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Predictive Model of the Effects on Lake Metabolism of Decreased Airborne Litterfall through Riparian Deforestation

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Abstract: *The importance of airborne allochthonous litter to the carbon and nutrient budgets of lakes has been seldom studied. We compiled data on the input of terrestrial litter to develop a simple and speculative model to predict the potential consequences of riparian deforestation on one aspect of lake metabolism, specifically the balance between phytoplankton production and plankton respiration. During the autumn of 1992, 56 litter traps were deployed around the littoral zones of four oligotrophic lakes in a densely forested region of northwestern Ontario, Canada. The airborne litter input was estimated to be 32 g dry weight per meter of forested shoreline per year. Allochthonous litter input per unit offshore distance was related to the size of riparian trees, their proximity to the shoreline, and the elevation of their canopy. Combining our data with those from other studies suggests that terrestrial litter can contribute up to 15% of the total carbon supply to oligotrophic lakes and up to 10% of the total phosphorus supply to lakes with a large surface area relative to that of their drainage basin. These results were incorporated into a simple model that predicts that removal of shoreline trees could increase the ratio of plankton production to respiration in oligotrophic lakes situated within small drainage basins. Such lakes may therefore shift from allotrophy to increasing autotropy (energy self-sustenance) following riparian deforestation.*

Modelo predictivo sobre los efectos de la disminución en el ingreso de detritos transportados por el aire a través de la deforestación ribereña sobre el metabolismo lacustre

Resumen: *La importancia de los detritos alóctonos transportados por el aire para el ciclo del carbono y los nutrientes ha sido poco estudiada. En el presente estudio compilamos datos sobre el ingreso al sistema de detritos terrestres, con la finalidad de desarrollar un modelo simple y especulativo para predecir las consecuencias potenciales de la deforestación ribereña sobre un aspecto del metabolismo lacustre, específicamente con respecto al balance entre la producción fitoplanctónica y la respiración del plancton. Durante el otoño de 1992, se colocaron 56 trampas para detritos alrededor de las zonas litorales de cuatro lagos oligotróficos en una región densamente forestal del noroeste de Ontario, Canadá. El ingreso de detritos transportatos por el aire fue de 32 g de peso seco por metro de costa forestal por año. El ingreso de detritos alócotonos por unidad de distancia a partir de la costa, fue relacionado con el tamaño de los árboles ribereños, su proximidad a la ribera y la altura de su fronda. La combinación de nuestros datos con aquellos tomados de otros estudios sugieren que los detritos terrestres pueden contribuir hasta un 15% del total de carbono suministrado a los lagos oligotróficos y hasta un 10% del total de suministro de fósforo en los lagos con una gran superficie en relación con sus cuencas de drenaje. Estos resultados fueron incorporados en un modelo simple, que predice que la remoción de árboles ribereños puede incrementar el cociente entre la producción planctonica y las tasas de respiración, en lagos oligotróficos situados dentro de pequeñas cuencas de drenaje. Dichos lagos podrían pasar de una alotrofía a una creciente autotrofía (energía auto-mantenida) después de una deforestación ribereña.*

Introduction

> Lakes are open ecosystems, and as such their metabolism and other characteristics strongly reflect the inputs of energy, water, and nutrients from their surroundings.
>
> —Likens and Borman (1979)

The scale of logging operations being undertaken within the boreal forests of Canada is extensive (Baskerville 1986), with, for example, contiguous clearcut areas in Ontario up to 20,000 ha in size (Flowers & Robinson 1976; Ontario Ministry of Natural Resources 1988*a*). Clearcutting around natural waterbodies might be expected to affect water quality therein (Christie 1990). To varying degrees all provinces allow harvesting from riparian zones immediately adjacent to lakes. In Ontario shoreline timber can be felled around "warmwater" lakes that are not thought to contain commercially important trout (Fig. 1) or around any body of water less than 4 ha in size (Ontario Ministry of Natural Resources 1988*b*). Protected trout lakes account for less than a third of the total number of lakes on the Canadian Shield of Ontario. With the exception of a study by Rask et al. (1993), what little information exists concerning the limnological repercussions of riparian tree removal around boreal lakes is restricted to natural, not anthropogenic, forces (e.g., Schindler et al. 1980). It is well established, however, that the input of litterfall to the forest floor is essential to providing the carbon and nutrients necessary for maintaining stand productivity (Van Cleve et al. 1983). Given that litterfall can also reach lakes through aerial transport (Szczpanski 1965; Gasith & Hasler 1976; Rau 1976; Hanlon 1981; Jones & Momot 1981), it is not surprising that studies have identified litter as a source of both carbon (Jordan & Likens 1976; Wissmar et al. 1977; Richey & Wissmar 1979) and nutrients (Goldman 1961; Dillon et al. 1986) to receiving waters. The aqueous release of carbon (Slack & Feltz 1968) and phosphorus (Culbert & France 1995) from terrestrial litter has the potential, therefore, to influence lentic metabolic processes.

