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THE INFLUENCE OF FOREST VEGETATION VARIABLES ON THE DISTRIBUTION AND DIVERSITY OF DRAGONFLIES IN A NORTHERN MINNESOTA FOREST LANDSCAPE: A PRELIMINARY STUDY (ANISOPTERA)

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Dragonfly communities were surveyed at 24 sites in 2 adjacent study regions, during the summer of 1994. In each of the 2 regions, 12 sites were grouped into 3 different study areas based on forest status. Forest status was determined by stand age and time since last logging disturbance, resulting in study areas defined as old-growth forest, mature second-growth forest, or recently clear-cut areas. Study sites within each forest-status study area included stream, pond, lake, and bog/swamp habitats. Recently-cleared forest areas exhibited the lowest species number and species diversity, while the greatest species number and diversity were found in the old-growth study areas. These differences were correlated with different vegetation structure variables characteristic of each forest-status study area. Furthermore, Beta-diversity, indicating changes in species composition across the forest-status gradient in each study area, was greater between the sites adjacent to the smallest old-growth forest "habitat island". These findings may be of importance in understanding dragonfly response to forest disturbance in the northern Minnesota landscape mosaic.

INTRODUCTION

The state of Minnesota is located along the upper shores of Lake Superior at the western periphery of North America's Great Lakes. This temperate, midcontinental region is dominated by a mixed hardwood-coniferous biome known as the Laurentian or Great Lakes Forest. Characterized by stands of red and white pines, the Great Lakes Forest also contains significant deciduous and coniferous elements of the adjacent eastern maple-basswood and boreal spruce-fir forests.

In pre-pioneering times, the forest landscape mosaic of northern Minnesota was primarily influenced by fire, wind disturbance and beaver activity. In the past cen-

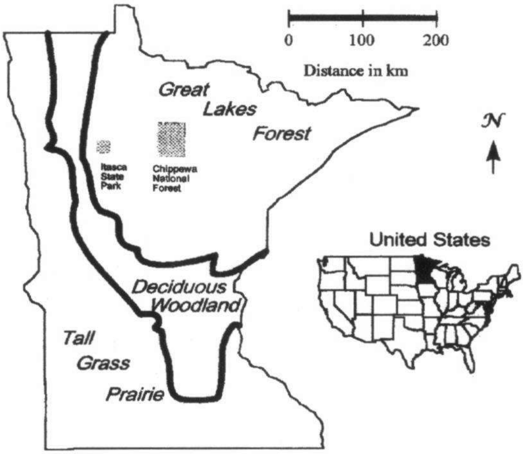

Fig. 1. Minnesota biomes.

tury, however, timber management has become the primary disturbance factor and has increased the patchiness of the forest landscape mosaic. As a result, the mixed-forest matrix is now part of a complex mosaic landscape that includes recent clear-cuts and young timber-managed forest stands, older second-growth forest dating from the turn-of-the-century logging era, and relict fragments of undisturbed old-growth pine-hardwood forest.

Further to the South and West of the Great Lakes forest, a narrow transition zone of aspen/oak woodland grades sharply into the tall-grass prairie biome of the Great Plains (Fig. 1). Although the Minnesota landscape is relatively flat, the remarkable conjunction of several major biomes (Great Lakes Forest, deciduous woodland, and tall-grass prairie) has resulted in levels of biodiversity that are ordinarily found only in mountainous regions where rapid biome shifts occur along a pronounced altitudinal gradient (TESTER, 1995).

Adding to the complexity of the landscape mosaic is the fact that the watersheds of three major North American rivers also meet in northern Minnesota, giving rise to the mighty Mississippi River as it flows South to the Gulf of Mexico; the Rainy River, which flows East to the Great Lakes and St Lawrence seaway; and the Red River of the North, which flows into the Hudson Bay of Canada (Fig. 2). Within these watersheds, aquatic and wetland habitats in the form of ponds and lakes, streams and rivers, and bogs, swamps, and marshes, cover extensive portions of the region. In some places, in fact, nearly 50% of the landscape is actually un-

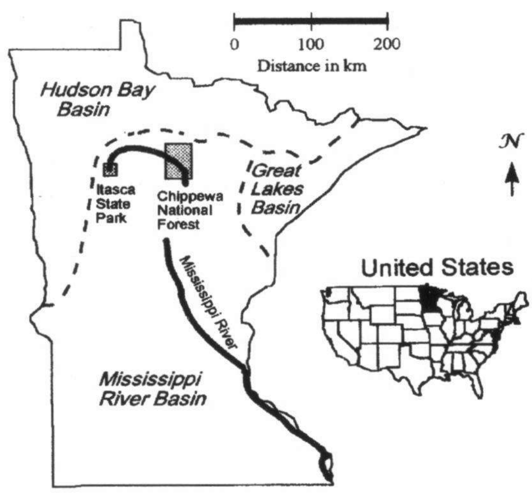

Fig. 2. Minnesota watersheds.

der water.

As a result of these landscape factors, northern Minnesota may be one of the most biologically diverse regions in the United States. Because its location is relatively remote and unsettled, however, much remains to be learned about the ecology and biogeography of northern Minnesota ecosystems. In particular, little is known about the dragonflies of the region, though it might be expected that their diversity would be great given the diversity of northern Minnesota's aquatic and terrestrial habitats. The likelihood of finding rare and threatened dragonfly species in such an area is high, especially where habitat is relatively undisturbed. In fact, recent research indicates that there are several rare and endangered dragonfly species adapted to similar habitats in the nearby state of Wisconsin and in the St Croix river valley of eastern Minnesota (SMITH et al, 1993; HAARSTAD, 1994).

