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Species richness - standing crop relationships
on an infertile shoreline in Nova Scotia

by

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Submitted in partial fulfilment of the requirements
for the degree of Master of Science at the
University of Ottawa
Ottawa Ontario



Irene Catherine Wisheu, Ottawa, Canada, 1987.

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ABSTRACT

Grime's species richness model was found to appropriately describe the species richness/standing crop and litter relationships of three out of four lakeshore areas. The shapes of the species richness curves varied however, among the four habitats as did a series of environmental measurements. These measurements indicated that infertility and to a lesser extent, damage by ice, wind, and waves, were limiting the amounts of standing crop and litter on the shorelines. Infertility may have also influenced community composition by acting as a stress and promoting the presence of stress-tolerant isoetids and stress-tolerant coastal plain species at low levels of standing crop and litter.

RESUME

Le modèle de Grime décrit bien la relation entre le nombre d'espèces, d'une part, et la biomasse sur pied et la litière, d'autre part, dans trois rivages lacustres sur les quatre étudiés. Ce pendant, la forme des courbes, ainsi qu'une série de paramètres environnemeutaux, varie d'un habitat à l'autre. Ces paramètres indiquent que la biomasse sur pied et la litière trouvées sur le bord du lac sont limitées principalement par l'infertilité du sol et aussi, mais d'une moindre part, par le dommage causé par la glace, le vent et les vagues. L'infertilité du sol peut influencer aussi la composition de la communauté; il agit en tant que stress et augmente, aux endroits à faible biomasse, la présence d'espèces tolérantes au stress, telles que les isoètes et les espèces de plaine côtière.

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INTRODUCTION

It has long been recognized that species richness varies from system to system. Describing, explaining, and ultimately predicting this variation is a fundamental goal in community ecology. To this end, several models have been proposed (Grime 1973, 1979 (see Appendix 1), Connell 1978, Huston 1979 and Tilman 1982).

A concept common to all of these models is that maximum species richness occurs at intermediate points on the gradients being measured. Grime's model (1973, 1979) is particularly attractive because changes in species richness occur along a standing crop and litter gradient. This easily defined and easily measured variable is an index of underlying stresses and disturbances. These two factors, which increase as standing crop and litter decreases, are keeping species richness low at low biomass sites since few species can tolerate extreme abiotic conditions. At high biomass sites, richness is also low since low levels of stress and disturbance allow competitive dominance by a few tall, fast-growing, rhizomatous species.

Grime's model therefore predicts not only the numbers of species in a given area, but the kinds of growth strategies that will be present as well. While dominant species occur at high biomass sites, either stress-tolerant or disturbance-tolerant species will occur where standing crop and litter is low. Where stresses are reducing productivity, stress-tolerant species will be present; small, slow-growing perennials, often species that are evergreen, insectivorous, or growing as rosettes. Where

disturbances are removing or destroying plant tissue, fast growing annuals will be present (Grime 1979).

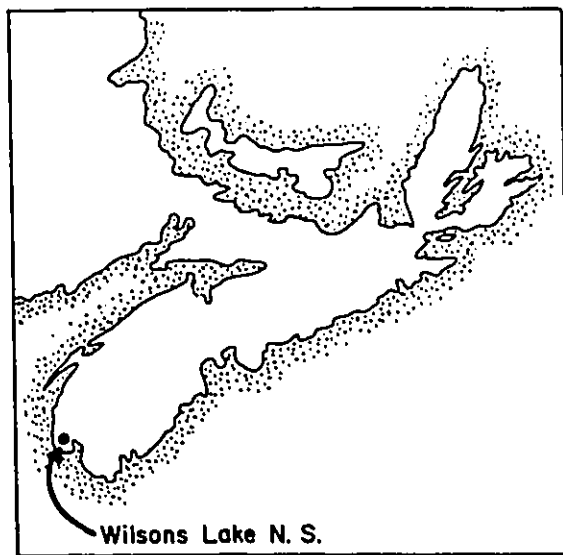
The increase in species richness that is predicted to occur at intermediate levels of standing crop and litter has been previously documented (Al-Mufti et al. 1977, Willems 1980, Bond 1981, Wheeler and Giller 1982, Walker and Peet 1983, Vermeer and Berendse 1983, and Day et al. in press). The standing crop values however, that correspond with maximum richness, are not always in accordance with the predicted values ($350-750\text{g/m}^2$, Grime 1979). Although this discrepancy has been briefly discussed (especially by Willems 1980), no one has specifically addressed whether species richness peaks from different communities are or should be similar. My objective was therefore, to establish species richness/standing crop and litter relationships for four shoreline areas, and then, to determine whether the relationships varied among the different wetland habitats. I also explored the environmental factors underlying standing crop gradients on shorelines. I correlating measures of stress and disturbance with standing crop and litter and I plotted the distributions of growth strategies along standing crop gradients, thereby testing whether "stress tolerators" increased with decreased standing crop and litter.

STUDY SITE

Wilsons Lake (43°55'N, 65°53'W) in the Tusket River system in Yarmouth Co., Nova Scotia, was chosen as the study site primarily because of the lake's exceptional species richness. Wilsons Lake is especially diverse due to the presence of disjunct populations of Atlantic coastal plain species (Fernald 1921, 1922, Roland and Smith 1969, Keddy 1985). Many of the disjunct species are nationally significant (Maher et al. 1978). Wilsons Lake contains two that are endangered (Pink coreopsis, Coreopsis rosea and Water pennywort, Hydrocotyle umbellata), one that is threatened (Plymouth gentian, Sabatia kennedyana), and three that are provincially rare (the Tubercled orchid, Habenaria flava; the Bladderwort, Utricularia resupinata; and the Panic-grass, Panicum longifolium). The Tusket River system is also noteworthy in that its shorelines experience extreme water fluctuations throughout the growing season. The water level at Wilsons Lake can change by over .25m in one day.

A second reason for choosing Wilsons Lake was its positioning on two distinct substrate types (Fig. 1). The north end of the lake is composed of glacial till that originated in the red bed terrane of the Fundy area (termed "red till" in this thesis). It was deposited during an early Wisconsinan glaciation (Grant 1977) and has produced broad, gently sloping gravel shorelines (Fig. 2a). The south end of the lake is on locally-derived glacial till (termed "local till" in this thesis) that dates from the late Wisconsinan (Grant 1977). More steeply sloping boulder shorelines mark the presence of this till type (Fig. 2b).

Figure 1. Map of the study site, Wilsons Lake, showing location and substrate types. Unmarked shorelines have been developed.



-  Red till
-  Local till
-  Mixed

Wilsons
Lake

0 1000
METRES

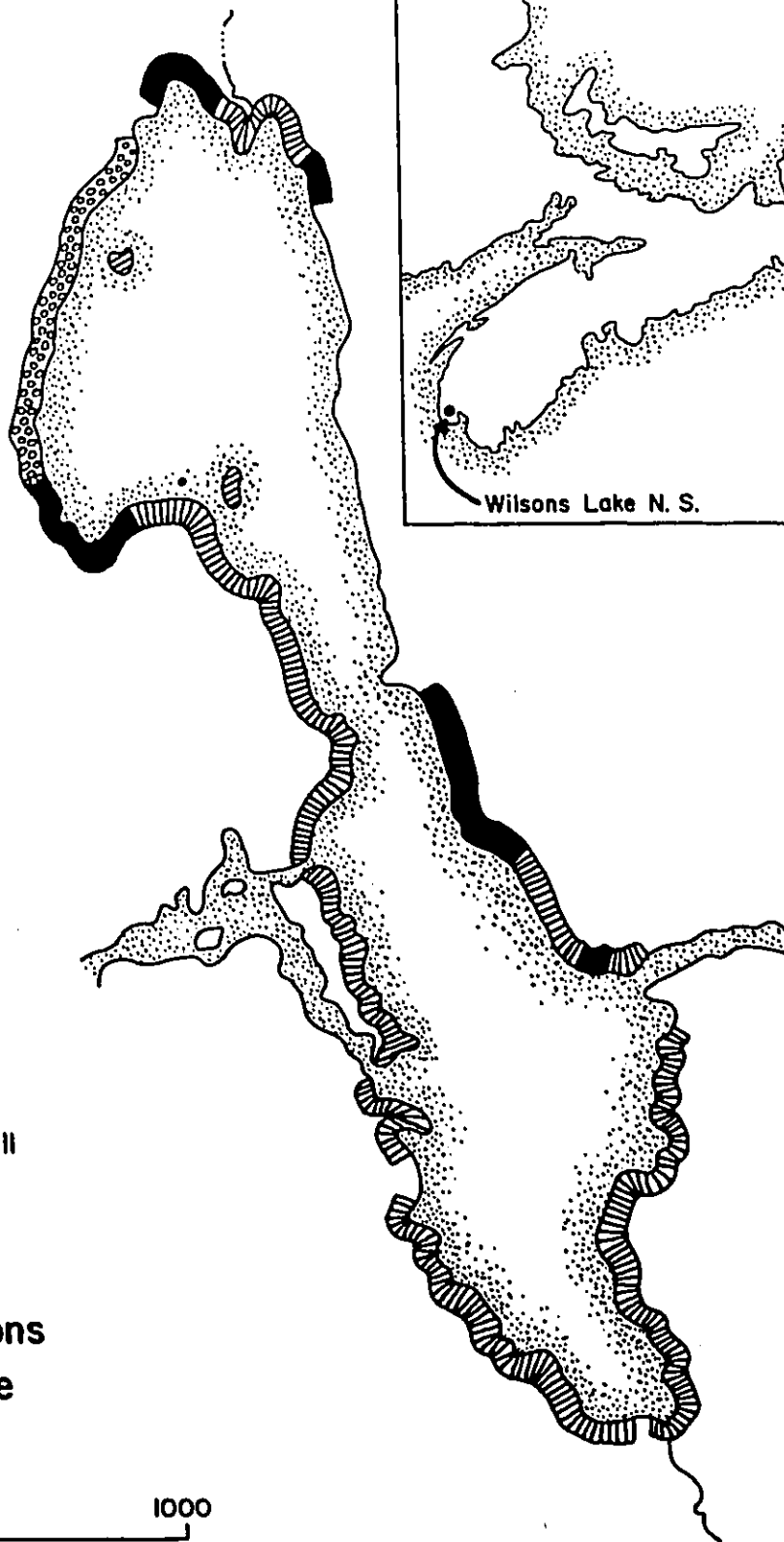


Figure 2. Contrasting shorelines at Wilsons Lake, Nova Scotia. Gently sloping, gravelly shorelines mark the presense of the glacially deposited red till at the north end of the lake (A). Local till at the south end of the lake produces steeper sloping boulder shorelines (B).

A



B



METHODS

From August 1 to August 26, 1984, 121 sites were chosen from four different habitats within Wilsons Lake. The sites were either 15 cm above or 15 cm below a zero-water level, the water's height on July 31, 1984, a typical low water level. Visual estimation indicated that this 30 cm wide range of elevation was the zone of maximum species richness. Sixty sites were located on local till (29 above and 31 below water). The remaining 61 sites were located on red till (31 above and 30 below water).

Since samples had to represent the full standing crop and litter gradient, sites could not be chosen randomly. To ensure that sites with the complete range of standing crop and litter were selected, locations were chosen from a boat on the basis of a visual approximation of the standing crop and litter present.

At each site, a 1 m by .25 m quadrat was positioned. The 1 m dimension was laid parallel to the shore since heterogeneity was more pronounced vertically than horizontally. From within each quadrat, all above ground standing crop and litter of vascular plants was collected and sorted as either litter or to species. Litter was defined as dead unattached material while standing crop was living and dead attached matter. All collected vegetation was separated to species, dried at 60°C for at least 24 hrs and weighed to the nearest .01 gm. When time and weather did not permit the standing crop to be separated to species in the field, the samples were bagged and transported for separation in the lab. All samples were collected within a short enough time span that there was no significant increase in standing crop

and litter due to the length of the sampling period ($p \geq .05$).

Whether species were evergreen was established by visual observation on May 12 to May 15, 1986. Species were considered as being evergreen when all or nearly all of the tissue associated with a normal summer growth form was intact. Partially evergreen species had only a portion of this tissue intact while species that were not evergreen experienced total destruction of above-ground tissue over winter. Roland and Smith (1969) was used to determine whether or not a species was part of the Atlantic coastal plain flora. Vouchers for all species have been deposited at the University of Ottawa (OTT) and/or at Agriculture Canada (DAO). Nomenclature is as found in Roland and Smith (1969) except for Xyris difformis Chapm. and Thelypteris palustris Schott.

Several environmental measurements were also taken. Conductivity was measured by a portable Metrohn conductometer from a slurry of approximately 50 ml wet soil standardized to 100 ml with distilled water. Ten 69.4 cc soil cores were also taken at each plot, five from each side of the quadrat. Percent organic content was calculated from a subsample's weight loss on ignition at 500° C for 12 hrs. Percent silt and clay was measured without dispersants using the wet-sieving and pipette method of Folk (1974).

These three measurements, conductivity, percent organic content, and percent silt and clay, were used to indicate soil fertility. Keddy (1984a) found strong correlations between direct measures of P, K, Mg, and Ca, and conductivity ($r^2 = .92 - .72$), loss on ignition ($r^2 = .86 - .77$), and percent silt and clay

2
($r^2 = .59 - .28$). Similar correlations were found in Gillfillan Lake, the lake upstream from Wilsons Lake (Keddy, unpublished data). Conductivity, a measurement which depends on the presence of ions, reflects nutrient availability since every essential plant nutrient occurs in either the anion or cation form (Thompson and Troeh 1973). Higher conductivity would therefore indicate greater concentrations of these molecules. Higher percentages of silt and clay and organic content also reflect greater fertility since nutrients are stored in soil by clay and organic matter (Thompson and Troeh 1973).

To measure ice scour, a series of ten 20 cm high x .6 cm diameter wooden pegs was positioned around the periphery of each plot and left in place for the winter. From July 7 to July 15, 1985, the plots were revisited and the remaining pegs collected and scored. A score of zero was given for an undamaged peg, one if a peg was cracked, and two if a peg was severed or removed. There was little difficulty in relocating the sites after the year's absence, so a plot score of twenty indicates ten missing pegs, not a lost plot. Soil depth was also recorded. This measurement was calculated as the mean distance that a 2 inch diameter auger could be driven into the soil, to a maximum of 25 cm, at five locations within each quadrat.

Another index of ice and wave damage was obtained from shrubs; greater wave damage and ice scour should push shrubs farther from the water line in exposed areas than in sheltered bays. Measurements of the elevation of the lower limit of the shrub zone were therefore also taken. An automatic level and a

surveying pole were used to record the height above the sampled plot at which shrubs began to grow. Notice that since low plots are 30 cm below high sites, the shrub zone is 30 cm further from them.

Data compiling, correlations, and multiple regressions were done using SPSS and SPSSX statistical package programming on an Amdahl mainframe computing system. When residuals of the regressions were plotted, slight heteroscedasticity occurred in some instances (see Appendix 2). Generalized least squares estimators were used to check that results did not differ once compensations were made for heteroscedasticity (Johnston 1984, Kennedy 1979, see Appendix 3. To test for differences in the species diversity/standing crop relationships, slopes and intercepts of the equations from the four habitats were compared (Kleinbaum and Kupper 1978, Zar 1974).

RESULTS

Changes in species richness along standing crop and litter gradients

Species richness (number of species per $.25 \text{ m}^2$ plot) ranged from 0 to 23 (Fig. 3). Standing crop and litter ranged from 0.1 to $145.2 \text{ g}/.25 \text{ m}^2$. The shortest standing crop and litter gradient occurred low on shores made of red till where the maximum recorded was $65 \text{ g}/.25 \text{ m}^2$ (Fig. 4). The highest standing crop and litter value was low on local till shores.

When all species richness and standing crop and litter values were analysed together, there was a significant polynomial relationship between species richness and the total biomass (Fig. 3). Comparison of F tests and r^2 values indicated that the second degree polynomial equation was a more appropriate descriptor of the relationship than either a linear equation ($p < .0001$, $r^2 = .35$) or a higher degree polynomial ($p \geq .05$). The superior fit of the polynomial equation signified that the species richness/standing crop relationship at Wilsons Lake is bitonic rather than monotonic.