There has been scarce discussion of the potential, much less realized, consequences of riparian clearcutting on the metabolism of nearby waters. Government forestry guidelines (Ontario Ministry of Natural Resources 1988*b*) explicitly state that because "much of the energy available to the food chain of lakes is fixed by phytoplankton and macrophytes through photosynthesis . . . the value of nearby timber for this purpose is not great." Increasing evidence suggests, however, that the belief in the energy self-sufficiency of oligotrophic lakes is misplaced (del Giorgio & Peters 1993). As a result, existing guidelines for buffer-strip management may be ineffectual in mitigating the effects of riparian clearcuts on the metabolism of Canadian Shield lakes and other similar oligotrophic lakes.

Our goal with this study was to demonstrate the influence of riparian (for this paper, synonymous with shore-

Figure 1. Examples of shoreline deforestation on the Canadian Shield near Atikokan, northwestern Ontario.

line) trees on airborne litter deposition to the littoral zones of four Canadian Shield lakes and to combine this with other data from the literature to determine the importance of airborne allochthonous litter to lake carbon and nutrient budgets. We integrated the information into a simple and speculative model to predict the potential consequences of riparian deforestation on lake metabolism, in particular the balance between phytoplankton production and plankton respiration (del Giorgio & Peters 1993).

Methods

Allochthonous litter traps were placed in the littoral zones of four lakes being studied by the Ontario Ministry of Natural Resources during the autumn of 1992. The study area is located in an unlogged region of northwestern Ontario, 50 km north of the town of Atikokan and 150 km southwest of the Experimental Lakes Area. These are small (26–57 ha) headwater lakes, situated in the transition zone between the northern boreal and Great Lakes–St. Lawrence forests (Rowe 1972). The lakes are ice-covered from November to April and are ultraoligotrophic.

Litter traps were built following the designs of Rau (1976) and Conners and Naiman (1984). Automobile innertubes were used as flotation collars and were anchored with rocks. To stabilize the trap, a deep plastic bucket with holes drilled in the bottom was wedged inside each collar and allowed to fill with water. A shallow plastic tub (0.05 m^2 in area) with small holes drilled in the bottom and with a side rim was secured within the top of each bucket with tape.

Each lake was divided into two or three sub-basins based on large-scale shoreline shape, as in France and Welbourn (1992). One site was randomly selected within each sub-basin, and three litter traps were placed 5 to 15 m apart at water depths from 0.5 to 2.0 m. Five additional traps were placed randomly around each lake's perimeter without consideration of sub-basin divisions. In total, 56 floating litter traps were used to quantify the airborne deposition of allochthonous litterfall to the four study lakes.

Traps were set during the last week of August and emptied at the end of September and at the end of October just before freeze-up. Thirty-three 0.05-m^2 plastic
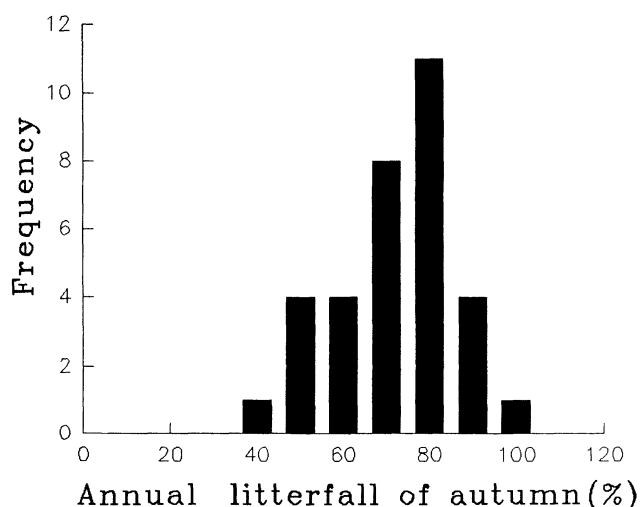
tubs were also set on the shore within the riparian zones near the floating traps. These terrestrial traps were emptied in September, October, the following June, and the following August to determine the annual rate of litterfall from which to correct autumnal values from the floating traps. Collected litter was frozen, then oven-dried at 60°C, and later weighed. Because the floating traps collected only material deposited directly on the lake surface, the estimates of allochthonous litter input represent minimum values. Lateral surface transport would be expected to increase the total amount of litter transported to these lakes by about 6% (France 1995).