During the summer of 1994, I conducted surveys of adult dragonflies (Anisoptera) at sites in six different study areas in and adjacent to the Itasca and Chippewa old-growth forests. Selection of study areas in each of these two regions was based on forest-status as determined by forest age and length of time since last major disturbance. This resulted in one old-growth, one mature second-growth, and one recently clear-cut study area for each region. Within each regions' forest-status study areas, dragonflies were surveyed at 4 sites which represented bog, stream, pond, and lake habitats. Vegetation was also surveyed to determine the characteristic tree species and vegetation structure of each forest-study area.

The purpose of this study was to determine the impact of timber-management on the community ecology and biogeography of dragonflies in a northern Minnesota mosaic landscape. The specific objectives of this study were to define a checklist for the dragonflies of northern Minnesota; to determine whether different forest-status areas (old-growth, second growth, and clear-cut) have characteristic dragonfly assemblages or communities; to examine whether differences between those communities may be attributable to differences in forest vegetation variables; and to identify uncommon and stenotypic dragonfly species that may serve as indicators for habitat quality based on their response to forest status and logging-related disturbance. This paper reports preliminary results as gathered in the 1994 field season. During the 1995 and 1996 field seasons, I investigated the possible role of the Mississippi River headwaters as a dragonfly habitat corridor linking undisturbed old-growth forest "islands" within the larger disturbed-forest landscape mosaic of the region (RITH-NAJARIAN, 1996). VAN TOL & VERDONK (1988) have suggested that odonates are integrative species which may serve a valuable function as bioindicators for environmental quality in aquatic/terrestrial ecotones. The role of dragonflies as indicator-species in northern Minnesota may become clearer with further research.

LOCATION OF STUDY SITES

Itasca State Park is located approximately 51.5 km Southwest of Bemidji, Minnesota (Fig. 3). Nearly twenty percent of the state's old-growth red and white pine forests are protected within the boundaries of this 4050-hectares park, although much of it experiences heavy recreational use. A separate 900-hectare wilderness area within the park was set aside in 1982 as an access-restricted state Scientific Natural Area, or SNA, encompassing 200-year old primary forest, several small lakes and shaded marshy ponds, a black spruce bog drained by a swift stream, and swampy areas abutting the western shore of Lake Itasca. The SNA is also a designated National Natural Landmark ecosystem, and is managed by state park officials under the advisement of the National Park Service (Dean Einwalter, National Park Service, pers. comm., 1994). State forest lands surrounding Itasca State Park have been heavily logged throughout this century, so the old-growth forests of the park form a "habitat island" in the larger landscape here. The park itself is surrounded by timber-managed forests of various ages and patch sizes, under the jurisdiction of county, state, and tribal (White Earth Chippewa Indian) management. Dragonfly surveys in the Itasca region were conducted at old-growth sites in the State Park SNA, as well as in second-growth and clear-cut forests in the Anchor Hill region of the adjacent White Earth State Forest.

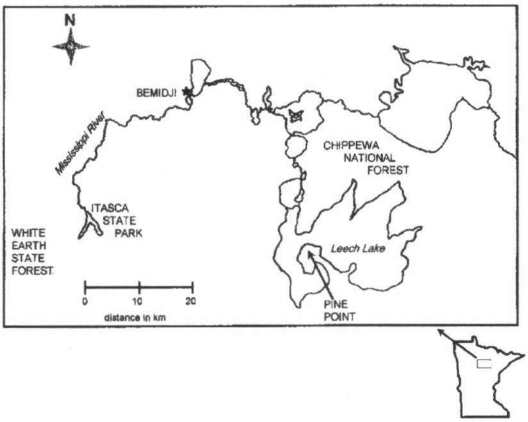

Fig. 3. Map of study regions, northern Minnesota, summer 1994.

Pine Point is a designated National Forest Research Natural Area (RNA) within the Walker Ranger district of the Chippewa National Forest. Located approximately 72 km South and East of Bemidji, Minnesota, its 225 hectares encompass 250-300 year-old white and red pine stands on a peninsula that reaches far out into Leech Lake. It is adjacent to timber-managed forests that are under federal (U.S. Forest Service) and tribal (Leech Lake Chippewa Indian) control. Since its designation as a Research Natural Area in 1932, all activities unrelated to research and education have been restricted, although residents of the neighboring Indian village of Onigum have been granted limited rights to hunt and collect firewood within it.

Although Pine Point is a part of the Chippewa National Forest, it is also a designated National Natural Landmark ecosystem and is managed in cooperation with the National Park Service. While it is a relatively small old-growth forest, it is nonetheless the largest example within the Chippewa National Forest and it has been spared the recreational impacts visited upon the similar old-growth forests at Itasca State Park. Within the Pine Point RNA are several unique bogs, a large swamp, several shaded marshy ponds, and extensive alder thicket with slow streams; additionally, the forest is surrounded on three sides by the large Leech Lake itself. The Forest Service lands South of Pine Point have been extensively logged, resulting in cleared and managed forests in various stages of succession. Thus, the Pine Point RNA is clearly an "island" in the larger forest landscape. Dragonfly surveys in the Chippewa National Forest region were conducted at old-growth sites at Pine Point, at sites in the adjacent second-growth forests of Onigum, and at clear-cut sites further South on Breezy Point.

MATERIAL AND METHODS

Prior to the beginning of the 1994 field season, a potential checklist was devised for the dragonflies and damselflies of northern Minnesota. This checklist was based on examination of specimens in the museum collections of the University of Minnesota and Cornell University; personal communication with odonatologists who have collected in the region (S. Dunkle, W. Smith, 1994); and literature review of Odonata surveys that had been conducted in other parts of Minnesota and in Wisconsin, North Dakota, and Manitoba (ALBY, 1968; BISCHOF, 1979; CARLSON et al., 1964; HAARSTAD, 1994; HAMRUM et al., 1965; HARRIS et al., 1991; MILLER, 1964; SMITH et al., 1993; WALKER, 1933). The checklist was revised after the 1994 field season, and later expanded following the 1995 field season.