To test for among-habitat variation, the species richness/standing crop and litter values were separated into four groups, the four sampled habitats, and the analyses were repeated. In 3 of these subsets, second degree polynomials once again fit the data better than either linear equations or third degree polynomials (Fig. 4). Comparing the equations from these different habitats (see Appendix 4) revealed that firstly, the three bitonic relationships were all uniquely shaped. Secondly,

the slopes and intercepts of the curves from low elevations on both shore types were indistinguishable. These two data sets were therefore recombined and reanalysed. The species richness/standing crop relationships of each of the three resulting subsets were again significantly different from one another (Fig. 5) and were also most appropriately described by bitonic equations.

Figure 3. Species richness values plotted against standing crop and litter for 121 lakeshore sites sampled from Wilsons Lake. The regression line

$$y = -2.9 + 17.5\log(x+1) - 4.6(\log(x+1))^2$$

is also shown ($p \leq .0001$, $r^2 = .40$). Note that in the equation, a value of 1 was added to the logged values of x to prevent the function from becoming undefined at zero.

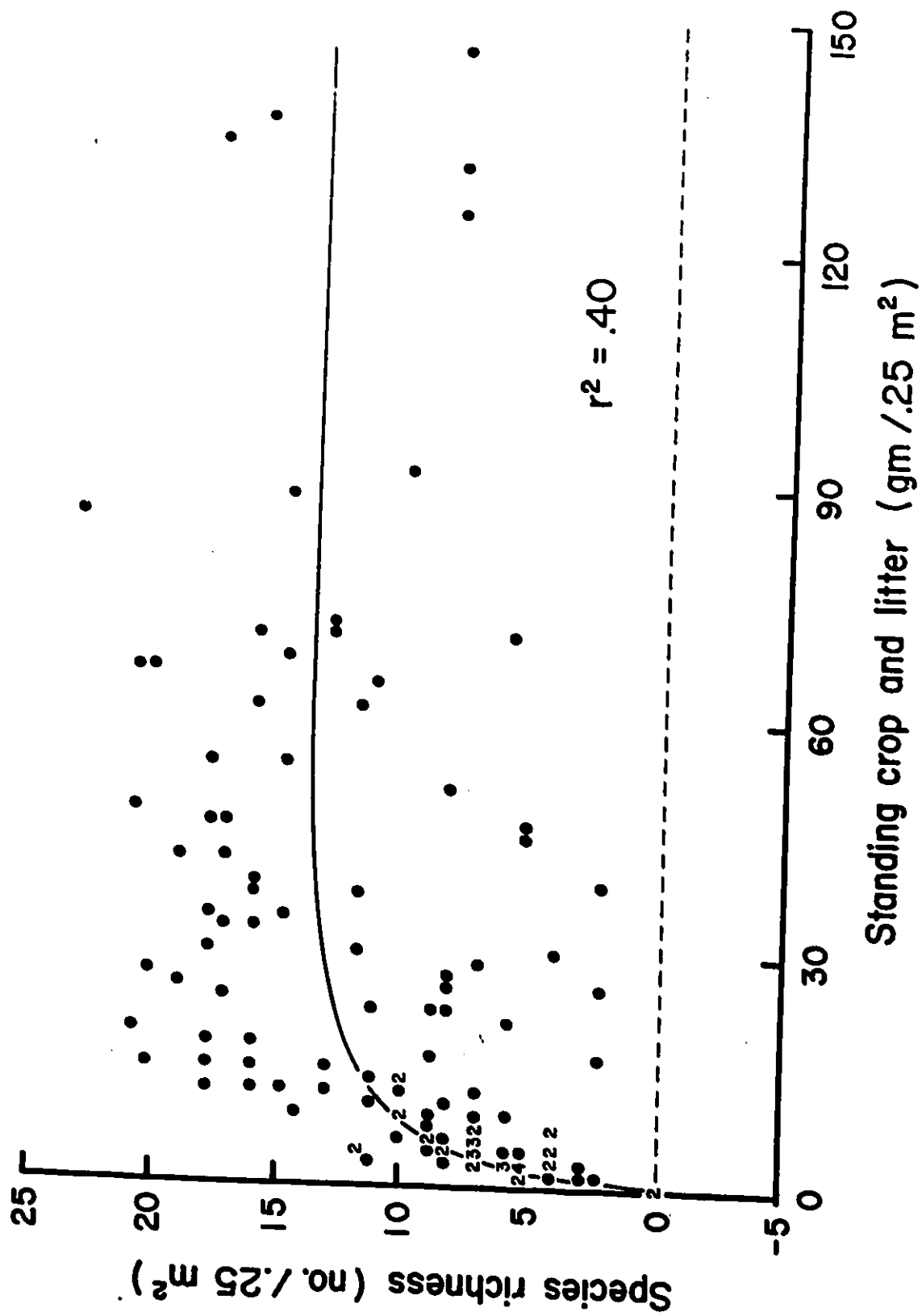


Figure 4. Species richness values plotted against standing crop and litter for each of the four sampled habitats at Wilsons Lake. High on shores made of red till, the points are most appropriately described by the regression equation

$$y = -5.5 + 26.9\log(x+1) - 7.9(\log(x+1))^2$$

($p = .0002$). Low on the same shore type, the equation is

$$y = 3.3 + 4.5\log(x+1)$$

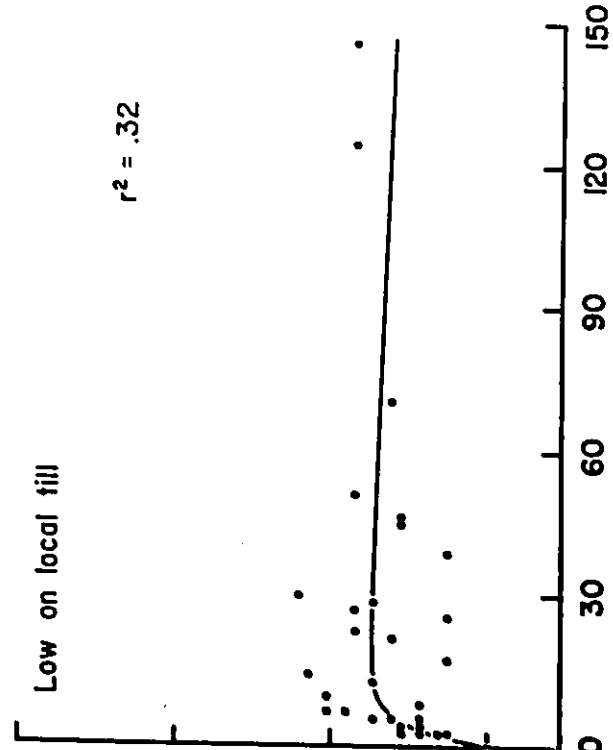
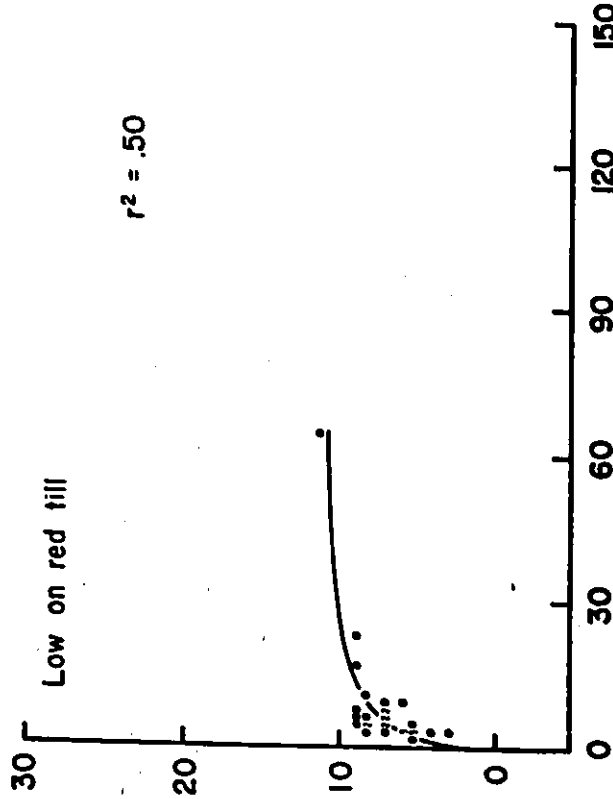
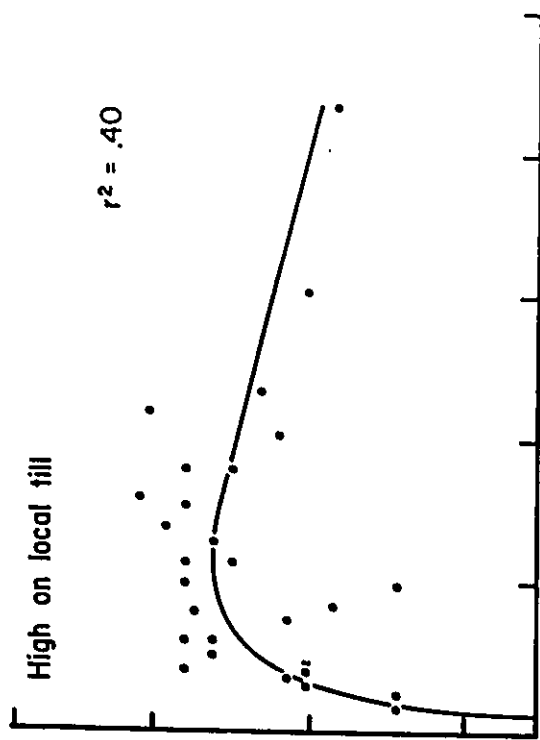
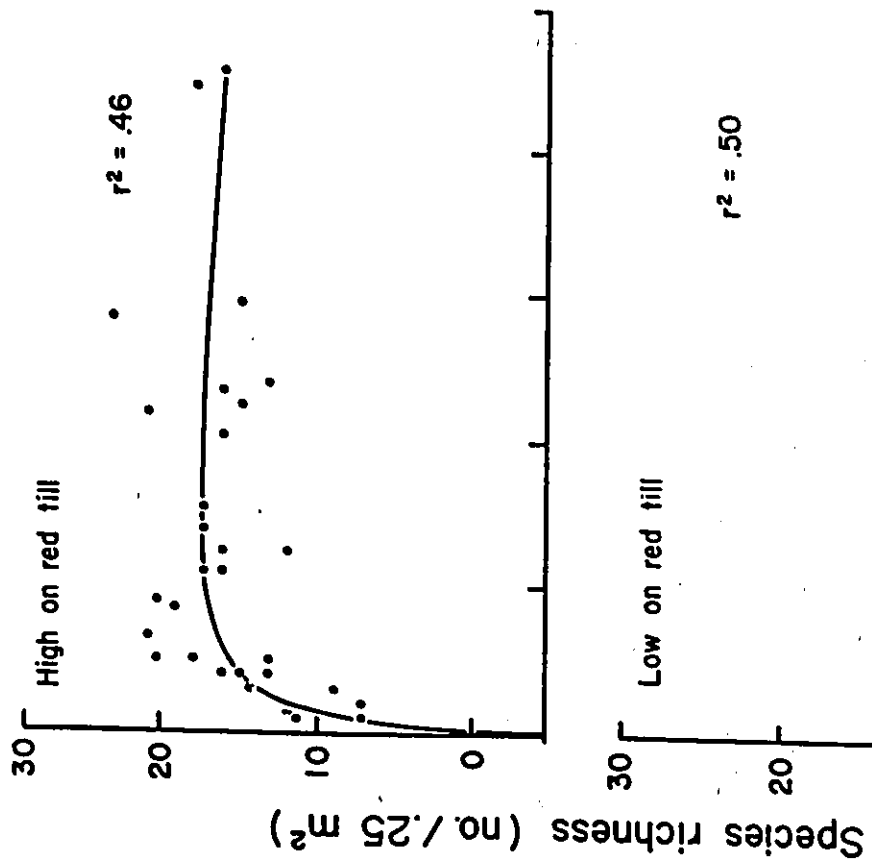
($p \leq .0001$). High on shores of local till, the equation

$$y = -36.3 + 66.8\log(x+1) - 21.4(\log(x+1))^2$$

is most appropriate ($p = .0014$), while lower on the same shorelines, the equation is

$$y = 0.6 + 9.1\log(x+1) - 3.1(\log(x+1))^2$$

($p = .0044$).

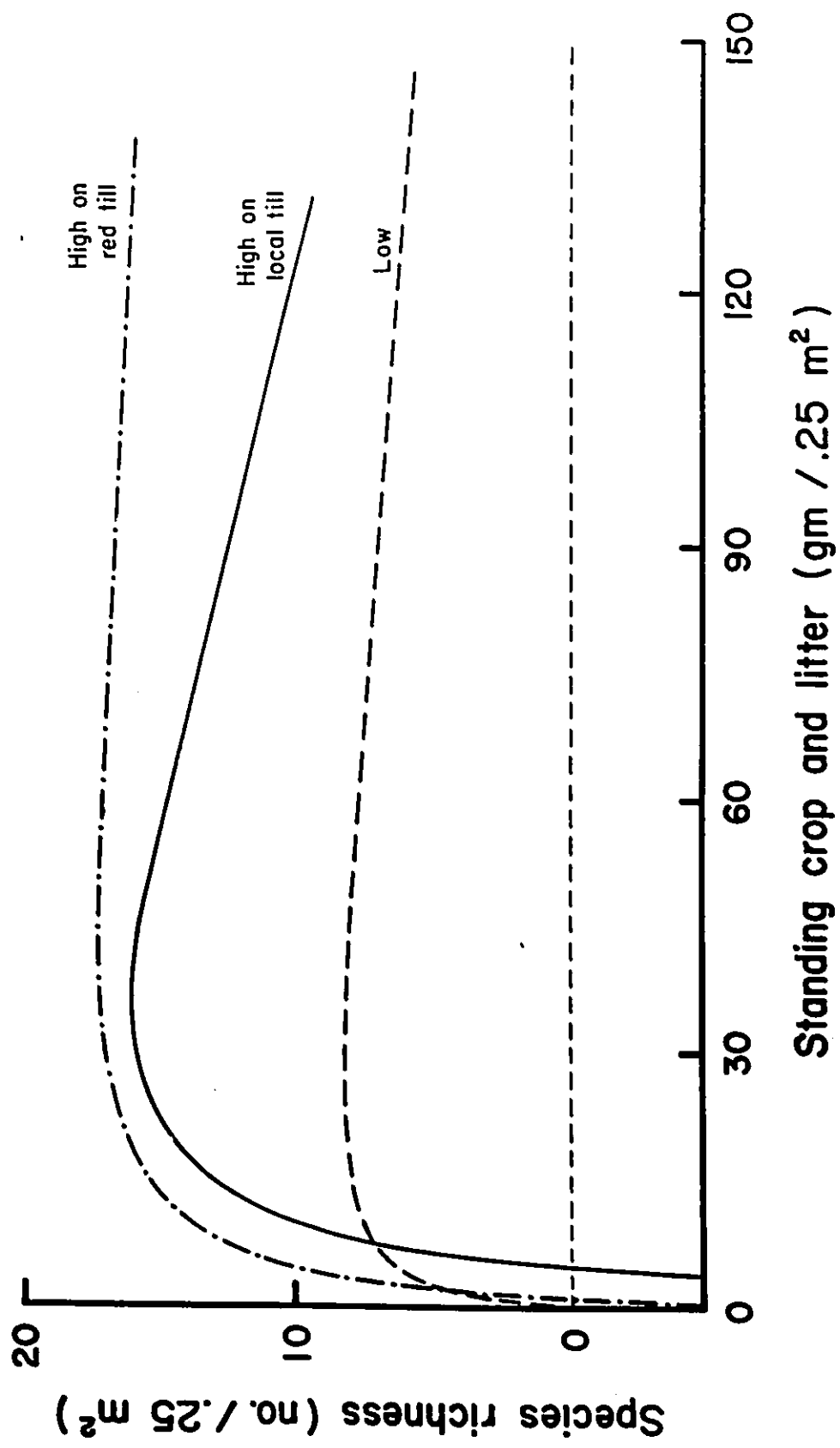


Standing crop and litter (gm/.25 m²)

Figure 5. Comparison of the regression lines. that most appropriately describe the four sampled habitats at Wilsons Lake. The two low shoreline habitats are here both described by the regression equation

$$y = .6 + 10.6\log(x+1) - 3.8(\log(x+1))^2$$

($r^2 = .32$, $p \leq .0001$).



