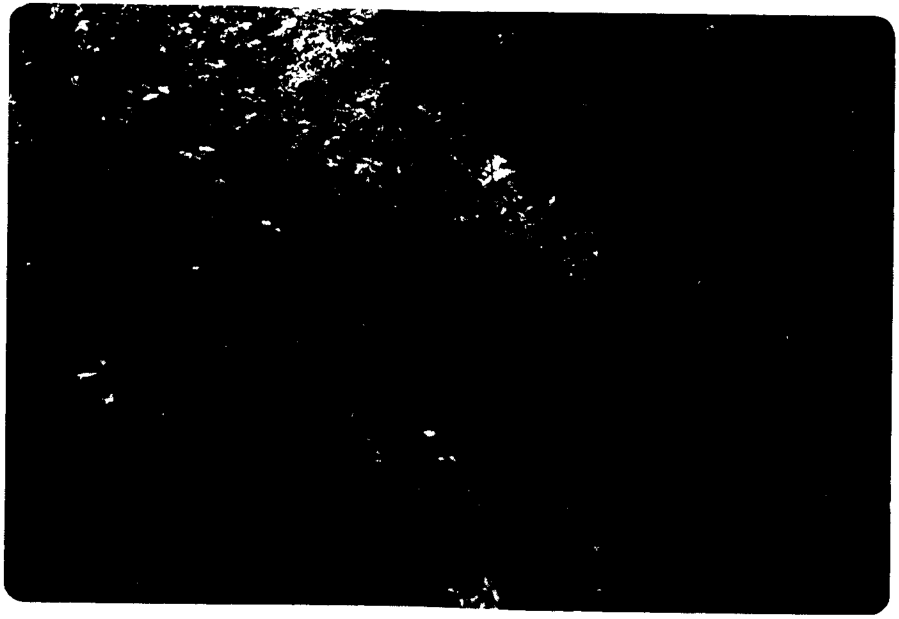
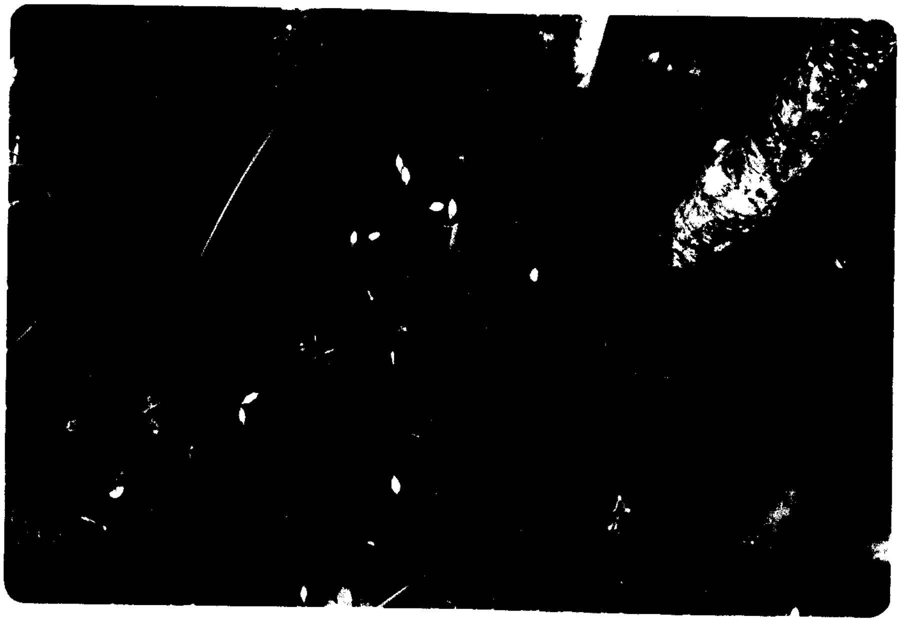


