

FIG. 4. A time-series plot of a robust  $t$ -ratio from 1937 to 1989. The  $t$ -ratio was formed by computing biweight means of the difference between clean and blighted slash pine pair members for each year and dividing this by robust standard error estimates (Hoaglin et al. 1983). A horizontal line marks 0.0, and vertical lines mark years 1956 and 1971.

browning appeared in the distal portions of the needles following the November–December 1970 event reported by Czabator et al. (1971). Snow (1989) reports that the needle blight problem is continuing and comments on an isolated incident near Collins, Mississippi, in 1986 where a wrecked railcar leaked chlorine gas. The pines were damaged within 30 mi<sup>2</sup> (1 mi = 1.6 km) of the site, and a species of *Lophodermium* was prevalent on all affected needles about 6 months after the accident. This demonstrates that fungi on needles can be secondary invaders rather than primary pathogens. Regardless of these innuendos to atmospheric pollution, cause and effect cannot be determined from our study. However, it does seem important to continue to monitor this recurring blight, to determine its yearly extent, and to try to ascertain its cause.

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## Sugar maple seed production and nitrogen in litterfall

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The influence of seed production on litterfall was studied for 2 years at five northern hardwood sites located across the Great Lakes region. Flower and seed litter contributed  $>1 \text{ Mg} \cdot \text{ha}^{-1}$  dry matter in several instances, accounting for as much as 34% of total litter deposition. Significant differences between years were measured for both foliar and reproductive litter inputs at the sites. Production of reproductive litter and foliar litter were negatively correlated at the stand level ( $r = 0.99$ ,  $P < 0.001$ ), suggesting a direct trade-off between leaf biomass and reproductive biomass. Bumper seed crops had a large impact on total aboveground N litterfall. Reproductive N flux was as high as  $41 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ . Averaged across both years and all sites, reproductive litter accounted for 36% of total N in aboveground litterfall (range = 14–61%). When compared with the amount of N returned in foliage, reproductive litter averaged 67% (range = 18–174%). Nitrogen uptake and return in litterfall can be underestimated, especially during periods of heavy seed production, if flowers and seeds are ignored. Periodic life-history events like seed production can play an important role in ecosystem-level processes like N cycling.

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L'influence de la production de semences sur la chute de litières a été étudiée pendant 2 ans sur cinq stations de feuillus nordiques localisées dans la région des Grands Lacs. Dans plusieurs cas, les fleurs et les semences ont contribué pour plus de 1 Mg·ha<sup>-1</sup> de matière sèche, ce qui représentait jusqu'à 34% du total de litières tombant au sol. Des différences significatives entre les années ont été mesurées à la fois dans les apports de litières foliaire et de reproduction dans toutes les stations. La production de litières de reproduction et de litières foliaires était négativement corrélée au niveau du peuplement ( $r = 0,99$ ,  $P < 0,001$ ) suggérant un échange entre la biomasse foliaire et la biomasse de reproduction. Les pics de production de semences ont un impact énorme sur la chute de litières totales épiées. Le flux de N relié à la reproduction était aussi élevé que 41 kg·ha<sup>-1</sup>·an<sup>-1</sup>. La litière de reproduction représentait en moyenne, pour toutes les années et toutes les stations, 36% du N total de la chute de litières épiées (étendue = 14-61%). Lorsque comparée à la quantité de N retournée par le feuillage, la litière de reproduction comptait en moyenne pour 67% (étendue = 18-174%). Le prélèvement de N et le retour par la chute de litières peuvent être sous-estimés, spécialement durant les périodes de production élevée de semences si les fleurs et les semences sont ignorées. Les événements qui reviennent de façon périodique, tels la production de semences, peuvent jouer un rôle important dans les processus, comme le cyclage de N, qui se déroulent à l'échelle de l'écosystème.