Description of habitats

Since the relationship between species richness and standing crop varied between habitats, I explored the differences among these areas. Table 1 summarizes the environmental factors measured in the four habitats.

The measurements taken to indicate soil fertility revealed significant differences between the two till types. The red till substrate was thicker in depth than the substrate present on local shores, but the soil there was less fertile. Red till had less silt and clay and a lower organic content than local till soils. Conductivity did not vary amongst the four habitats.

As with the measures of fertility, the measures of disturbance likewise revealed no differences between the high and low habitats. They did however, again reveal differences between the two till types. Both the height to the shrub zone and the damage sustained by pegs indicated that wave damage and/or ice scour was greater on red till than on local. On local till, the shrub zone was on average, 20 cm further down the shore than on red till shores.

Table 1. Mean values ($n \approx 30$) of various environmental measurements from Wilsons Lake. The measurements were taken either high or low on shorelines made of red till or from high or low on shorelines made of local till. Superscripts denote habitats that are not significantly different at $p \leq .05$. The original values of these and other measurements for each of the 121 sampled sites are presented in Appendix 5.

	high		low	
	red	local	red	local
Species richness (no./ $.25m^2$)	^a 15	^a 13	^b 7	^b 6
Standing crop and litter (g/ $.25m^2$)	^{ab} 38.80	^{ab} 35.73	^c 7.87	^{abc} 24.76
Litter (g/ $.25m^2$)	^{ab} 9.31	^{ab} 15.31	^a .95	^b 18.81
Loss on ignition (%)	^a 3.30	^b 17.44	^a 1.00	^b 13.38
Percent silt and clay	^a 9.72	^b 41.13	^a 9.70	^b 34.23
Conductivity ($\mu S/cm$)	^a 36.8	^a 39.4	^a 37.0	^a 32.6
Ice damage ¹	^{ac} 9	^{ab} 5	^c 11	^b 3
Soil depth (cm)	^a 23.0	^b 13.2	^a 20.6	^b 11.7
Height to shrubs (cm) ²	^{ab} 39	^a 18	^c 67	^{bc} 46

¹ Damage sustained by wooden pegs, on a scale from 0 (no damage) to 20 (high damage).

² When comparisons were performed with shrub measurements from a common shore height i.e., when 30 was added to the high habitat values, the results were as follows;

^a	^{ab}	^{ab}	^b
69	48	67	46

Description of standing crop and litter gradients

At Wilsons Lake, the standing crop and litter gradients ran parallel to fertility gradients. Loss on ignition, percent silt and clay, and conductivity, were all positively correlated with both standing crop and standing crop and litter (see Table 2). Soil depth, which was also positively correlated with total biomass, also reflected fertility since it correlated most often with other measures of fertility than with measures of disturbance (see Appendix 6).

As the total biomass and fertility gradients both increased, the disturbance gradients decreased. Peg damage, which indicates ice scour, was negatively correlated with standing crop and litter on the two red till shores. The height of the shrub zone, although not significant, also correlated negatively. Additional negative correlations are given in Appendix 6.

Overall, the two disturbance measures did not correlate often with total biomass. The fertility measures however, did. Although their importance varied among the different habitats, the four measures of fertility were often significant predictors of standing crop and litter (see Table 2 and Appendix 7). The standing crop gradients at Wilsons Lake seem therefore, to be most strongly reflecting an underlying fertility gradient rather than a gradient of disturbance.

Table 2. The relationship of standing crop (SC) or standing crop and litter (SC+L) with environmental measurements for the Wilsons Lake habitats ($n \approx 30$). The values shown are r (Spearman's rank correlation coefficients). The symbol ns indicates $p > .05$. Since the risk of accepting a false correlation increases with the number of correlations performed, only coefficients of $p \leq 0.001$ (***) were accepted and discussed. * $p \leq 0.05$

** $p \leq 0.01$

		high		low		all
		red	local	red	local	
loss on ignition	SC+L	.78***	.62***	.61***	.63***	.63***
(%)	SC	.75***	.57***	.65***	.65***	.45***
Percent silt and	SC+L	.50**	.58***	ns	.45**	.36***
clay	SC	.52**	.65***	ns	.65***	.24**
Conductivity	SC+L	ns	.32*	ns	.40*	.28***
($\mu\text{S}/\text{cm}$)	SC	ns	.50**	ns	.44**	.36***
Ice damage	SC+L	-.53***	ns	-.55***	ns	-.23**
	SC	-.56***	ns	-.59***	ns	ns
Soil depth (cm)	SC+L	.63***	.46**	.33*	.52***	.33***
	SC	.64***	.48**	.38*	.72***	.52***
Shrub zone (cm)	SC+L	ns	-.31*	ns	ns	ns ¹
	SC	-.31*	-.32*	ns	ns	ns ¹

1

Correlations were performed with shrub zone measurements from a common shore height.

Species distributions along standing crop and litter gradients

Plant species showed differential distributions along the four standing crop and litter gradients although distributions within one habitat were not always identical with another (Fig. 6). A species varied from habitat to habitat either in magnitude or in the range of its standing crop. Cladium mariscoides for example, was present at sites with less than $22 \text{ gm}/.25 \text{ m}^2$ of standing crop and litter low on red till but was absent at equivalent sites higher on the same shore. Cladium mariscoides was also absent from high shores of local till, demonstrating that the species' abundances were not related to the standing crop of the sites but rather, that distributions reflected underlying stresses (infertility) and disturbances.

The distribution of evergreen species

Evergreen species (those indicated in Figure 6) occurred throughout the gradients' lengths of the four habitats but their contributions to total standing crop varied noticeably from one point on the gradient to another. Evergreen species often made up a large percentage of the standing crop and litter at low biomass sites while at high sites, they were consistently rare (Fig. 7). Evergreen species were also particularly common in the lower habitats (see Table 3). There, they comprised 25 - 30% of all species found, but produced up to 69% of the standing crop.

The distribution of Atlantic coastal plain species

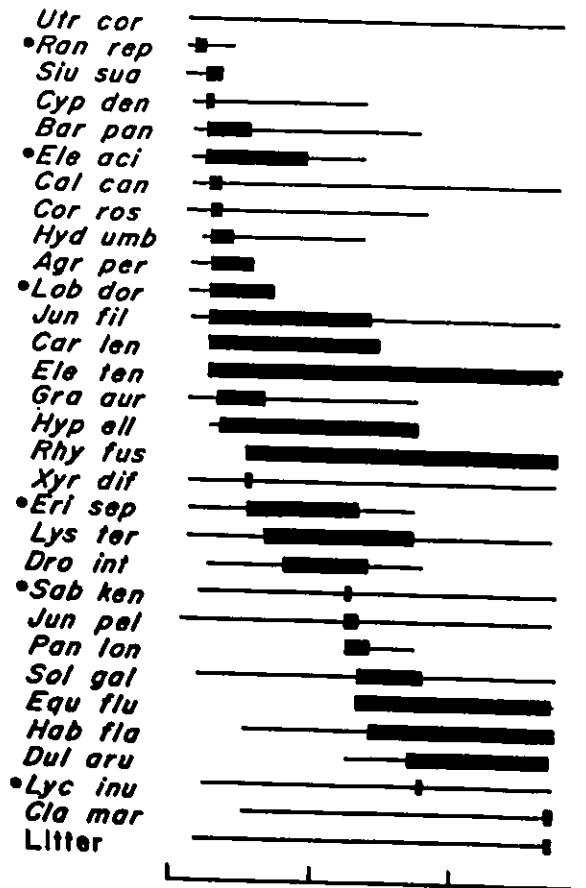
Unlike evergreen species, Atlantic coastal plain species occurred on each of the four shore types in approximately equal proportions (13 - 17% of all species present - Table 3); but their contribution to the total standing crop and litter was very different among the four habitats. Coastal plain species accounted for 29 - 35% of the total standing crop and litter high on red till but only 0.2% low on local shores. There were also differences in the contributions of these species along the standing crop and litter gradients. The proportion of standing crop contributed by coastal plain species increased with decreasing biomass (Fig. 8). Figure 8 also shows a similar distribution using only the species that have been classified as either endangered, threatened, or rare. This pattern is similar to that observed for evergreen species, even though there is minimal overlap in the two lists.

Figure 6. The distributions of plant species along standing crop and litter gradients of each of the four habitats from Wilsons Lake. Thin lines show the range of standing crop and litter values where the species' occurrence is $\geq 1\%$ of its total weight from all sites (thereby eliminating minor occurrences). Bold lines represent sites where the species occurred as $\geq 10\%$ of their total weight. Species that were encountered fewer than four times are not shown but are listed in Appendix 8. A circle (●) indicates that the species is evergreen.

Species names are abbreviated as follows: Agr per - Agrostis perennans, Bar pan - Bartonia paniculata, Cal can - Calamagrostis canadensis, Car len - Carex lenticularis, Cal mar - Cladium mariscoides, Cor ros - Coreopsis rosea, Lyp den - Cyperus dentatus, Dro int - Drosera intermedia, Dul aru - Dulichium arundinaceum, Ele aci - Eleocharis acicularis, Ele ten - Eleocharis tenuis, Equ flu - Equisetum fluviatile, Eri sep - Eriocaulon septangulare, Gly bor - Glyceria boreale, Gra aur - Gratiola aurea, Hab fla - Habenaria flava, Hyd umb - Hydrocotyle umbellata, Hyp ell - Hypericum ellipticum, Iso tuc - Isoetes tuckermani, Jun fil - Juncus filiformis, Jun pel - Juncus pelocarpus, Lob dor - Lobelia dortmanna, Lyc inu - Lycopodium inundatum, Lys ter - Lysimachia terrestris, Myr ten - Myriophyllum tenellum, Nym cor - Nymphoides cordata, Pan lon - Panicum longifolium, Pon cor - Pontederia cordata, Ran rep -

Ranunculus reptans, Rhy fus - Rhynchospora fusca, Sab ken -
Sabatia kennedyana, Siu sua - Sium suave, Sol gal - Solidago
galetorum, Utr cor - Utricularia cornuta, Vio lan - Viola
lanceolata, Xyr dif - Xyris difformis, Ela min - Elatine minima.

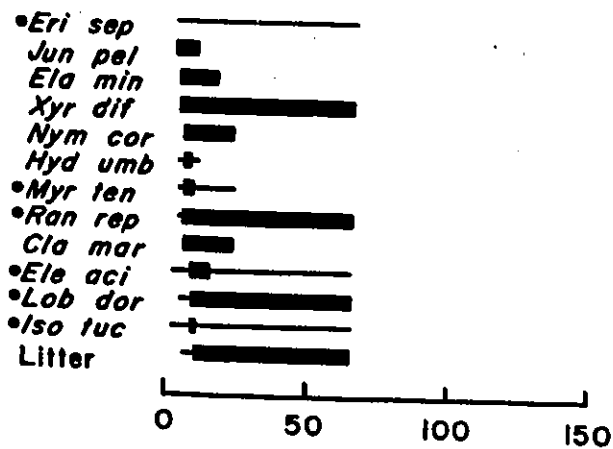
High on red till



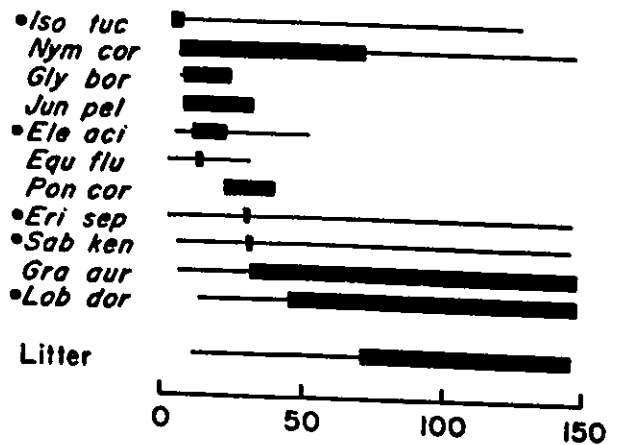
High on local till



Low on red till



Low on local till



Standing crop and litter (gm / .25 m²)

Figure 7. The contribution of evergreen species (those marked by a circle in Figure 6) to the standing crop and litter of each of 121 sites sampled from Wilsons Lake. The four habitats are represented as follows: high on shores of red till (O), low on shores of red till(●), high on shores of local till(□), low on shores of local till(■).