Several attributes of shoreline vegetation were measured to quantify the influence of riparian trees on the deposition of allochthonous litter: the inshore distance of the trees (>2 m in height) nearest to the floating traps, the girth (measured as diameter at breast height) of these trees, and the change in canopy height within the first 10 m inshore.

Results and Discussion

The Role of Riparian Vegetation

On average 75% of the annual litterfall within this study region of northwestern Ontario occurred during the autumn months of September and October (Fig. 2). Annual litterfall values from the floating traps were therefore determined as 1.33 times the autumnal values.

There was an inverse relationship between mean annual airborne litter deposition and the offshore distance of the floating traps (Fig. 3). Other studies have docu-

Figure 2. Frequency distribution of the proportion of annual litterfall that was deposited during the autumn months of September and October.
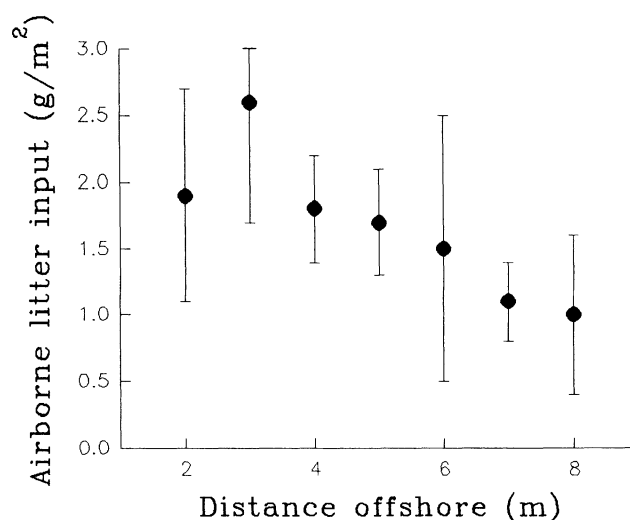
Figure 3. Deposition of mean airborne litterfall as a function of offshore distance in the four study lakes (combined data). Group sample sizes from left to right are 9, 9, 9, 6, 2, 2, and 4. Error bars denote ± one SD about grouped means. Spearman's R = −0.91; p = 0.005.

mented similar findings, describing the relationship as either linear (Mathews & Kowalczewsi 1969; Gasith & Hasler 1976) or exponential (Szczpanski 1965; Hanlon 1981; Conners & Naiman 1984) with respect to distance. Linear integration of the present data from the shoreline to 11 m offshore (the distance at which airborne litter transport ceases) indicated that the airborne litter input to the northwestern Ontario study lakes is 32 g dry weight per meter of forested shoreline per year. This value is considerably below the range of 135–354 per meter of forested shoreline recorded in the literature (Szczpanski 1965; Jordan & Likens 1975; Gasith & Hasler 1976; Hanlon 1981). There are at least four possible explanations for this discrepancy: (1) Over 90% of the litter input to these northwestern Ontario lakes is from coniferous trees that produce less litter than do the deciduous trees (Bray & Gorham 1964; Conners & Naiman 1984) that surround most of the other lakes studied. (2) The estimate of 354 g/m of forested shoreline for Mirror Lake was based on terrestrial transects (Jordan & Likens 1975), which greatly exaggerate the litterfall that actually reaches the lake's surface (Fig. 4) and, as a result, may be unrealistically high (Rau 1976). (3) Results from Szczpanski (1965) and Gasith and Hasler (1976) were based on only a single transect, and those of Hanlon (1981) on two transects, all placed to coincide with the most extensive shoreline forest growth. In contrast, the
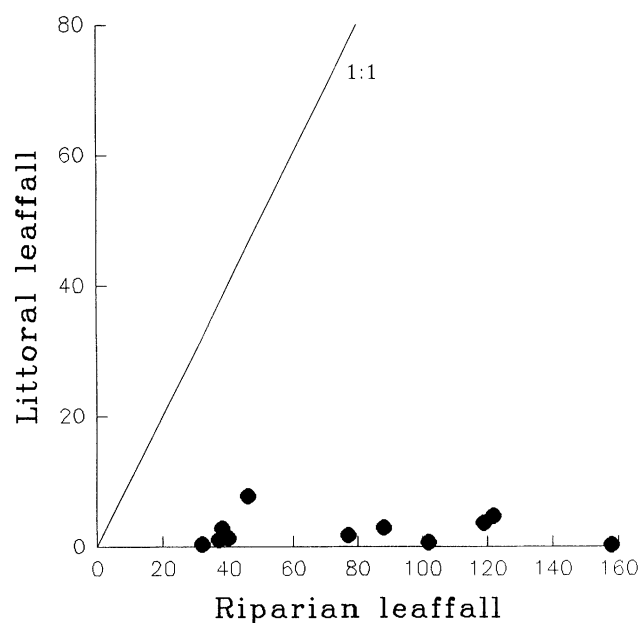
present results arise from integrating data from traps set randomly around the perimeters of four lakes without regard to shoreline vegetation. (4) Production of terrestrial litter declines with respect to climatic adversity and seasonality (Bray & Gorham 1964; Van Cleve et al. 1983), both of which are greater for the present study site than for the other regions investigated.

