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Area-species curve applies to gaps in a Canada hemlock (Tsuga canadensis (L.) carr.) forest in the Shenandoah National Park

Joseph John LaCroix

AREA-SPECIES CURVE APPLIES TO
GAPS IN A CANADA HEMLOCK (TSUGA CANADENSIS (L.)
CARR.) FOREST IN THE SHENANDOAH NATIONAL PARK

By

Joseph John LaCroix

I certify that I have read this thesis and find that, in scope and quality, it satisfies the requirements for the degree of Master of Arts/Science.

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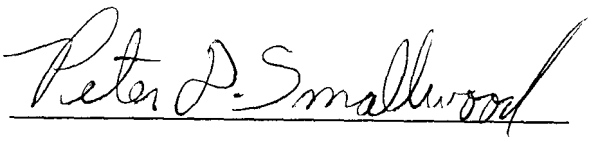

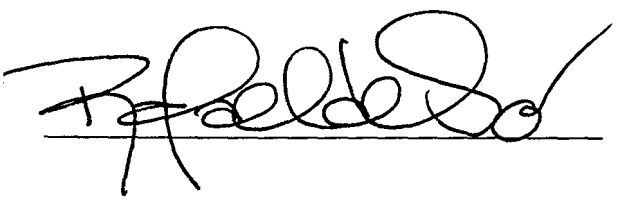

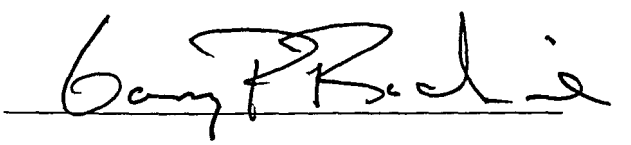

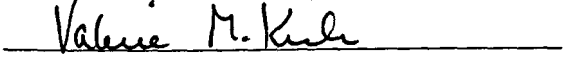

AREA-SPECIES CURVE APPLIES TO GAPS IN A CANADA HEMLOCK (TSUGA CANADENSIS (L.) CARR.) FOREST IN THE SHENANDOAH NATIONAL PARK

By

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AREA-SPECIES CURVE APPLIES TO GAPS IN A CANADA HEMLOCK (TSUGA CANADENSIS (L.) CARR.) FOREST IN THE SHENANDOAH NATIONAL PARK

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Master of Science in Biology

University of Richmond

Dr. John Bishop, Thesis Advisor

ABSTRACT: A typical area-species curve shows that species richness (number of species) and island size are positively correlated. I tested whether the area-species concept, which was developed using islands, could be applied to herbaceous plants in canopy gaps in a hemlock community.

I conducted studies in Limberlost, Shenandoah National Park. I measured the species richness of herbaceous plants in six gaps during the summer and fall of 1995 and eight gaps and one non-gap site in the spring of 1996. The two additional gaps in 1996 extended the upper range of gap sizes. I calculated the correlation between species richness and gap and quadrat size over all seasons (combined seasons) and each season separately (separate seasons).

Three hypotheses were tested: 1) as gap size increases so do species richness values, 2) as quadrat size increases so do species richness values,

and 3) within equal sized quadrats in different sized gaps, as gap size increases so do the species richness values.

Within separate seasons species richness values increased with an increase in gap size, but for combined seasons this relationship was not supported. As quadrat size increased there was an increase in species richness values. Within equal sized quadrats in different sized gaps, the values of species richness for separate seasons increased as gap size increased, but for combined seasons this relationship was not supported. Discrepancies between separate and combined seasons may be explained, in part, to the inclusion of the two larger gaps in the former case.

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INTRODUCTION

A primary principle of the classic theory of island biogeography is that the species richness (number of species) on an island will reach a dynamic equilibrium and this species richness will increase with island area and habitat diversity and decrease with island isolation (Buckley, 1981). Ecologists recognized the relationship between island size and species richness before any other diversity pattern, and the relationship has more to support it than any other rule about species diversity (Rosenzweig, 1995). Preston (1962) showed that the relationship between species richness and island size could be described according to a lognormal law, and called such a relationship the "species curve." This curve was the basis for MacArthur and Wilson's (1967) theory of island biogeography.

Islands can be defined as patches of habitat isolated from similar habitats by different, relatively inhospitable terrain (Simberloff, 1974). Canopy gaps can be considered "islands of light" in the dark forest. A gap is defined as the opening in the forest canopy extending to the base of the surrounding canopy tree (Runkle, 1981). I expected forest gaps to act as islands for herbaceous plants.

Canopy gaps create successional patches in forests and thereby play an important role in stand composition and dynamics of these forests (Clebesch and Busing, 1989). The formation of gaps can occur in more than

one way. For instance, a canopy tree may be blown over resulting in pits where the roots once resided, while another may die standing, leaving the soil relatively undisturbed. Different canopy-generated sites create a varied assortment of microsites, which in turn create sites suitable for one species and not another (Clinton and Boring, 1994). Individual tree mortality gaps tend to have highly localized effects on forest composition and structure (Clebesch and Busing, 1989). The predominant factors that produce gaps in the forests are high winds, glaze (ice) storms, and lightning (Runkle, 1985).

Other factors influencing the development of gaps are disease and pests which can cause the canopy tree to weaken, making it more susceptible to other natural factors such as wind and glaze storms. The woolly adelgid (Adelges piceae Annand) is one such pest that is spreading southward through the Canada hemlock (Tsuga canadensis (L.) Carr.) forests in the Appalachian mountains. Adelges piceae is native to Japan where its population is controlled by host resistance and natural enemies which are not found in the United States (McClure, 1995). Adelges piceae arrived in the Shenandoahs in 1990 and is now a threat to the hemlocks in this region (Nash and Spear, 1991). Adelges piceae severely reduces the growth and survival of Tsuga canadensis (McClure, 1991).

Species richness of herbaceous plants in hemlock forests tends to be low (Schafale and Weakley, 1990). Hemlock forests are relatively stable with

trees up to several centuries old (Schafale and Weakley, 1990). Tsuga canadensis is a medium to large tree in the pine family (Pinaceae) which can grow to more than thirty meters in height (Radford, et al., 1968). In the southern Appalachians it grows best at high elevations within ravines and open north-facing slopes where the soil is moist, acidic, and rocky (Schafale and Weakley, 1990). When a canopy gap forms in a hemlock forest there is a release of light formerly monopolized by the previously existing canopy tree (Phillips and Sure, 1990). In these "islands of light", which exist in an area of relative darkness, shade intolerant plants may compete with other plants for the newly available resources.

If the species-area curve is applied to these islands, a direct relation between the size of a sample area and species richness would be expected. This concept can be described by the power function:

$$SR = CA^z \qquad \text{(eq. 1)}$$

where SR = species richness (number of species), A = area of the island, C = a parameter that depends on the population density determined by the taxon and biogeographic region, and z = the change in species richness per unit area (MacArthur and Wilson, 1967). Most z values are found between 0.20 - 0.35 for isolated islands and falls between 0.12 and 0.17 for non-isolated sample areas (Preston, 1962).

Several studies have shown that there is a positive correlation between

island size and species richness in both terrestrial and aquatic ecosystems. In isolated pools of water, species richness increased with water volume (March and Bass, 1995). Within a subdivided field, islands of varying sizes were created by mowing a field and letting islands of flora grow, while keeping the surrounding areas mowed every two weeks. As the island size increased so did species richness (Holt, et al., 1995). Kohn and Walsh (1994) state that quadrat size, as well as gap size, play an important role in determining values of species richness and that data on species richness within quadrats of standard area reveal an increase in small-scale species richness on islands of increasing size . Therefore, I would expect quadrat size to have the same effect on species richness as gap size, and that quadrats of equal size found within islands of different sizes would be positively correlated with species richness.

I examined the species richness with respect to gap and quadrat size. I tested three hypotheses: 1) as gap size increases so do species richness values, 2) as quadrat size increases so do species richness values, and 3) within equal sized quadrats in different sized gaps, as gap size increases so do species richness values.

MATERIALS AND METHODS

Study Sites. This study was conducted in an area of the Shenandoah National Park known as "Limberlost" (Fig. 1) (Latitude 78°22'30"N, Longitude 38°34'00"W; 976-1006 meters in elevation), located in the Blue Ridge physiographic province of the Appalachian mountains near Luray, Virginia. "Limberlost" is a Canada hemlock forest consisting of predominantly Tsuga canadensis mixed with some scattered hardwoods, such as maples (Aceraceae) and birches (Betulaceae), with acidic, rocky, upland soils (Schafale & Weakley, 1990).