[Traduit par la rédaction]

### Introduction

Temperate forests periodically produce abundant seed crops. For example, from 1947 to 1958 Curtis and his students measured sugar maple (*Acer saccharum* Marsh.) seed production in a mesic forest in Green County, Wisconsin (Curtis 1959). Seed yield varied greatly, with number of seeds ranging from a high of 13 018 877 per hectare in 1953 to a low of 98 000 per hectare in 1958. Their data demonstrate substantial year to year variability, with seed yields greater than 10 000 000 per hectare in 3 of 12 years.

Few studies have addressed the impact of flower and seed production on aboveground, ecosystem-level fluxes of carbon and nutrients in temperate forests. Ovington (1963) warned that reproductive parts, if ignored, could confound measurement of energy flow and mineral circulation in forests. He reported that the dry weight of female catkins amounted to about 26% of leaf production and 31% of annual N flux in an aspen (*Populus tremuloides* Michx.) forest in Minnesota. Nielsen (1977) reported that total seed-fall (seeds + cupules) in a European beech (*Fagus sylvatica* L.) stand over 8 years ranged from 195 to 1960 kg·ha<sup>-1</sup> and emphasized that most of this mass entered the detritus pathway. The only report that demonstrates the impact of seed production on litter N flux comes from a Japanese beech (*Fagus crenata* Blume) forest. Kawada and Maruyama (1986) reported that in 1981, flower, seed, and cupule litter amounted to 52 kg N·ha<sup>-1</sup>, or about 58% of total annual N flux and 184% of annual foliar N flux.

The impact of reproductive parts on nutrient uptake, retranslocation, and leaching have often been ignored in calculating the nutrient dynamics of forest ecosystems. Also, no attempts have been made to correlate year to year variations in the fluxes of reproductive and foliar litter at the ecosystem level despite the fact that negative relationships between fruit and shoot production have been reported (Kozłowski 1971; Dick et al. 1990).

We measured litterfall and N flux for 2 years in five similar northern hardwood forests located across an 800-km geographic gradient in the Great Lakes States. Like Kawada and Maruyama (1986), we found flower and seed production can have a substantial impact on N flux. The purpose of this paper is to demonstrate how the production of a seed crop can influence estimates of N uptake, retranslocation, and litterfall in northern hardwood forests.

### Methods

The influence of seed production on litterfall was studied at five northern hardwood sites located across an 800-km acid deposition gradient in the Great Lakes region. The sites are part of an integrated study of the ecological effects of acid deposition on northern hardwood forests. All sites were situated on sandy, well-drained soils in second-growth northern hardwood stands dominated by sugar maple (Table 1). The overall area encompassed by each site was 5 to 6 ha. Within this area were three permanent 30 by 30 m measurement plots. Eight 0.5-m<sup>2</sup> wooden litter traps were randomly located on each 30 by 30 m measurement plot. Litter was collected from the traps on a monthly basis during the growing season and weekly in the autumn during the time of heaviest litterfall. Litter was sorted into leaves, woody material, and reproductive parts (flowers, fruits, seeds, etc.).

Samples were dried at 70°C for 48 h, after which the weight of each component from each trap was determined. The samples were composited annually by plot for chemical analysis. At the end of each sampling season (following complete litterfall), each composite was ground to pass a 20-mesh sieve and analyzed for total Kjeldahl N following sulfuric acid digestion (Technicon Industrial Systems 1977). Nitrogen content of litterfall was calculated by multiplying the N concentration of each litter component by the weight of the component.

Mean values for each component of litter flux at a site were compared between years using a two-sample *t*-test. The purpose of this analysis was to test for differences in litter production between years at a given site. Tests for differences among sites are not the focus of this report. The relationship between foliar litter production and reproductive litter production was examined using the linear (Pearson's product-moment) correlation coefficient. The purpose of this analysis was to determine if there was a linear relationship between changes in foliar litter flux and reproductive litter flux.