During the summer of 1994, surveys of adult dragonfly species (Anisoptera) were conducted at 12 different sites in and adjacent to Itasca State Park, and at an additional 12 sites in and adjacent to the Pine Point section of the Chippewa National Forest. The twelve sites in each study region represented pond, lake, stream and bog/swamp sites, grouped into 3 forest-status categories reflecting successional age and time since last major disturbance. This resulted in 6 study areas, 3 in each of the two separate study regions, with 4 undisturbed old-growth forest sites, 4 mature second-growth forest sites, and 4 recently cleared forest sites designated for surveys within each study area. From mid-May to mid-September of 1994, each study area was surveyed for four hours every other week. During surveys, relative abundance was noted for each adult dragonfly (Anisoptera) species present that day, and representative specimens were collected with standard insect nets and frozen for later identification. All identified specimens were preserved with acetone for future deposition in the University of Minnesota's Bell Museum in St Paul. In accordance with the current efforts of the Wisconsin Dragonfly Survey (W. Smith, director, pers. comm., 1994) collections were also made of the large dragonfly--sized damselfly *Calopteryx aequabilis* (Say) (Calopterygidae, Zygoptera), although smaller damselflies were not included in this study. A revised checklist for northern Minnesota dragonflies was determined at the end of the 1994 field season.

Data analysis was based on measures suggested and used by M. Samways and colleagues, whose pioneering insect conservation biology research has focused on dragonflies in both protected and

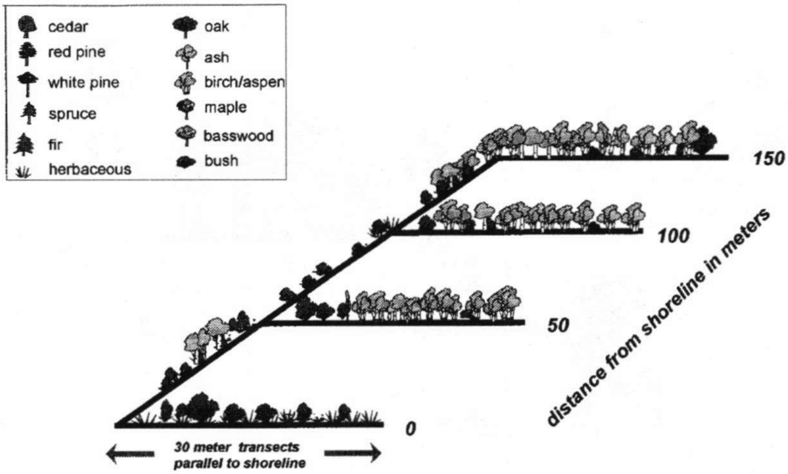

Fig. 4. Vegetation structure of recently logged forest, Anchor Hill, White Earth State Forest, Minnesota.

disturbed landscapes. (M.J. Samways, pers. comm., 1995; STEYTLER & SAMWAYS, 1995; SAMWAYS, 1989, 1993, 1994; SAMWAYS & MOORE, 1991). First, Schmidt's two-way five-level "Representative Spectrum of Odonata" ranking (RSO) was used to rank abundance and prevalence of each collected species, where species with high prevalence were ranked according to high, intermediate, or low abundance, and species with irregular distribution were ranked according to locally high or low abundance (SCHMIDT, 1985). The most common and abundant species at sites therefore received an RSO ranking of 5, and rare species received an RSO ranking of 1. Habitat preferences of an individual species were then determined according to the habitat characteristics of sites where the species exhibited its highest RSO rankings.

Dragonfly assemblages at sites within each of the study areas were treated as communities. Data for the presence, absence, and prevalence of individual species was used in community ecology data analysis to calculate species richness (S) and species diversity (H'). For these measures, S = total number of species per study area, and H' was calculated according to the equation:

$$H' = 1/N\ (N\log N - \Sigma n_i \log n_i)$$

using prevalence values for N and n_i (as per MAGURRAN, 1988). These values were compared to each other and to the maximum possible species diversity as determined by the log of the species richness for the whole study region, or H(max) = log S(max).

Cluster analysis and polar ordination were carried out as per MAGURRAN (1988) and BARBOUR et al. (1980), using Sorenson's Index to determine the similarity coefficients, or

$$C = 2j\ /\ (a+b)$$

where a and b represent the number of species at sites A and B respectively, and j is the number of species common to both sites. These techniques were used to investigate the composition of species in dragonfly communities, and to assess the relative similarity between study areas. Whittaker's Beta diversity [($\beta = S/(\alpha - 1)$), where S equals total number of species recorded in the whole system, and α equals average species richness of the samples in that system, as per MAGURRAN, 1988] was used to measure the differences in species diversity among the study areas at and adjacent to Itasca, compared to similar differences in the species diversity among Pine Point and adjacent National Forest study areas.