Gap Sampling. Samples were taken from each of six gaps during the summer and fall of 1995 and eight gaps in the spring of 1996 (Appendices I-IV). All gaps were sampled over a period of 3-5 days during each season. One non-gap site was studied in the spring of 1996 to obtain information on the herbaceous flora that was present outside canopy gaps.

Each gap boundary was defined by the base of the surrounding canopy trees according to the protocol established by Runkle (1981). Two criteria were used in gap selection: (1) the gap maker species had to be Tsuga canadensis and, (2) it had to be a canopy tree at the time of gap formation. These criteria were determined by observing the size of the trunk and/or the stump left in the ground. The gaps studied consisted of one to three tree falls per gap, and were chosen to represent a wide range of sizes. Rough sketches

of the dimensions, shape, and border trees were made for each gap. The areas of the gaps were estimated by utilizing NIH imaging software (NIH Image 1.60).

Sampling sites were established as follows. Two strings were extended from north-south and east-west across each gap. Markers were placed on the strings at intervals of one foot. Individual plants were counted within each of the one foot intervals between the strings.

The herbaceous flora and woody vegetation less than one meter in height was inventoried for all gaps during all sampling periods. The number of individual plants and location of each species in each quadrat was recorded. The plants were counted only if more than one half of the plant fell within the quadrat (Cox, 1996). Representative specimens of each species found within the quadrats were collected from outside the quadrats, returned to the University of Richmond, and identified. Twigs of the canopy trees bordering the gaps were also collected and identified to determine what species of canopy tree were present at the gap sites.

Plant Identification. Plant specimens were returned to the laboratory and identified to family, genus, and, if feasible, species. Nomenclature follows the Manual of the Vascular Flora of the Carolinas (Radford, et al., 1968). The specimens are now on file at the University of Richmond Herbarium (URV).

Data Analysis. The data from 5, 10, and 15 contiguous sampling sites were combined to yield estimates of species richness to determine the relationship between quadrat size and species richness. These combined data represent species richness for quadrats of 2.5, 5, and 10 ft^2 respectively.

A two-way parametric analysis of variance (ANOVA) was performed to ascertain the statistical significance of effects of seasons and gap size on species richness (Microsoft Excel 5.0c). The $\propto = 0.05$ was used as criterion for significance for all statistical tests.

Due to a flaw in experimental design, the singularity of data, a statistical problem where one variable is a combination of one or more of the other variables, precluded any statistical test of significance for the relationship between species richness and quadrat size (Tabachnick and Fidell, 1989).

In order to test the effects of seasons and gaps on species richness, equal sets of data were required. Two gaps contained 9 quadrats, and all others contained more than 9 quadrats. Nine values of species richness were selected at random for each of the other gaps. A matrix in which columns represented quadrats and rows represented gap and direction (N-S, E-W) was created. Quadrats in these later gaps were assigned numbers (ie. column 1, row1 = 1 and column 1, row 2 = 2). Data were eliminated in order to obtain 9 quadrats in each gap using a random numbers table (Appendix V)

(Dixon and Massey, 1957).

A least squares regression analysis was used to estimate the values of C and z in the following power function:

$$SR = CA^z \qquad \text{(eq. 1)}$$

as described previously.

RESULTS

The gaps were located approximately 0.3 miles east of Skyline Drive, and 100 yards north of the southern edge of the "Limberlost Access Trail" (Fig. 1). The gaps varied in shape and size (Fig. 2 and Appendix VI). The areas of the gaps ranged from 393-4190 ft^2. The gaps were near a small stream approximately 3-5 feet in width, and were relatively flat.

The gaps contained nineteen species of plants, seventeen of which were herbaceous (Table 1). Four species of herbaceous plants were found outside as well as inside the gaps. There were no species found in the forest that were not present within the canopy gaps.

Data from gaps 1-6 were used to test all hypotheses for combined seasons and data for gaps 7-8 were included for separate seasons. The species richness in gaps for combined seasons ranged from 6 to 14 and for separate seasons ranged from 3 to 11 (Table 2). As gap size increased so did the species richness values for separate seasons (Fig. 3). The relationship between gap size and species richness was statistically significant for separate seasons $P \leq 0.05$ (Table 3). This relationship was not supported for combined seasons. The relationship between species richness in the entire gap and gap size for separate seasons can be described by:

$$SR = 0.70A^{0.36} \qquad \text{(Eq. 1).}$$

where SR = species richness (number of species) and A = area of the gap.

The values of C (0.70) and z (0.36) were determined by a least squares regression analysis (Table 4).

The species richness nearly doubled between quadrats of 2.5 and 7.5 ft^2 within each gap for combined seasons and for separate seasons (Figs. 4-5 and Table 5). The effect of gap size on species richness in quadrats of 2.5 ft^2 in each gap was not statistically significant for combined seasons, but was statistically significant for separate seasons $P \leq 0.05$ (Fig. 6 and Tables 6 and 7).

DISCUSSION

The present study, for separate seasons, demonstrates a positive correlation between species richness and gap size. Species richness may be related to the numbers of microhabitats. The greater the microhabitat variety, the greater the species diversity (Rosenzweig, 1995). Kohn and Walsh (1994) state that as the area of an island increases, there are more numerous and diverse microhabitat types. The numbers of habitats supported by isolated islands of varying sizes demonstrated a direct correlation to the island size and the number of habitats found within that island. The larger island contained habitats ranging from bedrock to grasses, whereas smaller islands were more uniform.

The relationship between species richness and habitat diversity were also recognized in isolated pools of water. As the volume of water increased so did the species richness values found within these pools (March and Bass, 1995). The amount of vegetation and the microhabitat diversity which provided shelter from predators and hiding places for many invertebrates drastically increased the species richness values of those pools. The effect of area and habitat diversity were both found to be significant, but are so interrelated that one can serve as a surrogate for the other (Harner and Harper, 1976).

Other factors such as the availability of resources and variation of

insolation influence the species richness a given area can support. The availability of resources after a forest canopy tree dies is essential for floral growth on the forest floor. The immediate release of water and nutrients and the availability of light (insolation), which may not have reached that portion of the forest floor in hundreds of years, provide opportunistic species the resources to thrive. Within large gaps solar radiation is several times greater than in their smaller counterparts (Phillips and Sure, 1990). The colonization of pioneer species within larger gaps is enhanced by the higher insolation received by that gap (Holt, et al., 1995). This gradient is most evident in comparing the species richness within a gap and that found outside the gap in the darkness of the forest floor. In this study, only a very small percentage of those plants found within gaps were found outside of the gap. Limited resources, such as light, could have limited species richness outside the gaps. The difference in insolation also enhances a phenomenon known as edge effect. Edge effect occurs where the boundaries between two adjoining communities meet. This effect is influenced by the amount of edge availability and the contrast between vegetational communities. The contrast between adjoining plant communities and species richness typically are positively correlated (Smith, 1996).

The present study also demonstrates an increase in species richness values for equal sized quadrats within different sized gaps. Kohn and Walsh

(1994) showed that data on species richness within quadrats of standard area reveal an increase in small-scale species richness on islands of increasing size. The reasons for the increased species richness are unclear. There may be something inherent in larger gaps which influences species richness such as the diversity of microhabitats, space for propagule settlement and the amount of insolation that gap receives. I would expect microhabitat diversity to have the greatest influence on species richness, but further study must be done to determine what is inherent in these larger gaps which allows for the increased species richness.

Values of species richness on an island result from an equilibrium of immigrations and extinctions (Doak and Mills, 1994). According to MacArthur and Wilson's model, the rate of immigration of new species onto an island will decrease and the rate of extinction will increase with species richness (MacArthur and Wilson 1967). Within smaller islands, plants with high dispersal rates may increase the extinction risks due to the "wasted" seed production which is dispersed beyond the boundaries of the gap. The larger islands could also support larger and more dispersed populations, which have the capability to recolonize local vacant sites (Holt, et al., 1995).

The point where immigration equals extinction is known as the equilibrium point. As island size increases the equilibrium point will shift to a greater species richness value. On small islands, the equilibrium may be

reached within relatively short periods of time. Simberloff and Wilson (1970) found that values of species richness of (kinds of organisms) rebounded to equilibrium levels within one year of fumigation on small mangrove islands.