Data documenting the role of riparian vegetation in regulating the input of allochthonous litter are few and anecdotal. Rau (1976) recorded substantially lower litterfall from shoreline areas near a meadow or talus slope than from near coniferous trees; he believed that the proximity of trees was the primary factor determining the quantity of plant litter deposited at any given lake location. In support of this, Hanlon (1981) found that a sparsely wooded site exported less litter to the lake than a site where thick trees grew to the water's edge. Jones and Momot (1981) derived a "foliage index" that related both tree height and girth to litterfall on the water surface of their study ponds.

Several characteristics of the surrounding riparian vegetation were found to influence the quantity of litter deposited in our study lakes (Fig. 5). Airborne litter input per offshore distance increased in relation to tree girth, proximity of trees to the lakeshore, and the elevation change in canopy height within 10 m inshore (a measure of tree exposure to wind).

The demonstrated importance of riparian trees to allochthonous litter input helps to explain Odum and Prentki's (1978) finding that the magnitude of litter input can be directly related ($r = 0.90$, $n = 5$ lakes) to the extent of wooded shoreline. When the results for the present four study lakes and results from an additional three lakes from the recent literature are analyzed together with those compiled previously by Prentki and Odum for five lakes, and all data expressed as proportional decrease in litter input rather than as absolute amounts, a similar nonlinear relationship of litterfall to percentage forested shoreline exists, as found in the previous study (Fig. 6).

Litter as a Carbon and Nutrient Source

Del Giorgio and Peters (1993) found that plankton respiration exceeds phytoplankton photosynthesis in oligotrophic lakes; they suggested that these plankton communities must therefore consume more carbon than the algae can themselves produce. In other words, oligotrophic lakes must depend to a certain degree on allochthonous or external energy supplies. Hanlon (1981) hypothesized that in certain situations the contribution of particulate organic carbon from airborne plant litter to the overall lake budget could be as high as 25% of that produced by phytoplankton. Combining the present results with data from the literature demonstrates an increase in the proportional contribution of carbon from

