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Effects of long-term N fertilization on nitrate leaching and vegetation responses in a spruce stand after severe wind damage

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ABSTRACT

Wind damage in a forest stand can result in varying soil effects depending on the pre-history of the site, but areas with storm-felled trees can generally be expected to show more nitrate leaching than undamaged stands. Previous fertilization in such areas, especially with nitrogen (N) fertilizer, may further increase nitrate leaching. This study examined the effect of partial felling of a 42-year-old Norway spruce stand in the Skogaby experimental forest in Sweden during Storm Gudrun in 2005. Nitrate leaching was measured one year before and six years after the storm, in three experimental treatments: fertilization-irrigation with complete nutrient admixture (IF), fertilization with N-free nutrient admixture (V), and an untreated control (0). The 0 and IF treatments had some undamaged replicate plots, but V plots had no trees left after the storm. Compared with undamaged plots and the pre-disturbance level, nitrate leaching was significantly higher in all storm-felled plots, and in the soil solution nitrate dominated strongly over ammonium. Leaching peaked during the second and third post-storm years (2006–2007) and decreased to near pre-storm levels during the fifth and sixth years (2009–2010). Total nitrate leaching 2005–2010 was estimated to be 414, 233, and 218 kg N ha^{-1} in the damaged IF, 0, and V plots, respectively. Total nitrate leaching in undisturbed plots in the IF and 0 treatments was 37 and 0.3 kg N ha^{-1}, respectively. Ground vegetation coverage, biomass, and biomass N increased with time and were negatively correlated with nitrate discharge. However, plant uptake of N only partly explained the significant decline in nitrate leaching between 2006 and 2010. This decrease could also be explained by N immobilization in fungi decomposing woody roots with low N concentrations.

1. Introduction

Nitrogen (N) leaching often increases markedly following disturbances such as clear-cutting and storm-felling (Likens et al. 1970, Wiklander 1981, Grip 1982, Rosén 1982, Holmes and Zak 1999, Kreutzweiser et al. 2008, Futter et al. 2010, Löfgren et al. 2014b). This change in N flux is caused by the sudden imbalance between N mineralization and disrupted plant uptake. Nitrate (NO_3) is often the major form of N in discharge water during the post-disturbance period (Likens et al. 1970, Vitousek et al. 1982, Dahlgren and Driscoll 1994, Bergholm et al. 2015, Ring et al. 2018).

High nitrate-N leaching is undesirable because nitrification is an acidifying process and nitrate leaching is associated with increased leaching losses of base or acid cations (van Breemen et al. 1983). Nitrate leaching also means a loss of N from forest ecosystems and can cause eutrophication of surface waters and, although the effect is largely scale-dependent (Futter et al. 2010, Löfgren et al. 2014a), it can eventually contribute to eutrophication of marine and brackish waters (Boesch et al. 2006, Howarth and Marino 2006).

High chronic atmospheric deposition of N in forest soils is regarded as an environmental issue because it may lead to N saturation (Aber 1992). It is also a source of acidity, along with sulfur (S) deposition, because it increases the risk of nitrification and nitrate leaching occurring even in relatively young, undisturbed forests (Andersson et al. 2002, Gundersen et al. 2006, Akselsson et al. 2010, Vuorenmaa et al. 2018). However, the risk of N saturation and harmful consequences of high N deposition in Swedish forests has been disputed (Binkley and Högberg 2016). On a larger scale, atmospheric deposition of S and N still exceeds the critical loads for vast forested areas in Europe, despite reduced emissions of these compounds in recent decades (Hettelingh

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et al. 2017, Engardt et al. 2017, Forsius et al. 2021).

N fertilization of growing forests often increases net N mineralization, as a consequence of greater forest growth and litter production, and hence increasing N stocks in soil organic matter (Nohrstedt 2001, 2002, Laudon et al. 2011, Ring et al. 2015, 2018).

The intensity of forest harvesting can also influence nutrient losses. Several studies have demonstrated that N leaching following partial cutting (or shelterwood-cutting) is lower than after clear-cutting (Wang et al. 2006, Weis et al. 2006, Jerabkova et al. 2011). In the study by Jerabkova et al. (2011), high retention of trees (>70%) was found to be necessary to maintain uncut N-cycling conditions. Further, logging any slash remaining following final felling can increase nitrate-N concentrations in the humus layer or soil water (Staaf and Olsson 1994, Lindroos et al. 2016, Smolander et al. 2019). Hence, whole-tree harvesting can reduce nitrate leaching compared with stem-only harvesting.

Clear-cutting normally causes immediate loss of plant biomass and thereby reduces nutrient uptake (Palviainen et al. 2005). However, recovery of ground vegetation following cutting through recruitment from buried seeds and rhizomes is often rapid, and ground vegetation can therefore act as a significant N sink, potentially reducing N leaching (Dahlgren and Driscoll 1994, Kimmins et al. 2002, Fukuzawa et al. 2006, Hedwall et al. 2013, 2015, Bergholm et al. 2015). Vegetation control during site preparation for re-planting could therefore extend the period of enhanced N leaching (Palviainen et al. 2007). Further, there is evidence to suggest that greater richness in plant species and functional traits may result in higher primary production (Hector et al. 1999, Loreau et al. 2001, Tilman et al. 2001) and thus also higher N uptake. The reason for this effect is that presence of a large number of species, particularly species with complementary traits with respect to temporal and spatial pattern of nutrient uptake, increases the probability of soil resources being used more efficiently. In addition, long-term high N deposition or repeated N fertilization could influence the local stock of plant species available for recruitment after clear-cutting or storm-felling. Transgression of the critical load resulting from atmospheric N deposition in Europe has caused gradual replacement of oligotrophic species in favor of eutrophic plant species (Dirnböck et al. 2014). For example, Strengbom and Nordin (2008) found long-term residual effects of commercial N fertilization on ground vegetation in boreal forest following clear-cutting, with denser vegetation, lower evenness and biodiversity and higher Ellenberg's indicator value for N availability. However, a study by Olsson and Kellner (2006) on post-harvest residual effects of N fertilization observed reduced cover of epigeic lichens and mosses, but no effect on vegetation density and composition of vascular plants. Other fertilization experiments have found that liming, in contrast to N fertilization, can greatly increase plant species richness during the post-harvest period, with a positive correlation between pH in the humus layer and the number of vascular plant species (Olsson and Kellner 2002). These results suggest that N fertilization and liming treatments influence ground vegetation composition in independent and markedly different ways.

Another, often neglected, N sink is immobilization by decomposers of fresh coarse woody litter, e.g., roots, logs, and stumps left following final harvest (Brais et al. 2006, Palviainen et al. 2010). An examination of N sources and sinks following clear-cutting of a Norway spruce forest in southern Sweden concluded that N immobilization in below-ground tree biomass can be a significant N sink (Bergholm et al. 2015). This finding is consistent with model simulations by Hyvönen et al. (2013) demonstrating that N leaching can be higher following stump harvesting than stem-only harvesting because of the removal of major substrates for N immobilization in the soil. Studies of non-managed, semi-natural coniferous forests in southern Sweden that were seriously damaged by Storm Gudrun in 2005 (see section 2.2) and then suffered infestation by the European spruce bark beetle (*Ips typographus* L.) indicated that leaving huge amounts of large woody debris on-site can prevent excess N leaching (Löfgren et al. 2014b).

A long-term fertilization experiment was established at Skogaby, southwestern Sweden, in 1988 to investigate the effects of increased or decreased availability of nutrients and water to a Norway spruce (*Picea abies* (L.) Karst.) stand (Nilsson and Wiklund 1994). The Skogaby site was selected based on a combination of high atmospheric deposition of S and N in the region. The experimental treatments at the site commenced in 1988 and were discontinued in 2001. A complementary study of carbon (C) and N concentrations in soil was performed in 2004 (Rangfeldt 2005). In January 2005, southwestern Sweden was hit by Storm Gudrun (named Storm Erwin by the German Weather Institute), which caused severe damage to forests in the region (Valinger and Fridman 2011). In the Skogaby area, trees in around half of all experimental plots were completely blown down. Fortunately, in two treatments (an untreated control and a treatment consisting of complete nutrient (N, P, K, Ca, Mg, S) application in combination with irrigation), two out of four replicate plots were undamaged. Trees in all plots with N-free fertilization (P, K, Ca, Mg) were storm-felled, whereas plots with irrigation-only treatment were all undisturbed. The storm had inconsistent effects on plots with other experimental treatments.

The aim of this study was to examine the combined effects of previous nutrient fertilization and wind damage on N leaching and the interaction with ground vegetation recovery. Based on results from previous studies, five hypotheses were formulated and tested. These related to the the effect of previous fertilization with different nutrient admixtures on nitrate leaching (H1), the response of vegetation (H2-H4), and why nitrate leaching decreases rapidly a few years after disturbance (H5):

(H1) Experimental addition of N (together with other nutrients and water) to spruce forest plots results in higher leaching of nitrate-N, than in unfertilized plots and plots with N-free nutrient addition, after clearcut-like storm-felling.

(H2) N uptake by vegetation can quantitatively explain the reduction in nitrate leaching over time.

(H3) Species richness in ground vegetation is positively correlated with N uptake and rapid reduction in nitrate leaching.

