

Comparison of soil nutrient fluxes from tree-fall gap zones of an old-growth northern hardwood forest¹

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MCGEE, G. G., M. J. MITCHELL, D. J. LEOPOLD, AND D. J. RAYNAL (SUNY College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210-2778 U.S.A.). Comparison of soil nutrient fluxes from tree-fall gap zones of an old-growth northern hardwood forest. *J. Torrey Bot. Soc.* 134: 269–280. 2007.—The objective of this study was to assess nutrient losses, via soil solutes, from discrete zones of recent, single-tree gaps in an old-growth, northern hardwood forest. Growing season flux rates of all solutes did not differ between the “undisturbed” zones (areas 5 m away from gap-making trees) and “crownfall” zones (areas associated with fallen tree crowns) of the twelve tree-fallgaps we studied. Under assumptions of partial root gap formation (50% root mortality), total cation and anion fluxes were 2-fold greater, and DON and total N fluxes were 2- to 3-fold greater in the “proximate” zones (areas 0–2 m from stumps of snapped, gap-making trees) compared to the crownfall and undisturbed zones. The “pit” zones (areas of disturbed soil associated with tipped-up trees) exhibited 3- to 6-fold greater NH_4^+ , NO_3^- , and total dissolved N fluxes, and 2-fold greater total cation and anion fluxes than the undisturbed and crownfall zones. We estimated that proximate and pit zones associated with both recent and old tree-fall gaps accounted for 12% and 0.3%, respectively, of the total stand area in this old-growth forest. At the stand level, root throw pits contributed < 1% of the estimated NO_3^- , total dissolved N, total cations and total anions leaching from the system. Under assumptions of partial root gap formation proximate zones contributed 24–27% of the flux of these solutes. We conclude that the pit zones were inconsequential for nutrient loss and, while proximate zones contributed substantially more to nutrient losses from this system, the majority of nutrients leached from this system (~ 75%) were leached from undisturbed forest zones. Our results indicate that efforts to account for mechanisms of nutrient loss from old-growth forests must consider variation in leaching rates associated with discrete microenvironments within gaps, and focus greater attention on nutrient retention capacity of the live, intact forest matrix.

Key words: forest disturbance, nitrogen, nutrient retention.

Several factors such as climate, atmospheric deposition, disturbance/land-use history, species composition, soil nutrient pools, and stand age influence the internal cycling and retention of nutrients, especially nitrogen (N), from forests (see review by Fenn et al. 1998). Succession theory and some observational studies (Vitousek and Reiners 1975, Peet 1992, Hedin et al. 1995) suggest that old-growth forests have higher rates of nutrient loss than younger, aggrading stands (but see

Fisk et al. 2002, McGee et al. 2007). However, an understanding of the mechanisms accounting for age-dependent nutrient losses from forests has not been thoroughly pursued.

Old-growth forests have relatively high rates of mortality by canopy-dominant trees (Peet 1992) and processes occurring within canopy gaps may lead to localized nutrient losses. Canopy gaps created by tree-falls lead to spatially discrete microsites exhibiting higher light levels and soil temperatures, and greater soil moisture availability (Collins et al. 1985, Moore and Vankat 1986, Denslow et al. 1998, Ostertag 1998). Higher soil moisture and temperature, coupled with the delivery of readily decomposable twigs, foliage, and roots in canopy gaps may lead to elevated mineralization and nitrification rates within gaps. Some studies have found evidence of increased N mineralization and nitrification rates in surface soils within canopy gaps (Mladenoff 1987, Denslow et al. 1998). Tree mortality also leads to the creation of below-ground root gaps associated with the gap-making tree and neighboring canopy or understory trees that may be damaged and/or killed during gap creation (Sanford 1989, Parsons et al. 1994a,b,

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Bauhus and Bartsch 1996, Ostertag 1998, Denslow et al. 1998). Formation of root gaps may lead to localized disruptions in nutrient assimilation and hydrologic processes of plant/mycorrhizal systems. If tree falls result in the formation of root gaps, and if altered micro-environmental conditions within tree-fall gaps increase mineralization and nitrification rates, then canopy gaps may serve as sources of nutrient (particularly N) loss from old-growth forest ecosystems. While several studies have considered changes in soil nutrient availability within gaps, few have specifically investigated the role of gaps as sources of nutrient loss from forest ecosystems (Uhl et al. 1988, Parsons et al. 1994a, Bauhus and Bartsch 1995).

In addition, most gap-related research has focused on tree-fall zones associated with the obvious canopy openings; however, below-ground root gaps do not necessarily coincide with the canopy gaps (Sanford 1990). While some studies have considered nutrient loss from gaps, there has been little critical attention paid to the relative importance of within-gap microsites (e.g., Uhl et al. 1988). Root gaps clearly occur within pit-and-mound complexes associated with root-throws, and nutrient losses from root-throw pit zones have received some consideration (Vitousek and Denslow 1986). However, gap zones that are proximate to intact gap-maker stumps (associated with snapped trees) are also a likely location of root gaps (Wilczynski and Pickett 1993). If proximate zones associated with snapped and standing-dead trees are more abundant than root-throw pits in old-growth forests, they may be more important nutrient sources than pits. Investigations of nutrient loss from proximate zones have not been previously conducted.

The objectives of our study were to (1) investigate whether certain zones within recent, single tree-fall gaps (and in particular, zones proximate to the gap-maker stumps) serve as spatially discrete sources of nutrient loss in an old-growth, Adirondack northern hardwood forest; and (2) estimate the spatial extent of proximate and pit zones within this forest to evaluate their relative potential contributions to nutrient leaching at the stand level.