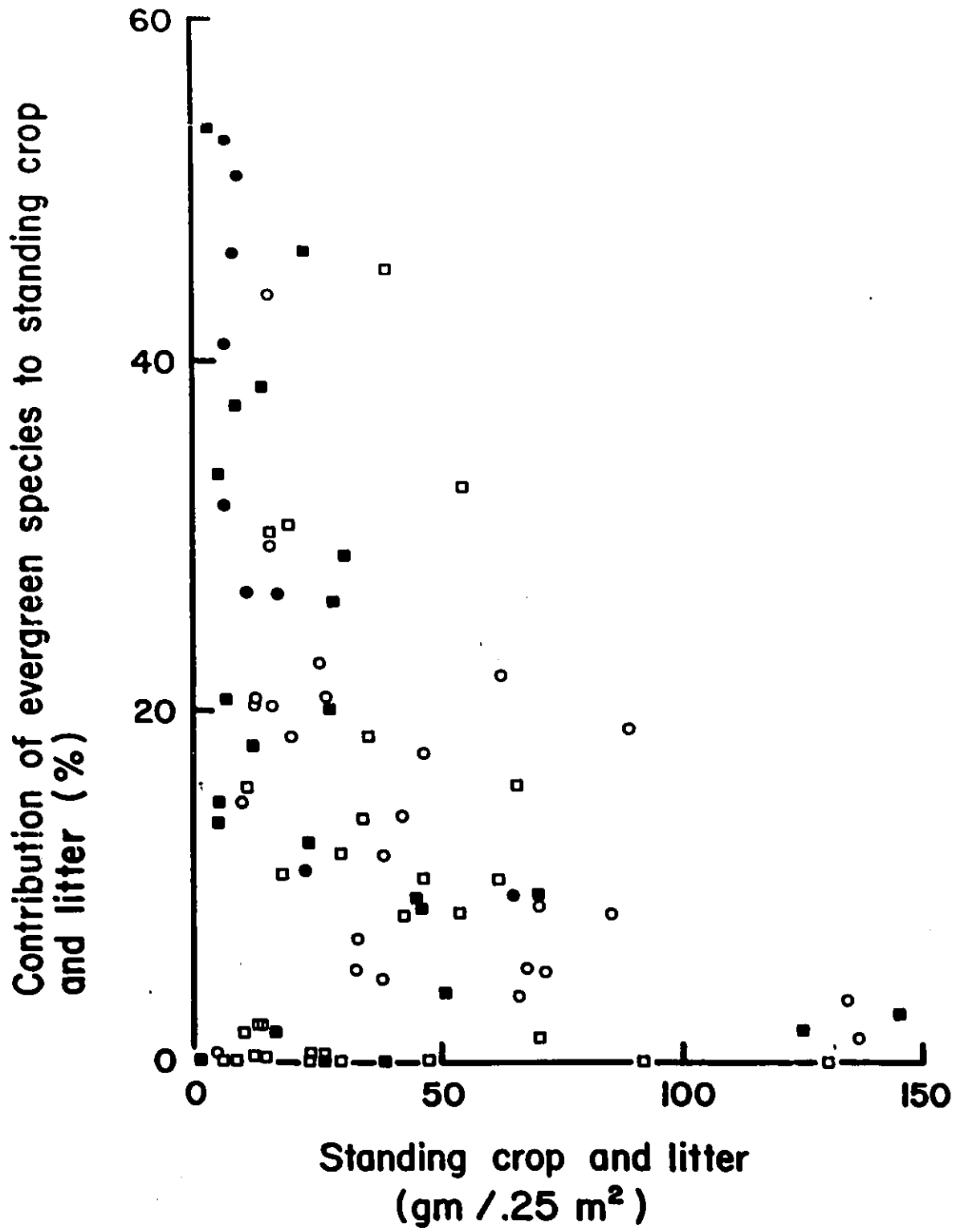
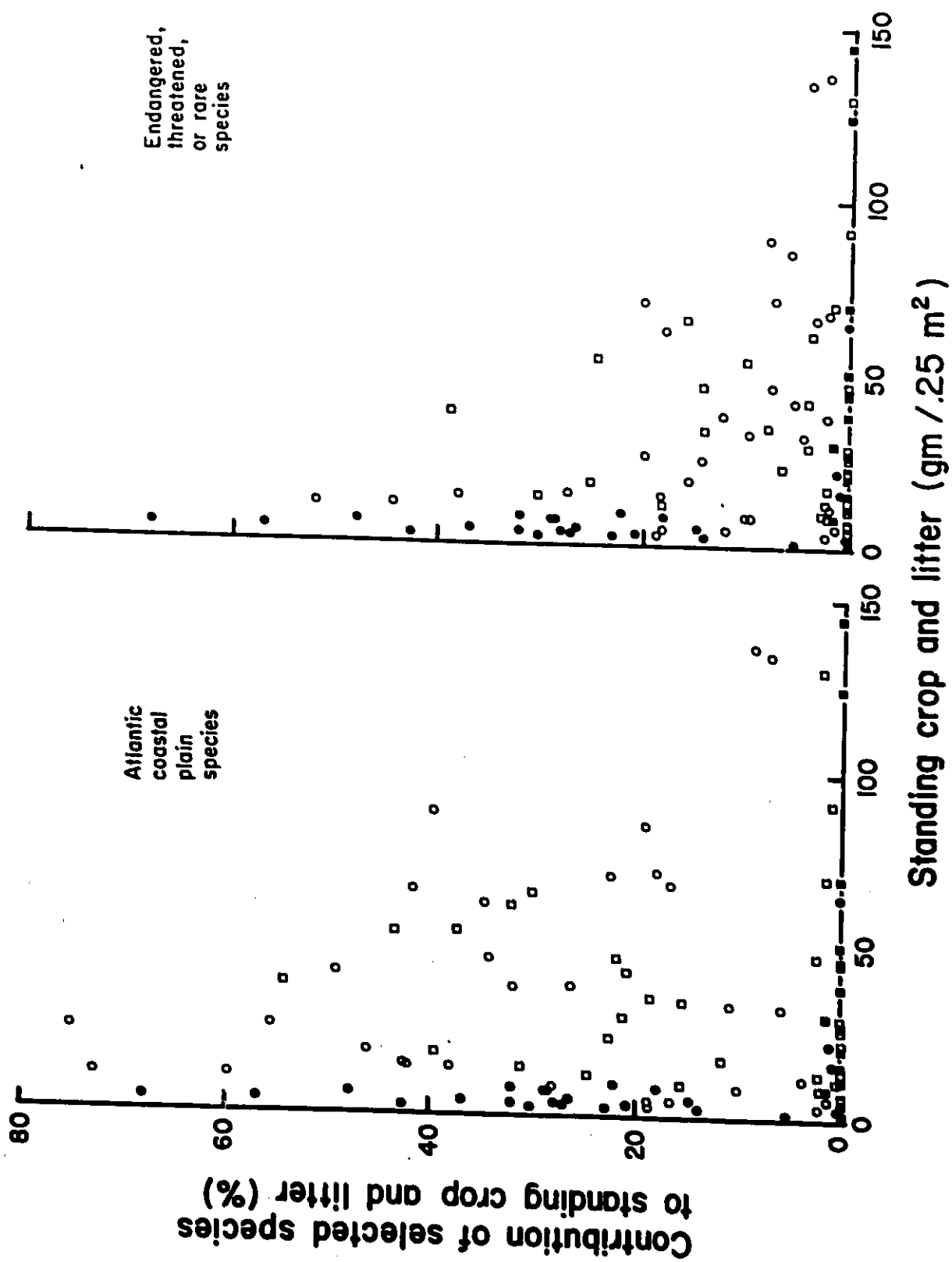


Table 3. Comparison of the numbers and abundances of selected species among four different habitats. Evergreen species are those indicated in Figure 6. The Atlantic coastal plain (ACP) species are as follows; Coreopsis rosea, Habenaria flava, Hydrocotyle umbellata, Lycopodium inundatum, Panicum longifolium, Polygonum hydropiperoides, Sabatia kennedyana, Solidago galetorum, and Xyris difformis. Superscripts denote habitats that are not significantly different at $p < .05$.

	high		low	
	red	local	red	local
No. of species / habitat	47	48	23	28
No. of evergreen species / habitat	8	7	7	7
% evergreen species / habitat	17.0	14.6	30.4	25.0
% evergreen species / quadrat	24.6 ^a	16.4 ^a	68.4 ^b	53.1 ^c
Contribution of evergreen species				
to standing crop and litter (%)	24.9 ^{ab}	9.4 ^a	66.0 ^c	32.0 ^b
to standing crop (%)	27.7 ^a	12.6 ^a	68.6 ^b	66.1 ^b
No. of ACP species / habitat	8	8	3	4
% ACP species / habitat	17.0	16.7	13.0	14.3
% ACP species / quadrat	30.7 ^a	21.6 ^b	13.4 ^c	2.6 ^d
Contribution of ACP species				
to standing crop and litter (%)	29.0 ^a	15.5 ^b	20.1 ^{ab}	0.1 ^c
to standing crop (%)	34.8 ^a	20.8 ^b	21.3 ^b	0.2 ^c

Figure 8. The contribution of selected species to the standing crop and litter of sites from within each of four habitats. Habitat designation are as in Figure 7. The Atlantic coastal plain species are listed in Table 3. Coreopsis rosea and Hydrocotyle umbellata are nationally endangered, Sabatia kennedyana is threatened, while Panicum longifolium, Habenaria flava, and Utricularia resupinata are provincially rare.



DISCUSSION

Application of Grime's model

The selection of bitonic rather than monotonic curves to describe the species richness/standing crop relationships illustrated that at Wilsons Lake, species richness decreased at high levels of standing crop and litter. The high values of standing crop however, at the four habitats, were not as high as what has been found in most other wetlands. Figure 9 compares the Wilsons Lake shorelines to a Typha dominated lakeshore. When the standing crop and litter gradient was thus extended, the bitonic relationship between species richness and standing crop became much more pronounced.

The ranges of standing crop values that correspond with maximum species richness were also lower at Wilsons Lake than in most other habitats (Appendix 9). The values were also not in accordance with the range predicted by Grime (350 - 750 g/m^2 , Grime 1979). As the present study shows though, maximum species richness will not and should not be expected to occur at similar points along different standing crop and litter gradients. Previous studies have also found species richness peaks outside the range of 350 - 750 g/m^2 (Appendix 9).

The reduction in species richness that occurs at high standing crop is thought to be due to competition by a few competitively dominant species (Grime 1979). This view is supported by Wilson and Keddy (1986a) who showed that species from areas with high standing crop have superior competitive abilities than those from less densely vegetated sites. The high

species richness at Wilsons Lake and other low standing crop sites, seems therefore, to be the result of factors reducing standing crop, reducing competition, and thereby preventing dominance.

Environmental factors and standing crop

Grime's prediction that both stresses and disturbances reduce standing crop is supported by the negative correlations between standing crop and the measures of disturbance that are presented in Table 2. As the amount of ice and wave damage increased, the amount of standing crop decreased. Wave action, by acting on different parts of the shorelines with different strength, had created disturbance gradients counter to the biomass gradients. Exposure to waves however, also affects fertility. Organic content and the proportion of silt and clay is lowered when exposure is intensified (Keddy 1982, 1983a). Wave action sorts out and removes fine nutritive particles. Exposure therefore, may also have created the nutrient stress gradient that underlies standing crop and litter. The positive correlations in Table 2 and a similar correlation in Wilson and Keddy (1986b) support Grime's prediction that low fertility (stress) can reduce standing crop.

Although both stress and disturbance are present at Wilsons Lake, disturbances appear to be of secondary importance. Ice and wave damage was a factor in controlling the standing crop gradient on only one till (red - Table 2), the till type that was described as being more disturbed (Table 1). On local till, boulders may have been physically protecting the flora and the

soil or perhaps, features of boulder shorelines in general were responsible. Local till shorelines are a series of bays and points while shorelines of red till are smooth (see Fig. 2).

The two tills were also different with respect to fertility, although neither till was very fertile. The lower organic content of red shorelines may be due to till differences with the glacially deposited till being more nutrient poor than local material. On local till, nutrient shortages may result from a shallow rooting zone. The characteristic boulders of this shoreline type reduce the space available for plants and may therefore be restricting the amount of standing crop and litter present. The overall infertility of these shoreline areas is also shown by the abundance of insectivorous plants in the genera Drosera and Utricularia.

Plant strategies as evidence of stress

Evidence for stress being the mechanism that affects species richness at low standing crop sites comes therefore, not only from the correlations of fertility measurements but from the morphologies of the species themselves. At Wilsons Lake, there was a virtual absence of annuals, a type of plant that should be common in disturbed areas (Grime 1979; only one species of annual was recorded, Elatine minima). This scarcity suggests that nutrient poor conditions have prevented annuals from exploiting gaps created by disturbances. Such nutrient poor conditions are also suggested by the presence of another type of plant.

There are a number of species at Wilsons Lake that share a similar growth form and habitat. These species, collectively

known as "isoetids", all have very short stems and rosettes of short stiff leaves (Hutchinson 1975). Eight of the species encountered during sampling are considered isoetids; Isoetes macrocarpon, Lobelia dortmanna, Eriocaulon septangulare, Elatine minima, Myriophyllum tenellum, Eleocharis acicularis, Juncus pelocarpus, and Gratiola aurea. A ninth species, Ranunculus reptans, is considered as an associated species as are Sphagnum spp. and other bryophytes (Boston and Adams 1987). All but three of these are evergreen, another characteristic common among isoetids; Juncus pelocarpus is partially evergreen.

Two other evergreen species are Lycopodium inundatum and Sabatia kennedyana. Sabatia is a small rosette plant that grows tall only when it bolts for flowering. Lycopodium has prostrate stems and very stiff, short leaves. Although not included in the list by Boston and Adams (1987), these two species do resemble isoetids in both form and habitat and will therefore be considered as such in the discussion to follow.

The isoetids at Wilsons Lake are all particularly abundant where standing crop and litter is low and in the submerged habitats. This distribution is consistent with previous reports of their being especially common in oligotrophic lakes and that they typically occur where the organic content of sediments is less than ~5% (Hutchinson 1975, Boston and Adams 1987).

Evergreenness is a feature that seems well suited to species growing in infertile areas (Grime 1979). Tissue conserved through winter is able to photosynthesize in the spring before a costly investment of new growth is made and before a canopy is formed overhead. Having evergreen tissue also compensates

species of low productivity by allowing each plant greater standing crop than if the species had high leaf turnover. Leaf turnover rates and annual productivity of isoetids is low (Boston and Adams 1975)

Even though isoetids are suited to and occur primarily on infertile soils, they are not restricted to such sites at Wilsons Lake. Of the eleven species previously listed, only Myriophyllum tenellum is restricted to sites with less than 5% organic content. Four species appear where organic content is 64%. All however, have maximum standing crop in sites with less than 25% organic content.

The short stature and creeping habit of isoetids may make them resilient to disturbances which eliminated competitive dominants (Spence 1982). The presence therefore, of isoetids in soil of greater fertility than expected may be a further indication that the sites are more heavily stressed and disturbed than at other lakes. Even though the stresses of infertility are the more important controlling factors at Wilsons Lake (Table 2), disturbances are also present. The fluctuating water levels typical of the basin and the ice, wind, and wave damage that the shores sustain may be keeping non-isoetids out of areas that are fertile enough to support them. Competition may therefore, be reduced in areas which isoetids can tolerate, but normally cannot occupy due to interspecific competition.

The physical structure of isoetids, their slow growth rates, and their ability to grow in nutrient poor soil are all suggestive of Grime's stress-tolerators. Boston (in press) likewise concluded that isoetids are stress-tolerators. Their

presence therefore supports one of Grime's mechanisms for changes in species richness. Stress-tolerators occur at low levels of standing crop and litter, indicating that stress (infertility) is reducing the number of species able to survive in these areas.

Stress and the presence of Atlantic coastal plain species

Stresses that keep biomass levels low at Wilsons Lake have also produced an exceptionally diverse flora (Fig. 9). The presence of rare, threatened and endangered Atlantic coastal plain species is, in large part, what sets Wilsons Lake apart from most other wetlands. These species occur in addition to the local flora, as at other lakes with similar disjunct populations of the species (Keddy 1981, 1984b). Their absence however, from other wetlands is not simply a function of limited dispersal. Within Wilsons Lake, these species have dispersed throughout the four habitats in roughly equal proportion, yet they do not occur in equal abundance. They are most abundant in the most infertile, disturbed habitat shorelines. This is consistent with the occurrence of other disjunct populations of these same species elsewhere (Keddy 1983b, 1984b).

The continued presence of Atlantic coastal plain species at Wilsons Lake may therefore be due to continued stress. An infertile till is being further depleted of nutrients by continuing water fluctuations and wave action. The stresses that result from infertility are apparently eliminating or hindering dominant species. The resulting reduction in competition, coupled with the coastal plain species' abilities to tolerate

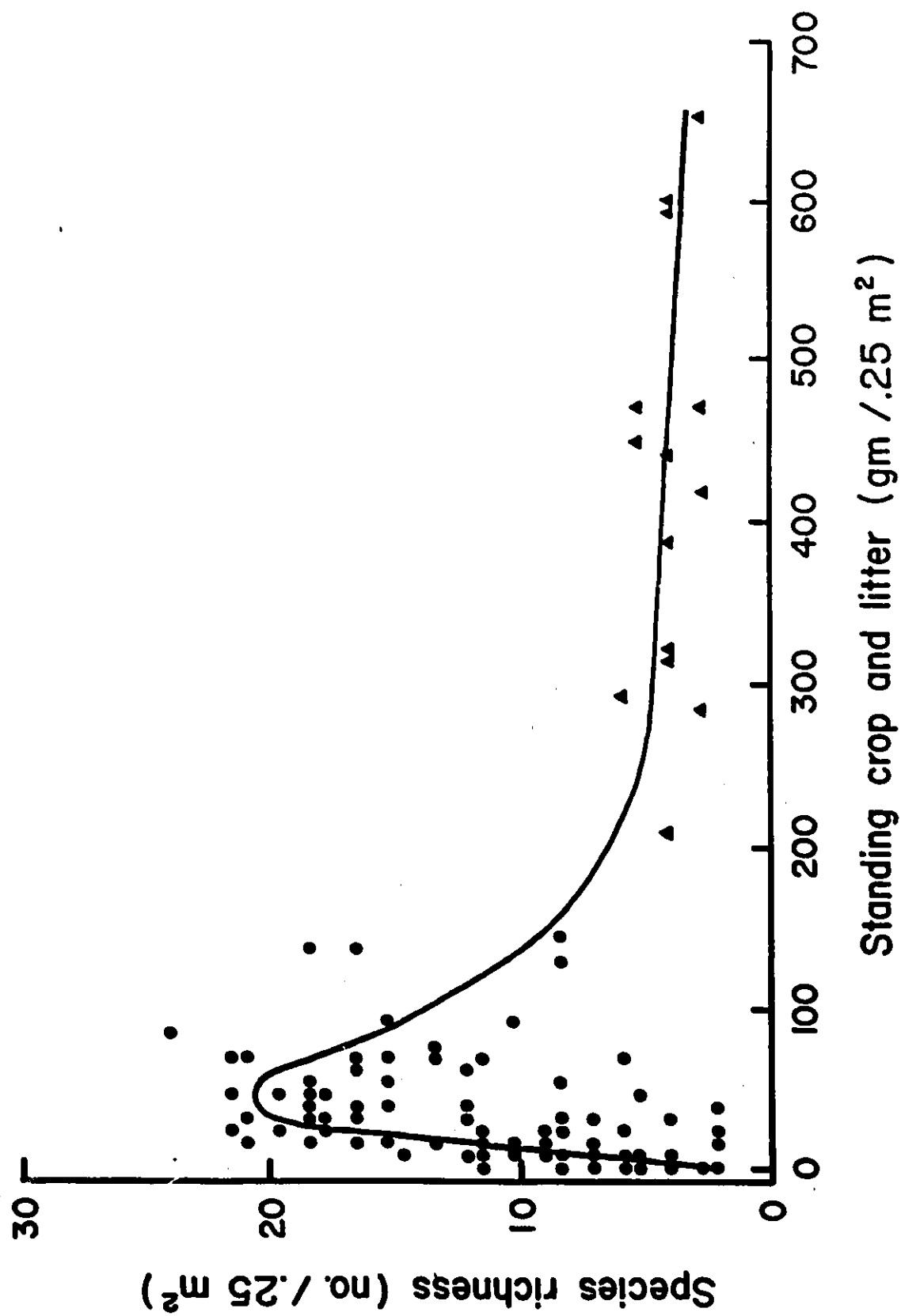
nutrient poor conditions, has apparently allowed the flora to persist far beyond its normal range in North America.