(H4) Treatments with previous addition of all nutrients and water will show greater plant biomass and higher N uptake following disturbance than treatments without N addition and water.

(H5) N leaching shows a peak at about two years post-disturbance, followed by a reduction because of re-colonization by ground vegetation.

2. Materials and methods

2.1. Study area

The Skogaby experiment is located 26 km southeast of the city of Halmstad (56°33′N, 13°13′E, 95–115 m a.s.l.) in southwestern Sweden, and 16 km from the Kattegatt Sea. The climate in the region is cold temperate and humid, with mean annual temperature of 7.6 °C and mean annual rainfall of 1140 mm (1961–1990) (Raab and Vedin 1995). However, during the period 1991–2000, precipitation in the area was about 5–10% higher than in the previous 30-year period (Alexandersson and Eggertsson Karlström 2001). The growing season lasts 200 days, starting in early April. During the period 1988–1998, atmospheric N deposition was on average 18 kg N ha^{-1} yr^{-1} (Bergholm et al. 2003).

The bedrock at the site is poor in basic minerals and dominated by gneiss. The area is located above the highest coastline, which means that the till has not been wave-washed in the past. The soil type is a loamy sandy till (4% clay, 32% silt, 64% sand) classified as an Albic podzol (IUSS Working Group WRB 2014, Tuyishime et al. 2022) (Haplic podzol according to former nomenclature). In 1987, before the experimental treatments were established, the pH (H_2O) in the humus layer, 0–10 soil layer, and 10–50 cm soil layer was 3.9, 4.1, and 4.5, respectively (Bergholm et al. 2003).

The study site was planted in 1966 with 3-year-old Norway spruce seedlings of two Polish provenances. The experimental treatments started in 1988, when the trees were 25 years old. At the time of Storm Gudrun, the stand was 42 years old. Thinnings were made in the winters of 1993–94 and 2001–02, with trees representing about 25% of the current basal area harvested on each occasion. All thinning residues were left at strip roads outside the plots. The spruce stand was the second generation of forest, following plantation of Scots pine in 1913 on *Calluna* heathland. Afforestation with conifers was a typical change in land-use of the region at that time (Malmström 1939).

2.2. Experimental design

The Skogaby experiment had a randomized block design with four replicates and plot size of 45 m × 45 m (original net plot size 25 × 25 m). Full details of the experiment are given in Bergholm et al. (1995) and Persson and Nilsson (2001). The treatments considered in this study consisted of liquid fertilization with a well-balanced mix of nutrients (irrigation + fertilization, treatment IF), an N-free nutrient admixture (treatment V), and a control (0, i.e., no application of water or fertilizers) (Supplement Table S1). The nutrient admixture used in the V treatment was a so-called 'vitality' fertilizer designed to mitigate harmfully high N deposition and low supply of other nutrients. A treatment consisting of irrigation only (I), with the same irrigation quantity as in treatment IF, was also included in this study. None of the replicate plots in the I treatment was damaged by the storm, so they served as an additional reference to storm felling. The irrigation water in treatments IF and I was taken from an adjacent small lake, and the irrigation load was on average 186 mm yr^{-1}, comprising between 3% and 47% of the annual throughfall.

On 8–9 January 2005, Storm Gudrun hit western Sweden from the west-southwest and caused major damage to the Skogaby experiment (Valinger et al. 2014). Two years later, the site was hit by another storm event, Storm Per, that brought down a few more trees still standing after the first storm. In about half of the entire experimental area, trees were completely or partly felled by the storms, and in one large part of the area all trees were felled (Fig. 1). Storm-felled trees were generally uprooted, but some were broken (resulting in snags). The stumps of uprooted trees mostly fell back after logging and clearing after the storm. Stems and logging residues (tops and branches) were harvested in 2005 after Storm Gudrun and again in 2007 after Storm Per. Less than half of the logging residues were harvested on these occasions. No further site preparation was performed before plantation of Norway spruce seedlings in 2008. Plots in the 0, V, and IF treatments were selected for this study because the 0 and IF treatments each had two completely storm-felled plots and two undamaged plots, albeit in different experimental blocks (Table 1). In one of the IF plots (block 3), one-third of the plot area was damaged, but the remaining stand in the plot was considered undisturbed (Fig. 1). All trees in all four plots in the V treatment were completely storm-felled. Thus, undamaged 0 and IF plots were used as undisturbed references to corresponding damaged plots, while the storm-felled plots in blocks 1 and 4 of the V treatment were used for comparison with the IF treatment in the same block. The V treatment plots in blocks 2 and 3 were used for comparison with the 0 plots in the same blocks (Table 1).

2.3. Pre-storm soil and stand conditions

The treatment program was terminated in 2001/2002, and C and N conditions in the soil were examined by Rangfeldt (2005) in autumn 2004, 3–4 months before the first storm (Table 2). In comparison with the 0 treatment, the IF treatment resulted in significantly higher net N mineralization rates (estimated by *in vitro* incubation according to Persson et al. 2000). The dominant component in estimated net N mineralization was ammonium-N (NH_4-N) in the 0 and V treatments,

Table 1
Pair-wise treatment comparison in mixed model statistical tests. Treatment V plots were storm-felled in all blocks, whereas treatments 0 and IF were storm-felled in different blocks. Treatment comparisons were therefore made separately for blocks 2 and 3, and 1 and 4, respectively.

Treatment comparison	Blocks included	Remark
0 – V	2, 3	V indicated as V_0
IF - V	1, 4	V indicated as V_{IF}
0 - IF	Not tested	

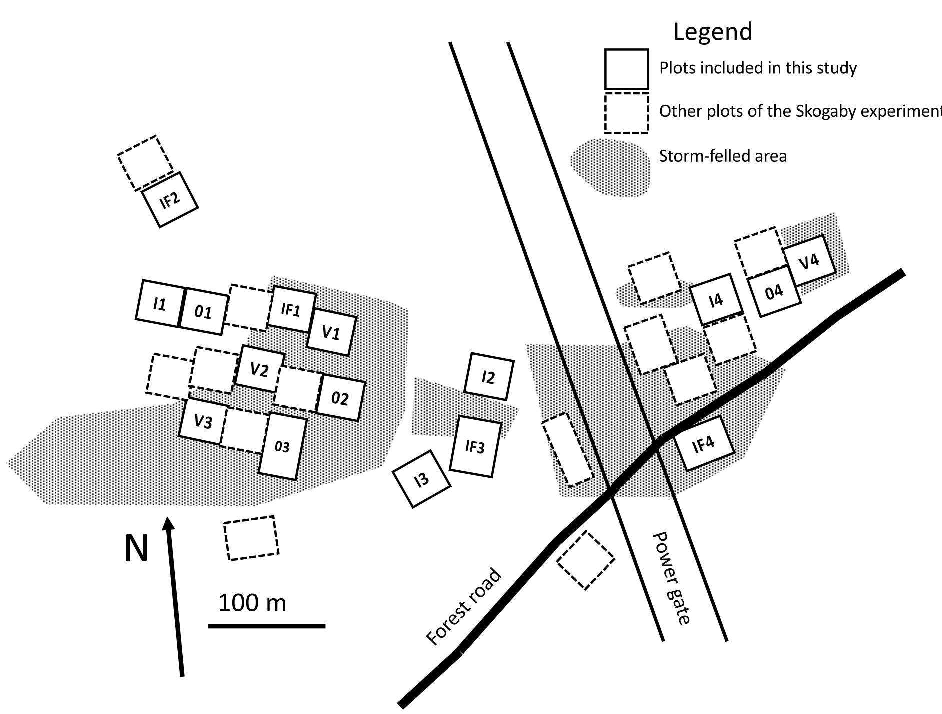

Fig. 1. Map of the Skogaby experimental site, showing the location of plots and of major storm-felled areas. Plots included in the present study are indicated by treatment symbol and block number. Treatments are control, no fertilization (0), vitality fertilization (V), irrigation-fertilization (IF), and irrigation (I).

Table 2
Pre-storm conditions in soil (2004), tree biomass (2001), and needle litterfall (2002–2004) in the 0, V, IF, and I treatments in the Skogaby experiment. Soil conditions are taken from Rangfeldt (2005) and Andersson et al. (2002) (*in situ* N-mineralization), and show treatment mean values (n = 4) with standard error (SE) within brackets. Aboveground and belowground tree biomass in 2001 following thinning in the same year was estimated using Marklund's (1988) allometric functions and diameter at breast height (DBH) (1.3 m) data. Significant differences between treatments are indicated with lower case letters. Results of statistical analyses on soils taken from Rangfeldt (2005).