BUCHWALD (1992) has indicated that dragonfly distribution may be influenced by shoreline veg-

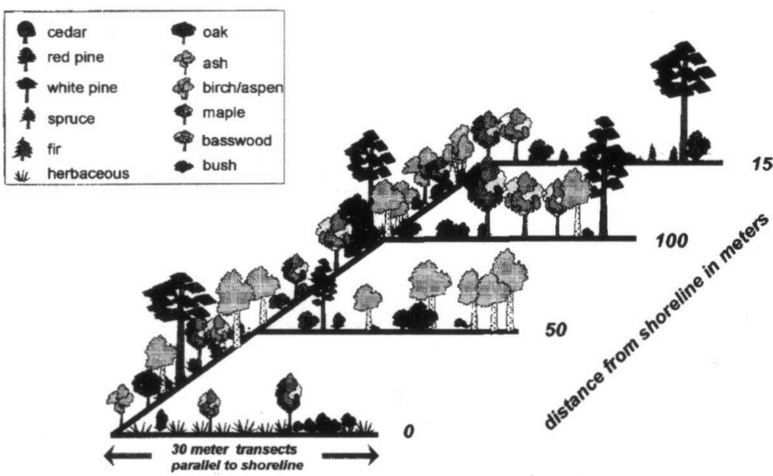

Fig. 5. Vegetation structure of mature second growth forest, Anchor Hill, White Earth State Forest, Minnesota.

etation and vegetation structure. Therefore, in addition to the dragonfly surveys, forest vegetation surveys were conducted at sites in each of the study areas. For each survey, tree species identification, density, diameter (dbh), and canopy coverage were determined along line transects for all trees encountered along a 30-meter lakeshore transect, along a 150-meter transect from shoreline into the adjacent forest, and along 3 additional 30-meter transects parallel to the shore at distances of 50 m, 100 m, and 150 m away (Figs 4, 5, 6). Trees were defined as having a trunk diameter (dbh) greater than 9 cm. Life forms (physiognomy) and percent coverage by each life form were also noted for all bryophytes, herbaceous plants, shrubs, saplings, and trees encountered along each line transect. The resultant data were used to determine the diversity of tree species (H', based on number of species and abundance of each species) and of physiognomic or structural diversity (H', based on number of life forms and percent coverage by each) for the vegetation at each survey site. The data also provided information about tree canopy coverage (shadiness), and about total basal area, density, and mean diameter of trees overall and for each species and each successional and habitat category (pioneer, mid, or late coniferous or deciduous, and lowland or upland coniferous or deciduous). Vegetation and dragonfly variables were then subject to regression analysis, using analysis of variance (ANOVA) and Spearman's Rank Correlation Coefficients to determine relationships between forests, forest variables, and dragonfly communities and species. Significance of analysis of variance was determined using p-values < 0.05. Significant correlation coefficients were determined using Siegel's Critical Values Table for Spearman's Coefficient (SIEGEL, 1956, as presented in GILBERTSON et al., 1995). Finally, cluster analysis and ordination were conducted for the forests in each survey area, with the results compared to the cluster analysis and ordination of their respective dragonfly communities.

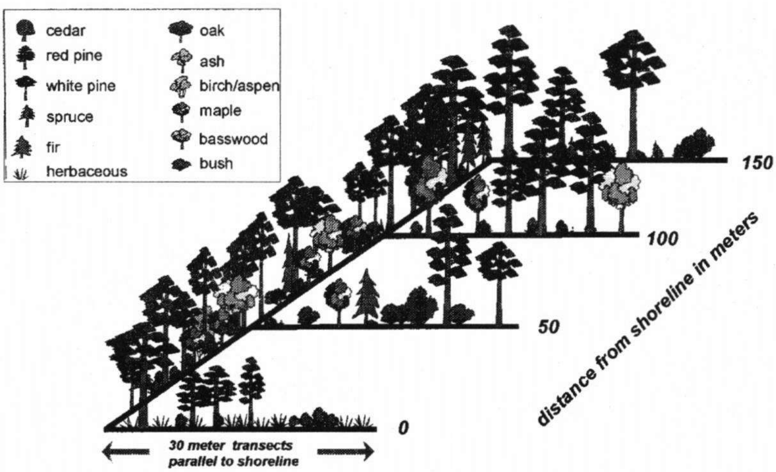

Fig. 6. Vegetation structure at Itasca Scientific Natural Area, Itasca State Park, Minnesota.

RESULTS

The checklist for northern Minnesota dragonflies collected in 1994 includes a total of 38 dragonfly (Anisoptera) species, in addition to the damselfly *Calopteryx aequabilis* (Tab. I). This species number was based on adult specimens collected, with confirmation of larval emergence based on presence of exuviae.

The most common and abundant of the species was the ubiquitous *Libellula* *quadrimaculata*, although *Aeshna canadensis*, *Libellula (Ladona) julia*, *L. pulchella*, and *L. (Plathemis) lydia* were also commonly found. Among the least common were several aeshnids (*Basiaeshna janata*, *Aeshna interrupta lineata*, *A. eremita*), cordulids (*Somatochlora minor*, *S. williamsoni*, *S. kennedyi*), gomphids (*Ophiogomphus rupinsulensis*, *Gomphus lineatifrons*), and libellulids (*Leucorhinia frigida*, *Sympetrum semicinctum*, *S. danae*, *Pachydiplax longipennis*) .

Out of the total possible number of species for the region, the greatest number were found in the old-growth areas at Itasca (30) and the Pine Point section of the National Forest (25) , and in the mature second growth area adjacent to Itasca (24) (Fig. 7). These species included many of the less common species for the region, some of whom appear to prefer mature forests in general, while others appear to be limited specifically to old-growth forest habitats (Tab. I).

In contrast, the fewest number of species were found in recently cleared forest areas near Itasca (17) and in the National Forest (13). Many of the clear-cut area dragonflies appeared to be common and widespread species adaptable to a wide range of habitats, as they were also found at all mature forest sites (Tab. I) .