Standing crop gradients and wetland conservation

Even though the exact nature of the species richness/standing crop and litter relationship varies from habitat to habitat, an important generalization can be made. Wetland sites of high standing crop, such as Typha dominated areas, can be expected to have and do contain far fewer species than areas with low standing crop and litter such as Wilsons Lake. The preservation of habitats with standing crop values that correspond to high species richness may therefore be paramount in maintaining maximum plant diversity. The conservation of a specific flora however, may depend on the preservation of particular sites. At Wilsons Lake for example, it was the low standing crop sites that contained the highest proportion of rare and endangered species.

Efforts to conserve a particular habitat should be centered on what is influencing the present levels of standing crop and litter. While competition may be important when standing crop is high, Grime's model (1979) and this study suggest that for low standing crop sites, stresses and disturbances should be considered. Increased disturbances for example, at Wilsons Lake could further reduce standing crop, but could also reduce the number of stress-tolerators. Changes to stresses or disturbances then, affect not only standing crop and species richness, but also the kinds of species that are present, changes which can all be predicted from Grime's model.

Figure 9. Species richness values as plotted along a standing crop and litter gradient. The values are from Wilson Lake, N. S., (●) and from a *Typha* stand at Presqu'ile Provincial Park, Ontario (▲), Gaudet and Moore unpublished data. Maximum richness occurred at low to intermediate levels of standing crop and litter. Line was fit by eye.



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APPENDIX 1

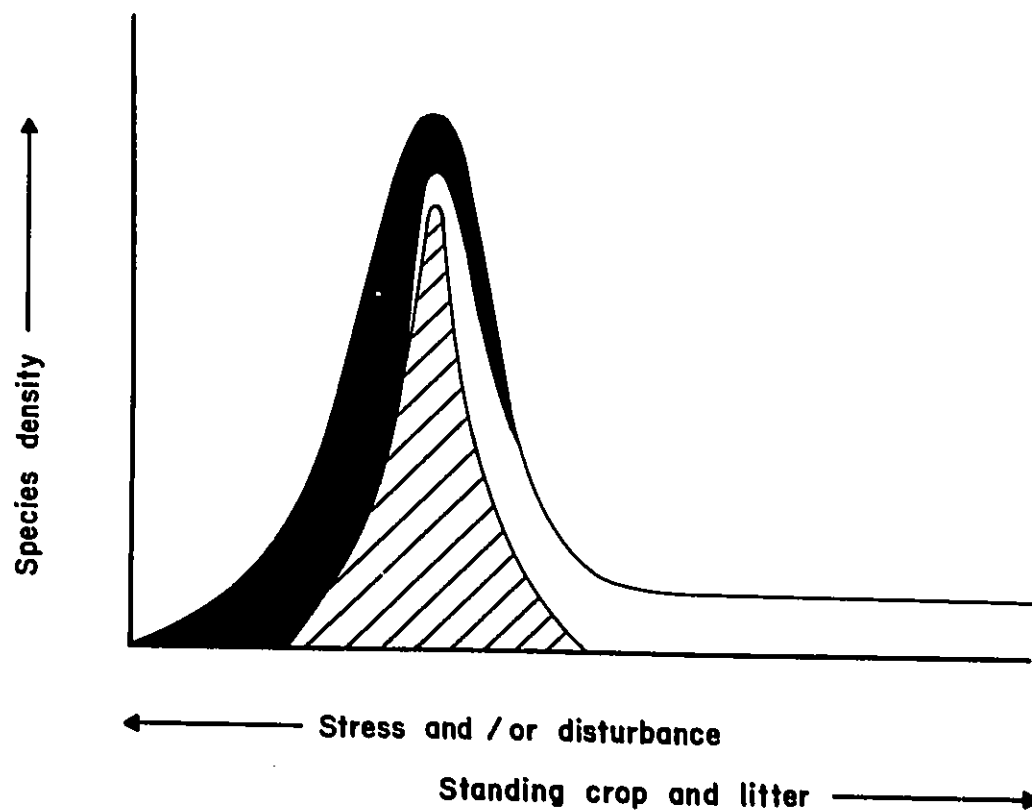
In order to explain variation in species richness, Grime (1973, 1979) proposed a coexistence model for herbaceous vegetation (Fig. 10). Maximum species density, recorded as the number of species per unit area, is found at sites of moderate stress and/or disturbance and moderate standing crop and litter (total biomass). Stresses are the phenomena which restrict photosynthetic production, such as water, light, and mineral nutrient shortages. Disturbance is the partial or total destruction and removal of vegetation both living and dead. This destruction can be the result of soil erosion, wind-damage, frosting, desiccation or fire. Herbivore and pathogen activities also cause destruction as do trampling, mowing, and ploughing (Grime 1979).

Grime (1979) also discussed the mechanisms which he thought produced the above pattern (Fig. 11). He proposed that in areas of high total biomass, low stress and/or disturbance permits competitive exclusion by a few dominant species. In areas of moderate total biomass, stress and/or disturbance reduces the competitive ability of the few dominants and allows less competitive species to coexist. Low species density and low total biomass is the result of few species being able to withstand extreme stresses and/or disturbances. The species that do occur at sites with low standing crop would therefore be either stress-tolerant species (defined by Grime, 1979, as being small, slow-growing, evergreen perennials) or disturbance-tolerant species (fast-growing annual ruderals). Dominant

species, those that would occur at the other end of the gradient, are defined as being very large, tussocky, rhizomatous, fast-growing perennials.

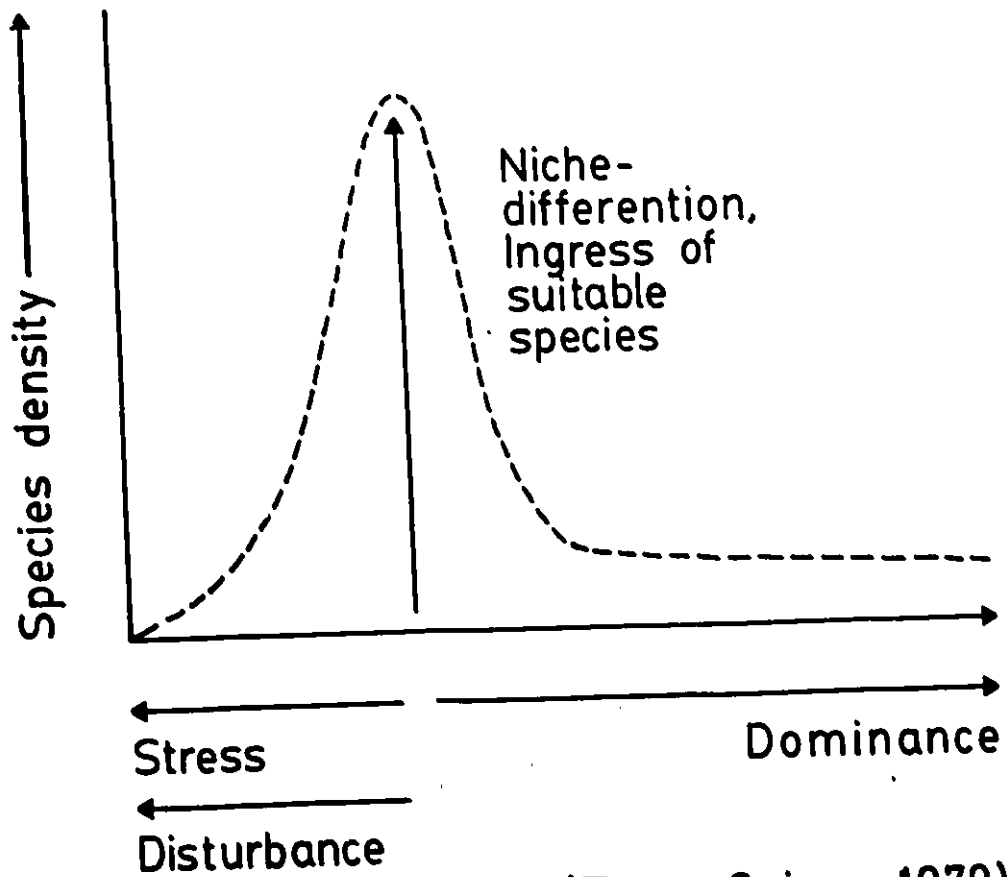
The usefulness of Grime's model is that once it is known to describe an area, predictions can be made as to the result of a manipulation (Fig. 12). Changes in total biomass and species density could be predicted, as could the presence or absence of a specific species if the species' range along the total biomass gradient is known. A rare plant for example, occurring only at sites of minimum biomass, could disappear if stresses affecting the sites were altered. The application of Grime's model to management is that it explains and predicts changes in species composition, allowing these changes to be controlled.

Figure 10. Model describing the impact of stress and/or disturbance on species density.



- ☐ Potential dominants
- ☒ Species adapted to stress or disturbance
- ☒ Remaining species (From Grime 1973 , 1979)

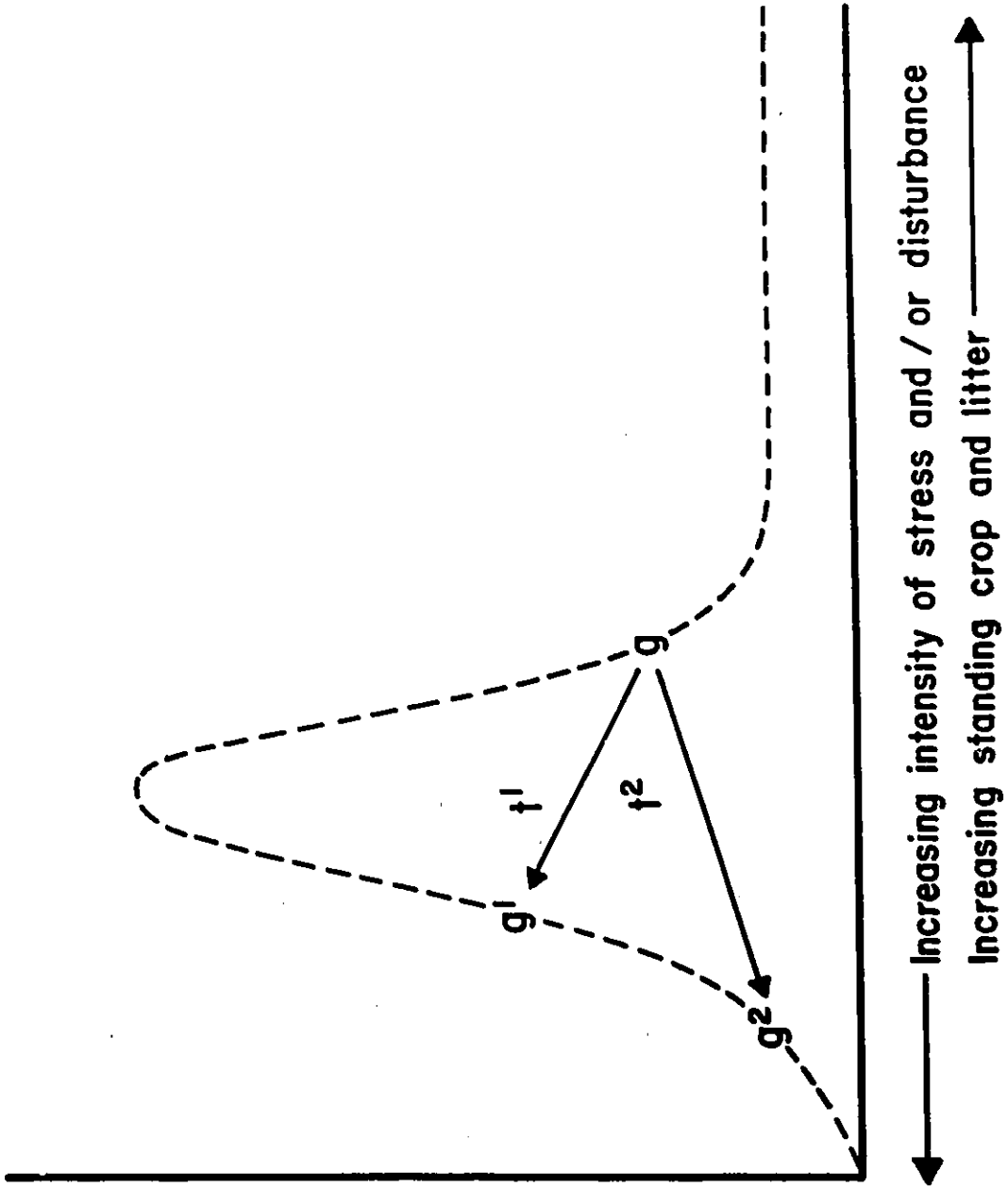
Figure 11. Model summarizing the impact of different processes on species density.



(From Grime 1979)

Figure 12. Diagram representing changes in species density which are associated with the changes in vegetation ($g_1 \rightarrow g_2$). The alteration is brought about when relatively undisturbed grassland is subjected to moderate (t_1) and severe (t_2) intensities of trampling (from Grime 1979).