	0	V	IF	I
Soil conditions and measured fine root biomass (2004)				
Total N stock (Mg ha^{-1})				
O-horizon	1.1 (0.0)^{a}	1.2 (0.0)^{a}	1.9 (0.0)^{b}	1.2 (0.0)^{a}
0–30 cm	3.2 (0.2)	3.7 (0.3)	3.3 (0.2)	2.9 (0.3)
Total	4.3 (0.2)	4.9 (0.3)	5.2 (0.3)	4.1 (0.2)
In vitro net N mineralization (N, kg ha^{-1} yr^{-1})				
O-horizon	36.3 (2.3)^{a}	34.1 (5.5)^{a}	95.5 (13.9)^{b}	58.3 (10.0)^{ab}
0–30 cm	34.8 (9.0)^{a}	51.6 (5.5)^{b}	52.2 (8.7)^{b}	57.1 (5.4)^{b}
Total	71.1 (7.1)^{a}	85.7 (10.4)^{a}	147.7 (21.6)^{b}	115.4 (14.9)^{a}
In situ net N mineralization (N, kg ha^{-1} yr^{-1})				
Total (O-horizon + 0–25 cm)	37		70	
C/N ratio				
O-horizon	29 (0.4)^{a}	30 (0.6)^{a}	26 (0.6)^{b}	30 (0.3)^{a}
0–30 cm	23 (1.1)	22 (0.4)	24 (1.4)	24 (0.8)
Fraction of NO_3-N in N-mineralization rate (%)				
O-horizon	0	0	23	0
0–30 cm	14	16	65	6
Total	7	9	38	3
Fine-root (0–2 mm) biomass (dry mass, Mg ha^{-1})				
O-horizon	3.64 (0.26)^{ab}	2.54 (0.12)^{c}	2.91 (0.27)^{bc}	3.94 (0.93)^{a}
Post-thinning biomass and litterfall				
Aboveground biomass 2001 (Mg ha^{-1})	133^{a}	134^{a}	181^{b}	142^{a}
Belowground biomass 2001 (Mg ha^{-1})	42^{a}	42^{a}	57^{b}	44^{a}
Roots (<5 cm) 2001 (Mg ha^{-1})	8.6^{a}	8.5^{a}	10.9^{b}	9.2^{a}
Annual needle litter fall 2002–2004 (g m^{-2} yr^{-1})	217	229	270	165

and nitrate-N in the IF treatment. According to Rangfeldt (2005), total net N mineralization ranged from 71 to 148 kg ha^{-1} yr^{-1}, with higher values in the IF treatment than in the other treatments. Fine-root biomass, estimated from soil cores, was significantly lower in the V treatment than in the 0 treatment. A stand inventory made at thinning in 2001 revealed significantly higher aboveground and belowground biomass in IF than in the 0, V, and I treatments (Table 2). These biomass estimates were based on Marklund's (1988) allometric functions for Norway spruce and diameter at breast height (DBH) (1.3 m) measurements on all trees in conjunction with thinning. Needle litterfall in 2002–2004 (prior to storm-felling) also indicated higher litter input in IF compared with the other treatments (Table 2).

2.4. Water balance and soil water flow

Water balance and daily soil water flow were simulated using CoupModel (Jansson 2012). CoupModel has been calibrated to fit the Norway spruce stands at Skogaby, through extensive measurements by Alavi and Jansson (1995), Alavi et al. (2001), and Alavi (2002). The same model set-up was used for simulation of soil water flux for the period 2004–2010.

The drivers of the model were measured data on daily precipitation, daily mean air temperature, humidity, wind speed, and solar radiation. All climate data except wind speed were recorded at Simlångsdalen, 19 km north of Skogaby. For periods where data from Simlångsdalen were lacking, climate data from SMHI meteorological stations in Knäred (precipitation), Ullared (air temperature), Torup (humidity and wind speed), and Växjö (insolation) were used. All values were adjusted for the Skogaby site using regression equations (Alavi 2002). Precipitation was further adjusted by + 7% as compensation for measurement losses due to sampling equipment aerodynamics.

An important parameter in CoupModel is leaf area index (LAI), which was modeled for the period 1998–2010 based on stand data. The thinning of the stand in winter 2001/2002 was considered in the model by reducing LAI (Supplementary Figure S1). An annual increase of 5% for LAI was considered following thinning (Alavi 2002). In undisturbed plots, it was assumed that LAI decreased by 5% due to increased shedding of foliage by the storm (Ulf Johansson, pers. comm., 2007), while LAI was assumed to decrease initially to zero in completely storm-felled areas. The LAI in storm-felled plots 2004–2010 was simulated based on measured above-ground biomass of *Deschampsia flexuosa* L. (Trin.), as this species dominated the ground vegetation. LAI was calculated from *D. flexuosa* biomass data using the following equation by Ring et al. (2003) and the seasonal change in biomass:

$$LAI = 0.00594 \times Drymass(g) \tag{1}$$

2.5. Soil water, wet deposition, and throughfall

N fluxes were quantified using the same methods as in Bergholm et al. (2003). Soil water was collected between August 1988 and May 2011 in ceramic tension lysimeters (P80) installed at 50 cm depth in the mineral soil. In total, 7 lysimeters were placed in each plot, located along a 2.5 m wide L-shaped sampling area in one corner of the net plot, with the acute angle pointing to the center of each plot. Some lysimeters were damaged by the storm and were replaced in 2005, always > 2 m from piles of residues to avoid a biased influence from these residues on soil water composition (Ring et al. 2015). Samples were collected approximately four times a year, mainly in spring and autumn. Samples from each lysimeter were stored frozen. Before analysis, pH and conductivity were measured on thawed samples. Samples of<50 mL were discarded, and the remaining samples were pooled by weight to a single sample per plot and sampling occasion, for further chemical analysis. The IF plot in block 3 was damaged to one-third by the storm. Soil water samples were pooled for the whole plot in 2004–2006, but samples from disturbed (2 lysimeters) and undisturbed parts (5 lysimeters) of the plot were thereafter pooled separately. In calculation of N leaching in undisturbed IF plots, lysimeter data from block 2 (2004–2010) and from undisturbed parts of block 3 (2006–2010) were used.

Prior to the storm, throughfall was sampled monthly in the four replicate 0 treatment plots, using six funnels per plot placed in a grid pattern and equipped with dark polyethylene containers for water collection. In the period 2005–2010, throughfall was only collected in the undamaged 0 plots. Open field (OF) precipitation was initially collected monthly on a storm-felled area at Skogaby, but this approach was replaced in 2006–2010 with measurements at least twice a month in the Tönnersjöheden experimental forest, Simlångsdalen (19 km north of Skogaby). Calibration between earlier OF precipitation data from Skogaby and Tönnersjöheden was performed based on data obtained from both locations during six months in 2005.

The amount of water in each collector for throughfall and OF precipitation was measured, and 100 mL per sample were stored in the freezer before chemical analysis. pH and conductivity were measured in each sample. Samples with highly divergent pH and conductivity values due to, e.g., bird droppings were discarded. Samples from throughfall and OF were combined on a volume basis. N deposition with throughfall and OF precipitation was calculated using the concentration of ammonium-N and nitrate-N on each sampling occasion multiplied by the amount of throughfall/precipitation at that sampling event.

2.6. Chemical analyses

The pH in soil water, throughfall, and OF precipitation was determined using a glass electrode. Inorganic N in soil water, throughfall, and OF precipitation samples was analyzed photometrically for ammonium-N and NO_2^--N + NO_3^--N (considered as nitrate-N) using a FIA STAR 5010 Analyzer. The N content in vegetation biomass (see section 2.7) was analyzed using a dry oxidation method (Carlo Erba NA 1500 instrument). Biomass samples were dried at 70 °C to constant weight and milled before analysis.

2.7. Deposition and substance transport

The amounts of N deposition in throughfall (per plot) and OF precipitation were summed annually. The daily concentration of ammonium and nitrate in the soil solution at 50 cm depth in the mineral soil was calculated by linear interpolation between sampling occasions. These values were multiplied by the simulated daily flow of water at that depth, and the amounts of N were summed annually.

2.8. Ground vegetation

Vegetation coverage analysis started in late July-early August 2006, one year after the storm. Vascular plant coverage was determined based on species in the L-shaped 66 m^2 sampling area for soil water, through a point-intercept method where plant coverage was estimated at 16 spots in each sampling area using a 0.5 m × 0.5 m wooden frame with height-adjustable legs and thin wires that divided the frame into smaller sections. Species hits were recorded at the reticle of wires (max. n = 16). This means that for 100% coverage by a species, a total of 256 hits within the sampling area was required. Other species observed in the frame, but not registered as a hit at a reticle, were recorded by presence (the score given was 0.5 of 1/16). Presence of other species observed within the plot, but not observed in the subplot frames, was given a score of 0.1 of 1/16. Species richness was calculated as the total number of vascular species observed in each plot.

Aboveground biomass of the ground vegetation was determined in the sampling area in conjunction with coverage analysis, using a 0.4 m × 0.4 m wooden frame at five sampling points per plot. Mosses were not included, and destructive sampling was not performed in spots used for plant coverage analyses. N concentration in aboveground biomass was calculated by multiplying N content in biomass (% of dry matter, d.m., see section 2.5) by biomass per unit area.

2.9. Relationship between N in soil water and vegetation coverage

A separate spot-scale study was made in early July 2008 to examine the relationship between vegetation coverage and soil water N content in storm-felled plots in the 0, V, and IF treatments. At this time after storm felling, N leaching was expected to be high and ground vegetation had not yet reached full coverage. In each plot, four 1 m^2 sampling squares were selected, based on the criterion of obtaining a range of vegetation coverage levels from zero to full coverage in each plot. The ground vegetation was still heterogeneous and vegetation-free spots were abundant in most plots. Plant coverage was estimated in the 1 m^2 sampling square, using the same method as applied for the main plots. Soil samples were taken with a 5-cm diameter steel corer to a depth of 20 cm in the mineral soil. The soil core was subdivided into humus layer and 0–10 and 10–20 cm mineral soil layers. The soil solution in the cores was expelled by centrifugation and then analyzed for nitrate and ammonium as described in section 2.5. Due to normal rainfall in June and July 2008, soil water availability was sufficient for extraction.