### Results

Total aboveground litter flux ranged from 3.9 to 5.4 Mg·ha<sup>-1</sup>. Site 4 produced an abundant seed crop in 1988, while sites 1, 2, and 3 produced abundant seed crops in 1989, especially sites 1 and 2 (Table 2). Reproductive parts (flowers and seeds) accounted for up to 34% of total litter production, and up to 59% of foliar litterfall (Table 2). At any given site, both foliar and reproductive litter production were often significantly different between 1988 and 1989 (Table 2). There was a significant negative correlation between relative differences in foliar litter and reproductive litter from 1988 to 1989 (Fig. 1).

TABLE 1. Selected site characteristics of five northern hardwood forests in the Great Lakes region

	Site 1	Site 2	Site 3	Site 4	Site 5
Latitude (N)	47°41'	46°52'	45°33'	44°23'	43°40'
Longitude (W)	90°44'	88°53'	84°51'	85°50'	86°09'
Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	31 (0.8)	32 (0.5)	30 (1.2)	30 (2.8)	30 (2.0)
Sugar maple basal area (%)	90 (7)	86 (7)	86 (8)	83 (5)	75 (13)
Canopy height (m)	20 (1)	24 (1)	27 (1)	28 (1)	24 (1)
Overstory age (years)	78 (13)	79 (15)	73 (6)	74 (11)	78 (5)
Mean annual temperature <sup>a</sup> (°C)	3.7	4.3	5.2	5.8	7.6
Growing degree-days <sup>b</sup> (>5.6°C)	1319	1528	1736	1944	2083
Precipitation (mm)					
Mean annual <sup>a</sup>	670	870	830	810	850
Growing season <sup>c</sup>					
30-year mean <sup>a</sup>	410	400	410	400	400
1988	610	410	270	230	290
1989	450	360	270	380	380
Soil great group	Haplorthod-Fragiorthod	Haplorthod	Haplorthod	Haplorthod	Haplorthod

NOTE: Standard deviations are in parentheses where applicable.

<sup>a</sup>For the nearest National Oceanic and Atmospheric Administration station (National Oceanic and Atmospheric Administration 1983).

<sup>b</sup>Phillips and McCulloch (1972).

<sup>c</sup>May through September.

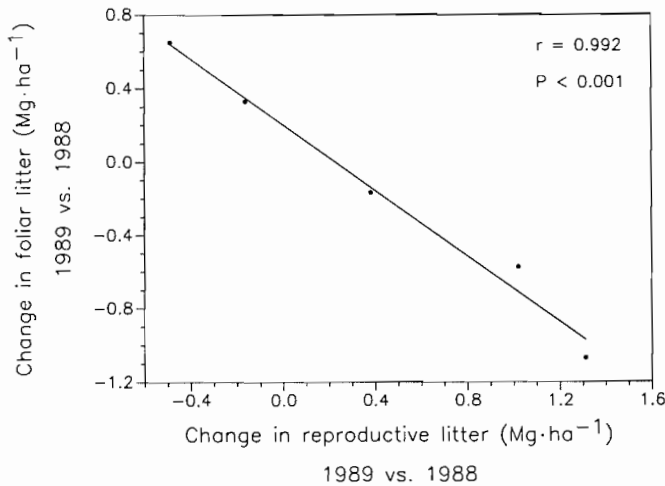


FIG. 1. Relationship between changes in reproductive and foliar litter fluxes over two complete growing seasons, 1988 and 1989.

Reproductive litter had a much higher concentration of total N than foliar litter (Table 3). The higher N concentration of these tissues had a large impact on the flux of N. For example, in 1989 the total "reproductive flux" was 39 and 42 kg N·ha<sup>-1</sup> at sites 1 and 2, respectively. Again, year to year differences were significant (Table 2), with N flux more than doubling at these sites in 1989 due to production of sugar maple flowers and seeds. Reproductive N flux was 153 and 173% of foliar N flux at sites 1 and 2, respectively, in 1989 (Table 2).