Methods. **STUDY SITE DESCRIPTION.** This study was conducted at the base of the

northern, lower slopes of Ampersand Mountain (44°15'00"N, 74°14'30"W; elevation 490 m), near Saranac Lake, New York, USA. Slopes ranged from 3–18% within the study area. This northern hardwood forest is dominated by *Acer saccharum* Marsh. and *Fagus grandifolia* L. (nomenclature follows Gleason and Cronquist 1991). Other common species include *Tsuga canadensis* (L.) Carr., *Picea rubens* Sarg., *Betula alleghaniensis* Britt., *Fraxinus americana* L., and *Tilia americana* L. This site has previously been characterized as an example of an old-growth northern hardwood forest (Woods and Cogbill 1994, McGee et al. 1999, McGee et al. 2007). The site is located within New York's Adirondack Forest Preserve, and no logging has occurred there since it was incorporated into the Preserve in the mid-1890's. Prior to that time, it is likely that only large-diameter *P. rubens* trees were selectively cut from the stand (McMartin 1994). Canopy dominant *A. saccharum* at this site ranged up to 90 cm diameter at breast height (dbh) and have attained ages from 160–240 years (McGee 1998).

GAP SELECTION. In May 1999, we located several single-tree gaps created by fallen mature (> 50 cm dbh) *Acer saccharum* trees within a 15-ha area of the study site. Gap ages in 1999 were estimated at 1- to 2-years based upon the gravitropic reorientation of vascular plants growing on disturbed root throws and/or of perennial, saprotrophic polypores (e.g., *Ganoderma applanatum* (Pers. Ex Wall.) Pat.) that were established while the trees were upright. Many of the tree-falls (and 10 of the 12 that were eventually selected) were oriented in a northerly to northeasterly direction, and thus were likely caused by a directional wind event. We included only large (> 50 cm diameter at breast height) *Acer saccharum* tree-falls for several reasons. First, *A. saccharum* and *Fagus grandifolia* dominated this site, and tree-falls of other species were not sufficiently abundant to adequately replicate. Second, the effort involved in replicating tree-falls among several species would have been prohibitive. Finally, the use of recent *F. grandifolia* tree-falls would be problematic due to current, widespread mortality of this species by the beech bark disease complex at this site as is typical for other forest stands in the Adirondacks (Forrester et al. 2003). Although nutrient cycling processes associated

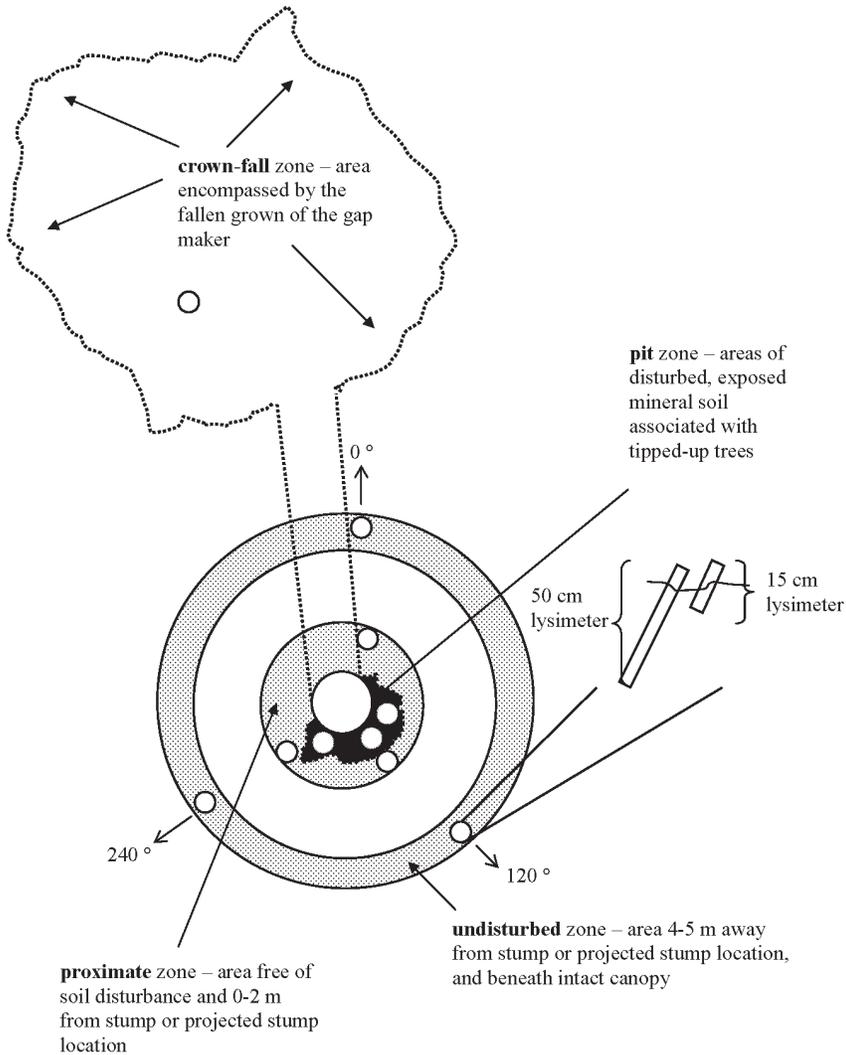


FIG. 1. Schematic diagram of gap zones used for exploring soil solution nutrient concentrations in 2–3 year-old *Acer saccharum* tree-falls in an old-growth northern hardwood forest at Ampersand Mountain, New York. Three pairs of lysimeters (paired 50- and 15-cm lengths) were placed within the pit, proximate, and undisturbed zones. One lysimeter pair was placed within the crown-fall zone.

with beech bark disease are worthy of evaluation, such determinations were beyond the scope of this investigation.