2.10. 9 statistical analyses

The Skogaby experiment originally had a randomized block design with four blocks and with one replicate of each treatment in each block (n = 4). Mixed-model ANOVA was applied to test the effect of treatment and year in storm-felled plots, based on the original blocking. Treatment, year, and interactions between treatment and year were considered fixed effects, and block was considered as a random effect. Dependent variables were nitrate-N leaching, vegetation coverage, biomass, biomass N, and species richness. Due to the disturbed design of the experiment, the two storm-felled 0 plots (blocks 2 and 3) were compared with V plots in the same block (hereafter denoted V_0), and the two storm-felled IF plots (blocks 1 and 4) were compared with V plots in the same block (hereafter denoted V_{IF}). Thus, no direct comparison of the 0 and IF treatments was made (Table 1). In addition, two-way ANOVA was used to test the effect of treatment and block by year, using the same block design as above. Correlation (row-wise method) analyses were made between nitrate leaching, vegetation coverage, biomass, biomass N, and species richness. Correlation analyses were performed by year, and for the period 2006–2010. All statistical analyses were performed in JMP version 15.0.

3. Results

3.1. Water flux

Precipitation in storm-felled plots (OF measurements) was on average 1370 mm yr^{-1} during the period 2005–2010, which was 54% higher than the water flux in throughfall in the undisturbed plots (888 mm yr^{-1}). Open-field precipitation during this period was 20% higher than the site average for the period 1989–1998. The highest annual precipitation in storm-felled plots (1681 mm) occurred in 2007 (Fig. 2).

The simulated LAI range was 6–9 in undisturbed forest and 0.2–1.5 in storm-felled plots (Supplementary Figure S1). The much lower LAI reduced transpiration and increased infiltration in the storm-felled plots, so simulated runoff below 50 cm depth in storm-felled plots was twice as large (1070 mm) as in the undisturbed plots (550 mm) during the period 2005–2010. A linear regression between storm-felled (SF) and undisturbed forest plots (UF) with respect to simulated daily infiltration (I) at the soil surface resulted in the regression equation $= 1.25 + 1.14 \times I_{UF}$ ($R^2 = 0.791$). The corresponding regression equation for daily runoff at 50 cm depth (Q) was $Q_{SF} = 1.13 + 1.18 \times Q_{UF}$ ($R^2 = 0.68$).

3.2. Inorganic N concentration in soil water

Inorganic N concentration in soil water before the storm (2003–2004) was very low in all treatments (<0.01 mg L^{-1}) (Fig. 3). It

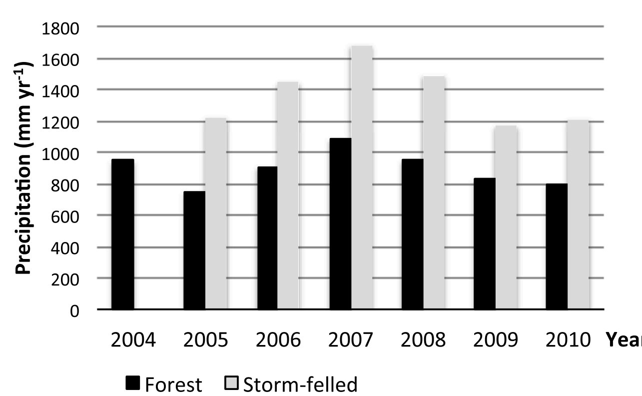

Fig. 2. Precipitation (mm yr^{-1}) in undamaged forest (black) and storm-felled (grey) experimental plots before (2004) and after (2005–2010) storm-felling in January 2005.

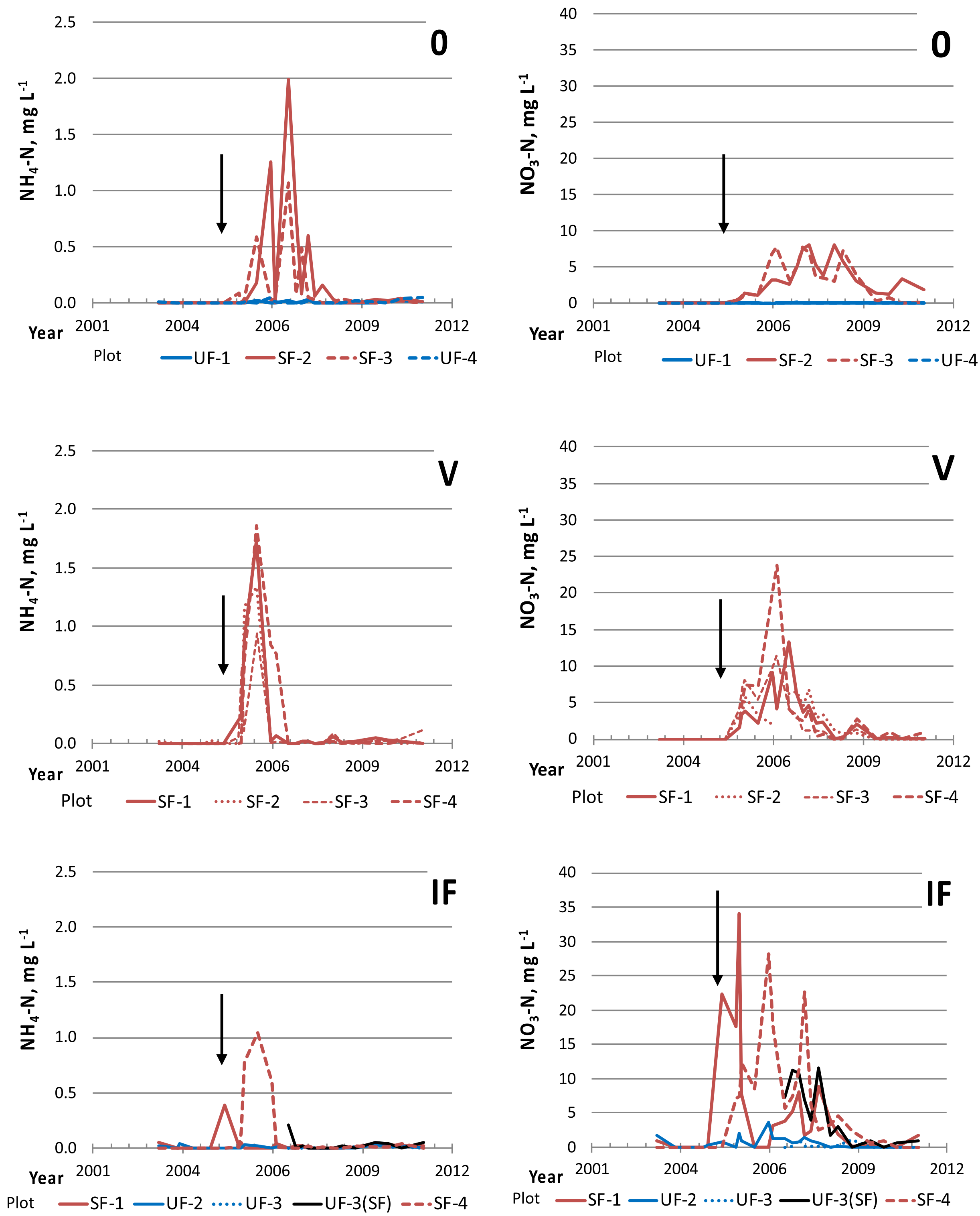

Fig. 3. Concentrations of NH_4^+-N (left panel) and NO_3-N (right panel) in soil water at 50 cm soil depth in the 0, V, and IF treatments at Skogaby, 2003–2011. Arrows indicate the storm-felling event (January 2005). Storm-felled (SF) plots are indicated by red lines and undisturbed (UF) plots by blue lines, while different numbers (1–4) indicate blocks. For the IF treatment, 'UF-3'indicates the undisturbed part of IF block 3 (2007–2010), while 'UF-3(SF)' indicates the storm-felled part of the same plot and period (black solid line). The sampling in 2004–2006 did not separate storm-felled from undisturbed parts of the plot (data not shown). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

remained low (<0.01 mg L^{-1}) in the 0 plots with undamaged trees and relatively low in the undamaged IF plots (range 1–5 mg L^{-1}) after the storm in January 2005. Elevated ammonium-N concentrations in soil water were observed in storm-felled 0, IF, and V plots (Fig. 3). The highest peaks in ammonium-N concentrations were found in 0 plots, where they also occurred later (2006–2007) than in V and IF plots.

In contrast to ammonium-N, nitrate-N concentrations peaked earlier in disturbed IF plots (2005–2007) and were higher than in disturbed 0 plots (2006–2008). In the V plots, peaks in nitrate-N concentrations were lower than in IF plots, but higher than in 0 plots, and the period of peak levels was shorter (2006–2007).