A substantial flux of C and N can occur in spring. For example, 1012 kg·ha<sup>-1</sup> of litter fell at site 4 during May and June of 1988 (64% reproductive, 14% wood, 22% foliar), or 20% of the total annual litter flux (Fig. 2). Most of the 646 kg·ha<sup>-1</sup> of reproductive litter during this period was composed of sugar maple flowers. If we assume their N concentration was 2%, this would amount to 13 kg N·ha<sup>-1</sup>, or 22% of the total aboveground N returned to the soil in a single year. When sugar maple flowers abun-

dantly, there can be significant fluxes of C, N, and very likely other nutrients in the spring.

### Discussion

Flowers and seeds can represent a significant carbon flux in northern hardwood forests, and they should not be ignored in mass balance calculations. Reproductive flux was >1 Mg·ha<sup>-1</sup> in several instances (Table 2), equivalent to as much as 59% of foliar litter dry weight. The data of Curtis (1959) suggest that major seed crops occur once every 4 or 5 years. Whether or not this C and N enters the detritus pathway is another question. Nielsen's (1977) data suggest this is a distinct possibility, and Curtis (1959) demonstrated that at least one of every pair of sugar maple seeds is empty. The flowers, empty seeds, and seed wings obviously become detritus.

The negative linear relationship between reproductive biomass and foliar biomass (Fig. 1) is well documented for individual shoots (Kozlowski 1971; Dick et al. 1990). Our results suggest that if stands are of relatively uniform composition, heavy seed production will result in lower stand leaf area and foliar biomass (Fig. 1). The flowers of sugar maple occur on determinant shoots and develop before the leaves in spring. How much developing seeds draw from stored reserves is unclear. Developing seeds and seed wings are green and have N concentrations >2%. They have, as far as we know, an unknown photosynthetic capacity at the stand level. Both the flowers and fruits of trees may be sufficiently active photosynthetically to pay a major fraction of the carbon cost of their own structure and that of the ripened seed (Bazzaz et al. 1979). There may be a direct trade-off between seed and leaf production along the determinant shoots of sugar maple (Fig. 1). Such a trade-off was recently reported for lodgepole pine (*Pinus contorta* Dougl.) (Dick et al. 1990). An interesting question is whether or not heavy seed production alters stand-level growth efficiency, or simply leaf area.

Bockheim and Leide (1990) review the three types of nutrient transfers that commonly are considered in the estimation of nutrient uptake at the ecosystem level,

TABLE 2. Aboveground litter biomass and N fluxes in five northern hardwood forests over the course of 2 complete years