From the available tree-falls, we randomly selected twelve for study. The tree-falls were comprised of two categories hereafter referred to as “tip-ups” and “snaps.” Tip-ups included exposed root masses with associated pits and disturbed mineral soils. Snaps were defined as trees that broke near their base (within 2 m of the ground). Root systems of snapped trees remained intact in the ground, and therefore no zones of disturbed soils were associated with this type of tree-fall. Four spatial zones,

the “pit,” “proximate,” “crown-fall,” and “undisturbed” zones, were defined around each tip-up, while three spatial zones, the pit, proximate, and crown-fall zones, were defined around each snap (see Fig. 1).

TREE-FALL AREA. The surface area directly affected by each tree-fall was determined by surveying the outline of the gap-maker and calculating the area of the polygon. We included the area surrounding each stump or tip-up that was beyond the canopy of live, adjacent trees, as well as the entire crown-fall zone, which always encompassed the associat-

ed canopy gap. However, because the upper boles and crowns of the gap-makers often fell past neighboring trees without causing substantial canopy damage, the crown-fall zones often encompassed areas beyond the influence of the canopy gap. The tree-fall polygons resembled asymmetric "dumbbells" with a large lobe associated with the crown-fall zone, a smaller lobe associated with the proximate zone, and a narrow central portion associated with the tree bole.

LYSIMETER INSTALLATION AND SAMPLING. Estimations of nutrient loss from the respective gap zones were based on analyses of soil solution from porous cup, tension lysimeters placed at rooting depth (15 cm deep) and below the rooting depth (50 cm deep). Tension lysimeters have been used extensively to study relationships between soil solution and elemental cycling in forest ecosystems (Shepard et al. 1990, Johnson and Lindberg 1992, Mitchell et al. 2001a). Lysimeters were evacuated overnight to a tension of 40 kPa. At this tension both gravitational water and interstitial soil solution (Brady and Weil 2002: 208–210) were collected.

Tension lysimeters were installed in May–June 1999. Pairs of lysimeters were installed at 45° angles, with their porous cups positioned at either 15-cm or 50-cm below the ground surface (Fig. 1). Three lysimeter pairs were installed in each of the pit, proximate, and undisturbed zones; one lysimeter pair was installed in each crown-fall zone. Lysimeter clusters in the proximate and undisturbed zones were located at 0°, 120° and 240° from the gap-maker's stump to incorporate possible variation due to microenvironmental gradients (e.g., shade, light, temperature) within the gaps (e.g., Collins and Pickett 1987). The single lysimeter pairs within each crown-fall zone were randomly located within the area encompassed by the fallen tree's branches. Lysimeter clusters within the pit zones were placed in the pit walls.

Our study included observations in six snaps and six tip-ups. The tip-ups included all four gap zones, while the snaps, by definition, lacked pit zones. Each tip-up had three pairs of lysimeters installed in the pit, proximate and undisturbed zones, and one pair of lysimeters in the crown-fall zone, for a total of 10 pairs (20 lysimeters). Each snap had three pairs of lysimeters installed in the

proximate and undisturbed zones, and one pair in the crown-fall zone, for a total of 7 pairs (14 lysimeters).

Soil solution was collected monthly with samples being bulked in each of the 12 gaps, by depth and zone, in proportion to the volume of solution collected from each lysimeter. Elevated NO_3^- concentrations were observed in soil solution from June to November 1999, presumably due to soil disturbance associated with the lysimeter installations (Shepard et al. 1990). Therefore, the data presented here include only samples taken from May–October 2000.

SOIL SOLUTION ANALYTICAL METHODS. Solution samples were stored at 4°C prior to analyses. All samples were analyzed for pH within two days and N solutes within two weeks of collection. Soil solution pH was determined potentiometrically. Samples were analyzed for NO_3^- , Cl^- and SO_4^{2-} (detection limits 0.5, 0.7 and 0.8 $\mu\text{mol L}^{-1}$, respectively) on a Dionex 2000 ion chromatograph and for NH_4^+ (detection limit 0.2 $\mu\text{mol L}^{-1}$) on a Bran Luebbe AA3 auto analyzer. Total dissolved N (TDN) was determined on a Bran Luebbe AA3 auto analyzer after filtration and persulfate oxidation (Ameel et al. 1993). Dissolved organic N (DON) was determined by the difference of TDN and inorganic N ($\text{NO}_3^- + \text{NH}_4^+$). Cation (Al^{3+} , Ca^{2+} , Mg^{2+} , K^+ , Na^+) concentrations were analyzed using a Perkin Elmer 3300 DV inductively coupled plasma-atomic emission spectroscopy (ICP-AES). Dissolved organic carbon (DOC) was determined by the persulfate-ultraviolet oxidation method (Greenberg et al. 1992, Standard Method 5310) using a Tekmar-Dohrmann Phoenix 8000, UV-Persulfate TOC Analyzer.