3.3. Fluxes of inorganic N in deposition and runoff

N deposition in 2004–2010 was on average 10.2 kg ha^{-1} yr^{-1} in storm-felled plots (OF precipitation) and 14.8 kg ha^{-1} yr^{-1} in forest plots (measured as throughfall), and contained nitrate and ammonium in similar proportions (Table 3). The higher average deposition in undamaged plots was mostly an effect of the higher throughfall deposition during 2007–2010.

Annual losses of inorganic N at 50 cm soil depth mainly consisted of nitrate (Fig. 4). Leaching of ammonium-N was 1.6% of total inorganic N in the forest and 4.9% in storm-felled plots. In the following, only leaching of nitrate-N is discussed. Leaching of nitrate-N in storm-felled plots showed a bell-shaped curve that reached maximum levels during the second and third year following disturbance and approached pre-disturbance levels in the fifth and sixth year. In both comparisons (0 *vs* V_0, IF *vs* V_{IF}), nitrate leaching showed significant differences between years, but no significant difference between the treatments (mixed model tests). Two-way ANOVA revealed significantly higher nitrate leaching in the 0 and IF treatments than in the V treatment in 2008 and 2009, indicating a treatment effect on differences in temporal dynamics at onset and decline of leaching in storm-felled plots. Nitrate leaching in V_0 plots increased and declined earlier than in 0 plots. Leaching started earlier and declined later in IF than in V_{IF} plots (Fig. 4). In the undisturbed plots, nitrate-N leaching was substantially lower than in the storm-felled plots, i.e., on average 0.05, 0.17, and 5.3 kg ha^{-1} yr^{-1} in 0, I, and IF plots, respectively (Fig. 4, right panel).

Accumulated nitrate leaching 2005–2010 was not significantly (p = 0.18) different in disturbed 0 (233 kg N ha^{-1}) and V_0 (180 kg N ha^{-1}) plots, but was significantly higher in IF (414 kg N ha^{-1}) than in V_{IF} plots (256 kg N ha^{-1}) ($p < 0.01$) (Fig. 5). This indicates that accumulated leaching was also lower in disturbed 0 than in disturbed IF plots, because leaching was lower in V_0 than in V_{IF}.

3.4. Vegetation development and N content

There was no significant difference between treatments across years (mixed model) with respect to ground vegetation biomass or N stocks in biomass. However, tests for single years using two-way ANOVA revealed significantly higher biomass and higher N stocks in biomass in the V treatment than in the 0 and IF treatments in the latter part of the period (Fig. 6a and 6b). The N content in aboveground biomass reflected the temporal changes in vegetation coverage, with the highest mean values of N stocks in V and the lowest in IF plots (Fig. 6b).

Vegetation analyses commenced in 2006, the second summer after storm-felling. Vegetation coverage in the first summer after the storm was thus not recorded, but the degree of cover was probably low as the ground vegetation in undisturbed plots was dominated by mosses and had virtually no field layer. In the following years (2006–2010), wavy hairgrass (*Deschampsia flexuosa*) was initially the dominating species in the 0 treatment, and this species later became dominant in all storm-felled plots, followed by *Betula pendula* Roth, *Carex pilulifera* L., *Rubus idaeus* L., and *Calluna vulgaris* (L.) Hull. In addition, *Senecio sylvaticus* L. was abundant in the V treatment, together with *R. idaeus* and *Agrostis capillaris* L. (Fig. 6c, 6d, Supplementary Table S2). Vegetation coverage was significantly higher in the V treatment than in the 0 and IF treatments in the initial years (two-way ANOVA), and a significant effect of treatments was revealed by the mixed-model test (Fig. 6c).

Species richness was significantly influenced by the treatments (mixed model), with the highest number of species in V plots (Fig. 6e). The species in V plots mostly consisted of forbs and graminoids (Supplementary Table S2).

Table 3
Annual deposition of inorganic N (NO_3-N + NH_4-N), kg ha^{-1} yr^{-1}) at Skogaby. Open-field precipitation estimated in storm-felled plots and throughfall in undisturbed forest.

Year	Open-field precipitation			Throughfall		
	NH_4-N	NO_3-N	Sum N_{inorg}	NH_4-N	NO_3-N	Sum N_{inorg}
2004	6.5	6.2	12.7	3.6	4.1	7.7
2005	4.0	5.0	9.0	6.1	7.1	13.2
2006	6.9	7.8	14.7	8.3	7.3	15.6
2007	4.7	6.2	10.9	7.3	7.0	14.3
2008	3.9	5.7	9.6	9.7	9.2	18.9
2009	2.9	4.1	7.0	11.8	10.4	22.2
2010	3.7	3.6	7.3	5.4	6.4	11.8
Total	32.6	38.6	71.2	52.2	51.5	103.7
Average 2004–2010	4.7	5.5	10.2	7.5	7.4	14.8

3.5. Correlation between nitrate leaching and vegetation coverage

Nitrate leaching in 2006–2010 was generally negatively correlated with ground vegetation biomass, N stocks in biomass, vegetation coverage, and species richness (Table 4), supporting our first hypothesis (H1). However, the correlations were not very strong except for the positive correlation between vegetation biomass and N content in the same biomass. This was expected, and indicated little variation in N concentrations in the above-ground biomass. The highest negative correlation for independent measures was between vegetation coverage and nitrate leaching (r = −0.65). Correlation analyses by year showed that correlations between leaching and vegetation variables changed markedly over time. The strongest negative correlations occurred in 2008, 1–2 years following the peak in nitrate leaching in 2006–2007 (Fig. 4, Fig. 6f).

3.6. Vegetation coverage and inorganic N in soil water

A negative relationship between vegetation coverage and inorganic N in soil water was observed in the spot tests conducted in July 2008 (Fig. 7). In spots with full plant coverage (100%), nitrate and ammonium concentrations were all low, particularly in the 0–10 cm mineral soil layer. A similar negative relationship between vegetation coverage and soil water nitrate concentration was observed at plot scale for the period 2006–2010 (Fig. 8). The graph in Fig. 8 indicates treatment effects in the time trajectory of changes in plant coverage and nitrate leaching. In IF plots, nitrate concentrations declined and reached their lowest values at only about 50% vegetation coverage, whereas low concentrations were associated with fuller vegetation coverage in 0 and V plots.

4. Discussion

4.1. General effects of storm-felling and clear-cutting

Storm Gudrun caused severe disturbances to the Skogaby spruce stand that in many respects resembled the effects of clear-cutting, as all trees were felled over large parts of the study area, leaving a mixture of broken stems and uprooted trees. Storm-felled trees and some of the logging residues were harvested one year after the storm, so it was not surprising that soil water N concentrations and N leaching was markedly elevated in storm-felled plots across all treatments. The findings for the 0 treatment plots were in agreement with observations in other studies of high nitrate leaching following Storm Gudrun. For example, at the regional scale in southern Sweden, soil water nitrate concentrations increased for 1–4 years, with the highest nitrate concentrations (3–8 mg L^{-1}) in disturbed areas where all trees had blown down (Hellsten et al. 2015). Löfgren et al. (2014b) found large variations in nitrate concentrations in soil water for a semi-natural Norway spruce forest in southeast Sweden that was partly felled by the storm and later attacked by bark beetle. Soil water in the recharge area in that study showed

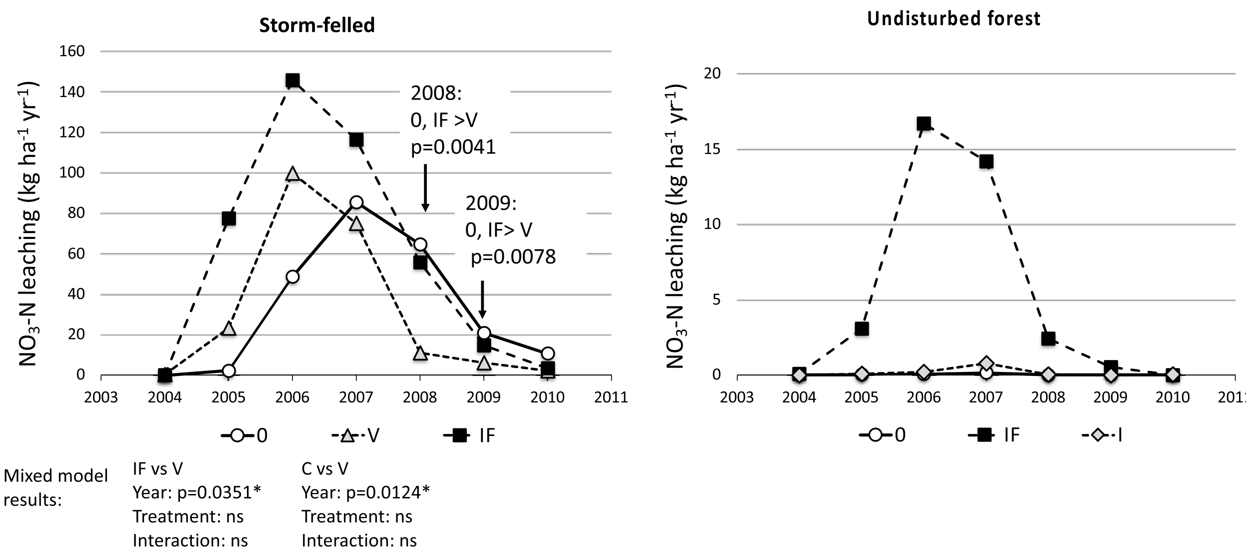

Fig. 4. Mean annual (n = 2) NO_3-N leaching at 50 cm soil depth in storm-felled 0, V, and IF plots at Skogaby, 2005–2010 (left panel), and corresponding leaching in undisturbed forest plots in the 0, I and IF treatments (right panel). Data from 'undamaged' IF block 3 in 2005–2006 are excluded because soil water from the damaged part of the plot was included in analyses, but data from the same plot in 2007–2010 included only samples from the undamaged part. All plots of the I treatment were undisturbed (i.e., n = 4). The main storm-felling event occurred in January 2005. Results of mixed model tests and ANOVA by year are shown for $p < 0.05$.