Table I

Checklist of Odonata species collected at 24 sites northern Minnesota, U.S.A., summer 1994

ZYGOPTERA
Calopteryx aequabilis Say

ANISOPTERA
Anax junius (Drury) @
Aeshna canadensis Walker + @
Aeshna umbrosa Walker
Aeshna constricta (Say)
Aeshna eremita Scudder - *
Aeshna l. lineata Walker - *
Basiaeshna janata (Say) - *
Hagenius brevistylus Selys
Ophiogomphus rupinsulensis Walsh - *
Gomphus vastus Walsh
Gomphus graslinellus Walsh
Gomphus spicatus Hagen
Gomphus lineatifrons Calvert -
Arigomphus cornutus (Tough)
Macromia illinoiensis Walsh
Somatochlora williamsoni Walker -
Somatochlora minor Calvert -
Somatochlora minor Calvert -
Somatochlora kennedyi Walker -
Cordulia shurtleffi Scudder
Epitheca spinigera (Selys) @
Epitheca canis (McLachlan) @
Epitheca cynosura (Say) @
Dorocordulia libera (Selys)
Leucorrhinia glacialis Hagen
Leucorrhinia hudsonica Selys
Leucorrhinia proxima Calvert
Leucorrhinia frigida Hagen -
Leucorrhinia intacta Hagen
Libellula pulchella Drury @, +
Libellula quadrimaculata Linnaeus +,@
Libellula (Plathemis) lydia Drury @, +
Libellula (Ladona) julia Uhler @, +
Sympetrum danae (Sulzer) -
Sympetrum rubicundulum (Say) @
Sympetrum vicinum (Hagen) @
Sympetrum obtrusum (Hagen)
Sympetrum semicinctum (Say) - , *
Pachydiplax longipennis (Burmeister) -

* = found only at old-growth forest sites
@ = found throughout clear cut, second-growth, and old-growth forest sites
\+ = most common
\- = least common

Species diversity, which measures species richness in conjunction with abundance, is similarly high in the old--growth study areas, intermediate in the second growth areas, and low in the clear cut areas (Fig. 8). It appears that there are strong correlations between forest-status of each study area (recently cleared, mature second growth, old--growth) and both species number (correlation coefficient of r = 0.90) and species diversity (correlation coefficient of r = 0.87), with a trend towards greater species richness and diversity with increasing forest age. Furthermore, cluster analysis and ordination of the dragonfly fauna of each study area demonstrated that the species composition of old-growth study areas are very similar to each other as well as each being high in richness and diversity (Figs 9, 10). This appears to be true despite their isolation from each other within the larger timber-managed landscape. In contrast, the recently-cleared study areas not only have low species number and diversity, but their species compositions also differ considerably, both from each other and from the adjacent second-growth and old-growth areas nearby.

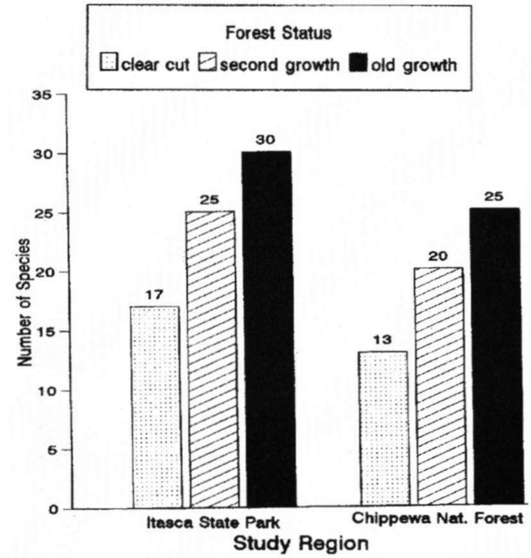

Fig. 7. Number of Anisoptera species according to forest status in northern Minnesota study regions, May-September 1994 (total 39 species overall).

It is interesting to note that the species composition of the Itasca second-growth study area appears to be more like both old-growth study areas, while the National Forest second-growth area is less similar to both the adjacent old-growth area and the Itasca second-growth area. These findings are consistent with the Whittaker's Beta-diversity assessment, which indicates that the differences between the National Forest study areas ($\beta = 1.02$) are greater overall than the differences between the Itasca study areas ($\beta = 0.65$).

As listed in Table II, a total of 28 tree species were encountered in surveys at the dragonfly study areas. Although *Populus tremuloides* was present in seedling and sapling form at each clear-cut study area, tree species diversity was zero in these areas as there were no species of tree size. A significantly larger number of tree species (22 at Itasca, 16 in the National Forest) (Fig. 11) and a greater species diversity (0.88 and 0.85 respectively) (Fig. 12) were found at the mature second--growth study areas. Old-growth study areas had the greatest number of species

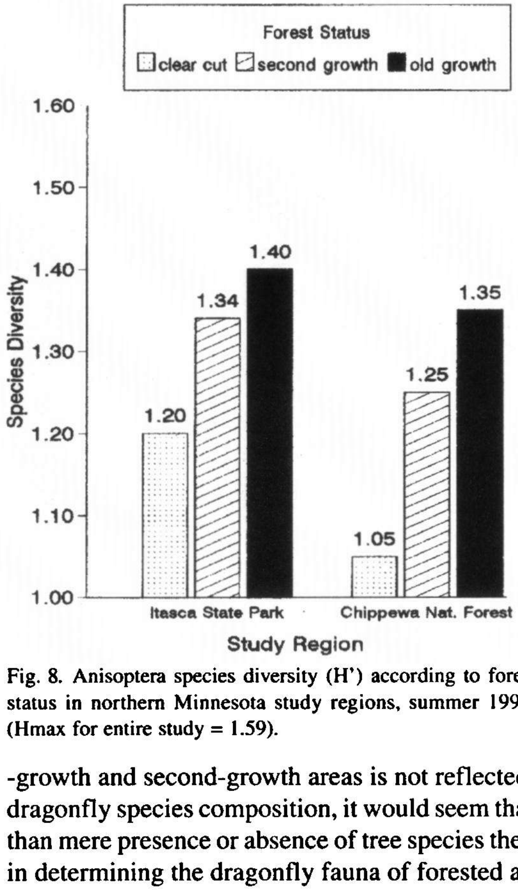

Fig. 8. Anisoptera species diversity (H') according to forest status in northern Minnesota study regions, summer 1994. (Hmax for entire study = 1.59).