SOIL NUTRIENT FLUX ESTIMATIONS. Soil solution flux rates were estimated by combining the measured, monthly solute concentrations obtained from the 50-cm deep lysimeters with monthly water flux estimates using the BROOK90 simulation model (Federer 1995). We have successfully used the BROOK2 and BROOK90 models to estimate water fluxes in several Adirondack watersheds and forest stands (Mitchell et al. 1996, 2001b). Water flux estimates were made using inputs of daily precipitation and minimum and maximum temperatures from the Saranac Lake, NY weather station, which is 12 km from the

study site. The BROOK 90 model calculates soil water leaching rates as the difference between measured precipitation and calculated evapotranspiration rate of the forest system.

We applied this model to estimate nutrient fluxes from the four gap zones using the following assumptions. Root systems were clearly disrupted within the root throw pits and, therefore, we assumed complete disruption of hydrologic cycling and nutrient retention processes by root/mycorrhizal networks in the pits. The soil water flux rates through these pit zones equaled precipitation. Deep soil solute concentrations were elevated in the proximate zones for some, but not all solutes (presented in Results), indicating apparent partial disruption of soil/root/mycorrhizal systems within the proximate zones. Therefore, we applied the BROOK 90 model to the proximate zones using two different assumptions to estimate a potential range of nutrient fluxes from these zones. First, a conservative nutrient flux estimate from the proximate zones was made by assuming that the root/mycorrhizal networks of neighboring canopy trees and saplings immediately surrounding the gap makers were capable of retaining local hydrologic control, and therefore no root gap formed within the proximate zones. A less conservative assumption was that a partial root gap was formed within the proximate zones and, therefore, we modeled nutrient flux rates by assuming that evapotranspiration capacity was diminished by 50% within the proximate zones. Monthly soil water fluxes at 50 cm were multiplied by concentrations to obtain monthly solute fluxes. Monthly fluxes were summed over the entire sampling period to estimate total nutrient fluxes.

VEGETATION SAMPLING. Density and basal area of woody vegetation were estimated in the respective zones in each of the tree-falls. Trees (≥ 5.0 cm dbh) were tallied and their breast height (1.40 m) diameters measured on 5-m radius plots surrounding each crown-fall zone lysimeter cluster and within 5-m of the edge of the gap-maker's stump (or projected stump). This scheme created a circular area from which the gap-maker's basal area was subtracted. Therefore, the area of sample plots in the crown-fall zones were all 78.5 m², while those surrounding the gap-maker stem ranged from 86.7–93.5 m². Saplings and woody

shrubs (< 5.0 cm dbh and ≥ 1.0 m tall) were tallied and their diameters measured (at breast height or, if < 1.4 m tall, at the terminus of the current year's growth) on 1-m radius plots centered at each lysimeter cluster. Estimates of sapling density and basal area within each gap zone at each of the 12 gaps represented averages of three samples in the pit, proximate and undisturbed zones, and values from one sample in the crown-fall zone, respectively.

GAP ZONE ABUNDANCE SAMPLING. Stand-level abundance of pit and proximate zones was estimated by sampling along seven 200 \times 20 m belt transects that were randomly located along a randomly oriented 400-m long baseline. All stumps and tip-ups that occurred within each belt transect were located. The species, diameter (tops of stumps or breast height equivalents of tip-ups) and decay class (following McGee et al. 1999) were determined for each standing and downed dead tree ≥ 25.0 cm diameter that occurred within the belt transects. We were particularly interested in determining the abundance of recently fallen stems (decay stage "1", sensu McGee et al. 1999; wood solid and with twigs, small branches, and bark intact), which would have gap zone conditions similar to those we instrumented in the recent sugar maple tree-falls. The proximate zones around each dead tree were defined, as before, as the concentric zone from 0–2 m away from the edge of each stump (or, in the case of tip-ups, the projected stump location). The areas associated with the pit and proximate zones were calculated for each belt transect and averaged among the seven transects to estimate the area of each zone within the stand.

EXPERIMENTAL DESIGN. Since the zones surrounding each of the twelve gap-makers were not independent of each other, the gap-makers were considered blocking factors for statistical analyses. The proximate, undisturbed, crown-fall, and pit zones were replicated 12, 12, 12, and 6 times, respectively. Solution samples from one of the pits consistently had extremely high NH₄⁺, DON, DOC, and K⁺ concentrations, resulting in large means and standard errors for the pit zones. Observations of DOC in soil solution during field sampling suggested that the high concentrations probably resulted from just one of the three lysimeter pairs at this location, and

we believe that one lysimeter was installed into or directly under a decaying root. Therefore, we chose to remove this outlier from the analyses, resulting in five replicates for the pit zones. Also, the 15-cm lysimeter in one of the crown-fall zones repeatedly failed to produce sufficient sample volume for analysis. Therefore the crown-fall zone was replicated 11 times for comparisons at 15 cm and 12 times at 50 cm. We applied ANOVA with an incomplete block design (PROC GLM, SAS Institute 2000) to test for differences in soil solution chemistry among the four zones while accounting for differences among the gap-makers (blocks) and unequal replication of the different zones. The observation for each replicate consisted of bulked soil solution averaged over nine monthly samples. Differences among the zones were identified using Tukey's HSD test in order to control for the experiment-wise error rate associated with the multiple comparisons. Data were square-root transformed prior to analyses to achieve normality. Densities and basal areas of canopy and subcanopy woody vegetation were compared using ANOVA for a completely randomized design (PROC GLM, SAS Institute 2000).

Results. CHARACTERISTICS OF GAPMAKERS AND TREE-FALL AREAS. Diameters of the twelve gap-making trees ranged from 52–95 cm and averaged 75 ± 5 cm (± 1 SE). The lengths of the fallen trees ranged from 24–29 m and averaged 26.2 ± 0.5 m. The twelve tree-fall areas ranged from 88–230 m² and averaged 158 ± 13 m².