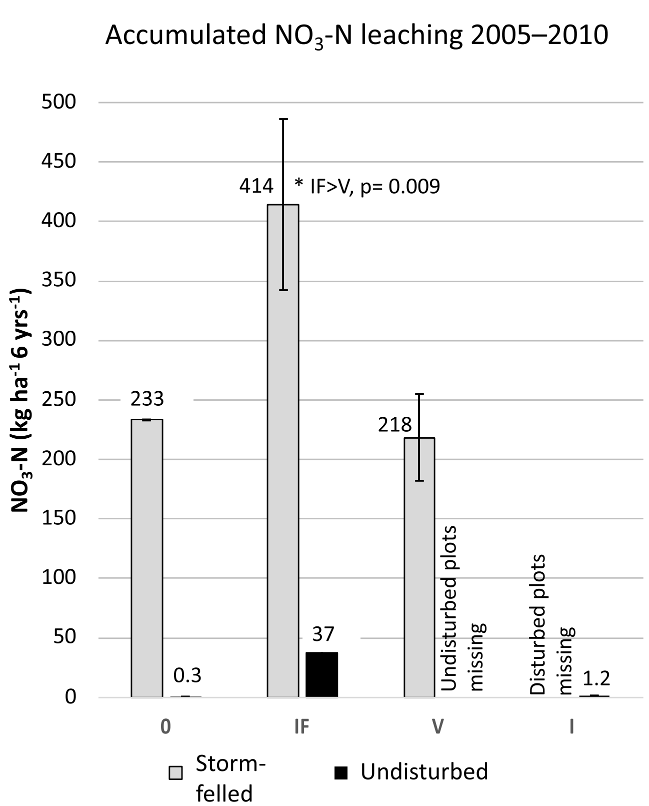

Fig. 5. Treatment means (±SE) of accumulated NO_3-N leaching (kg ha^{-1}) at 50 cm depth during the period 2005–2010. A significant difference between V and IF is indicated (ANOVA). Grey bars = storm-felled stand, black bars = undisturbed stand.

concentrations > 5 mg NO_3-N L^{-1}.

Annual nitrate leaching in storm-felled plots in all treatments at Skogaby was higher than values reported in most other comparable studies of clear-cutting in the Nordic countries. A literature review of average losses of total N following clear-cutting in the Nordic countries reported an increase from 1.3 (range 0.9–2.0) before harvest to 4.9 (range 2.3–9.5) kg ha^{-1} yr^{-1} up to 5 years after harvesting (Bloem et al. 2020). Higher fluxes were found in studies in Norway, which were assumed to be an effect of the higher precipitation in Norway than in other Nordic countries (Bloem et al. 2020). The high precipitation at Skogaby may thus have contributed to the high N losses at this site.

In a wider geographical perspective, the C/N ratio in forest soils tends to decrease along a gradient from northern Sweden to southern Germany, with ratios below 25 associated with higher N supply to plants and increased probability of high nitrate leaching and gaseous losses of nitrous oxide (N_2O) following clear-cutting (Högberg et al. 2021). N losses from clear-cut areas are also reported to be higher in southern Sweden (temperate, hemi-boreal) than in the boreal northern regions, although the period with elevated nitrate flux is shorter in southern Sweden than in northern Sweden and Finland (Grip 1982, Rosén 1982, Ring 1995, Kubin 1998, Löfgren 2007, Futter et al. 2010).

The decreasing C/N gradient from northern Sweden to southern Germany is also associated with increasing chronic N deposition, which is considered to increase the risk of nitrate leaching following clear-cutting and even from growing forests. Within southern Sweden, there is also a west-to-east gradient from high to low N deposition. Akselsson et al. (2004) predicted that nitrate laverage > 20 kg ha^{-1} yr^{-1} in the western area near Skogaby and < 5 kg ha^{-1} yr^{-1} at the same latitude in eastern Sweden. The predicted gradient in nitrate leaching is in accordance with the deposition gradient, and higher leaching in the west was reinforced by higher runoff. Thus, nitrate leaching at Skogaby, and in the study by Örlander et al. (1997) at Tönnersjöheden near the west coast, appears to be at the high end in a Swedish context. However, the N leaching at Skogaby is comparable to nitrate leaching from clear-cut Norway spruce forests reported by Huber et al. (2010) for southern Germany (Höglwald) and Ireland (Ballyhooly).

The German Höglwald site is an example of N saturation in Europe, indicated by the fact that nitrate leaching (≈ 40 kg ha^{-1} yr^{-1}) in uncut stands was higher than N deposition (throughfall ≈ 25 kg ha^{-1} yr^{-1}) (Huber et al. 2010, Binkley and Högberg 2016). Nitrate leaching from undisturbed 0, V, and I plots at Skogaby was negligible, despite this region having received N deposition of the same order of magnitude as in Höglwald. There was thus no strong evidence of N saturation in the 0 plots at Skogaby before storm-felling. Differences in stand age and nutrient demand were probably a contributing factor to the differences

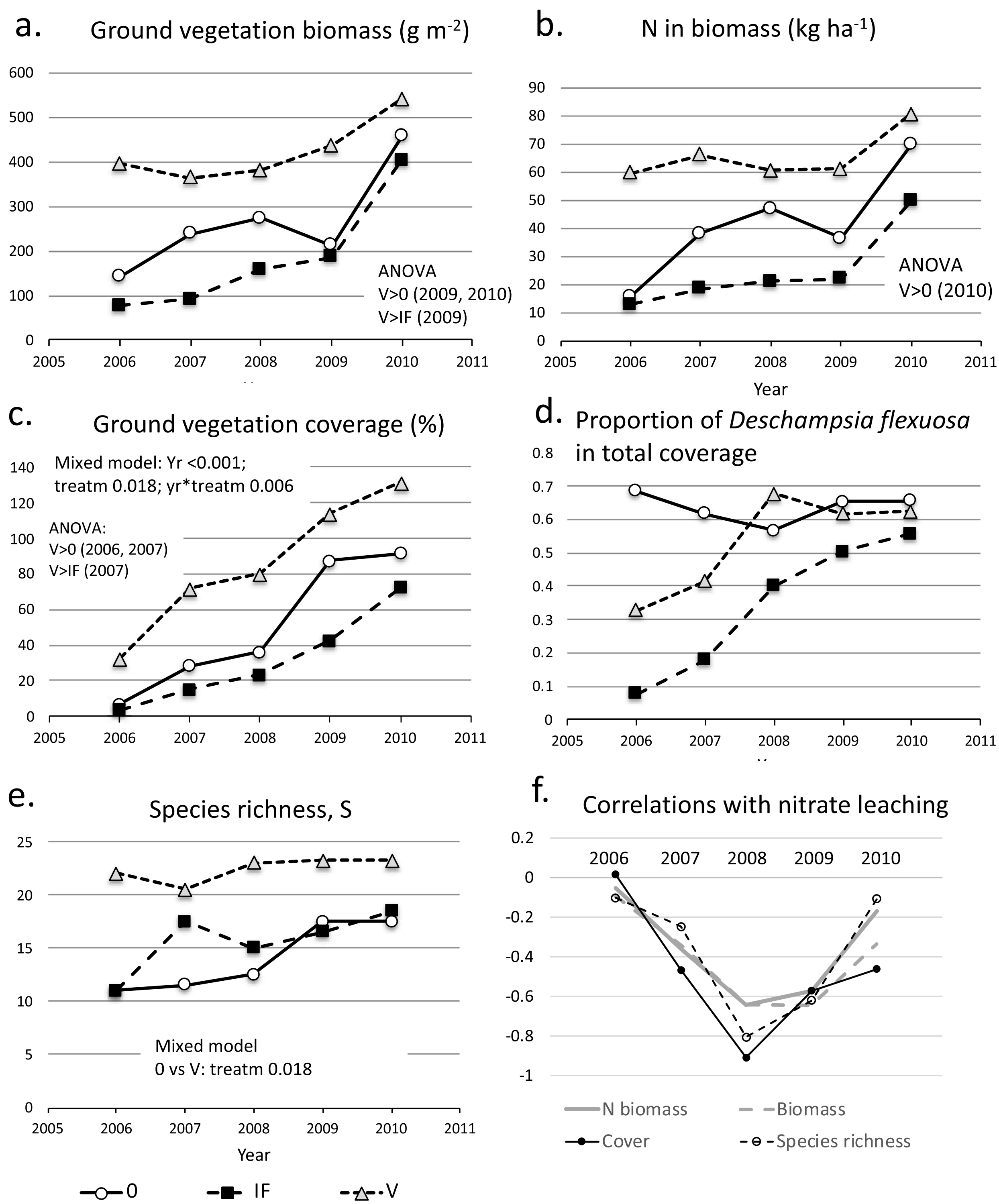

Fig. 6. a-f) Ground vegetation changes in storm-felled 0, V, and IF plots at Skogaby during the period 2006–2010. Results (p-values) of mixed model tests are shown for $p < 0.05$, and significant differences between treatments by year (ANOVA) for (a), (b), (c), and (e). The observations started in 2006, one year after storm-felling. (a) Aboveground summer biomass of ground vegetation (kg dry matter (d.m.) ha^{-1}), (b) aboveground summer nitrogen stocks in biomass (kg N ha^{-1}), (c) ground vegetation coverage (%), (d) proportion of *Deschampsia flexuosa* in total ground vegetation coverage, (e) species richness, and (f) correlations by year between nitrate leaching and vegetation biomass, N in biomass, plant coverage, and species richness.