(23 at Itasca, 22 at the National Forest), but tree species diversity was much greater at Itasca compared to the National Forest site (1.67 vs. 0.86).

Cluster analysis (Fig. 13) and ordination (Fig.14) of the study-area forests indicate that the clear-cut areas are like each other but are markedly different from any of the mature forest areas. The species composition of second-growth and old-growth forest areas, however, appear to be quite similar, although the second-growth area in the National Forest is somewhat less like its counterpart at Itasca or either of the old-growth areas. Since this pattern of similarity between tree species composition of old-growth and second-growth areas is not reflected by a corresponding similarity in dragonfly species composition, it would seem that forest vegetation variables other than mere presence or absence of tree species themselves may be important factors in determining the dragonfly fauna of forested areas.

In terms of the vegetation characteristics of different forest-status areas, there appear to be significant positive correlations in trends toward greater tree species richness, density, diversity, and successional diversity, with increase in forest age (Tab. III). There are also corresponding increases in basal area and size (dbh) of trees, especially in the later successional trees. Positive correlations also in-

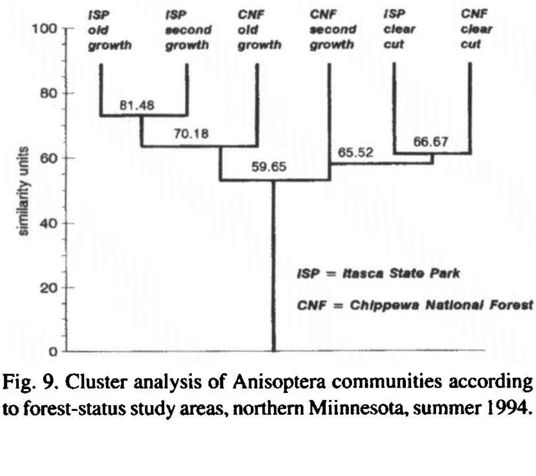

Fig. 9. Cluster analysis of Anisoptera communities according to forest-status study areas, northern Miinnesota, summer 1994.

dicate an important trend toward greater physiognomic or structural diversity in old-growth forest areas, along with more herbaceous growth along shore and more extensive canopy coverage along shore and throughout the adjacent forest. Analysis of variance of vegetation variables per forest status category also demonstrate the significance of these correlations.

Significant correlations also occur between dragonflies and vegetation variables in the northern Minnesota landscape. It appears that dragonfly species richness and diversity, which increase according to forest status or age in general, are specifically influenced by higher tree species richness and diversity; greater tree size, successional diversity, and overall diversity of vegetation structure; and less disturbance of shoreline vegetation. Thus, while some individual species of dragonflies do appear to prefer forested areas in general, the structural characteristics of the older, less disturbed forest areas also seem to be the most important positive influ-

Table II

Tree species at study sites in and adjacent to Itasca State Park and Chippewa National Forest, Mississippi Headwaters Region, northern Minnesota, U.S.A.

Abies balsamea (L.) Mill	Balsam Fir
Acer negundo L.	Box Elder
Acer rubrum L.	Red Maple
Acer saccharum Marsh.	Sugar Maple
Acer spicatum Lam.	Moose Maple
Betula papyrifera Marsh.	Paper Birch
Carprinus caroliniana Walt.	American Hornbeam
Fraxinus pennsylvanica Marsh.	Green Ash
Fraxinus nigra Marsh.	Black Ash
Larix laricina (DuRoi) K. Koch	Tamarack, Larch
Ostrya virginiana (mill.) K.Koch	Eastern Hophornbeam, Ironwood
Picea glauca (Moench) Voss	White Spruce
Picea mariana (Mill.) BSP	Black Spruce
Pinus banksiana Lamb.	Jack Pine
Pinus resinosa Ait.	Red Pine
Pinus strobus L.	Eastern White Pine
Populus balsamifera L.	Balsam Poplar
Populus grandidentata Michx.	Big-toothed Aspen
Populus tremuloides Michx.	Quaking Aspen
Prunus virginiana L.	Chokecherry
Quercus ellipsoidalis E.J. Hill	Northern Pin Oak
Quercus macrocarpa Michx.	Bur Oak
Quercus rubra L.	Red Oak
Salix nigra Marsh.	Black Willow
Thuja occidentalis L.	Eastern Cedar
Tilia americana L.	Basswood, Linden
Ulmus americana L.	American Elm
Ulmus rubra Mulh.	Slippery Elm

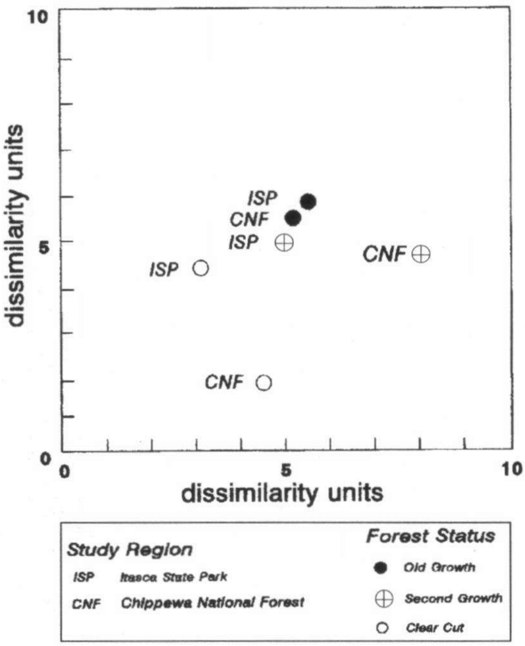

Fig. 10. Ordination of Anisoptera communities according to forest-status study areas in northern Minnesota, summer 1994.

ences on overall dragonfly species diversity and faunal composition.