Figure 4. Disparity between amounts of riparian and littoral autumnal leaffall. Data are averages of three closely associated traps placed on the shore and three similar floating traps anchored in the water, both groups located near one another. Littoral data from each offshore trap were empirically converted to the expected shoreline value (offshore distance = 0) from the overall relationship presented in Figure 3.
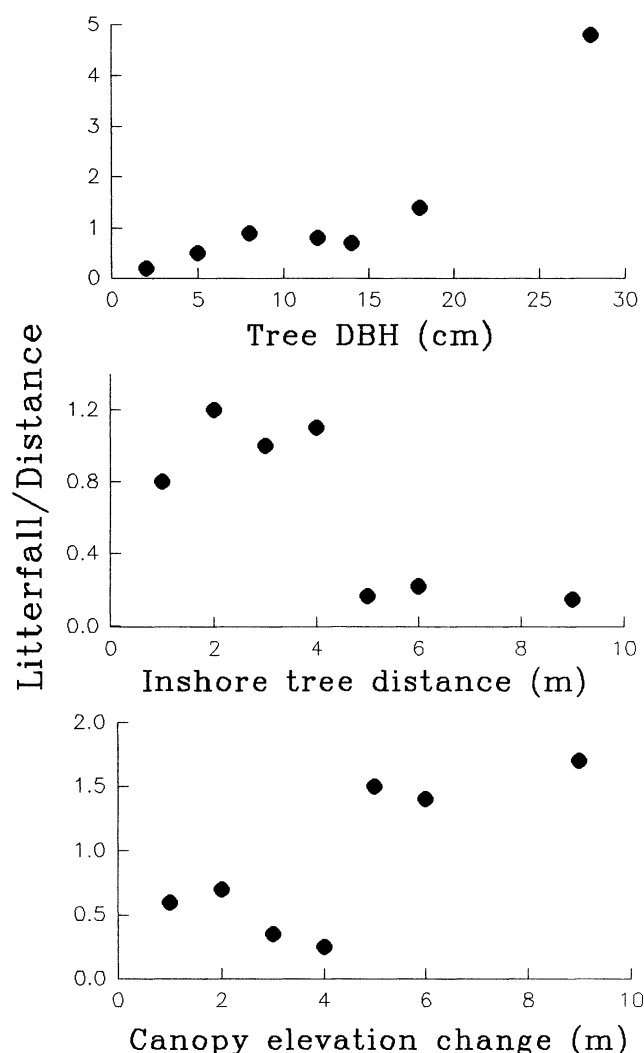
Figure 5. Influence of riparian vegetation on the quantity of litterfall deposited per unit offshore distance in the study lakes. Data are means from 5 to 20 trap-specific values per grouping. Spearman's Rs with respect to litterfall deposition are 0.75 (p = 0.05) for tree girth (diameter at breast height), −0.71 (p = 0.07) for inshore distance of trees, and 0.64 (p = 0.13) for canopy elevation change within the first 10 m inshore.

airborne litterfall to the total lake-carbon budget with increasing oligotrophy (Fig. 7). In eutrophic lakes terrestrial plant litter is a minor source of carbon, comprising less than 2% of the annual supply. In oligotrophic lakes, however, terrestrial plant litter can contribute from 10% to 15% of the total carbon budget and may therefore be an important energy source for sustaining plankton respiration. Lake surface area (Gasith & Hasler 1976) and residence time (Groeger & Kinnel 1983) may both modify the contribution of allochthonous energy to lakes.

Likens and Borman (1979) found that terrestrial litter accounted for about 5% of the total measured phospho-
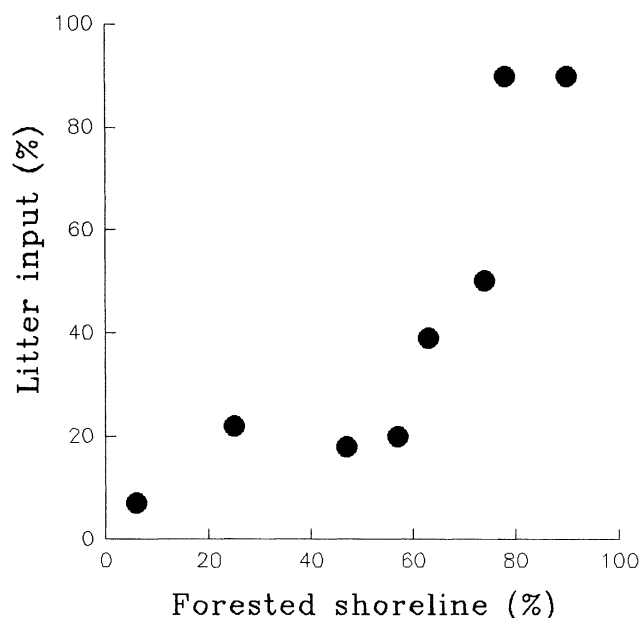

Figure 6. Relationship between airborne litter input and percentage of forested shoreline. Litterfall data are expressed for eight lakes as a proportion of the average amount of litter deposited in four lakes (three from this study and Marion Lake from Odum and Prentki [1978]) that are completely surrounded by shoreline trees.

rus input to Mirror Lake, New Hampshire. Dillon et al. (1986) empirically determined that terrestrial litter could contribute from 2% to 8% of the phosphorus input to Canadian Shield lakes and suggested that this might be a significant nutrient source for lakes with smaller watersheds than those they studied. These data permit generation of a relationship describing the proportion of the total phosphorus input to lakes supplied directly by plant litter based on the ratio of lake to drainage-basin area (Fig. 8). In those lakes in which this "hydraulic drainage ratio" approaches 0.5, allochthonous plant litter can contribute up to 10% of the total phosphorus supply and may measurably influence phytoplankton production.