Potential
species
density

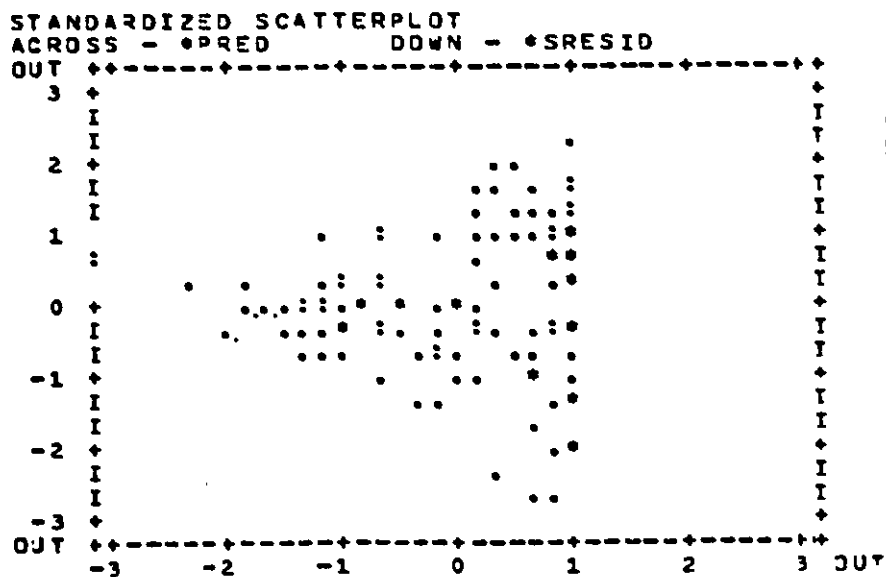


APPENDIX 2

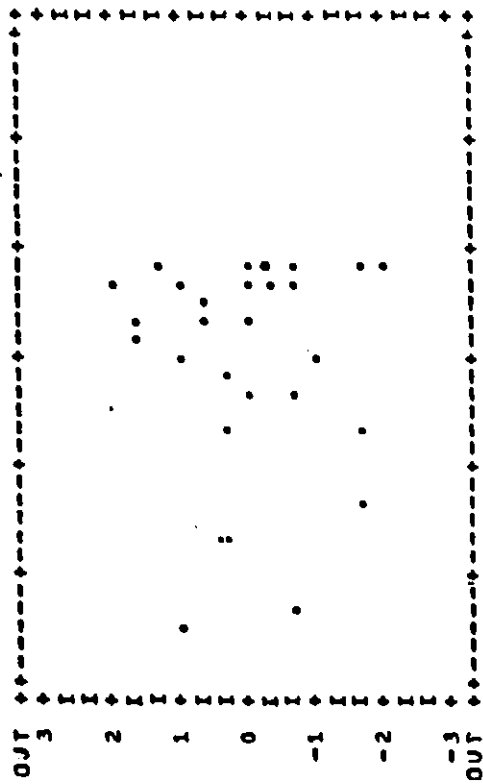
Plotted residuals of the Wilsons Lake habitats. Studentized residuals, along the horizontal axis, are plotted against the standardized predicted values. The symbols are as follows;

. one
: two
* three

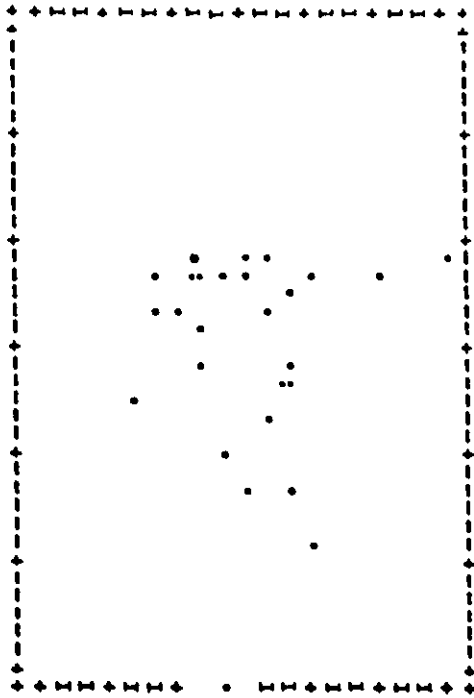
ALL HABITATS



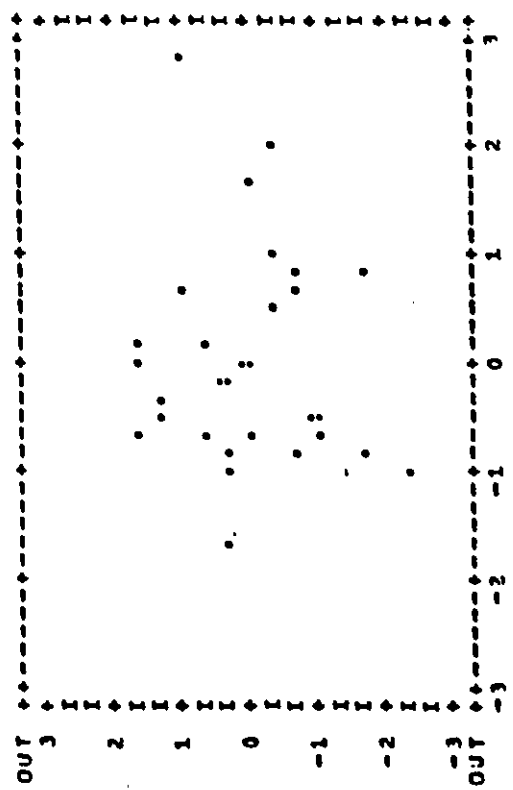
HIGH ON RED TILL



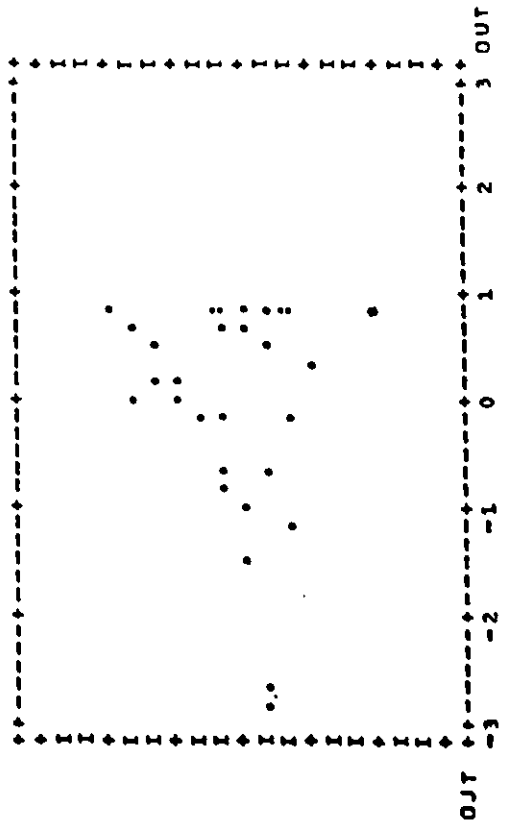
HIGH ON LOCAL TILL



LOW ON RED TILL



LOW ON LOCAL TILL



APPENDIX 3

In this thesis, interest in regression equations centered on the shape of the plotted equations. Does species richness (the dependent variable) increase infinitely, or does it level off or decrease at high values of standing crop and litter? Slight heteroscedasticity within the Wilsons Lake data sets could affect the shape of these plotted equations, especially at high values of the independent variable.

To check whether the shapes of the equations shown in figures 3 and 5 are distorted because of heteroscedasticity, the regression analyses were repeated using GLS (generalized least squares) techniques (Johnston 1984, Kennedy 1979). The technique involves transforming variables so that variances become equal and heteroscedasticity no longer occurs. The classical regression equation

$$y = a + bx + cx^2$$

where y = species richness

and $x = \log(\text{standing crop} + \text{litter} + 1)$

was therefore transformed to become

$$y/x = a/x + b + cx.$$

The equations that result from this new model have homoscedastic disturbances and are plotted in Fig. 13. The equations shown are as follows; from all habitats

$$y = 7.5 - 0.3/\log(x + 1) + 5.7\log(x + 1) - 3.0(\log(x + 1))^2$$

$(r^2 = .18, p < .0001)$, from high on shores of red till

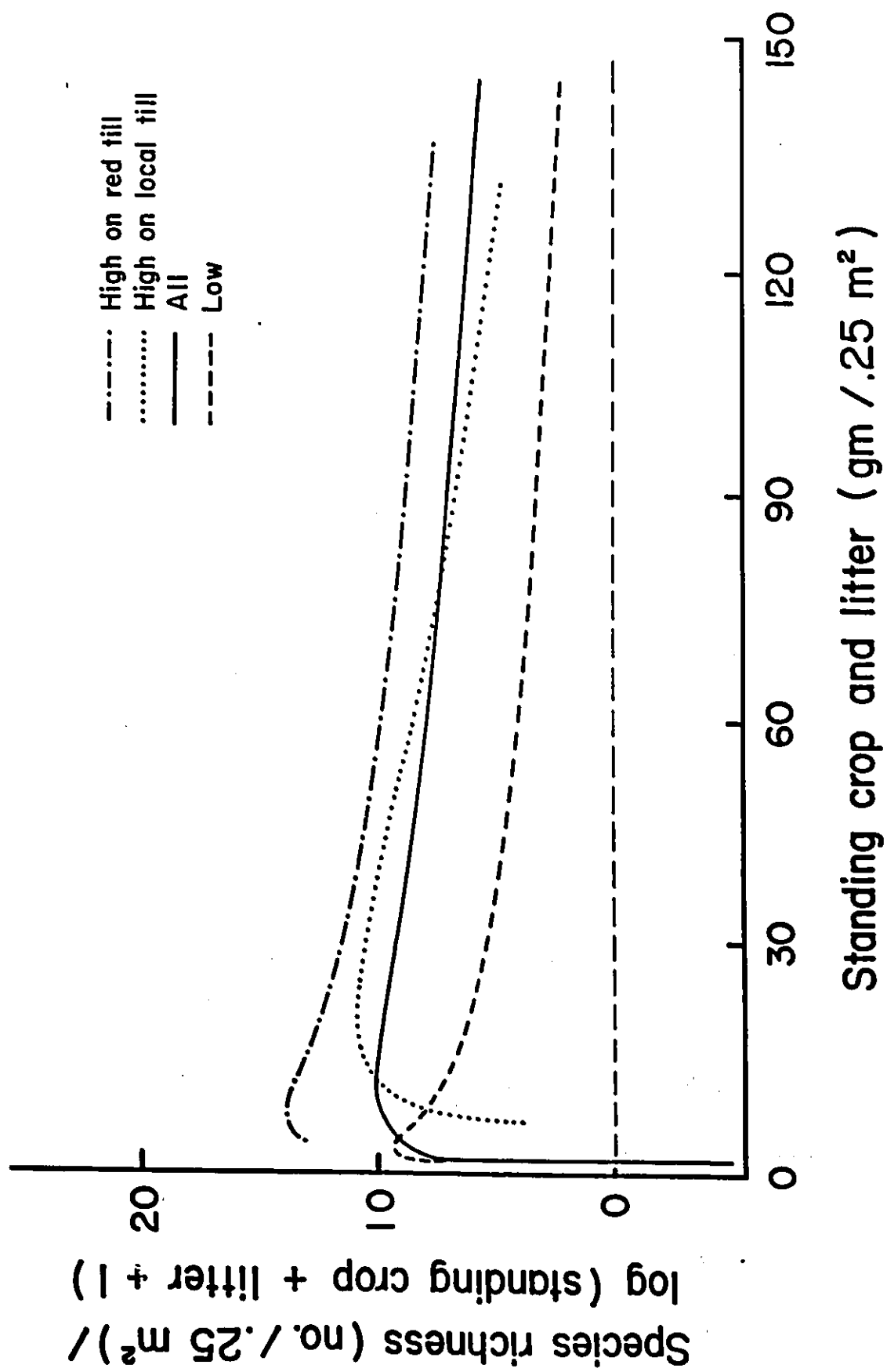
$$y = 26.2 - 5.1/\log(x + 1) - 7.6\log(x + 1)$$

$(r^2 = .41, p = .0006)$, from high on shores of local till

$y = 62.4 - 33.4/\log(x + 1) - 19.8\log(x + 1)$
 $(r^2 = .30, p = .0101)$, and from low on both shore types.

$y = 12.7 - 0.4/\log(x + 1) - 4.7\log(x + 1)$
 $(r^2 = .54, p < .0001)$. Note that the dependent variable of these new curves once again decreases at high values of standing crop and litter. This similarity of pattern suggests that the shape of the species richness/standing crop and litter relationships shown in figures 3 and 5 are not unduly affected by heteroscedasticity.

Figure 13. GLS regression lines for the shoreline habitats from Wilsons Lake. Note that the independent variable that has been plotted is standing crop and litter, not the log of this value + 1. This discrepancy alters the shape of the curve in that the horizontal axis is not compressed at the lower values. The positioning of the dependent variable is not affected but visualizing the graph's meaning is easier. Note also that since division by the log of 1 is impossible, the curves do not extend to the intercept.



APPENDIX 4

To test whether the species richness/standing crop and litter relationships differed among the four habitats from Wilsons Lake, the equations describing these relationships were compared statistically. Similar relationships would be described by identical equations, equations that would produce parallel lines with intercepts that coincide.

Testing for parallelism

To test for parallelism, the following equation from Kleinbaum and Kupper (1978) was used;

$$F(xz,yz/x,y,z) = \frac{SS_{reg}(x,y,z,xz,yz) - SS_{reg}(x,y,z)}{MS_{resid}(x,y,z,xz,yz)} \quad (1)$$

where $x = \log(\text{standing crop} + \text{litter} + 1)$

$$y = (\log(\text{standing crop} + \text{litter} + 1))^2$$

and $z = 0$ or 1 , a dummy variable indicating the habitat types of the two data sets being compared.

Example

To compare the regression equations describing the data set from high on shores of red till to the data set from high on shores of local till, the data sets of the two habitats were recombined and fitted with the following equation;

$$r = a + bx + cy + dz$$

where r = species richness and a , b , c and d are regression parameters. Values from the resulting "analysis of variance"

table are reproduced below.

ANALYSIS OF VARIANCE

	DF	SUM OF SQUARES	MEAN SQUARE
REGRESSION	3	483.00	161.00
RESIDUAL	56	721.19	12.88
F = 12.50 SIGNIF F = 0.0000			

The same data set was also fitted with this second equation.

$$r = a + bx + cy + dxz + cyz + fz \quad (2)$$

yielding the following results;

ANALYSIS OF VARIANCE

	DF	SUM OF SQUARES	MEAN SQUARE
REGRESSION	5	539.59	107.92
RESIDUAL	54	664.60	12.31
F = 8.77 SIGNIF F = 0.0000			

Applying equation 1 to these results yields

$$F_{2,54,.95} = \frac{539.59 - 483.00}{12.31} = 4.60.$$

Since 4.60 is greater than $F_{2,54,.95}^*$ (3.17), the lines describing the species richness/standing crop and litter relationships of the two high habitats are not parallel.

Testing for coincident intercepts - example

When equation 2 was applied to the combined high habitats data set, the significance of the change in F after the addition

of the z variable was .02. Since this value is less than the probability level of .05, the intercepts of the equations describing high shores of red till and high shores of local till are not identical.

This lack of coincidence is supported by the "significance of T" values that were printed with the initial fitting of polynomial equation to each data set. When

$$r = a + bx + cx^2 \quad (3)$$

was first used to describe the data set from high on shores of red till, the significance of T for the constant (a) was .33. Since this value is greater than .05, the intercept (a) is the same as zero.

When equation 3 was used to describe the data set from high on local shores, the significance of T for the same constant was .01. The intercept of this equation is therefore not the same as zero.

Summary

The following tables summarize the results of the tests for parallelism, coincidence, and 0 intercept. The symbol (+) indicates similarity between the two sites being compared.

Comparing for parallelism

	high on red	high on local	low on red	low on local
high on red	+			
high on local	-	+		
low on red	-	-	+	
low on local	-	-	+	+

Note that only the lines from the two low habitats are parallel.

Comparing intercepts

	high on red	high on local	low on red	low on local
high on red	+			
high on local	-	+		
low on red	+	-	+	
low on local	+	-	+	+
intercept = 0	+	-	+	+

Note that only the equation from the high local shoreline data set has an intercept indistinguishable from 0. Also, since the slopes and intercepts of the two low habitat equations are indistinguishable, the species richness/standing crop and litter relationships are taken to be the same. The data sets were therefore recombined and the analyses were repeated.

Since the following two tables show that each of the three habitats are described by uniquely shaped regression line equations, the species richness/standing crop and litter relationships along the three shorelines also differ.

Comparing for parallelism

	high on red	high on local	low
high on red	+		
high on local	-	+	
low	-	-	+

Comparing intercepts

	high on red	high on local	low
high on red	+		
high on local	-	+	
low	-	-	+
Intercept = 0	+	-	+

APPENDIX 5

Physical factor measurements and species' weights for each of the 121 sampled sites at Wilsons Lake. Data is presented as a printout of a mainframe computing system file. An indentation marks the beginning of each new line of data. Each line contains the following information:

Site number (from 1 to 121), till type (red = 0, local = 1), height on shore (low = 1, high = 2), species richness (no./ $.25m^2$), standing crop ($g/.25m^2$), standing crop and litter ($g/.25m^2$), percent silt and clay (missing values = 0), loss on ignition (%), missing values = 0), ice damage (damage sustained by wooden pegs. 20 = no damage, 0 = high damage, scale is reversed in thesis), conductivity ($\mu S/cm$, missing values = 0), soil depth (cm, value is sum of five measurements, maximum possible is 100, thesis used mean value where maximum possible is 25), height to shrub zone (cm).