Species richness often increases with island size and can be described according to a power function in which the exponent "z" ranges from 0.20-0.35 for isolated islands. The value of "z" found in this study was 0.36. This value is larger than one would expect for non-isolated sample areas which are typically between 0.12 and 0.17, but is more closely related to the values of isolated islands. Greater values of "z" have been recorded in many instances. Analysis of breeding land and freshwater birds on four islands in the Gulf of Guinea yielded a z-value of 0.49 (Hamilton and Armstrong, 1965), and an even higher z-value of 0.72 was recorded for cave dwelling species in the Greenbriar Valley system of West Virginia (Culver, et al, 1973). Lower values of "z" (0.12-0.17) are found where non-isolated sample areas occur (MacArthur and Wilson 1967). Reduced z-values occur within non-isolated sample areas because of transient immigration which takes place from surrounding habitats into the non-isolated sample area (Rozensweig, 1995).

There are two possible explanations for the high z-value found in this study. First, there are few data points which limit the confidence of the accuracy of the z estimate. One or two outliers could significantly change the value of z. Secondly, the gaps represent isolated islands, and immigration

rates (i.e., introduction of propagules) could be low. I would expect to have a low transient immigration rate within hemlock gaps due to the absence of herbaceous plants in the forest proper, and according to Rozensweig (1995) such low immigration leads to high values of "z".

The present study provides insight into how species richness is affected by the size of canopy gaps which have resulted due to the loss of the eastern hemlock. The destruction of the eastern hemlock cove forest caused by the woolly adelgid is occurring at an alarming rate and the species composition of this forest will vastly change in years to come.

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Table 1. Plant taxa in gaps. The symbol (*) denotes species within and without gaps. The symbol (**) indicates non-herbaceous species.

Lycopodiaceae
    Lycopodium lucidulum Michaux
Osmundaceae
    Osmunda cinnamomea L.
Aspidiaceae
    Dryopterus spinulosa (Mueller) Watt
Pinaceae
    Tsuga canadensis (L.) Carr.**
Poaceae
    Glyceria melicaria (Michaux) Hubbard
Cyperaceae
    Carex crinita Lam.
Liliaceae
    Clintonia umbellulata (Michaux) Morong *
    Maianthemum canadense Desf. *
    Veratrum viride Aiton
Betulaceae
    Betula lutea Michaux f **
Lauraceae
    Lindera benzoin (L.) Blume
Oxalidaceae
    Oxalis acetosella L. *
Balsaminaceae
    Impatiens sp.
Violaceae
    Viola blanda Willd.
Apiaceae
    Hydrocotyle americana L.
    Angelica triquinata Michaux
Rubiaceae
    Mitchella repens L. *
Asteraceae
    Eupatorium sp.
    Aster acuminatus Michaux

Table 2. Species Richness in gaps for combined and separate seasons.

Gap	Gap Size (ft^2)	Species Richness (# species)			
		Combined	Separate		
			Spring	Summer	Fall
1	393	6	6	3	6
2	438	11	8	5	7
3	917	14	10	10	8
4	950	12	10	8	9
5	1045	12	8	10	9
6	1376	13	11	10	10
7	2913		10		
8	4190		11		

Table 3. Analysis of variance (ANOVA) for effects of gap size and seasons on species richness for separate seasons.

ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Gap Size	59.11	5	11.82	8.51	<0.05	3.33
Season	4.11	2	2.06	1.48	0.27	4.10
Error	13.89	10	1.38			
Total	77.11	17				

Table 4. Regression analysis of species richness $\log_{10}$ (# species) and gap size $\log_{10}$ (ft^2).

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.73
R Square	0.54
Adjusted R Square	0.51
Standard Error	0.10
Observations	20

ANOVA

	df	*SS*	*MS*	*F*	Significance F
Regression	1	0.20	0.20	20.69	0.00
Residual	18	0.17	0.01		
Total	19	0.37			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	-0.16	0.24	-0.67	0.51	-0.65	0.34
Gap Size	0.36	0.08	4.55	<0.05	0.19	0.53

Table 5. Species richness (# species) for different sized quadrats within the same gap for combined and separate seasons. Values under species richness: mean ± standard deviation.

	Species Richness	
Quadrat Size (ft^2)	Combined	Separate
2.5	4.7 ± 1.5	3.3 ± 1.0
5.0	6.1 ± 1.6	4.5 ± 1.3
7.5	7.2 ± 1.5	5.8 ± 1.4

Table 6. Species richness (# species) for quadrats of equal size (2.5 ft²) for combined and separate seasons. Values under species richness: mean ± standard deviation.

Gap Size (ft²)	Combined	Separate		
		Summer	Fall	Spring
393	2.4 ± 1.5 (27)	1.8 ± 1.1 (9)	1.1 ± 0.8 (9)	1.9 ± 1.3 (9)
438	3.1 ± 2.8 (27)	2.2 ± 1.9 (9)	1.0 ± 1.0 (9)	1.6 ± 1.5 (9)
917	6.0 ± 1.1 (36)	3.3 ± 1.8 (12)	3.0 ± 2.1 (12)	2.5 ± 1.1 (12)
950	5.9 ± 1.8 (33)	2.6 ± 1.4 (11)	1.8 ± 1.5 (11)	3.8 ± 1.7 (11)
1045	5.9 ± 1.4 (36)	3.5 ± 1.7 (12)	3.0 ± 2.1 (12)	3.3 ± 1.4 (12)
1376	4.8 ± 1.6 (39)	3.4 ± 1.2 (13)	2.9 ± 0.8 (13)	3.2 ± 1.4(13)
2913				3.9 ± 1.4 (15)
4190				4.7 ± 2.1 (19)

Table 7. Analysis of variance (ANOVA) for effects of season and gap on species richness in quadrats of 2.5 ft^2 for separate seasons.

ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Season	15.72	2	7.86	3.18	<0.05	3.06
Gaps	89.60	5	17.92	7.26	<0.05	2.28
Interaction	13.40	10	1.34	0.54	0.86	1.90
Within	355.56	144	2.47			
Total	474.27	161				

Figure 1. Approximate locations of gaps 1-6 and gap 8 (gap 7 could not be relocated). (Map provided by the Shenandoah National Park Service in Luray, Virginia).