in N status and nitrate leaching, as the Höglwald forest was approximately 90 years of age and the Skogaby stand was 42 years at storm-felling. The N stocks in the O-horizon and the upper mineral soil (0–30 cm) at Höglwald (4.0 Mg ha^{-1}) were similar to the stocks at Skogaby (Table 2), but C/N ratio was lower at Höglwald (O-horizon including litter 25, mineral soil 0–30 cm 17.5) (Kreutzer and Weiss 1998), indicating potential for higher N mineralization rate in relation to N stocks compared with Skogaby.

Table 4
Correlations across treatments and years between NO_3-N leaching (kg ha^{-1} yr^{-1}) and nitrogen stocks in ground vegetation biomass (kg N ha^{-1}), vegetation biomass (kg dry matter, d.m., ha^{-1}), vegetation coverage (%) and number of species (plot^{-1}) in storm-felled plots in the 0, IF, and V treatments at Skogaby 2006–2010 (total n = 160). Significant correlation coefficients >|0.5| in bold.

	NO_3-N leaching	Biomass N	Biomass d.m.	Vegetation coverage	Number of species
Nitrate leaching	1.00				
Biomass N	−0.31	1.00			
Biomass	−0.37	**0.97**	1.00		
Coverage	**−0.65**	**0.61**	**0.61**	1.00	
Number of species	−0.37	0.55	0.55	**0.60**	1.00

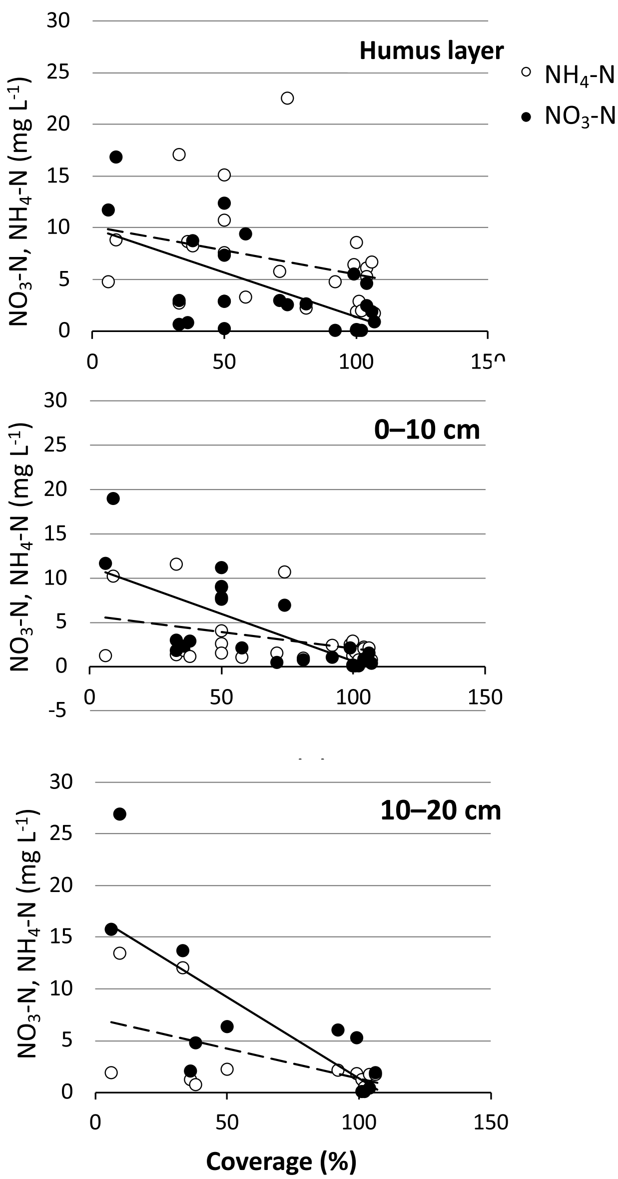

Fig. 7. Soil water concentrations of NH_4-N and NO_3-N (mg L^{-1}) in different soil horizons in relation to vegetation coverage (%) in July 2008, the third year following storm-felling at Skogaby. The data show spot-scale (≈ 1 m^2) correlations between plant coverage and NO_3-N (filled symbols, solid regression line) and NH_4-N (open symbols, dashed regression line) in soil water, measured in storm-felled 0, V, and IF plots.

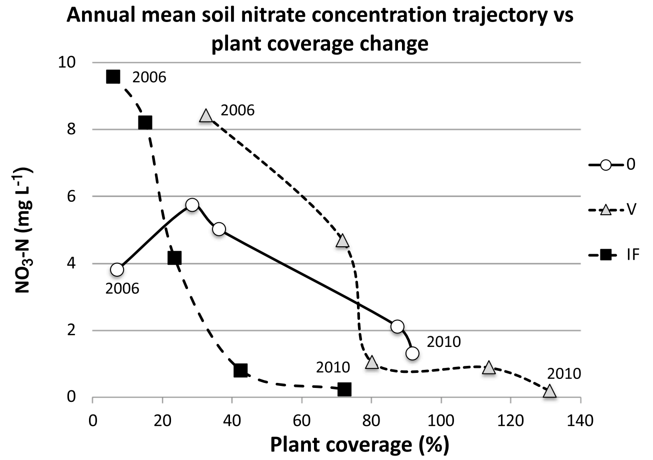

Fig. 8. Change in NO_3-N concentrations (mg L^{-1}) in soil water (50 cm) in relation to vegetation coverage (%) during 2006–2010. Means for treatments 0, V, and IF (n = 2), measured at the plot scale. Each line shows the time trajectory going from left (2006) to right (2010). The storm-felling event occurred in January 2005.

4.2. *Vegetation response to treatments and effect of vegetation on N leaching*

The V treatment enhanced the establishment of ground vegetation in terms of coverage and species richness. Surprisingly, the IF treatment had no such effects despite its substantial content of base cations (Supplementary Table S1). The effect of V was likely due to the dolomite component in its fertilizer mixture, although the pH increase in the V treatment was relatively small (0.35 units) in comparison with the 0 treatment (Rangfeldt 2005). Other studies in Sweden have demonstrated that previous applications of calcite lime, dolomite lime, and wood-ash can increase species richness in vegetation recovery following clear-cutting (Olsson and Kellner 2002, Bergholm et al. 2015). The mechanism behind this effect is not well known. However, a large part of the additional species in the V treatment were probably recruited from the soil seed bank (Supplementary Table S2), indicating that the V treatment stimulated breaking of seed dormancy in these species.

Our hypothesis that rapid establishment of ground vegetation facilitates a rapid reduction in nitrate leaching (H2) was supported in a general sense by the negative correlation between vegetation coverage and nitrate leaching. The fact that the negative correlation reached the maximum value one year after the peaks in nitrate leaching indicates that vegetation control of leaching gradually became more marked. Unexpectedly, the negative correlation between nitrate leaching and vegetation variables was stronger for plant coverage than for biomass or N stocks in biomass. This difference might reflect shortcomings in sampling very heterogeneous vegetation. A larger area was used in coverage measurements (4 m^2) than in vegetation biomass sampling (0.8 m^2) in each plot. Hypothesis H2 was also supported by the spot-scale analyses of nitrate concentrations in relation to vegetation coverage. However, that spot-scale study was made in early July, when plant N demand can be expected to be highest, and the results may therefore give a biased view of the average conditions across all seasons. Nevertheless, the results clearly demonstrate the potential for N retention by plants, as there was little nitrate-N available at 10–20 cm soil depth under full vegetation coverage. This agrees with findings in similar studies of N dynamics following clear-cutting in southern Sweden (Hedwall et al. 2015, Bergholm et al. 2015). However, our hypothesis H3, that high species richness contributes to low nitrate leaching, received limited support from the results obtained in this study. This probably reflected the marked dominance of *D. flexuosa* (Fig. 6d). Thus, the high number of additional species established in the V treatment seemed to have a relatively restricted incremental effect on plant N uptake.