The tree-falls did not cause substantial mortality to neighboring vegetation. Sapling densities ranged from 0.05 to 0.24 stems m⁻² in the four tree-fall zones (Figure 2a). The pit zones tended to have the lowest average sapling densities, but no statistically discernible differences were detected among the zones. Similarly, no differences were detected in sapling basal areas, which ranged from 0.14–0.45 cm² m⁻² among the four zones (Figure 2b). Total tree (≥ 5.0 cm dbh) densities did not differ between the areas within a 5 m radius of the gap-makers' stumps/projected stumps (515 ± 84 stems ha⁻¹) and within 5 m of the lysimeters placed in the crown-fall zones (528 ± 68 stems ha⁻¹). However, tree basal areas in the crownfall zones (33.9 ± 8.7 m² ha⁻¹) were 3-fold greater ($P = 0.03$) than the basal areas directly

surrounding the gap-maker stumps or projected stump locations (12.0 ± 3.3 m² ha⁻¹).

MICROSITE SOIL SOLUTION CHEMISTRY. Average NH₄⁺, NO₃⁻, DON, TDN, Ca²⁺, K⁺, Mg²⁺ concentrations in deep (50 cm) soil solution ranged from 1–2, 39–94, 10–25, 53–129, 157–191, 10–54, 28–53 $\mu\text{mol}_C \text{ L}^{-1}$ ($\mu\text{mol L}^{-1}$ for DON and TDN) respectively, across the four gap zones during the course of the sampling period (Table 1). No differences existed in soil solute concentrations between the undisturbed zones and crown-fall zones (Table 1). When differences in soil solute concentrations were detected among the four tree-fall zones, the pit and proximate zones tended to have higher concentrations than the undisturbed and crown-fall zones. In the shallow (15 cm) soil horizons the proximate zones consistently tended to have the highest concentrations of N solutes and DOC. In the deep (50 cm) soil horizons, concentrations of Mg²⁺ and K⁺ were 2-fold and more than 5-fold greater, respectively, in the proximate zones than the undisturbed zones. Likewise deep soil solution DON concentrations were 1.9- to 2.5-fold greater in the proximate zones than in the undisturbed and pit zones, and DOC concentrations were 2.1- to 2.9-fold greater in the proximate zones than in the undisturbed and pit zones.

MICROSITE NUTRIENT FLUX RATES. Without exception, the modeled nutrient flux rates for the pit and/or proximate zones were greater than the undisturbed and/or crownfall zones, and the pit zones typically had the highest modeled nutrient flux rates (Table 2). Estimated nutrient fluxes from the proximate zones were influenced by the model assumptions. Even under the conservative assumption of no root gap formation, the soil nutrient flux rates from the proximate zones were still greater than from the undisturbed and/or crownfall zones for Mg²⁺, K⁺, Ca²⁺, DON, DOC, total cations, and total anions. With the assumption of partial root gap formation in the proximate zones, higher nutrient flux rates were estimated, and flux rates from the proximate zones differed from the undisturbed and/or crownfall zones for Mg²⁺, K⁺, Ca²⁺, Al³⁺, Cl⁻, SO₄²⁻, DON, TDN, DOC, total cations, and total anions.