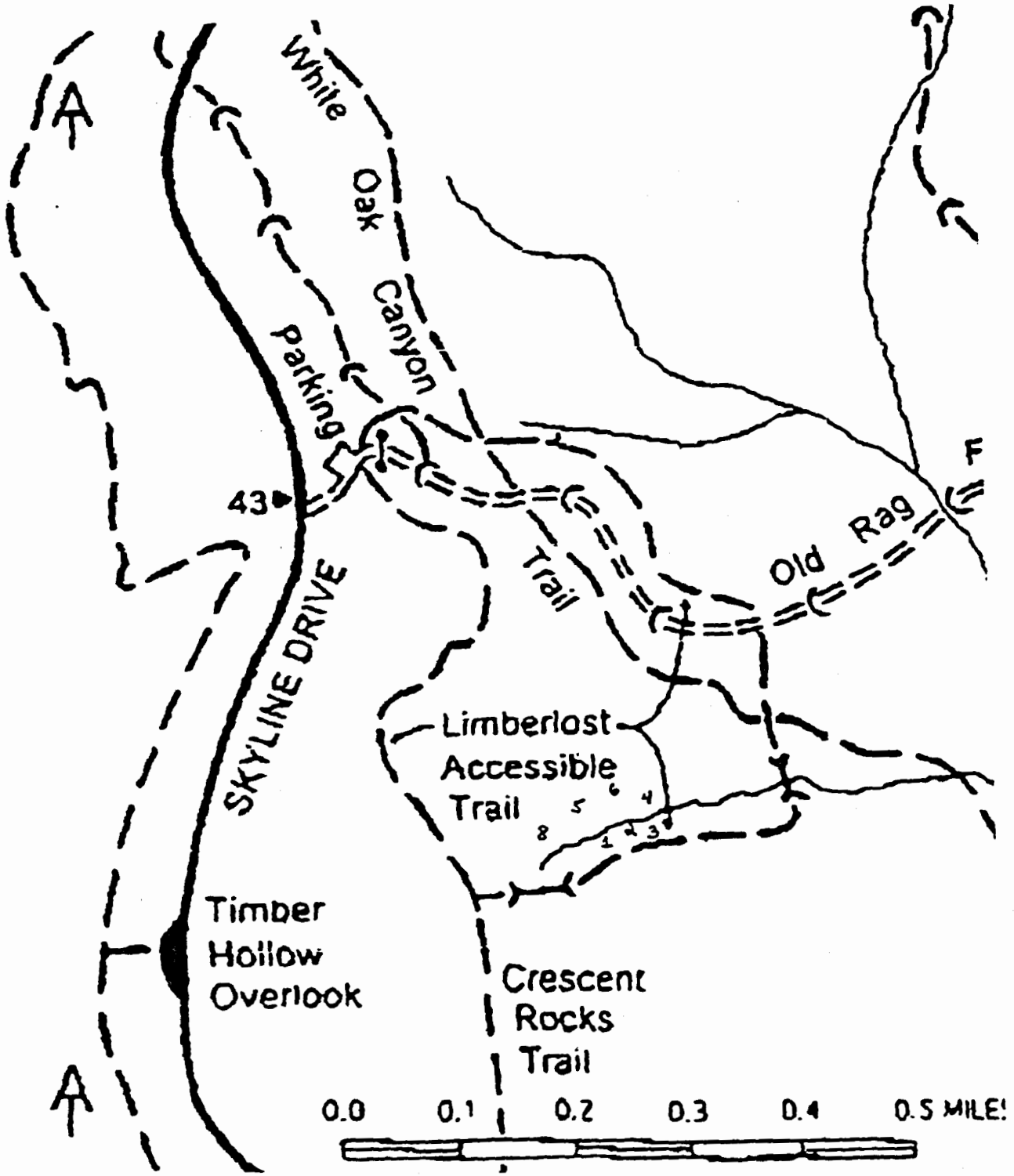
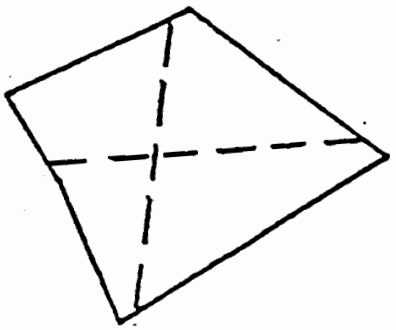
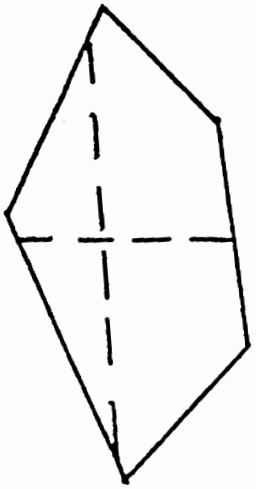

White Oak Canyon
Parking
43
SKYLINE DRIVE
Trail
Old Rag
F
Limberlost
Accessible
Trail
Timber
Hollow
Overlook
Crescent
Rocks
Trail
0.0
0.1
0.2
0.3
0.4
0.5 MILE

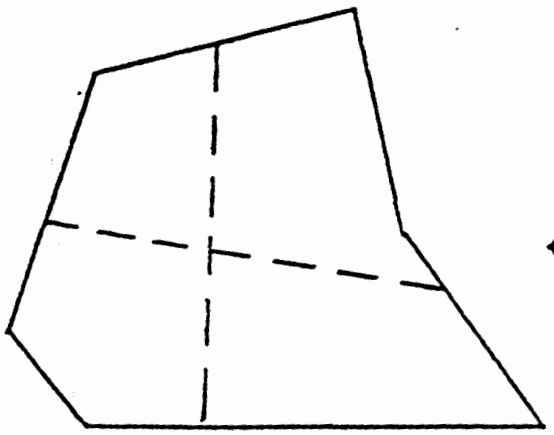
Figure 2. Diagrams of gaps 1-8. Dotted lines represent the transects. Numbers in parentheses are gap sizes (ft^2).



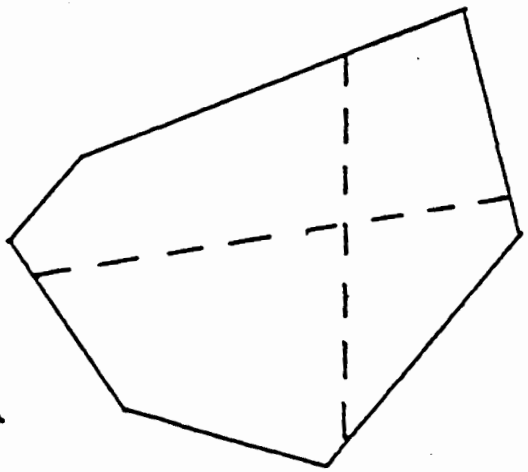
Gap 1 (393)



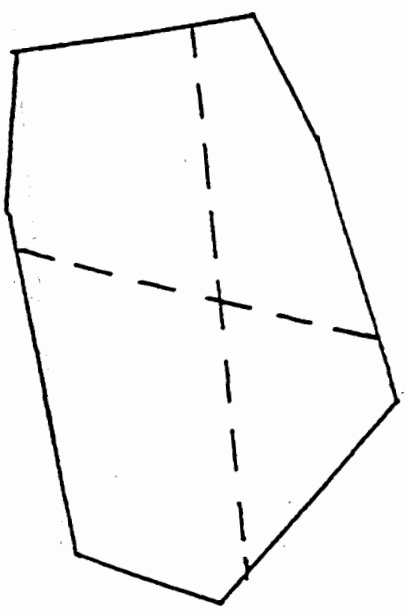
Gap 2 (438)



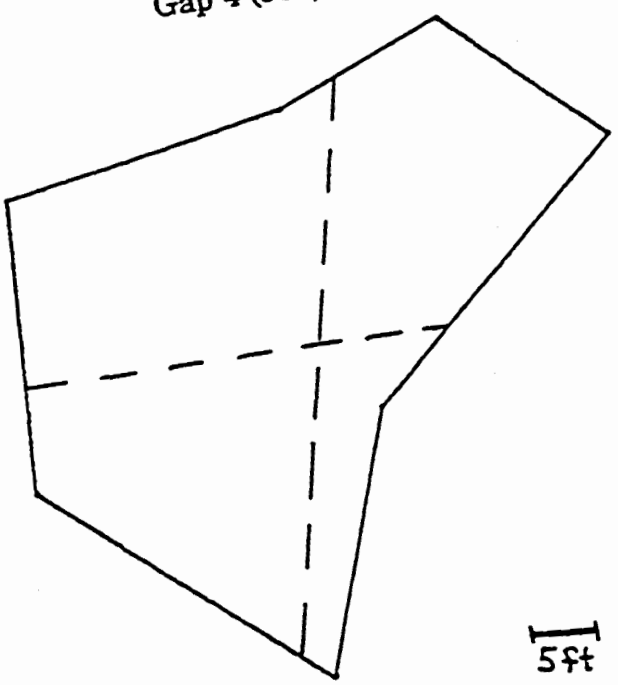
Gap 3 (917)



Gap 4 (950)

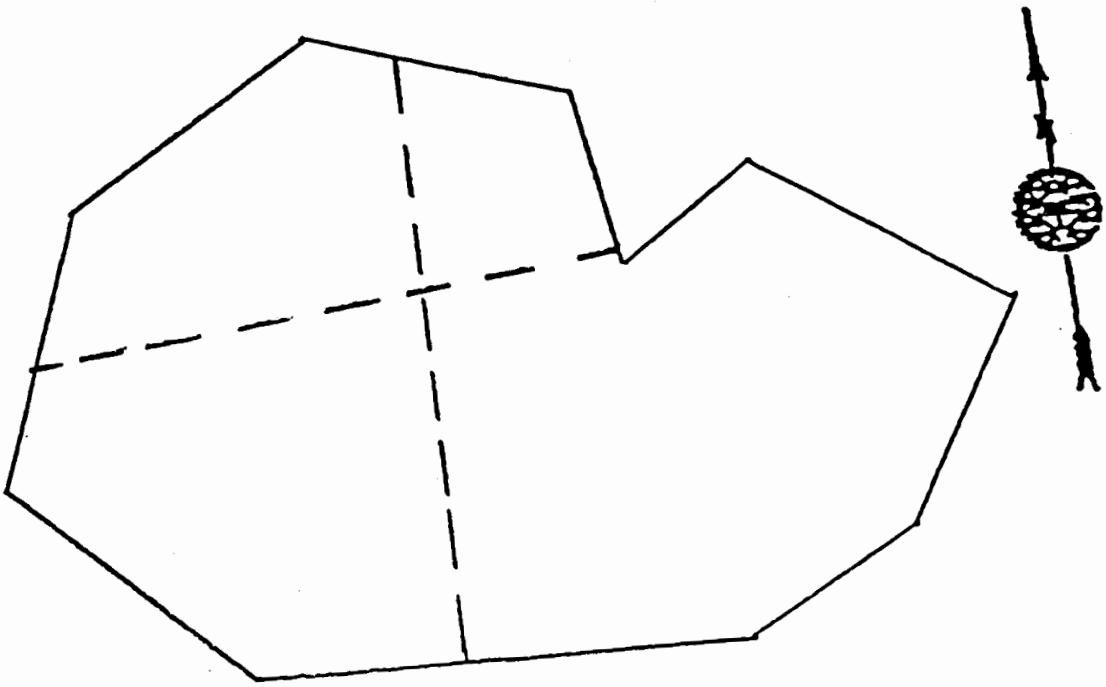


Gap 5 (1045)