Predicted Effects of Deforestation

Riparian reserves have often been recommended to ameliorate the effects of timber harvesting on aquatic systems, but these discussions usually address the role of shoreline trees in buffering the water from elevated temperatures and sediment influxes (reviewed by Freedman 1982). The importance of allochthonous litter in structuring the energy flow within lotic waters is well known (McDowall & Fisher 1976; Fisher 1977; Conners & Naiman 1984), as is its ability to provide both a food source and habitat to lentic macroinvertebrates (Rau 1980; France 1994). How the function of terrestrial
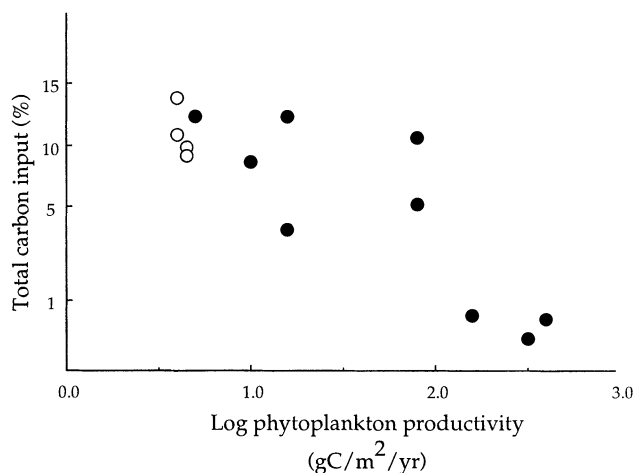
Figure 7. Relationship between the proportion of the annual carbon input to lakes arising from the deposition of airborne litterfall and phytoplankton production (Spearman's R = −0.84; p = 0.001). Open circles denote data from the present study lakes in northwestern Ontario and closed circles indicate data from Szcspanski (1965), Jordan and Likens (1975), Wissmar et al. (1977), Gasith and Hasler (1976), Odum and Prentki (1978), Hanlon (1981), and Jones and Momot (1981).

plant litter in the energy balance of lakes may be altered through riparian clearcutting is unknown, however.

Decreased phosphorus input to lakes will result in decreased primary production. Combining data from Figs. 6 and 8 allows predictions to be made of the consequences of different levels of deforestation on phytoplankton production as brought about through reduced litter input (Fig. 9). From Fig. 8 the percentage of total phosphorus
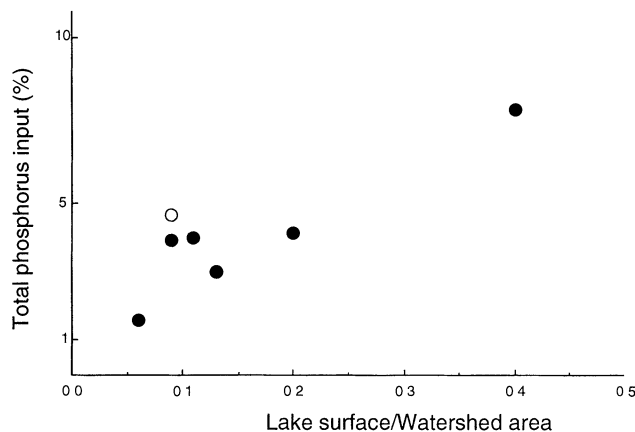

Figure 8. Influence of the ratio of lake to watershed area on the proportion of the total phosphorus input to lakes in central Ontario that arises from airborne litter transport (Spearman's R = 0.66; p = 0.09). Closed circles are from Dillon et al. (1986), and the open circle is from Likens and Borman (1979).
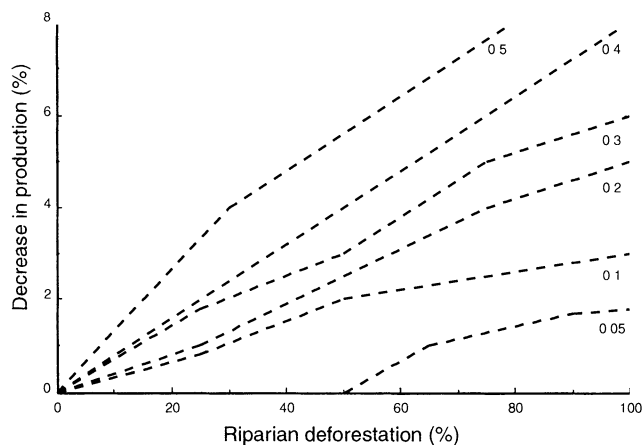