Site	Litter biomass			Litter N content		
	1988	1989	$P^a$	1988	1989	$P^a$
<b>Foliar litter flux (kg·ha<sup>-1</sup>)</b>						
1	3134 (73)	2561 (250)	0.01	26.4 (2.4)	25.5 (2.3)	0.34
2	3823 (153)	2754 (59)	<0.01	30.6 (2.2)	23.9 (1.3)	<0.01
3	4095 (235)	3583 (213)	0.02	32.7 (2.8)	34.7 (1.8)	0.18
4	3418 (148)	4068 (357)	0.02	29.6 (1.3)	38.7 (1.8)	<0.01
5	3895 (385)	4225 (412)	0.18	30.5 (3.8)	36.7 (5.7)	0.10
<b>Reproductive litter flux (kg·ha<sup>-1</sup>)</b>						
1	357 (55)	1377 (73)	<0.01	8.0 (1.0)	39.1 (1.2)	<0.01
2	306 (62)	1617 (137)	<0.01	5.5 (2.0)	41.5 (6.3)	<0.01
3	779 (36)	1161 (302)	0.05	17.3 (0.8)	28.2 (8.3)	0.04
4	1202 (127)	715 (181)	<0.01	28.3 (3.5)	15.9 (4.1)	<0.01
5	785 (145)	622 (115)	0.10	16.2 (1.2)	12.6 (3.7)	0.09
<b>Woody litter flux (kg·ha<sup>-1</sup>)</b>						
1	430 (114)	529 (109)	0.17	2.9 (0.8)	4.2 (1.0)	0.07
2	763 (124)	411 (65)	<0.01	3.6 (0.4)	2.9 (0.9)	0.11
3	360 (80)	610 (239)	0.08	2.4 (0.4)	4.8 (1.3)	0.02
4	391 (105)	348 (126)	0.34	2.1 (0.4)	2.3 (0.7)	0.35
5	397 (137)	514 (101)	0.15	2.0 (0.3)	2.9 (0.5)	0.02
<b>Total litter flux (kg·ha<sup>-1</sup>)</b>						
1	3920 (158)	4467 (308)	0.03	37.2 (0.6)	68.8 (3.0)	<0.01
2	4891 (126)	4782 (86)	0.14	39.8 (2.6)	68.2 (6.6)	<0.01
3	5234 (291)	5355 (159)	0.28	52.4 (3.9)	67.6 (5.5)	<0.01
4	5011 (69)	5131 (369)	0.31	60.0 (3.1)	56.9 (4.0)	0.17
5	5077 (518)	5361 (562)	0.31	48.7 (3.1)	52.2 (9.1)	0.28
<b>Reproductive litter as a % of foliar litter</b>						
1	11.4	53.8		30.3	153.0	
2	8.0	58.7		18.0	173.5	
3	19.0	32.4		52.7	81.3	
4	35.2	17.6		95.7	41.0	
5	20.2	14.7		53.2	34.4	
<b>Reproductive litter as a % of total litter</b>						
1	9.1	30.8		21.5	56.8	
2	6.2	33.8		13.9	60.8	
3	14.9	21.7		32.9	41.7	
4	24.0	13.9		47.2	27.9	
5	15.5	11.6		33.3	24.2	

NOTE: Values are presented as the mean and standard deviation in parentheses for three plots per forest site.

<sup>a</sup>Significance probability of two-sample *t*-test for differences between 1988 and 1989 flux means.

including: (i) nutrient accumulation within the tree, (ii) return of nutrients from the tree to the soil, and (iii) internal cycling within the tree. Their paper summarizes many of the equations that have been used to calculate nutrient uptake in forests. Any equation that does not account for reproductive litter will underestimate nutrient uptake at the stand level. During bumper seed years in sugar maple forests this underestimate can be high, e.g., 42 kg N·ha<sup>-1</sup> for our site 2 in 1989 (Table 2). Pollen also has a high N content, and it too is usually ignored in estimates of uptake.

Flowers and seeds from our study sites had a N concentration that was usually greater than 2% (Table 3). We do not know if there was any N retranslocated from seeds prior to seedfall, but substantial retranslocation seems unlikely owing to the relatively high protein content of seeds. Obviously,

flower and seedfall can represent a major flux of N from sugar maple trees; up to 173% of foliar N flux (Table 2). Where does this N come from? It seems reasonable to consider that some may come from stored reserves that accumulate through time. Otherwise, uptake from the soil must be much greater in bumper seed years. It is also reasonable to consider that when a major seed crop occurs, storage of N during the following dormant season may be affected. A common assumption in calculations of nutrient retranslocation is that retranslocated nutrients are accounted for by sampling the woody biomass during the dormant season. Major problems with this approach are that we still do not know where retranslocated nutrients are stored in many mature trees, or how the size of the retranslocated pool of nutrients varies from year to year. For example, Pregitzer