STAND-LEVEL NUTRIENT FLUX RATES. The total number of dead trees ≥ 25 cm diameter

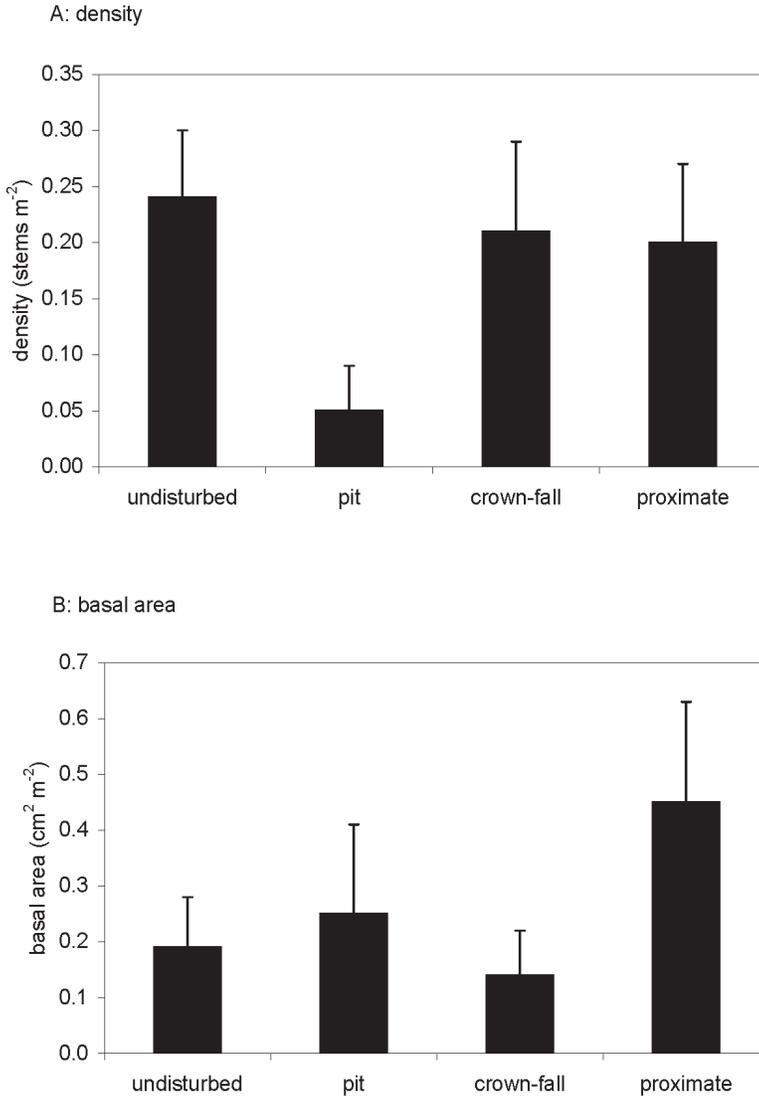


FIG. 2. Mean (± 1 SE) densities (Panel A) and basal areas (Panel B) of saplings (< 5.0 cm dbh and ≥ 1.0 m tall) in respective tree-fall zones in an old-growth northern hardwood forest at Ampersand Mountain, New York ($n = 12, 6, 12,$ and $12,$ for undisturbed, pit, crown-fall, and proximate zones, respectively).

averaged 79 ± 3 ha⁻¹ across the study site. Of this total, 13 ± 3 ha⁻¹ were tip-ups, and 66 ± 4 ha⁻¹ were snaps and standing dead trees. The pit and proximate zones comprised 0.3 ± 0.3 and $11.8 \pm 0.8\%$ of the total forest area, respectively. These stand-level gap zone estimates included dead trees of all species and of much greater stages of decay than the *Acer saccharum* trees used in the tree-fall zone soil solution characterizations. Recent tree-falls of decay stages similar to the twelve instrumented *A. saccharum* tree-falls (decay stage "1"; sensu McGee et al. 1999) accounted for 3% and 10%

of all the tips and snaps, and represented 0.009% and 1.2%, respectively, of the study site area.

Our estimates of stand-level nutrient fluxes from both recent and old tree-falls suggest that the pit zones account for $< 1\%$ of the TDN, cation, and anion flux from this forest. Estimates of stand-level nutrient flux rates from the proximate zones depended on assumptions of root gap formation. Under the assumption of no root gap formation, the proximate zones yielded 18% of the TDN, and 17% of the summed cations and anions

Table 1. Mean (\pm 1 SE) soil solution ion concentrations in shallow and deep soils of respective tree-fall zones during the 2000 growing season (May–October) in an old-growth northern hardwood forest at Ampersand Mountain, New York. Significant differences among means are indicated with different superscript letters (Tukey's HSD test; significance levels are * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$).

	$\mu\text{mol L}^{-1}$										$\mu\text{mol L}^{-1}$			
	N	H ⁺	Na ⁺	Mg ²⁺	K ⁺	Ca ²⁺	Cl ⁻	SO ₄ ²⁻	NH ₄ ⁺	NO ₃ ⁻	DON	TDN	DOC	Al ³⁺
15-cm														
Undisturbed	12	16 (3)	17 ^b (1)	29 (3)	12 (3)	202 (41)	10 (1)	83 ^b (4)	3 (1)	85 ^{ab} (13)	22 ^{ab} (3)	104 ^{ab} (14)	954 ^{ab} (136)	9 ^{ab} (2)
Pit	5	8 (4)	34 ^a (6)	46 (10)	36 (28)	243 (55)	14 (3)	125 ^a (11)	1 (1)	133 ^{ab} (57)	18 ^{ab} (14)	129 ^{ab} (54)	470 ^b (227)	4 ^b (3)
Crown-fall	11	15 (4)	26 ^{ab} (4)	29 (3)	17 (6)	148 (19)	10 (1)	90 ^{ab} (9)	4 (2)	63 ^c (20)	20 ^c (3)	74 ^b (17)	830 ^b (170)	9 ^{ab} (2)
Proximate	12	16 (4)	21 ^b (1)	54 (13)	27 (8)	234 (51)	10 (1)	105 ^{ab} (15)	4 (2)	127 ^{bc} (20)	46 ^a (11)	165 ^{bc} (23)	1456 ^c (229)	11 ^a (1)
Significance level			***					*		*	**	**	**	**
50-cm														
Undisturbed	12	6 (1)	30 (4)	28 ^b (4)	10 ^b (4)	157 (14)	9 (1)	113 (6)	2 (1)	39 (8)	13 ^b (2)	53 (10)	361 ^b (76)	3 (1)
Pit	5	7 (2)	37 (4)	33 ^{ab} (6)	37 ^{ab} (30)	180 (48)	10 (1)	127 (11)	1 (1)	94 (32)	10 ^b (2)	129 (52)	268 ^b (99)	3 (1)
Crown-fall	12	10 (3)	34 (5)	31 ^{ab} (4)	15 ^{ab} (5)	166 (16)	12 (2)	125 (5)	1 (1)	61 (20)	17 ^{ab} (4)	77 (26)	404 ^{ab} (83)	4 (1)
Proximate	12	7 (2)	33 (3)	53 ^a (13)	54 ^a (25)	191 (21)	13 (3)	128 (15)	1 (1)	63 (19)	25 ^a (5)	88 (23)	773 ^a (278)	4 (1)
Significance level				*	*						**	**	**	**

leached from this stand. Assuming partial root gap formation, the proximate zones yielded 28%, 24%, and 27% of the TDN, total cations, and total anions leached from the stand.