Figure 9. Empirically predicted decreases in phytoplankton production caused by reductions in the airborne input of total phosphorus in allochthonous litter as produced by different levels of riparian deforestation in relation to watershed drainage ratios from 0.05 to 0.5.

input can be equated to the percentage decrease in production in Fig. 9. For example, complete riparian deforestation will remove about 2% of the total phosphorus input to lakes having drainage ratios of 0.05 (Fig. 8). As a result, primary production will be about 2% lower, as indicated in Fig. 9 by the termination point at complete riparian deforestation for the bottommost dashed isopleth for lakes with 0.05 drainage ratios. Similarly, complete riparian deforestation will remove about 8% of the total phosphorus input to lakes having drainage ratios of 0.4 (Fig. 8). Primary production in such lakes will be lowered by about 8%, as indicated in Fig. 9 at the point where the dashed isopleth for lakes with 0.4 drainage ratios intersects the point of complete deforestation. Less extensive riparian deforestation will of course cause less severe reductions in primary production through decreased litter input. The precise nature of this reduction can be obtained from the relationship in Fig. 6 that was used to calculate the paths of the isopleths in Fig. 9.

Decreased carbon input to lakes will result in decreased respiration rates. Combining data from Figs. 6 and 7 allows predictions to be made of the consequences of different levels of deforestation on plankton respiration as brought about through reduced litter input (Fig. 10). From Fig. 7 the percentage of total carbon input can be equated to the percentage decrease in respiration in Fig. 10. For example, complete riparian deforestation will remove about 2% of the total carbon input to lakes having productivities of 300 mg C m^{-2} per year (log 2.5; Fig. 7). As a result, respiration will be about 2% lower, as indicated in Figure 10 where the dashed isopleth for lakes of 300 mg C m^{-2} intersects the point of complete riparian deforestation. Similarly, complete deforestation

will remove about 16% of the total carbon input to lakes having productivities of 5 mg C m^{-2} per year (log 0.5; Fig. 7). Respiration will consequently be reduced by about 16%, as indicated in Fig. 10 by the termination point at complete riparian deforestation for the topmost dashed isopleth for lakes with productivities of 5 mg C m^{-2}. Less extensive riparian deforestation will cause less severe reductions in plankton respiration through decreased litter input. The precise nature of this reduction can be obtained from the relationship in Fig. 6, which was used to calculate the paths of the isopleths in Fig. 10.

This simple model suggests that in oligotrophic lakes (< 10 mg autochthonous C m^{-2} year^{-1}) with small drainage basins (> 0.4 drainage ratio), half to complete shoreline deforestation can produce decreases of about 4% to 9% in phytoplankton production (Fig. 9) and of 8 to 17% in plankton respiration (Fig. 10).

The limnological extent of these deforestation effects within a regional context for northwestern Ontario can be estimated by combining morphometric and phytoplankton data for a group of Shield Lakes from the nearby Experimental Lakes Area (Brunskill & Shindler 1971; Shearer et al. 1987*a*, 1987*b*) with results from the present predictive model. Because respiration is reduced more than production in the model, the ratio between the two will increase with riparian deforestation (Fig. 11). Lakes should therefore become more self-sustaining or autotrophic when their riparian zones are logged. Recent data for a small Finnish lake (Rask et al. 1993) substantiates this prediction. In this respect our study supports Wissmar et al. (1977) in implying "the probable dependence of many lakes in coniferous forests upon allochthonous inputs and their sensitivity to land-based perturbations."
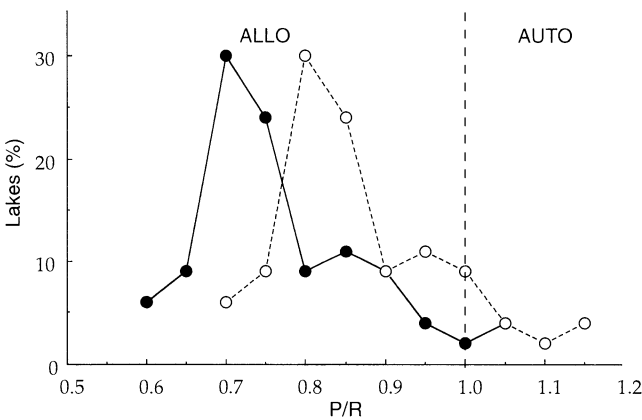
Figure 11. Empirically predicted regional consequences of complete shoreline deforestation on lake metabolism (plankton production [P]: respiration [R]) for small, oligotrophic lakes in northwestern Ontario. ALLO = predominantly allochthonous energy sources, and AUTO = predominantly autochthonous energy sources. Closed circles denote proportional distribution of lakes before clearcutting and open circles indicate the effects of complete shoreline clearcutting.