Till type (repeat entry), height on shore (repeat entry), visual estimate of standing crop and litter (from 1 to 5, used to insure representational sampling of gradient), date of sampling (August, 1984), lake water level at sampling time (zero-water level = 29.5 cm).

Weight (gm) of the following species (a weight of .005 indicates that the sample weighed less than .01 gm): Acer rubrum, Agrostis perennans, Aster tradescanti, unknown Asteraceae, Bartonia paniculata, Calamagrostis canadensis, Carex limosa/paupercula (either of these species; a more accurate identification could

not be made), Carex lenticularis, Carex stricta, Carex bullata,
Carex oligosperma, Cladium mariscoides, Coreopsis rosea, Cyperus
dentatus, Drosera intermedia, Dulichium arundinaceum, Eleocharis
acicularis, Eleocharis smallii, Eleocharis tenuis , Equisetum
fluviatile, Eriocaulon septangulare, Glyceria boreale, Gratiola
aurea, Habenaria flava, Hydrocotyle umbellata, Hypericum boreale,
Hypericum ellipticum, Isoetes tuckermani, Juncus canadensis,
Juncus filiformis, Juncus militaris, Juncus pelocarpus, Leersia
oryzoides, Lobelia dortmanna, Lycopodium inundatum, Lycopus
uniflorus, Lysimachia terrestris, Myriophyllum tenellum, Nuphar
variegatum, Nymphaea odorata, Nymphoides cordata, Thelypteris
palustris, Osmunda regalis, unknown dicot A, Panicum longifolium,
unknown dicot B, Polygonum hydropiperoides, Pontederia cordata,
Ranunculus reptans, Rhexia virginica, Rhynchospora fusca, Sabatia
kennedyana, Sagittaria latifolia, Scirpus cyperinus, Scirpus
subterminalis, Scirpus validus, blank entry (disregard),
Potamogeton oakesianus, Sium suave, Solidago galetorum, Spartina
pectinata, blank entry (disregard), Utricularia cornuta,
Utricularia purpurea (not rooted in plots, disregard),
Utricularia resupinata, Eleocharis robbinsii, Vaccinium
macrocarpon, Viola lanceolata, Xyris difformis, Elatine minima.

1	1.0	1	5	4.75	45.11	5.52	5.75	18.00	22.40	83.00	70.00
1 1 4 1	28.0										
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	3.97	0.00	0.00	0.02	0.00	0.00			
0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.49	0.00	40.36							
2	1.0	2	8	2.54	26.10	6.21	5.54	15.00	29.60	41.00	40.00
1 2 2 1	28.0										
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.02	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.12	0.00	0.00	0.00					
0.00	0.00	0.00	0.09	0.00	0.00	2.18	0.00				
0.00	0.00	0.005	0.00	0.00	0.00	0.00					
0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.10	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.005			
0.00	0.00	6.62	0.00	23.56							
3	1.0	1	2	12.15	15.94	53.16	35.74	20.00	35.10	40.00	53.00
1 1 5 2	26.5										
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
11.89	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	6.63	3.79							
4	1.0	2	8	56.94	129.97	79.82	37.19	18.00	44.80	125.00	20.00
1 2 5 2	26.5										
0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00				
0.00	2.62	0.00	0.00	0.00	0.00	0.00					
0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.03				
0.00	0.00	0.00	0.01	0.00	15.38	0.00					
31.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	2.37					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	1.53	1.20	73.03							
5	1.0	1	7	7.00	7.15	4.77	.81	12.00	41.00	107.00	87.00
0 1 4 3	26.5										
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	1.18	0.00	0.00	0.28	0.72	0.00	0.00				
0.00	3.41	0.00	0.00	1.40	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.005			
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.005	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				

0.07 0.00 0.005 0.00 5.44
 41 1.0 1 8 2.95 50.99 35.82 39.05 20.00 36.40 78.00 94.00
 1 1 4 7 19.0
 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.78 0.00 0.00 0.00 0.92 0.00 0.41
 0.00 0.00 0.00 0.00 0.02 0.00 0.00
 0.00 0.00 0.00 0.27 0.00 0.00 0.00 0.00
 0.00 0.00 0.38 0.00 0.00 0.00 0.00
 0.00 0.00 0.12 0.00 0.00 0.00 0.05 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.09 0.00 0.00 0.00 0.00
 0.00 0.00 0.01 6.64 48.04
 42 1.0 2 10 5.69 13.83 15.24 5.19 10.00 28.00 .00 65.00
 1 2 2 7 19.0
 0.00 0.00 0.00 0.00 0.00 0.00 2.95 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.005 0.00 0.00 0.00 0.02 0.00 0.85
 0.00 0.00 0.00 0.02 0.005 0.00 0.85
 0.00 0.21 0.00 0.00 0.00 0.00 0.47 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 0.00 0.31 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 8.14
 43 .0 2 20 23.69 26.39 5.79 1.80 20.00 29.90 125.00 132.00
 0 2 3 8 19.0
 0.00 0.20 0.00 0.00 0.005 0.00 0.00 0.00
 0.00 0.00 0.00 6.83 0.56 0.00 0.07
 0.00 0.28 0.00 0.00 0.00 0.14 0.00 0.12
 0.18 0.03 0.00 0.03 0.00 0.00 0.81
 0.00 0.37 0.00 0.00 0.43 0.00 0.02 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.15 0.00 0.00 4.48 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 8.43
 0.00 0.00 0.005 0.00 0.00 0.00 0.00 0.00
 0.55 0.00 0.88 0.00 2.70
 44 .0 1 9 10.83 22.24 2.50 .70 4.00 31.60 125.00 98.00
 0 1 3 8 19.0
 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 8.18 0.00 0.00 0.00
 0.00 0.01 0.00 0.00 0.00 2.28 0.00 0.00
 0.00 0.22 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.04 0.00 0.00 0.00 0.08
 0.00 0.00 0.01 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.01 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 0.005 0.00 0.00 0.00
 0.00 0.00 0.02 0.00 11.41
 45 1.0 1 9 3.30 5.68 43.26 20.69 15.00 62.90 113.00 87.00
 1 1 3 9 18.5
 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 1.63 0.00 0.00 0.00
 0.00 0.75 0.00 0.00 0.00 0.30 0.00 0.32
 0.00 0.00 0.00 0.00 0.01 0.00 0.00
 0.00 0.005 0.00 0.11 0.00 0.00 0.00 0.00
 0.00 0.00 0.17 0.00 0.00 0.00 0.00
 0.00 0.00 0.01 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00
 0.00 0.00 0.00 0.00 0.00 0.00 0.00

0.00	0.00	0.22	0.005	2.38															
46	1.0	2	18	48.76	53.91	44.80	20.84	12.00	60.00	53.00	119.00								
1	2	5	9	18.5															
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.04											
0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.00												
2.39	0.005	0.00	1.09	4.17	0.06	0.00	0.30												
0.41	0.00	0.00	0.02	0.00	0.00	0.00	1.97												
0.00	10.13	0.00	0.005	0.15	0.00	4.21	0.00												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.38	0.00											
0.00	0.00	0.00	0.00	0.00	0.00	0.005	17.90												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00											
0.00	0.00	16.94	0.005	5.15															
47	1.0	1	11	7.23	12.99	53.16	13.04	19.00	22.20	125.00	93.00								
1	1	5	9	18.5															
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00											
0.00	0.00	0.00	1.15	0.00	0.00	0.00	0.00												
0.00	3.42	0.00	0.00	0.76	1.06	0.10	0.07												
0.00	0.00	0.00	0.00	0.21	0.00	0.02													
0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00												
0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00												
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.00											
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00											
0.00	0.00	0.005	4.10	5.76															
48	1.0	2	20	62.05	65.56	43.48	19.32	8.00	21.90	54.00	61.00								
1	2	5	9	18.5															
0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00											
0.00	0.00	0.00	0.00	1.62	0.00	0.005													
6.72	0.005	0.00	0.98	3.12	0.005	0.00	14.47												
0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.22												
0.00	3.09	0.00	0.04	2.54	0.00	0.43	0.00												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.86												
0.00	0.00	0.00	0.00	0.00	0.00	13.28	7.74	0.00											
0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.51												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00											
0.28	0.00	6.39	0.00	3.51															
49	.0	2	16	52.61	70.27	15.03	5.43	18.00	46.40	118.00	61.00								
0	2	4	10	20.0															
0.00	0.00	0.00	0.00	0.005	0.00	0.00	0.00												
0.00	0.00	0.00	26.40	0.28	0.00	0.005													
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18												
0.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00												
0.00	0.86	0.00	0.00	1.34	0.00	0.02	0.00												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.36												
0.00	0.00	0.005	0.00	0.00	9.36	4.98	0.00												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19												
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.00											
0.10	0.00	0.00	0.00	17.66															
50	.0	1	8	3.79	3.90	5.98	.88	16.00	42.90	125.00	95.00								
0	1	4	10	20.0															
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00												
0.00	0.16	0.00	0.00	0.00	2.47	0.00	0.00												
0.00	1.05	0.00	0.00	0.02	0.00	0.00													
0.00	0.00	0.00	0.005	0.00	0.00	0.00	0.02												
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00												
0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00											
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00												
0.00	0.00	0.00	0.005	0.00	0.00	0.00	0.00												

0.12	0.00	0.00	0.00	7.83							
56	.0	1	7	4.38	4.51	9.31	1.06	12.00	35.20	125.00	105.00
0	1	4	11	22.0							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.28	0.00	0.00	0.00	2.56	0.00	0.00				
0.00	1.44	0.00	0.00	0.005	0.00	0.00					
0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.08				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.005	0.09	0.005	0.13							
57	.0	1	8	3.81	4.02	17.14	.85	14.00	41.00	125.00	102.00
0	1	4	12	25.0							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.57	0.00	0.00	0.00	1.52	0.00	0.00				
0.00	0.83	0.00	0.00	0.67	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.005	0.005	0.01	2.40	0.21							
58	.0	2	7	5.98	5.98	13.95	2.75	19.00	26.80	95.00	73.00
0	2	1	12	25.0							
0.00	0.00	0.00	0.00	0.005	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.08	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.005	0.00	1.75				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.73	0.00	0.00	0.00	0.00	0.005	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	3.41	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00							
59	.0	2	18	97.47	133.96	24.33	8.93	17.00	46.00	125.00	67.00
0	2	5	12	25.0							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	61.67	0.01	0.00	0.03					
1.83	0.005	3.87	0.04	16.15	0.005	0.00	0.00				
0.47	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	1.43	0.00	0.00	0.00	0.00	0.09	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.005	0.00	2.87	4.87	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	4.11					
0.00	0.00										

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0.00	0.00	0.11	0.33	2.68								
81	1.0	1	5	4.34	46.04	26.51	7.15	20.00	31.40	65.00	85.00	
1	1	3	14	36.0								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.38	0.00	0.00	0.00	3.16	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.005	0.00	0.00					
0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00					
0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.08	0.64	41.70								
82	1.0	1	2	14.89	26.12	74.47	32.88	20.00	37.80	125.00	64.00	
1	1	5	14	37.0								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	14.67	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.21	11.23								
83	1.0	1	7	6.00	11.28	49.59	15.38	16.00	37.70	95.00	52.00	
1	1	4	14	37.0								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
1.98	0.02	0.08	0.00	1.87	2.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.005	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.005	0.00	5.28								
84	1.0	1	6	2.12	3.92	10.84	2.80	20.00	32.70	.00	131.00	
1	1	1	15	42.0								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.23	0.00	0.00	0.00	0.26	0.09	0.00					
0.00	0.00	0.00	0.00	0.01	0.00	0.00						
0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00					
0.00	0.00	1.50	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	66.12	1.80								
85	1.0	1	6	20.93	21.72	50.20	3.77	18.00	29.30	125.00	85.00	
1	1	5	15	42.0								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	8.55	0.00	0.00	0.00	1.52	1.13	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.005	0.00	0.00	0.00	0.00						
0.00	0.00	9.72	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					

0.00	0.00	0.09	0.005	0.79							
86	1.0	1	4	2.75	7.35	14.33	2.52	19.00	17.70	.00	61.00
1	1	2	15	42.5							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	1.60	0.00	0.00	0.00	0.59	0.00	0.00				
0.00	0.00	0.00	0.00	0.53	0.00	0.00					
0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.005	1.30	4.60							
87	1.0	1	8	5.92	145.17	72.26	10.08	16.00	29.00	125.00	63.00
1	1	2	15	43.0							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.03	0.17	0.00	0.00	0.00	1.05	0.00	1.40				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	2.73	0.00	0.00	0.00	0.00				
0.00	0.00	0.49	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00			
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.00			
0.00	0.00	0.005	0.005	139.25							
88	1.0	1	12	27.24	30.12	73.58	23.51	20.00	45.20	125.00	52.00
1	1	5	15	44.5							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	2.10	0.00	0.00	0.11	6.07	0.00	1.86				
0.00	0.00	0.005	0.00	0.02	0.00	0.00					
0.00	0.005	0.00	0.09	0.00	0.00	0.00	0.00				
0.00	0.00	0.005	0.00	0.00	0.00	0.00					
0.00	0.00	16.55	0.00	0.00	0.00	0.42	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.005	0.05	0.005	2.88							
89	1.0	1	10	8.65	9.07	72.32	15.03	18.00	42.70	115.00	54.00
1	1	4	15	44.5							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.13	0.00	0.00					
0.00	4.20	0.00	0.00	0.31	3.53	0.00	0.10				
0.00	0.00	0.00	0.00	0.05	0.00	0.00					
0.00	0.005	0.00	0.005	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.32	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00											

0.00	0.005	0.005	0.27	1.22								
91	1.0	1	5	1.10	2.01	11.92	.96	5.00	37.60	70.00	45.00	
1	1	1	16	48.5								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.15	0.00	0.00	0.00	0.83	0.00	0.005					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.005	0.005	0.91								
92	.0	2	17	17.99	32.90	7.16	1.61	6.00	31.90	125.00	123.00	
0	2	2	16	67.5								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	9.37	0.99	0.00	0.39						
0.00	0.005	0.00	0.00	0.02	0.09	0.00	0.26					
0.00	0.03	0.00	0.00	0.00	0.00	0.00	4.17					
0.00	0.05	0.00	0.03	0.00	0.00	0.00	0.01	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.03	0.00	0.00	0.00	2.19	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25					
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.00				
0.10	0.00	0.00	0.00	14.91								
93	.0	2	13	10.61	11.60	3.36	2.35	4.00	40.20	125.00	58.00	
0	2	2	16	70.5								
0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.86					
0.00	0.00	0.00	0.00	0.15	0.20	0.00						
0.00	0.13	0.00	0.00	0.00	0.005	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.12					
0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.08	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	2.16	0.00	0.00	0.00	0.07	0.00				
0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
0.21	0.00	0.31	0.00	0.99								
94	.0	2	16	49.17	62.24	.00	.00	20.00	55.60	125.00	42.00	
0	2	5	17	90.0								
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	16.92	0.04	0.00	0.10						
0.97	0.00	1.13	0.28	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.14	0.00	0.00	0.00						
0.00	3.34	0.00	0.00	3								