SITE 11

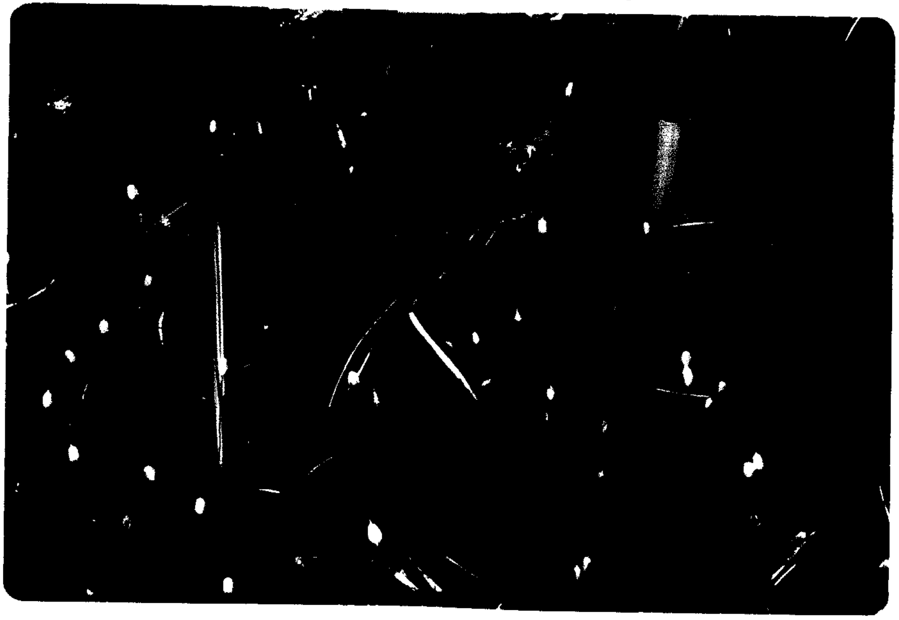
SITE 10

SITE 11

CLOSEUP VIEW OF MORPHOLOGY AT EACH SITE



P. commune on site 9A - low light site



P. commune on site 1 - low light site

P. commune on site 9A - low light site

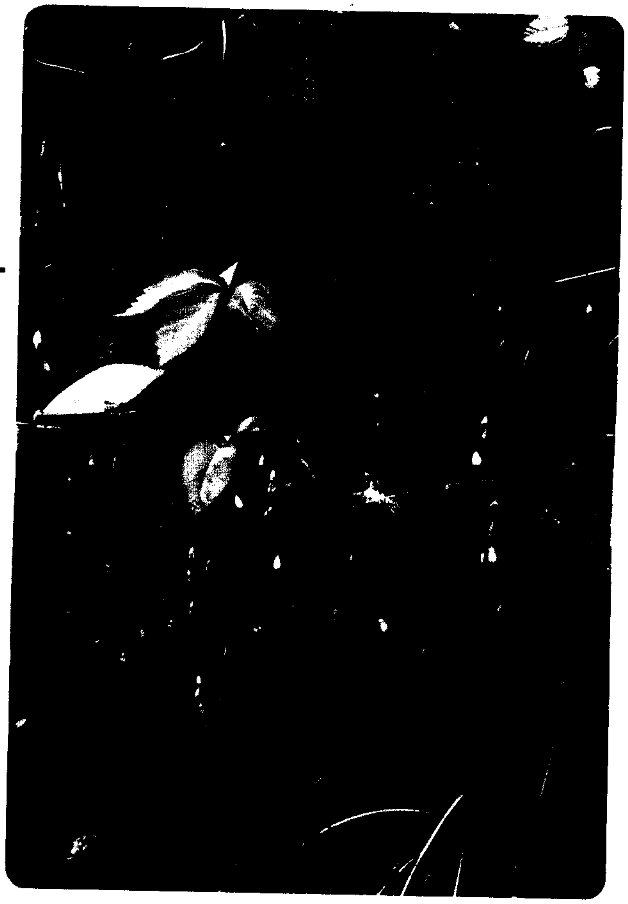
P. commune on site 1 - low light site

<u>P</u>. <u>juniperinum</u> on site 11 - low light site

<u>P</u>. <u>commune</u> on site 6 - moderate light site

P. *juniperinum* on site 11 - low light site

P. *commune* on site 6 - moderate light site



Both species on site 3 - moderate light site

Both species on site 3 - moderate light site

P. commune on site 9B - moderate light site

Both species on site 7 - high light site

P. commune on site 9B - moderate light site

Both species on site 7 - high light site

P. juniperinum on site 10 - high light site

P. juniperinum on site 5 - high light site

P. *juniperinum* on site 10 - high light site

P. *juniperinum* on site 5 - high light site

COMPARATIVE ECOLOGY
OF
POLYTRICHUM COMMUNE HEDW. AND
POLYTRICHUM JUNIPERINUM HEDW.

APPROVED: ______________________________
Michael S. Adams
Associate Professor of Botany
August 25, 1975