Discussion. Our results suggest that localized disruptions in the biological processes responsible for cycling and retaining nutrients were associated with specific microsites within single treefalls in this old-growth forest. We detected no differences in soil leachate chemistry between the crown-fall zones and undisturbed forest zones, which is consistent with the one other study that made similar microsite comparisons (Uhl et al. 1988). The lack of elevated nutrient concentrations in soil leachate within the crown-fall zones may be due several factors. First, it is possible that by the time we located, instrumented and sampled these tree-fall gaps (approximately two years after their establishment), we missed any short-term response to disturbance. Others have reported only short-term (1–6 months) increases in N mineralization (Denslow et al. 1998) and NO₃⁻ leaching (Uhl et al. 1988) in the crown-fall zones of single-tree gaps. Second, microenvironmental changes within the crown-fall zones of these relatively small single-tree gaps may not have been extreme enough to stimulate high net mineralization and nitrification rates (e.g., Vitousek and Denslow 1986, Mladenoff 1987, Parsons et al. 1994a, Denslow et al. 1998). Third, given the abundance of advance regeneration and canopy vegetation, and lack of soil disturbance, root/mycorrhizal networks and free-living soil microbial communities may have remained sufficiently intact within the crown-fall zones to maintain biotic control on nutrient cycling processes there.

The proximate zones displayed elevated concentrations of DOC, DON, Mg²⁺, and K⁺ in deep soil leachate and the likely sources of these elements were the decaying stumps and associated root systems (Fahey et al. 1988). Although NO₃⁻ and TDN concentrations were elevated in the shallow soils of the proximate zones relative to the crownfall and undisturbed zones, these differences did not persist into the deeper soils. Elevated NO₃⁻ concentrations in the forest floor of the proximate zones suggests increased net nitrification rates, but apparently the residual, live root/mycorrhizal systems were sufficient to retain N and hence diminish NO₃⁻ leaching to

Table 2. Mean (SE) estimated soil solute fluxes from tree-fall zones during the 2000 growing season (May–October) in an old-growth northern hardwood forest at Ampersand Mountain, New York. Flux estimations for the proximate zones are presented using two assumptions: (1) no root gap formation with subsequent maintenance of local hydrologic control by surrounding vegetation; and (2) partial (50%) root gap formation and subsequent partial localized disruption of hydrologic control by vegetation. Significant differences ($P < 0.05$) among means are indicated with different superscript letters (Tukey's HSD test). Two sets of superscripts denote independent sets of pair-wise comparisons that include either the proximate zones without root gap formation (lower case letters) or proximate zones with partial root gap formation (capital letters).

Microsite	mmolc m ⁻² growing season ⁻¹										mmol m ⁻² growing season ⁻¹			mmolc m ⁻² growing season ⁻¹	
	Na ⁺	Mg ²⁺	K ⁺	Ca ²⁺	Al ³⁺	H ⁺	NH ₄ ⁺	NO ₃ ⁻	Cl ⁻	SO ₄ ²⁻	DON	TDN	DOC	Σ cations	Σ anions [‡]
Undisturbed	^b 6 ^B (1)	^b 6 ^B (1)	^{ab} 3 ^B (1)	^{bc} 35 ^B (4)	0.7 ^B (0.1)	^b 1.0 ^B (0.3)	^b 0.2 ^B (0.1)	^b 9 ^B (1)	^b 2 ^B (0.1)	^b 23 ^B (2)	^b 3 ^B (1)	^b 11 ^B (2)	^b 74 ^B (16)	^{bc} 51 ^B (6)	^c 42 ^B (2)
Pit	^a 15 ^A (3)	^a 12 ^A (2)	^{ab} 13 ^{AB} (10)	^a 66 ^A (14)	0.8 ^{AB} (0.3)	^a 2.7 ^A (0.6)	^a 0.6 ^A (0.2)	^a 33 ^A (10)	^a 5 ^A (1)	^a 58 ^A (7)	^{ab} 4 ^{AB} (1)	^a 47 ^A (17)	^b 107 ^B (39)	^a 109 ^A (9)	^a 95 ^B (11)
Crownfall	^b 6 ^B (1)	^c 5 ^B (1)	^b 2 ^B (1)	^c 27 ^B (4)	0.5 ^B (0.1)	^{ab} 1.4 ^{AB} (0.4)	^b 0.1 ^B (0.1)	^b 11 ^B (4)	^b 3 ^B (1)	^b 22 ^B (2)	^b 3 ^B (1)	^b 12 ^B (3)	^b 55 ^B (8)	^c 43 ^B (6)	^c 41 ^B (4)
Proximate – no root gap	^b 6 (1)	^{ab} 10 (3)	^a 11 (5)	^{ab} 41 (5)	0.8 (0.2)	^b 1.1 (0.4)	^b 0.2 (0.1)	^{ab} 14 (3)	^{ab} 3 (1)	^b 29 (4)	^a 5 (1)	^b 19 (4)	^a 152 ^A (53)	^b 70 (11)	^b 65 (13)
Proximate – partial root gap	^b 6 ^B (1)	^c 5 ^B (4)	^b 2 ^B (8)	^c 27 ^B (6)	1.4 ^A (0.3)	^{2.1} 1.4 ^A (0.7)	^{0.3} 0.1 ^B (0.1)	²⁴ 14 ^{AB} (7)	⁷ 7 ^A (2)	⁴⁹ 49 ^A (6)	⁹ 9 ^A (2)	³² 32 ^A (8)	²⁷² 272 ^A (97)	¹¹² 112 ^A (17)	¹¹³ 113 ^A (24)

[‡] Total anions account for negative charges associated with dissolved organic carbon using parameters and equations of Mitchell et al. (2001b).