Ecological Consequences

There are at least two potential ecological consequences if the predictions from our theoretical model become realized. First is decreased phytoplankton production: Because most lakes are regulated through resources (de Melo et al. 1992), decreased primary productivity resulting from riparian deforestation might be expected to be transmitted up the foodweb (Peters 1986) and thereby produce lower biomasses at all trophic levels. Because sport fishing is the largest recreational activity on the Canadian Shield, lower biomasses may therefore carry serious regional economic consequences. Second is increased autotrophy: Because contaminant uptake by aquatic organisms is affected by respiration (Neely 1979), the metabolic balance between production and respiration may influence the movement and ultimate fate of such chemicals within ecosystems. An increase in energy self-sustenance in lakes with deforested shorelines may therefore exacerbate bioaccumulation up a more direct foodweb.

Study Limitations and Managerial Implications

Environmental managers should be able to predict and evaluate effects of anthropogenic perturbations rather than act upon damage that has already become manifest. This means extrapolative methods are required (National Research Council 1981). Although we describe a "first-generation" model, unencumbered by rigid satisfaction of a large set of tenets, we follow the belief of Minns et al. (1986) that production of such models are
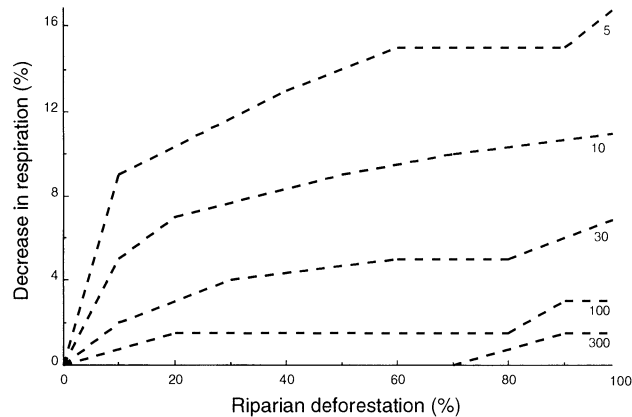

Figure 10. Empirically predicted decreases in plankton respiration caused by reductions in the airborne input of carbon in allochthonous litter as produced by different levels of riparian deforestation in relation to phytoplankton productivities from 5 to 300 g C m^{-2} per year.

beneficial because they generate hypotheses that are testable with further experimentation or observation and because they form the basis for development of more complete and realistic future models.

The present speculative model will be tested in the future by two independent means: experimental deforestation of two of the watersheds monitored in this study (planned to take place following several additional years of background data collection) and a synoptic survey of previously clearcut riparian zones of different ages. Cursory analysis of preliminary survey data indicates that the reduction of airborne litter input from riparian clearcutting will not be merely an ephemeral phenomenon but rather decadal in duration.

Model predictions of reductions of less than 10% in primary production and less than 20% in plankton respiration, which would increase autotrophy by about 0.2 in terms of production-to-respiration ratios, may not be serious enough to necessitate revisions to existing buffer-strip guidelines. Other limnological effects that are expected to result from riparian deforestation, such as elevated temperatures and sediment influxes (Freedman 1982), may have much more immediate consequences to lake health through their direct influence on organism viability. But it is the cumulative impact of a whole suite of smaller, often initially independent repercussions that poses the most serious threat to maintaining biotic integrity. In this respect, predicted alterations in lake metabolism (allotrophy toward increasing self-sustenance or autotrophy) may prove to be ecologically significant through an indirect, as yet unrecognized, synergistic role with other more-overt aquatic effects of riparian deforestation.

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