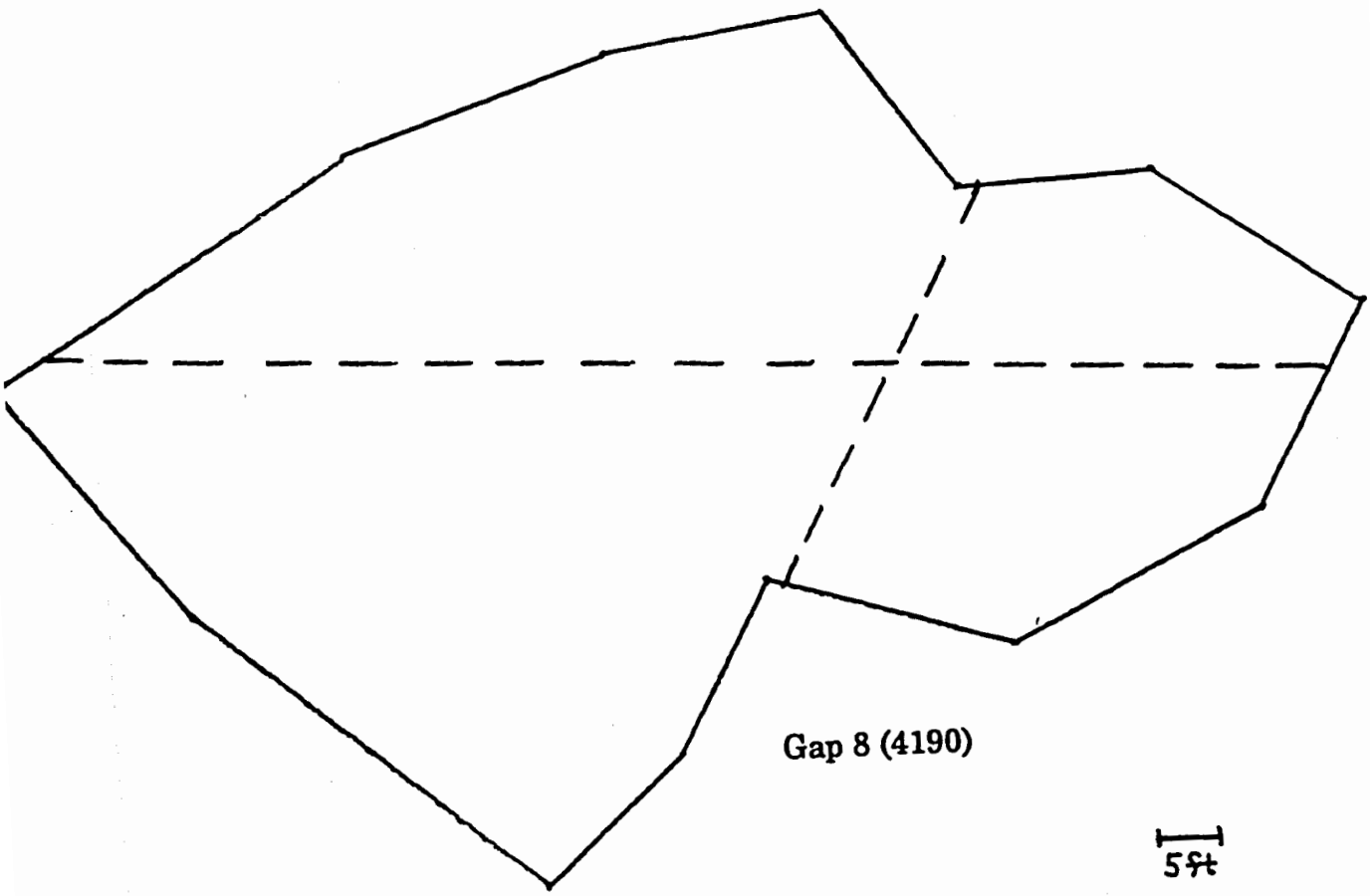


Gap 6 (1376)

5ft



Gap 7 (2913)



Gap 8 (4190)

Figure 3. Species richness (# species) versus gap size (ft^2) for separate seasons.

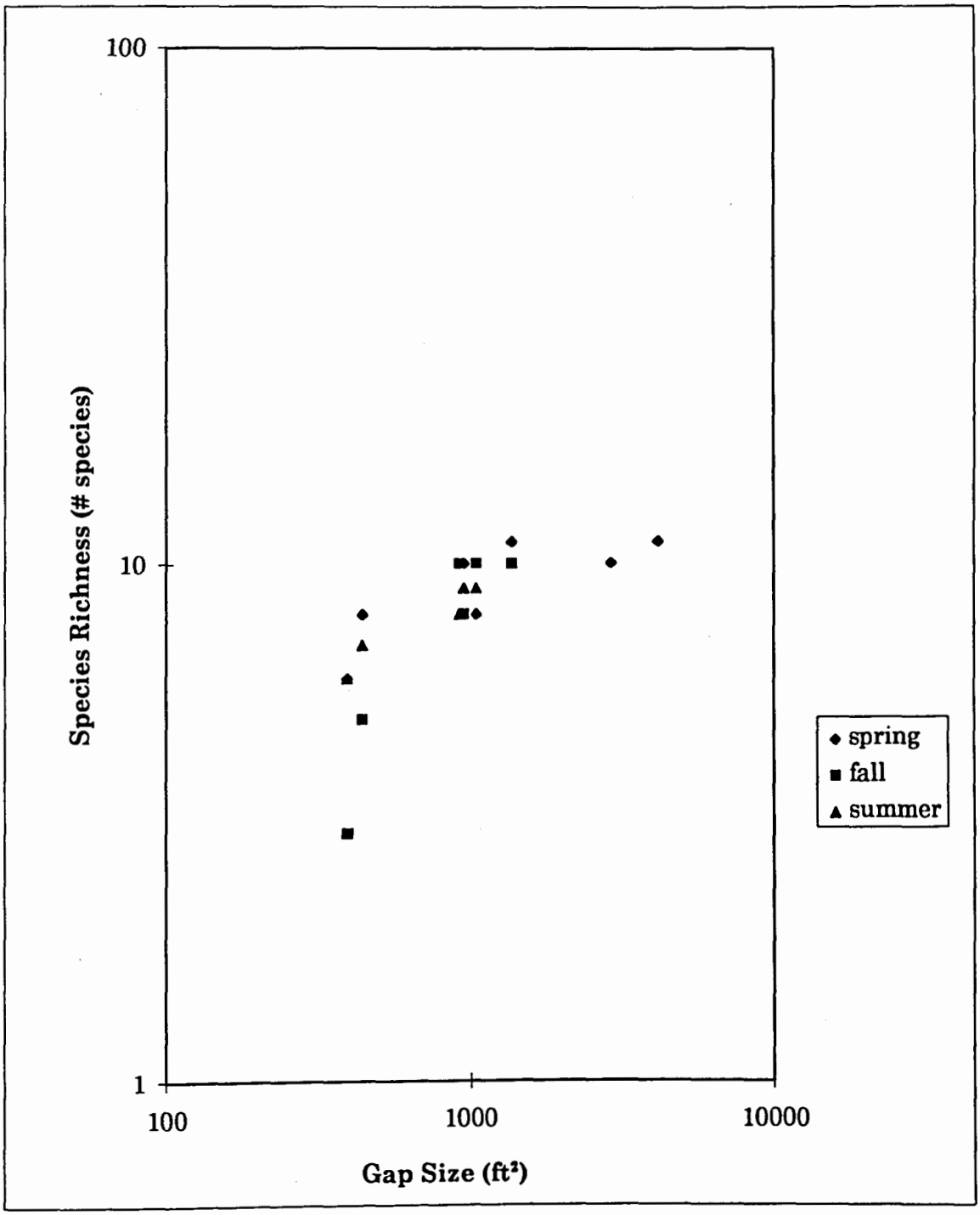

100
10
1
Species Richness (# species)
100
1000
10000
Gap Size (ft²)
spring
fall
summer

Figure 4. Species richness (# species) versus quadrat size (ft^2) for combined seasons. Values for species richness are means for seasons combined.