DISCUSSION

If the dragonfly assemblages or communities within the undisturbed old-growth forest areas of Itasca State Park and the Pine Point section of the Chippewa National Forest are viewed as controls, or as being most representative of dragonfly communities in northern Minnesota under natural (pre-logging era) conditions, it would appear that disturbance caused by timber--management in the forest landscape does indeed affect dragonflies by impacting on their species number, species diversity, and faunal species composition. The impact appears to be greatest in forest areas that have been recently harvested and cleared, with some degree of recovery in second-growth forest habitats. It is interesting to note, however, that recovery of dragonfly communities appears to be a slow process, with species number and diversity lagging in the second-growth sites even several decades after disturbance.

Furthermore, although the dragonfly species composition of the old-growth study areas are similar, the species number and species diversity of the Itasca old-growth sites are higher and the difference between the Itasca old-growth sites and Itasca second-growth sites appears to be much less than between old-growth and second--growth sites in the National Forest. We might speculate that the differences in species number and diversity is attributable to an island biogeography effect, whereby larger "island" size results in greater number and diversity of species. Indeed, the protected old-growth study area at Itasca may be seen as a "patch" of 900 hectares embedded within a larger relatively undisturbed old-growth forest "island" of 4050 hectares, as compared to the 225 hectare old growth "island" at Pine Point in the National Forest. The greater similarity between the dragonfly populations of the Itasca second-growth and old-growth study areas, in contrast to those in the National Forest, could be due to the fact that the larger number of dragonfly species within the larger Itasca old-growth "island" serves as a larger resource base from which recovery and recolonization could occur in the adjacent second growth forests. In addition to island size per se, however, the matter of connectivity may also be a consideration. The Itasca old-growth study area occurs as a "patch" in a larger old-growth "island" completely surrounded by and connected to timber-managed forests of different ages; the smaller National Forest old-growth "island" at Pine Point is really an isolated resource "patch", separated from most other National Forest areas by its location on the tip of a long peninsula in a large lake. Migration of species from the Pine Point area into adjacent areas in the National Forest is thus limited by being channeled through the southern end of the peninsula; few species (other than large gomphids, e.g. *Hagenius brevistylus*) are likely to migrate to forest areas in other directions over the large expanses of open water.

While timber-management and fragmentation of the northern Minnesota forest landscape may have an important and demonstratable effect on dragonfly biogeography in

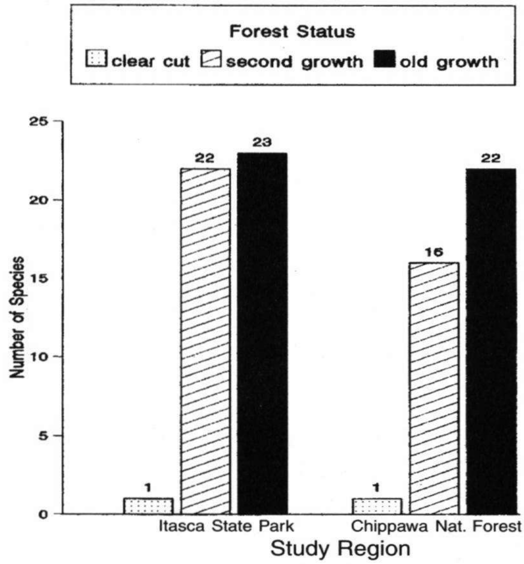

Fig. 11. Number of tree species according to forest status in northern Minnesota study regions, summer 1994 (total 28 species in study overall).

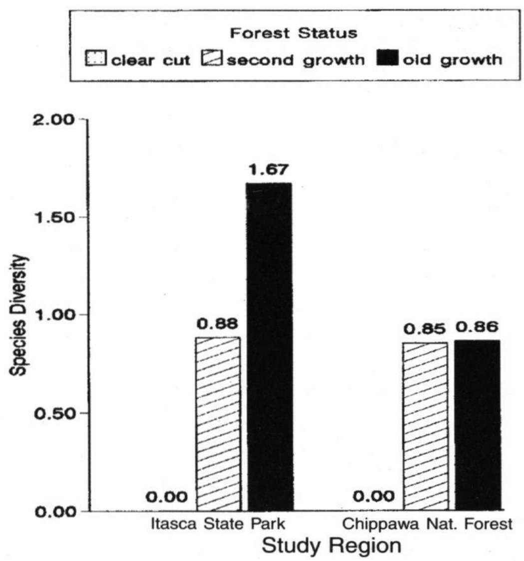

Fig. 12. Tree species diversity (H') according to forest status in northern Minnesota study regions, summer 1994.

Table III
ANOVA p-values and correlation coefficients (r) for forest vegetation and dragonfly variables, northern Minnesota, summer 1994