Table 3. Estimated stand-level soil solute fluxes from tree-fall zones during the 2000 growing season (May–October) in an old-growth northern hardwood forest at Ampersand Mountain, New York. Flux estimations for the proximate zones are presented using two assumptions: (1) no root-gap formation or disruption of localized hydrologic control by vegetation; and (2) partial (50%) root gap formation and subsequent partial localized disruption of hydrologic control by vegetation. The undisturbed and crownfall zones are combined as “background” condition since no differences were previously found in concentrations and flux rates of all solutes between these zones.

Microsite	molC ha ⁻¹ growing season ⁻¹							mol ha ⁻¹ growing season ⁻¹				molC ha ⁻¹ growing season ⁻¹			
	Na ⁺	Mg ²⁺	K ⁺	Ca ²⁺	Al ³⁺	H ⁺	NH ₄ ⁺	NO ₃ ⁻	Cl ⁻	SO ₄ ²⁻	DON	TDN	DOC	Σ cations	Σ anions [‡]
Background	53	49	20	276	5	10	2	86	21	201	24	99	567	413	363
Pit Zones	<1	<1	<1	2	<1	<1	<1	<1	<1	2	<1	1	3	3	3
Proximate Zones – No root gap	7	12	13	50	1	1	<1	16	4	34	6	22	179	83	77
Proximate Zones – Partial root gap	12	20	20	76	2	2	<1	28	7	58	11	38	321	132	133
Total w/ no root gaps in proximate zones	60	61	33	326	6	11	2	103	25	237	30	122	749	499	443
Total w/ partial root gaps in proximate zones	65	69	40	352	7	12	2	115	28	261	35	138	891	548	499

‡ Total anions account for negative charges associated with dissolved organic carbon using parameters and equations of Mitchell et al. (2001b).

the lower mineral soils. The single tree-fallgaps we studied averaged ~ 160 m² in area, including the crownfall zones. Therefore, the proximate zones were about half this area and, according to the available literature, too small for the formation of complete root gaps. For instance, others (Parsons et al. 1994b, Bauhus and Bartsch 1996, Denslow et al. 1998) have shown that gaps > 250–700 m² were required before root tip density and fine root growth rates approached zero, thereby leading to elevated NO₃⁻ leaching (Parsons et al. 1994a, Bauhus and Bartsch 1995). Sanford (1989) and Ostertag (1998) demonstrated that single-tree gaps contained ~ 20–50% lower fine root biomass (Sanford 1989, Ostertag 1998) than intact forest microsites. Furthermore, others (e.g., DeBellis et al. 2002) have demonstrated that communities of both vesicular-arbuscular mycorrhizae (VAM) on *Acer saccharum* and ectomycorrhizae (ECM) on *Betula alleghaniensis* remain unaffected, and colonization rates increase on seedlings in gaps up to 1000 m² following partial cuts. Given this information, we modeled nutrient flux rates from the proximate zones using conservative estimates of root gap formation (0 and 50% root mortality).

It was evident that complete root gaps formed within the disturbed pits, and the pit zones had among the highest NO₃⁻ and TDN concentrations in both the shallow and deep soils. Although our data indicate the presence of saplings within the disturbed root throw pits their presence was attributed to our sampling design that included stems within a 1 m radius of a point centered at each lysimeter cluster. When lysimeters were placed at a pit wall some live stems outside of the disturbed zone were included. There were, however, no live woody stems rooted within the disturbed root throw pits and the root systems of neighboring trees were severed at the pit walls.

Our estimates for stand-level nutrient leaching from this old-growth northern hardwood forest depended upon the assumptions for root gap formation within the proximate zones (0% or 50% root mortality). Furthermore, these assumptions were applied to proximate zones surrounding recently dead trees as well as long-dead trees. Therefore, we may have overestimated nutrient fluxes from the proximate zones when applying the assumption of partial root gap formation

since many of the stumps may have been > 10–20 years old and so root/mycorrhizal systems probably had sufficient time to reestablish. Nonetheless, our measurements of growing season soil leachate nutrient concentrations and estimations of nutrient flux through soil leachate were consistent with other studies of northern hardwood forests (Foster et al. 1992, Mitchell et al. 1992, 2001a).

Prevailing models of nutrient retention and loss during forest stand development suggest that greater rates of nutrient loss from old-growth forests result from gaps associated with relatively frequent mortality of canopy-dominant trees (Vitousek and Reiners 1975, Bormann and Likens 1979, Vitousek 1985, Peet 1992). Our estimates indicated that the pit zones, although having high soil solute nutrient concentrations and having lost biotic control on the localized hydrologic and nutrient cycles, comprised only a small proportion of the stand area, and were therefore inconsequential for stand-level nutrient losses from this forest system. The proximate zones surrounding both recent and long-dead trees and stumps comprised a greater proportion (12% area) of the forest than pit zones and these proximate zones accounted for ~ 25% of the TDN, cations, and anions leached from the system under the most liberal assumption (50% root gap formation) applied in this study. Therefore, the vast majority (~ 75%) of nutrients were leached from undisturbed microsites in this forest. Our results support alternative hypotheses of nutrient loss from old-growth systems suggesting that chronic, stand-level nutrient losses occur due to the abundance of live, but aging and senescent trees, which collectively lead to low net primary productivity and nutrient demand (Sprugel 1985, Gower et al. 1996).

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