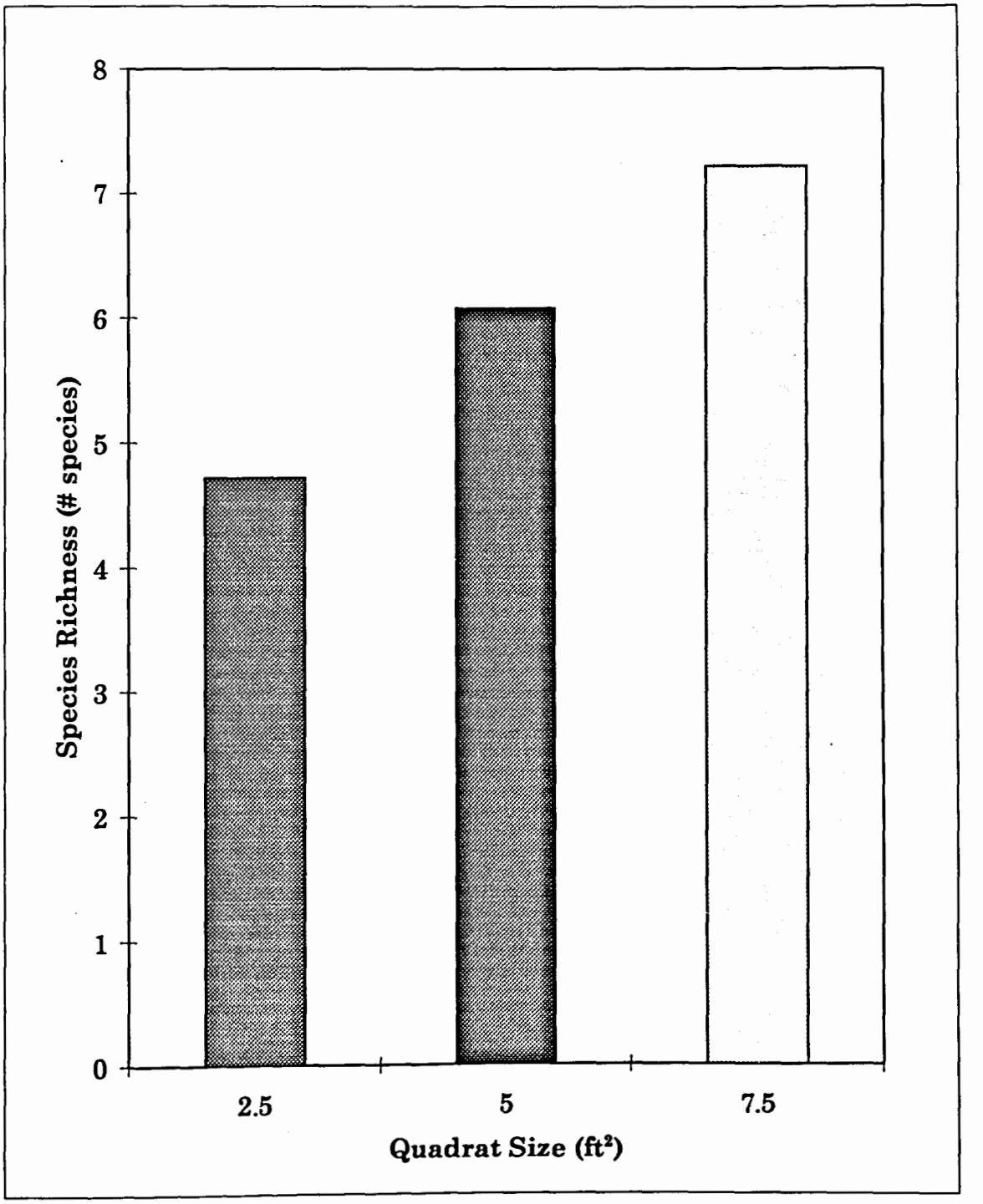

8
7
6
5
4
3
2
1
0
Species Richness (# species)
2.5
5
7.5
Quadrat Size (ft²)

Figure 5. Species richness (# species) versus quadrat size (ft^2) for separate seasons. Values for species richness are means for separate seasons.

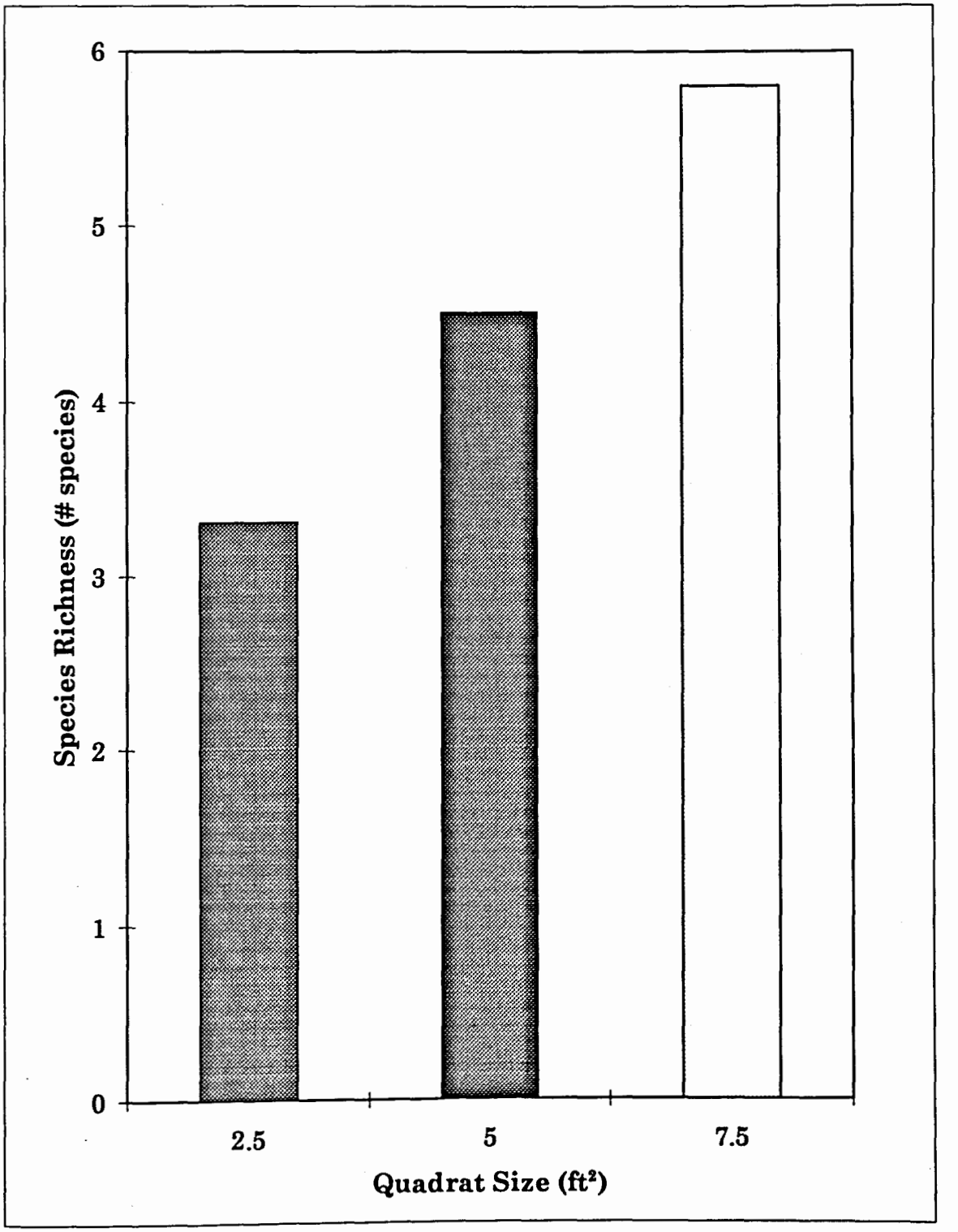
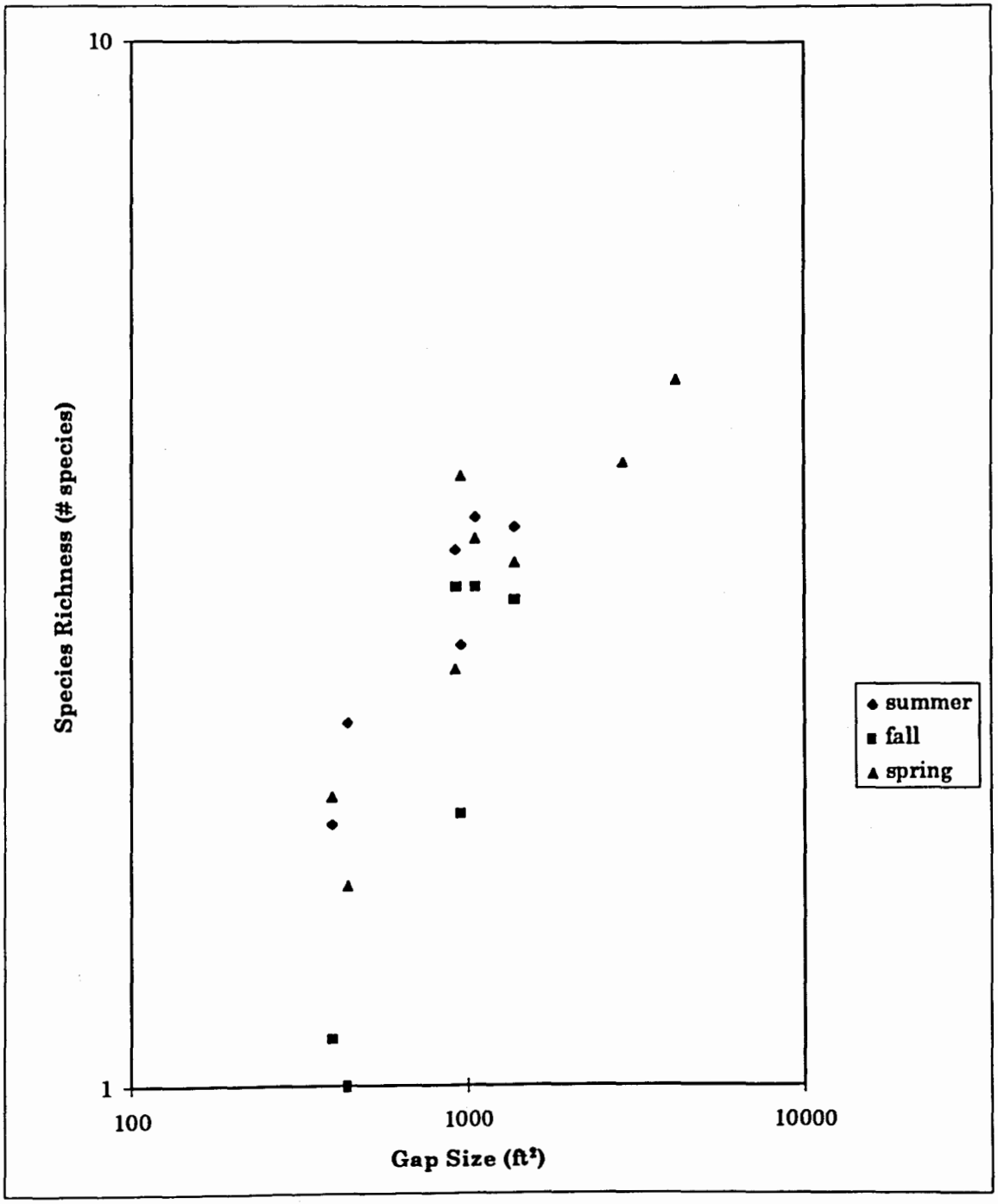