0.00	0.00	0.01	0.00	4.39									
96	.0	2	20	13.24	15.41	3.41	1.10	2.00	53.90	120.00	60.00		
0	2	2	18	88.5									
0.00	0.24	0.00	0.00	0.01	0.00	0.00	2.21						
0.00	0.00	0.00	0.00	1.17	0.00	0.26							
0.00	0.005	0.00	0.00	0.05	0.03	0.00	0.47						
0.00	0.03	0.00	0.08	0.00	0.00	2.53							
0.00	0.23	0.00	0.00	0.00	0.00	0.42	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.06							
0.00	0.00	0.00	0.14	0.00	0.00	2.95	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	2.10							
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00						
0.25	0.00	0.83	0.00	2.17									
97	.0	2	12	5.07	5.07	2.18	.67	5.00	35.10	111.00	50.00		
0	2	1	18	87.0									
0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.91	0.04	0.005							
0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.33						
0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.01	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	3.64	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00						
0.00	0.00	0.00	0.005	0.00	0.00	0.00	0.00						
0.04	0.00	0.00	0.00	0.00									
98	.0	2	11	3.37	3.38	5.79	.52	.00	40.10	44.00	52.00		
0	2	1	18	86.0									
0.00	0.005	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.63	0.00	0.01							
0.00	0.005	0.00	0.00	0.00	0.005	0.00	0.005						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	2.35	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.005						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01						
0.00	0.00	0.00	0.00	0.005									
99	1.0	2	16	16.35	17.26	36.56	9.63	20.00	43.50	37.00	82.00		
1	2	3	19	81.0									
0.00	0.03	0.00	0.00	0.005	0.04	0.00	0.00						
2.66	0.00	0.00	0.00	0.00	0.00	0.00	0.005						
0.00	0.00	0.00	0.55	0.00	0.00	0.00	10.16						
0.25	0.00	0.00	0.09	0.00	0.00	0.67							
0.00	0.00	0.00	0.15	1.61	0.00	0.01	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00						
0.03	0.00	1.64	0.74	0.91									
100	1.0	2	10	2.15	11.29	2.53	.65	19.00	33.80	75.00	102.00		
1	2	1	19	80.0									
0.00	0.04	0.00	0.23	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.005						
0.39	0.00	0.00	0.01	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.005	0.00	0.005	0.03	0.00	1.43	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.005						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						

76

0.17	0.00	0.70	0.00	2.55									
106	1.0	2	19	28.47	42.47	47.89	21.04	20.00	44.20	38.00	11.00		
1	2	2	20	73.0									
0.00	0.00	0.00	0.00	0.00	0.005	0.005	0.00	12.94					
0.00	0.00	0.00	0.00	1.16	0.00	0.10							
0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.92						
0.15	0.00	0.00	0.04	0.00	0.00	0.00							
0.00	0.00	0.00	0.08	3.15	0.00	0.16	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00							
0.00	0.00	0.00	0.00	0.00	4.96	0.33	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	4.02							
0.00	0.00	0.005	0.00	0.00	0.00	0.34	0.02						
0.03	0.00	10.43	0.00	14.00									
107	1.0	2	11	8.89	10.01	24.82	6.32	9.00	31.20	5.00	55.00		
1	2	2	21	69.5									
0.00	0.00	0.00	0.00	0.00	0.00	0.005	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.005						
0.00	0.00	0.00	0.50	0.00	0.005	0.00	5.27						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.36						
0.00	0.00	0.00	0.005	1.30	0.00	0.19	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.005	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.17	0.16	1.12									
108	1.0	2	12	30.63	61.77	72.19	10.91	8.00	41.00	125.00	26.00		
1	2	5	21	69.0									
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04						
5.70	0.00	0.00	1.62	0.00	0.00	0.00	0.005						
0.03	0.00	0.00	0.00	0.00	0.00	0.00	1.63						
0.00	0.00	0.00	0.00	4.30	0.00	0.01	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.13	0.00					
1.85	0.00	0.00	0.00	0.00	0.00	0.00	12.86						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
0.46	0.00	25.58	0.00	31.14									
109	1.0	2	18	31.25	35.13	73.42	14.60	4.00	39.40	125.00	49.00		
1	2	4	21	69.5									
0.00	0.005	0.00	0.00	0.00	0.005	0.00	0.00	0.00					
0.00	0.00	0.00	0.00	0.05	0.00	0.08							

0.00	0.00	0.00	0.005	1.42									
111	1.0	2	16	33.06	38.71	72.66	18.58	20.00	33.90	125.00	21.00		
1	2	4	22	69.0									
0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08						
4.73	0.00	0.00	3.85	1.33	0.00	0.00	1.65						
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.13	0.00	0.005	2.57	0.00	0.11	0.00						
0.00	0.00	0.00	0.00	0.005	0.00	0.00							
0.00	0.00	0.00	0.00	0.00	0.00	14.98	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	2.34							
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.02						
1.09	0.00	1.72	5.90	5.65									
112	.0	2	21	16.99	19.12	5.11	1.69	1.00	36.70	125.00	77.00		
0	2	4	23	60.5									
0.00	0.00	0.00	0.00	0.005	0.05	0.00	1.91						
0.00	0.00	0.00	0.00	0.99	0.01	0.40							
0.00	0.005	0.00	0.00	0.00	0.005	0.00	0.57						
0.00	0.15	0.00	0.03	0.00	0.00	4.23							
0.00	0.005	0.00	0.005	0.75	0.00	0.00	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00							
0.00	0.00	0.00	0.95	0.00	0.00	1.83	0.00						
0.00	0.00	0.00	0.00	0.00	0.005	4.99							
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00						
0.10	0.00	0.005	0.00	2.13									
113	.0	2	15	47.77	67.67	25.04	10.35	13.00	41.90	125.00	17.00		
0	2	5	23	60.5									
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.00	0.00	0.00	29.98	0.02	0.00	0.57							
0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00						
0.11	0.00	0.00	0.00	0.00	0.00	5.57							
0.00	0.005	0.00	0.00	2.41	0.00	0.005	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00							
0.00	0.00	0.00	0.00	0.00	0.005	1.27	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	7.37							
0.005	0.00	0.005	0.00	0.00	0.00	0.00	0.00						
0.06	0.00	0.005	24.96	19.90									
114	.0	2	13	47.16	71.34	24.00	7.33	17.00	43.60	125.00	44.00		
0	2	5	23	59.5									
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.49						
0.00	0.00	0.00	26.87	0.00	0.00	0.13							
0.00	0.00	0.00	0.73	2.53	0.00	0.00	0.00						
1.64	0.00	0.00	0.00	0.00	0.00	2.44							
0.00	0.08	0.00	0.00	0.18	0.00	0.03	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00							
0.00	0.00	0.00	0.00	0.00	0.00	3.56	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	7.34							
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00						
0.14	0.00	0.00	41.05	24.18									
115	.0	2	17	35.28	42.04	14.75	5.77	12.00	45.40	125.00	32.00		
0	2	4	24	56.5									
0.00	0.00	0.00	0.00	0.005	0.02	0.00	0.00						
0.00	0.00	0.00	11.22	0.07	0.00	1.34							
0.00	0.005	0.00	1.35	0.00	0.00	0.00	0.005						
0.00	0.005	0.00	0.00	0.00	0.00	0.00							
0.00	0.21	0.00	0.00	3.73	0.00	0.42	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	0.00							
0.005	0.00	0.00	0.00	0.00	0.00	2.17	0.00						
0.00	0.00	0.00	0.00	0.00	0.00	14.56							
0.00	0.00	0.005	0.00	0.00	0.00	0.00	0.00						

80

APPENDIX 6

The interrelationships of the environmental measurements from four different habitats from Wilsons Lake. The values shown are r^2 (Pearson correlation coefficients - presented first) and r (Spearman correlation coefficients). Since the risk of accepting a false correlation increases with the number of correlations performed, only coefficients of $p \leq 0.001$ should be accepted. Measurement abbreviations are as follows; Loss on I - loss on ignition (%), Silt/clay - percent silt and clay, Conduct - conductivity ($\mu\text{S}/\text{cm}$), Ice dam - ice damage (damage sustained by wooden pegs), Soil - soil depth (cm), Shrub - height to shrub zone (cm). Asterisks have the following meanings; * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Pearson correlations

All habitats r^2	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.44***				
Conduct	.13***	.04*			
Ice dam	.09***	.12***	ns		
Soil	ns	ns	.08***	ns	
Shrub	.05**	.18***	ns	.08***	ns

2
High on red till (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.82**				
Conduct	.11*	ns			
Ice dam	.27**	.30***	ns		
Soil	ns	ns	ns	.21**	
Shrub	.28***	.24**	.12*	ns	ns

2
High on local till (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.19**				
Conduct	.40***	ns			
Ice dam	ns	ns	.12*		
Soil	ns	.47***	.19*	ns	
Shrub	ns	.18**	ns	.15*	.26**

2
Low on red till (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	ns				
Conduct	ns	.13*			
Ice dam	.13*	ns	ns		
Soil	ns	ns	ns	.24**	
Shrub	ns	ns	ns	ns	ns

Low on local till ² (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.30***				
Conduct	.26**	.18**			
Ice dam	ns	ns	ns		
Soil	.15*	.39***	.11*	ns	
Shrub	ns	ns	ns	ns	ns

Spearman correlations

All habitats (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.78***				
Conduct	.17*	ns			
Ice dam	-.47***	-.37***	ns		
Soil	ns	ns	.24**	ns	
Shrub	-.37***	-.43***	-.21*	.31***	ns

High on red till (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.86***				
Conduct	ns	ns			
Ice dam	-.57***	-.55***	ns		
Soil	.47**	ns	ns	-.46**	
Shrub	-.54***	-.49**	-.33*	ns	ns

High on local till (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.64***				
Conduct	.51**	.37*			
Ice dam	ns	ns	-.39*		
Soil	ns	.67***	.44*	ns	
Shrub	ns	-.42*	-.40*	.42*	-.50**

Low on red till (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	ns				
Conduct	ns	ns			
Ice dam	-.70***	ns	ns		
Soil	.49**	ns	ns	-.53***	
Shrub	ns	ns	ns	ns	ns

Low on local till (r)

	loss on I	Silt/clay	Conduct	Ice dam	Soil
Silt/clay	.72***				
Conduct	.55***	.47**			
Ice dam	ns	ns	ns		
Soil	.52***	.61***	ns	ns	
Shrub	ns	ns	-.31*	ns	ns

1

Correlations were performed with shrub zone measurements from a common shore height.

APPENDIX 7

The relationship of standing crop (SC) or standing crop and litter (SC+L) with environmental measurements for the Wilsons Lake habitats ($n \approx 30$). The values shown are r^2 (Pearson correlation coefficients), which represent the proportion of variance in standing crop accounted for by the environmental measure. The measurements of height to shrub zone were not significant in any of the cases ($p \geq .05$, indicated by ns) and are therefore not shown. Since the risk of accepting a false correlation increases with the number of correlations performed, only correlations of $p \leq 0.001$ should be accepted.

		high		low		all
		red	local	red	local	
loss on ignition	SC+L	.45***	.30***	.81***	ns	.14***
(%)	SC	.50***	.10*	.90***	.11*	.02*
Percent silt and	SC+L	.32***	.26**	ns	.09*	.11***
clay	SC	.35***	.28**	ns	.38***	.03*
Conductivity	SC+L	ns	ns	ns	ns	.03*
($\mu\text{S}/\text{cm}$)	SC	ns	ns	ns	.10*	.05**
Ice damage	SC+L	.27***	ns	ns	ns	.05**
	SC	.33***	ns	ns	ns	.03*
Soil depth (cm)	SC+L	.14*	.12*	ns	ns	.03*
	SC	.16*	.16*	ns	.36***	.12***

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

APPENDIX 8

A list of all plant species encountered during sampling at Wilsons Lake, Nova Scotia. The presence or absence of each species within each of the four habitats is indicated. The symbol "*" indicates that the species is evergreen, while "#" indicates that the species is considered part of the Atlantic coastal plain flora.

	high		low	
	red	local	red	local
<u>Acer rubrum</u>	+	-	-	-
<u>Agrostis perennans</u>	+	+	-	-
<u>Aster tradescanti</u>	+	+	-	-
<u>Bartonia paniculata</u>	+	+	-	-
<u>Calamagrostis canadensis</u>	+	+	-	+
<u>Carex limosa/paupercula</u>	+	+	-	-
<u>Carex lenticularis</u>	+	+	-	-
<u>Carex stricta</u>	-	+	-	-
<u>Carex bullata</u>	-	+	-	-
<u>Carex oligosperma</u>	-	+	-	-
<u>Cladium mariscoides</u>	+	-	+	+
# <u>Coreopsis rosea</u>	+	+	+	+
<u>Cyperus dentatus</u>	+	-	-	-
<u>Drosera intermedia</u>	+	+	-	-
<u>Dulichium arundinaceum</u>	+	+	-	+

	<u>Elatine minima</u>	-	-	+	+
*	<u>Eleocharis acicularis</u>	+	+	+	+
	<u>Eleocharis robbinsii</u>	-	-	+	-
	<u>Eleocharis smallii</u>	+	-	-	+
	<u>Eleocharis tenuis</u>	+	+	-	-
	<u>Equisetum fluviatile</u>	+	+	+	+
*	<u>Eriocaulon septangulare</u>	+	+	+	+
	<u>Glyceria boreale</u>	-	-	+	+
	<u>Gratiola aurea</u>	+	+	+	+
#	<u>Habenaria flava</u>	+	+	-	-
#	<u>Hydrocotyle umbellata</u>	+	-	+	+
	<u>Hypericum boreale</u>	+	+	-	+
	<u>Hypericum ellipticum</u>	+	+	-	-
*	<u>Isoetes tuckermani</u>	+	+	+	+
	<u>Juncus canadensis</u>	+	+	-	-
	<u>Juncus filiformis</u>	+	+	-	+
	<u>Juncus militaris</u>	-	+	-	+
	<u>Juncus pelocarpus</u>	+	+	+	+
	<u>Leersia oryzoides</u>	+	+	-	-
*	<u>Lobelia dortmanna</u>	+	+	+	+
**	<u>Lycopodium inundatum</u>	+	+	-	-
	<u>Lycopus uniflorus</u>	-	+	-	-
	<u>Lysimachia terrestris</u>	+	+	-	+
*	<u>Myriophyllum tenellum</u>	-	-	+	-
	<u>Nuphar variegatum</u>	-	-	-	+
	<u>Nymphaea odorata</u>	-	-	-	+
	<u>Nymphoides cordata</u>	+	+	+	+

<u>Osmunda regalis</u>	+	+	-	-
# <u>Panicum longifolium</u>	+	+	-	-
# <u>Polygonum hydropiperoides</u>	-	+	-	-
<u>Pontederia cordata</u>	+	+	+	+
<u>Potamogeton oakesianus</u>	-	-	-	+
* <u>Ranunculus reptans</u>	+	-	+	+
<u>Rhexia virginica</u>	+	-	-	-
<u>Rhynchospora fusca</u>	+	+	-	-
*# <u>Sabatia kennedyana</u>	+	+	-	+
<u>Sagittaria latifolia</u>	-	+	-	-
<u>Scirpus cyperinus</u>	-	+	-	-
<u>Scirpus subterminalis</u>	-	-	+	-
<u>Scirpus validus</u>	+	-	+	-
<u>Sium suave</u>	+	+	+	-
# <u>Solid. zo. galetorum</u>	+	+	-	-
<u>Spartina pectinata</u>	+	-	-	-
<u>Thelypteris palustris</u>	-	+	-	-
<u>Utricularia cornuta</u>	+	+	+	+
<u>Utricularia resupinata</u>	-	-	+	-
<u>Vaccinium macrocarpon</u>	+	+	-	-
<u>Viola lanceolata</u>	+	+	-	-
# <u>Xyris difformis</u>	+	+	+	+
Unknown Asteraceae	-	+	-	-
Unknown dicot A	-	+	-	-
Unknown dicot B	+	-	-	-

APPENDIX 9

Standing crop and litter values that correspond with maximum species richness in an assemblage of habitat types. Notice that standing crop and litter is expressed as $\frac{g}{m^2}$ and not $\frac{g}{.25m^2}$.

site	habitat type	Standing crop and litter ($\frac{g}{m^2}$) at maximum species richness	Reference
Wilsons Lake N.S., Canada	Occasionally flooded gravel lakeshore	200	Wisheu and Keddy
	Occasionally flooded boulder lakeshore	140	
	Frequently flooded lakeshore	100	
Ottawa River Ont. Canada	Riverine wetland	312	Day et al. im press
Green Swamp N.C., USA	Pine-wiregrass savannas	280	Walker and Peet 1983
Gelderse Vallei Netherlands	Reed swamp, grass- land, road verges	400-500	Vermeer and Berendse 1983
Westbroekse Zodden Netherlands	Grassland Fens	400-500 400-500	
	Wet grassland	425	
Norfolk Broadland Britain	Herbaceous fen	1500	Wheeler and Giller 1983
N.E. Europe	Chalk grasslands	150-350	Willems 1980
Sheffield Britain	Grassland, woodland tall herb community	510	Al-Mufti et al. 1977, Grime 1979