	ANOVA p-value for forest status (based on stand age)	Correlation coefficient (r) for forest status (based on stand age)*	Correlation coefficient (r) for dragonfly species number*	Correlation coefficient (r) for dragonfly species diversity*
# Trees at site	0.0006	0.91	0.80	0.83
# Tree species at site	0.005	0.91	0.92	0.91
Tree species diversity	0.07	0.89	0.94	0.87
Total tree basal area	0.01	0.97	0.87	0.84
Mean tree diameter (DBH)	0.03	0.93	0.90	0.85
Structural diversity	0.005	0.82	0.84	0.86
Successional diversity	0.01	0.96	0.82	0.84
DBH-upland deciduous	0.01	0.96	0.81	0.81
DBH-late deciduous	0.05	0.79	0.82	0.79
DBH-lowland coniferous	0.01	0.84	0.64	0.68
Basal area-lowland coniferous	0.005	0.85	0.64	0.64
DBH-upland coniferous	0.007	0.75	0.82	0.82
Basal area-upland coniferous	0.03	0.90	0.78	0.78
DBH-late coniferous	0.009	0.73	0.81	0.81
Basal area-late coniferous	0.02	0.91	0.79	0.79
DBH-upland trees	0.005	0.98	0.86	0.86
Basal area-upland trees	0.007	0.98	0.85	0.85
DBH-mid successional trees	0.007	0.87	0.88	0.88
Basal area-mid successional trees	0.005	0.98	0.79	0.79
DBH-late successional trees	0.02	0.83	0.82	0.82
Basal area-late successional trees	0.02	0.70	0.68	0.68
Percent bush coverage at shoreline	(-) 0.02	-0.87	-0.76	-0.76
Percent herbaceous cover at shoreline	0.001	0.96	0.97	0.87
Percent canopy coverage over entire site	0.009	0.97	0.82	0.82
Dragonfly species diversity	0.09	0.87	0.97	1.00
Dragonfly species number	0.07	0.90	1.00	0.97

* Correlation coefficients are significant at r = 0.82 and above for six study areas (SIEGEL, 1956); other correlations are weak

the region, the effects may be indirect as well as direct. The direct effect of forest--clearing is to remove trees, shade, and other structural elements of forest vegetation which may be important to stenotypic adult dragonfly species. In the post--harvest environment, however, the indirect effects of timber management may also result in alteration of the aquatic habitats of dragonfly larvae. Soil from denuded shorelines may slump into nearby bodies of water; logging slash may be deposited in or near ponds and stream in recently cleared areas; and the dominance of young aspen growth in post-clear-cut areas often results in an increase in favorable beaver habitat and subsequent beaver activity within them. All of these effects result in the damming of streams and stagnation of ponds and small lakes. Although logging is not allowed directly along the shorelines of larger lakes and streams, the shoreline forest buffers are often no more than a few hundred meters wide at best (McGREGOR, 1992). As such, logging activity near these bodies of water may result in increased overland flow and siltation from the run-off from recently logged areas. These changes in aquatic habitats could affect dragonflies in their larval stages as well as when they are adults.

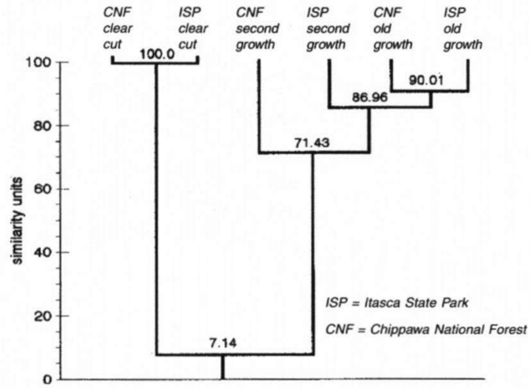

Fig. 13. Cluster analysis of forests at Anisoptera study areas in northern Minnesota, summer 1994.

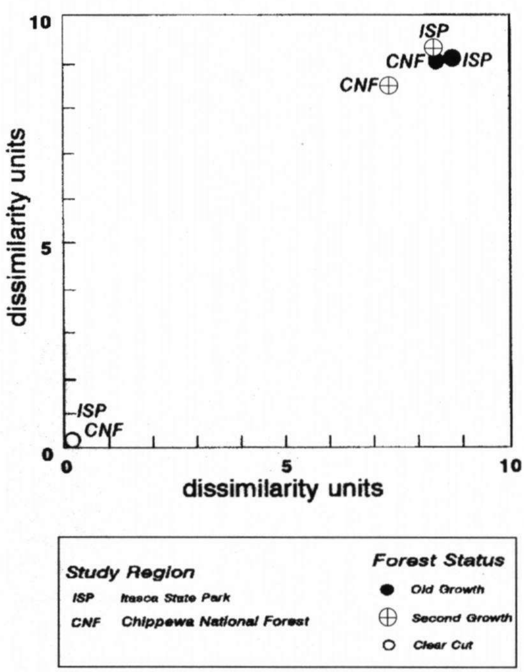

Fig. 14. Ordination of forests at Anisoptera study areas in northern Minnesota, summer 1994.

CONCLUSIONS

Disturbance related to timber-management activities may have an important impact on the biogeography and ecology of dragonflies in northern Minnesota. Such disturbance may have direct and indirect effects, resulting in decline in dragonfly species number and diversity and affecting dragonfly community species composition in timber-managed areas. Protected old-growth forest areas appear to be "habitat islands" representing pre-logging area dragonfly communities, and may serve as resource patches for the recolonization of adjacent disturbed sites. For the purposes of dragonfly conservation, it seems that preservation of larger old-growth "patches" could result in greater diversity of dragonflies. Establishing connectivity between smaller or more isolated patches could similarly enhance species flow and diversity. Though efforts are now being made to establish protected areas of "potential old-growth" throughout northern Minnesota, it may be many years before these patches will actually achieve old-growth status or have an adequate degree of connectivity between them through the larger matrix of the disturbed forest landscape.

Though a large portion of the initial river corridor of the Mississippi Headwaters is buffered on each side by a 300-meter wide old-growth riparian forest, it remains to be determined whether the river can actually serve as a habitat corridor connecting dragonfly communities of isolated old-growth "habitat islands" at Itasca State Park and the Chippewa National Forest, and whether the corridor itself is wide enough to buffer the effects of nearby logging activities. Furthermore, for environmental monitoring purposes, it remains to be determined whether changes in dragonfly communities may also indicate important changes throughout the ecosystems of the aquatic and terrestrial ecotones in northern Minnesota forests.

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