6
5
4
3
2
1
0
Species Richness (# species)
2.5
5
7.5
Quadrat Size (ft²)

Figure 6. Species richness (# species) versus gap size for 2.5 ft^2 quadrats for separate seasons. Values of species richness are averages for separate seasons.


10
1
100
1000
10000
Species Richness (# species)
Gap Size (ft²)
summer
fall
spring

Appendix I. Key for raw data tables (appendices II-IV).

Dir	Direction along transect studied
G	Gap
1, 2, ...	Location within the transect (ie. 1 = first foot on that transect)
A, B, ...	Plant taxa (see below)

Code	Family	Genus species (author)
A	Aspidiaceae	Drypoterus spinulosa (Muiler)
B	Lauraceae	Lindera benzoin (L.)
C	Asteraceae	Aster acuminatus (Michaux)
D	Liliaceae	Mainthemum canadense (Desf.)
E	Oxalidaceae	Oxalis acetosela (L.)
F	Apiaceae	Angelica triguinata (Michaux)
G	Lycopodiaceae	Lycopodium lucidulum (Michaux)
H	Osmundaceae	Osmunda cinnamomea (L.)
I	Liliaceae	Clintonia umbullata (Michaux)
J	Rubiaceae	Mitchella repens (L.)
K	Asteraceae	Eupatorium sp.
L	Violaceae	Viola blanda (Willd)
M	Balsaminaceae	Impatiens sp.
N	Pinaceae	Tsuga canadensis (L.)
O	Poaceae	Glyceria melicaria (Michaux)
P	Betulaceae	Betula lutea (Michaux)
Q	Liliaceae	Veratrum viride (Aiton)
R	Poaceae	Glyceria melicaria (Michaux)
S	Poaceae	Carex crinita (Lam.)
T	Apiaceae	Hydrocotyle americana (L.)

Appendix II. Raw Data showing presence (1) or absence (empty) of plant taxa in Gaps 1-6 for summer 1995.

Date: 8/14/95																						
Gap: 1																						
Direction: N-S																						
			Species																			
			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
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	26					1	1															
	27						1			1												
	28				1		1	1														
	29						1			1												
	30				1		1															
Date: 8/1495																						
Gap: 1																						
Direction: E-W																						
			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
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	14																				
	15																				
	16																				
	17						1														
Date: 8/15/95																					
Gap: 2																					
Direction: N-S																					
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	30																				

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Gap: 2																				
Direction: E-W																				
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	29					1	1						1							
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Gap: 3																				
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	29		1			1															
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Gap: 3																					
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Gap: 4																						
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Gap: 6																					
Direction: E-W																					
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	25																				
	26																				

Appendix III. Raw Data showing presence (1) or absence (empty) of plant taxa in Gaps 1-6 for fall 1995.

Date: 10/13/95																						
Gap: 1																						
Direction: N-S																						
			Species																			
			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
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	2																					
	3																					
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	29						1				1			1								
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Date: 10/13/95																						
Gap: 1																						
Direction: E-W																						
			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
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	17																				
Date: 10/13/95																					
Gap: 2																					
Direction: N-S																					
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Appendix IV. Raw Data showing presence (1) or absence (empty) of plant taxa in Gaps 1-8 for spring-summer 1996.

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Gap: 8																					
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Appendix V. Random numbers table