TABLE 3. Concentrations of total N in northern hardwood litter

	Site 1	Site 2	Site 3	Site 4	Site 5
<b>1988 litterfall N (%)</b>					
Foliage (all species)	0.84 (0.06)	0.80 (0.04)	0.80 (0.04)	0.87 (0.05)	0.78 (0.03)
Sugar maple foliage	0.76 (0.05)	0.70 (0.04)	0.74 (0.03)	0.84 (0.05)	0.71 (0.03)
Woody litter	0.66 (0.05)	0.48 (0.04)	0.67 (0.06)	0.55 (0.05)	0.54 (0.21)
Reproductive litter	2.25 (0.10)	1.78 (0.32)	2.22 (0.13)	2.35 (0.07)	2.09 (0.02)
<b>1989 litterfall N (%)</b>					
Foliage (all species)	1.00 (0.04)	0.87 (0.04)	0.97 (0.01)	0.96 (0.08)	0.87 (0.07)
Sugar maple foliage	0.96 (0.06)	0.80 (0.08)	0.92 (0.09)	0.90 (0.10)	0.80 (0.09)
Woody litter	0.96 (0.02)	0.68 (0.10)	0.81 (0.10)	0.68 (0.15)	0.56 (0.05)
Reproductive litter	2.84 (0.11)	2.56 (0.18)	2.41 (0.11)	2.24 (0.33)	2.00 (0.25)

NOTE: Values are presented as the mean and standard deviation in parentheses for three plots per forest site.

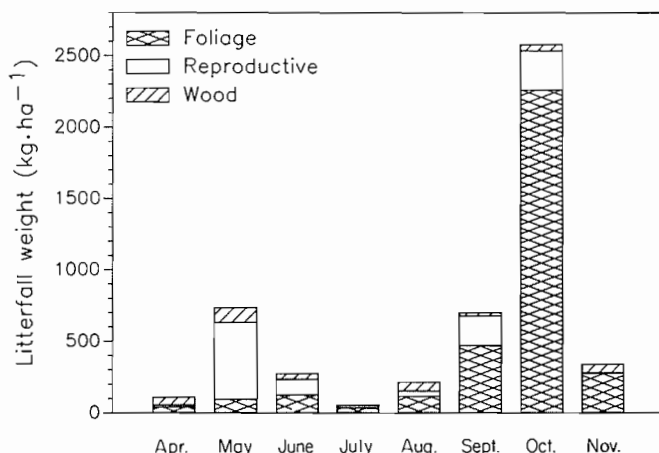


FIG. 2. Monthly litterfall at site 4 during 1988.

et al. (1990) found that in young hybrid poplars most N was stored in large structural roots. Root storage of nutrients has been ignored as a possibility in most nutrient cycling studies. Smaller twigs are another probable site for local storage of nutrients during the dormant season. It is likely that many of the allometric equations and sampling schemes used to estimate nutrients in the perennial tissues of large trees do not estimate twig nutrient content very accurately. Bockheim and Leide (1990) conclude that studies that more clearly elucidate the retranslocation-reutilization process in forests are necessary. We certainly agree with this conclusion. The use of tracers like  $^{15}\text{N}$  may be one way to understand better the process of retranslocation.

Some scientists have recognized the importance of bridging the gaps between ecosystem, physiological, community, and population ecology (Shugart and Bonau 1988; Vitousek and Walker 1989). As this study very clearly demonstrates, a simple life-history event like the production of a seed crop can have a profound impact on ecosystem processes like the flux of C and N in aboveground litterfall. There may even be "trickle-down" impacts of seed production on such factors as nutrient and carbohydrate storage, and perhaps even stand leaf area in the year(s) following seed production. Our results seem to give credence to the call for a more population-based and physiologically based understanding of ecosystem-level processes.

### Acknowledgements

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**Erratum: Organic matter and mineral distribution in an old-growth *Acer saccharum* forest near the northern limit of its range<sup>1</sup>**

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In this article on page 1335,  $\text{cmol}_c \cdot \text{kg}^{-1}$  above columns 7 to 13 of Table 5 should read  $\text{cmol} \cdot \text{kg}^{-1}$ . No other tables are affected by this change.

On page 1338 in Table 9, the value 380 020 in column 3 should read 38 020. In the same table, values for Wishart Lake mineral soil Ae available P, K, Ca, and Mg should read 1, 11, 111, and 9, respectively. The column totals are correct.

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