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3	42	26	89	53	19	64	50	93	03	23	20	90	25	60	15	95	33	47	64	35	08	03	36	06	
4	01	90	25	29	09	37	67	07	15	38	31	13	11	65	88	67	67	43	97	04	43	62	76	59	
5	00	70	99	70	80	15	73	61	47	64	03	23	66	53	98	95	11	68	77	12	17	17	68	33	
6	08	57	47	17	31	07	27	68	50	36	69	73	61	70	65	81	33	98	85	11	19	92	91	70	
7	01	01	08	05	45	57	18	24	06	35	30	34	26	14	86	79	90	74	39	23	40	30	97	32	
8	26	97	76	02	02	05	16	56	92	68	66	57	48	18	73	05	38	52	47	18	62	38	85	79	
9	57	33	21	35	05	32	54	70	48	90	55	35	75	48	28	46	82	87	09	83	49	12	56	24	
10	79	64	57	53	03	52	96	47	78	35	80	83	42	82	60	93	52	03	44	35	27	38	84	35	
11	52	01	77	67	14	90	56	86	07	22	10	94	05	58	60	97	09	34	33	50	50	07	39	98	
12	80	50	54	31	39	80	82	77	32	50	72	56	82	48	29	40	52	42	01	52	77	56	78	51	
13	45	29	96	34	06	28	89	80	83	13	74	67	00	78	18	47	54	06	10	68	71	17	78	17	
14	65	54	02	00	86	50	75	84	01	36	76	66	79	51	90	36	47	64	93	29	60	91	10	62	
15	59	46	73	48	87	51	76	49	69	91	82	60	89	28	93	78	56	13	68	23	47	83	41	13	
16	48	11	76	74	17	46	85	09	50	58	04	77	69	74	73	03	95	71	86	40	21	81	65	44	
17	12	43	56	35	17	72	70	80	15	45	31	82	23	74	21	11	57	82	53	14	38	55	37	63	
18	35	09	98	17	77	40	27	72	14	43	23	60	02	10	45	52	16	42	37	96	28	60	26	55	
19	91	62	68	03	66	25	22	91	48	36	93	68	72	03	76	62	11	39	90	94	40	05	64	18	
20	89	32	05	05	14	22	56	85	14	46	42	75	67	88	96	29	77	88	22	54	38	21	45	98	
21	49	91	45	23	68	47	92	76	86	46	16	28	35	54	94	75	08	99	23	37	08	92	00	48	
22	80	33	69	45	98	26	94	03	68	58	70	29	73	41	35	53	14	03	33	40	42	05	08	23	41
23	44	10	48	19	49	85	15	74	79	54	32	97	92	65	75	57	60	04	08	81	22	22	20	64	13
24	12	55	07	37	42	11	10	00	20	40	12	86	07	46	97	96	64	48	94	39	28	70	72	58	15
25	63	60	64	93	29	16	50	53	44	84	40	21	95	25	63	43	65	17	70	82	07	20	73	17	90
26	61	19	69	04	46	26	45	74	77	74	51	92	43	37	29	65	39	45	95	93	42	58	26	05	27
27	15	47	44	52	66	95	27	07	99	53	59	36	78	28	48	82	39	61	01	18	33	21	15	94	66
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33	35	96	31	53	07	26	89	80	93	54	33	35	13	54	62	77	97	45	00	24	90	10	33	93	33
34	59	80	80	83	91	45	42	72	68	42	83	60	94	97	00	13	02	12	48	92	78	56	52	01	06
35	46	05	88	52	36	01	39	09	22	86	77	28	14	40	77	93	91	08	36	47	70	61	74	29	41
36	32	17	90	05	97	87	37	92	52	41	05	56	70	70	07	86	74	31	71	57	85	39	41	18	38
37	69	23	46	14	06	20	11	74	52	04	15	95	66	00	00	18	74	39	24	23	97	11	89	63	38
38	19	56	54	14	30	01	75	87	53	79	40	41	92	15	85	66	67	43	68	06	84	96	28	52	07
39	45	15	51	49	38	19	47	60	72	46	43	66	79	45	43	59	04	79	00	33	20	82	66	95	41
40	94	86	43	19	94	36	17	53	06	51	34	88	88	15	53	01	54	03	54	56	05	01	45	11	76
41	98	08	62	48	26	45	24	02	84	04	44	99	90	88	96	39	09	47	34	07	35	44	13	18	80
42	33	18	51	62	32	41	94	15	09	49	89	43	54	85	81	88	69	54	19	94	37	54	87	30	43
43	80	95	10	04	06	96	38	27	07	74	20	15	12	33	87	25	01	62	52	98	94	62	46	11	71
44	79	75	24	91	40	71	96	12	82	96	69	86	10	25	91	74	85	22	05	39	00	38	75	95	79
45	18	63	33	25	37	98	14	50	65	71	31	01	02	46	74	05	45	56	14	27	77	93	89	19	36
46	74	02	94	39	02	77	55	73	22	70	97	79	01	71	19	52	52	75	80	21	80	81	45	17	48
47	54	17	84	56	11	80	99	33	71	43	05	33	51	29	69	56	12	71	92	55	36	04	09	03	24
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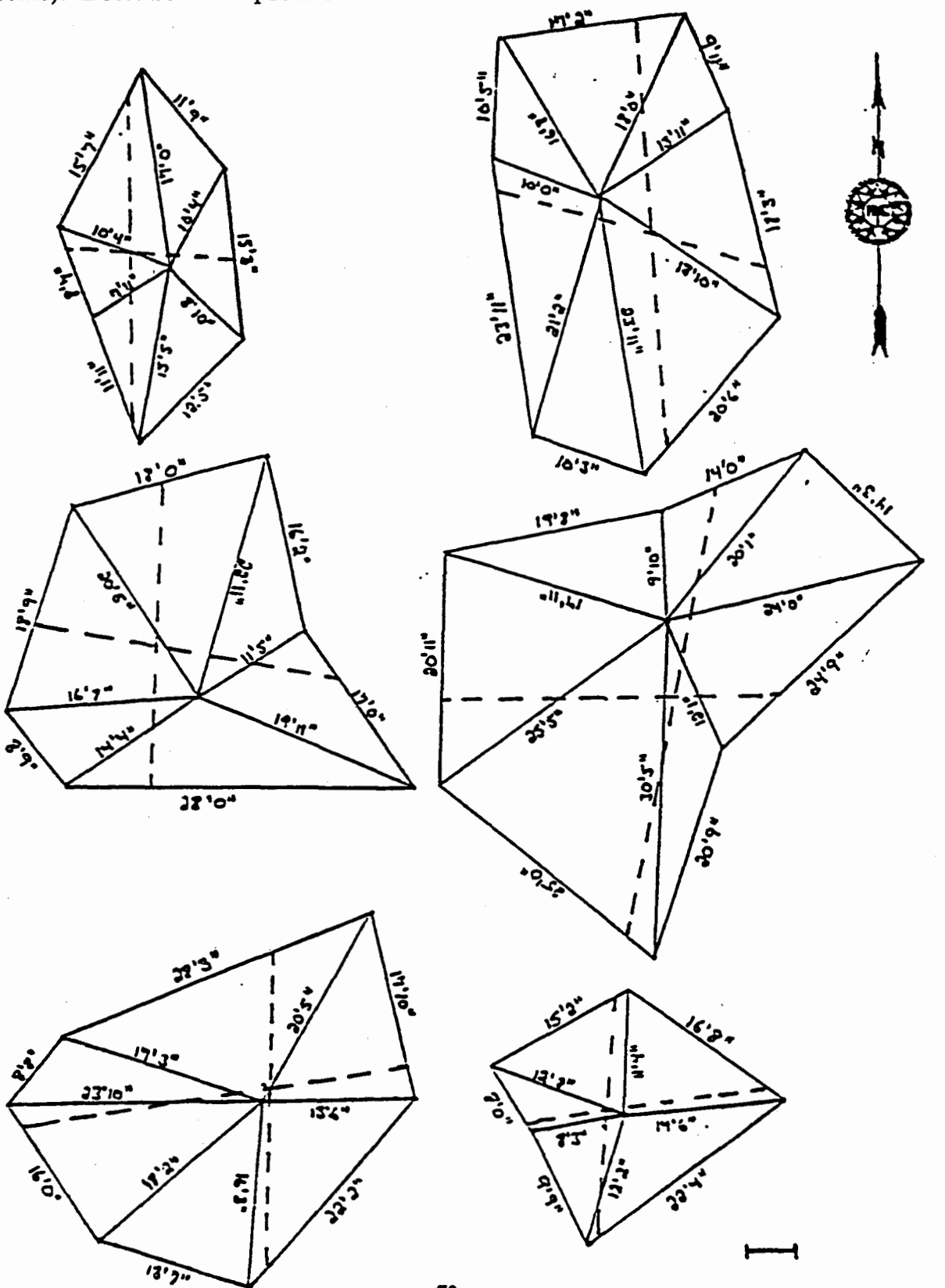
49	48	32	47	79	28	31	24	96	47	10	02	29	53	68	70	32	30	75	75	46	15	02	00	99	94
50	69	07	49	41	38	57	60	70	22	76	35	38	48	32	14	69	49	96	62	43	37	51	00	38	46

* This table is reproduced with permission from tables of the RAND Corporation.

Appendix VI. Diagrams of the measurements for gaps 1-6 (diagrams are to scale). Dotted lines represent he transect directions



VITA

Joesph John LaCroix, son of John and Violet LaCroix was born in Huntingdon, Quebec. He grew up in upstate New York and received his high school education at Lake Placid High School in Lake Placid, New York. He graduated in 1990 and continued his education at Clarkson University where he majored in biology and graduated in May, 1994. In the fall of 1994 he went on to the University of Richmond where he is now attending for a Masters of Science in biology.