The biomass and N content in ground vegetation in storm-felled plots were larger in the V than in the IF treatment, and thus our hypothesis H4 was rejected. The fast recovery of vegetation in the V treatment compared with IF may have shortened the period of high N leaching in V. However, despite slow vegetation recovery in IF plots, which at most reached 50% plant coverage, nitrate concentrations in soil water declined to near baseline values. This suggests that leaching in IF plots declined due to causes other than merely plant uptake.

4.3. Effects of previous fertilization on N leaching

The results supported our hypothesis H1 in several ways. Cumulative nitrate leaching was higher in IF plots than in V_{IF} plots, and nitrate-N concentrations were occasionally more elevated also in undisturbed IF plots compared with undisturbed 0 and I plots. The higher (accumulated) leaching in IF plots seemed to be due to the combination of higher peak fluxes and earlier onset of nitrate flux compared with V and 0 plots.

The higher leaching in IF plots can have several causes. Fertilizer N can have a direct influence on N leaching if fertilization occurs shortly before disturbance, but that was not the case in Skogaby. Repeated fertilization causes increased leaching if fertilization results in increased forest growth, and hence increased soil organic matter accumulation and ultimately higher N mineralization rates. A qualitative change in soil organic matter, such as a decrease in C/N ratio, can also result in increased N mineralization. In accord with this, it has been concluded that predicted nitrate leaching is more strongly correlated with N field mineralization rate than with previous N inputs from deposition and fertilization (Andersson et al. 2002). That study examined indicators of N leaching in forests, including that at the Skogaby site (treatments 0 and IF, before storm-felling). The higher initial nitrate leaching in the IF treatment seen in the present study was therefore likely an effect of the higher N stock, and significantly lower C/N-ratio (26 *vs* 29) in the O-horizon and higher N net mineralization rate than in the 0 and V treatments (Table 2). In addition, the higher nitrate-to-ammonium ratio of mineralized N reported by Rangfeldt (2005, Table 2) indicated a high activity of nitrifying microorganisms in the IF plots prior to the disturbance.

To facilitate comparison between the present study and other similar field studies, a compilation of accumulated N leaching the first four years following clear-cutting or storm-felling is provided in Table 5. All sites contained Norway spruce stands and, except for the Höglwald site in southern Germany and the Aneboda site in Sweden, all included long-term fertilization prior to clear-cutting. In parallel with the present study, Hedwall et al. (2013) examined nitrate fluxes in soil water and dynamics in a fertilization experiment following clear-cutting at Asa (114 km northeast of Skogaby). The treatment at Asa was similar to that at Skogaby with respect to total N dose, duration of fertilizer treatment, nutrient proportions in fertilizer admixture, and fertilizer effect on C sequestration in tree biomass, ground vegetation biomass, and N content. Despite these similarities, nitrate leaching in Asa was only a fraction of that in Skogaby (Table 5). This indicates that factors other than N fertilizer load or differences in biomass were more significant explanations for the differences between Asa and Skogaby. Runoff at Skogaby was about twice that at Asa, suggesting that water availability was particularly important.

Table 5
Four-year accumulated NO_3-N leaching (kg ha^{-1} 4 yrs^{-1}) following clear-cutting or storm-felling (this study) at Swedish field N fertilization experimental sites and the German Höglwald site.

Site	Lat. Long.	Disturbance	Precip./ runoff mm yr^{-1}	Treatment[a]	N fertilization[b] accum. dose, N, kg ha^{-1}	Mean C seq. in tree biomass in excess of control[c] (Mg ha^{-1} yr^{-1})	4-year accumulated nitrate-N leaching^2 N, kg ha^{-1}	Reference
Skogaby,	56°33′N	Undisturbed		0			0.3	This study
Sweden	13°13′E	Undisturbed		IF	890	2.11	34	
		Storm-felled	1270/980	0			201	
		Storm-felled		IF V	890	2.11 0	398 209	
		Storm-felled						
Asa, Sweden	57°08′N 14°45′E	Clear-cut	730/530	0, SOH			55	Hedwall et al. 2013
		Clear-cut		0, WTH			61	
		Clear-cut		F, SOH	1000	2.75	82	
		Clear-cut		F, WTH	1000	2.75	38	
Farabol, Sweden	56°26′N 14°35′E	Clear-cut	670/544	0			50	Bergholm et al. 2015
		Clear-cut		U-F	600	0.61	27	
		Clear-cut		Lime			29	
		Clear-cut		S			75	
Aneboda[d]	57°05′N	Undisturbed	840/370	Semi-natural forest			0.1	Löfgren et al. 2014b
Sweden	14°32′E	Storm-felled	780/320	Semi-natural forest			0.8	
		Storm-felled + bark beetle killed	790/310	Semi-natural forest			2.0	
Höglwald	48°29′N	Undisturbed					162	Huber et al. 2010
Germany	11°04′E	Clear-cut,	947/898	SOH, Planted			331	
		Clear-cut,	947/702	SOH, Natural regeration			115	

[a] Treatments are: 0 = control; IF = repeated fertilization and irrigation; SOH = stem-only harvest; WTH = whole-tree harvest; F = repeated fertilization; U-F = repeated urea-N fertilization; Lime = calcite limestone; S = elemental sulfur (acidification). Treatment IF is described in Table 1, nutrient proportions in treatment F (N:P:K:Ca:Mg) were 100:32:58:7:18 (Albaugh et al. 2009).

[b] Accumulated N dose at Skogaby (1988–2001), Asa (1988–2003), Farabol (1976–1985).

[c] Effect of N fertilization on growth: mean carbon sequestration in tree biomass in excess of control (0), from Hyvönen et al. (2008).

[d] Aneboda data shows situation before Storm Gudrun, the first 4 years after storm-felling by 15%, and 4 years following attack by bark bettles where most spruce trees were killed.

The study at Asa also included different harvesting treatments. Leaving logging residues on-site at Asa increased accumulated leaching during the first four years to a small extent in control plots, but caused substantial increases in fertilized plots. Logging residues were partly harvested at Skogaby, so the influence of residues left on-site was likely lower than in the slash retention treatment at Asa.

Nitrate leaching following clear-cutting at the Farabol experiment (850 km east of Skogaby) was of the same order of magnitude as reported for Asa (Table 5). N leaching in the Farabol urea plots was lower than in control plots (Ring et al. 2003). An N budget indicated that uptake in ground vegetation and immobilization in stump and tree root biomass were important N sinks, and that treatment differences in leaching were largely due to differences in vegetation development (Bergholm et al. 2015). N immobilization in coarse woody debris was probably also the major cause to low nitrate discharge from the semi-natural forest at Aneboda (Table 5; Löfgren et al. 2014b).

Nitrate leaching at the German Höglwald site was already very high in an undisturbed stand, and clear-cutting of the Norway spruce stands resulted in a further increase in nitrate leaching during the first year (Table 5). Accumulated four-year leaching approached the level in storm-felled Skogaby plots.

4.4. Decline in nitrate leaching to pre-disturbance levels after six years

A major finding in this study was that for all treatments, nitrate leaching showed a bell-shaped curve with maximum leaching at 2–4 years after storm-felling followed by rapid declines to approach pre-disturbance levels. This decline in leaching can be due to simultaneous changes in inorganic N sources and sinks. As shown above, vegetation recovery was probably a significant N sink, but does not fully explain the decline in nitrate leaching, especially in storm-felled IF plots. Thus, our hypothesis H5 was only partly supported by the results. A decline in N sources can be an effect of a decrease in easily degradable N compounds originating from the harvested stand, e.g., slash, fine roots and dead mycorrhizal fungi. On the other hand, decay of stumps and coarse roots can cause substantial N immobilization, lasting for several years, due to low N concentration and slow decomposition rate (Brais et al. 2006, Palviainen et al. 2010, Hyvönen et al. 2013, Löfgren et al. 2014b, Bergholm et al. 2015). Denitrification was another potential N sink at Skogaby, considering the high precipitation and abundance of nitrate. However, denitrification was not measured at the site and remains an unknown process.

We can only speculate about the role of N immobilization in nitrate leaching at Skogaby. The belowground biomass of fine and coarse root biomass at the time of storm-felling had been influenced by the previous treatments. The V treatment had lower fine root biomass than the 0 and IF treatments (Rangfeldt 2005, Table 2), whereas total belowground biomass was highest in the IF treatment. At the time of thinning four years before storm-felling, belowground biomass was 35% greater in IF than in the 0 and V treatments (Table 2). Further, N dynamics (immobilization and net mineralization of N) can be expected to proceed more rapidly in decomposing fine roots than in coarse dead wood, and a lag-phase in colonization by decomposers can be expected to increase with increasing physical dimensions of the litter (Hyvönen et al. 2001). Thus, the relatively high initial nitrate leaching in V plots despite rapid vegetation establishment can be partly explained by initially lower N immobilization rates in fine-root litter. On the other hand, in the late phase of the study period immobilization in woody litter of coarser dimensions could have been more important. This lag in N immobilization is a possible explanation for why nitrate leaching in IF plots was reduced despite lower vegetation coverage compared with the V and 0 treatments.

5. Conclusions

Analysis of N leaching following storm-felling of a Norway spruce stand showed three main characteristics consistent with earlier findings for similar systems and conditions. These were: (1) a marked increase in nitrate leaching compared with pre-disturbance conditions, (2) a dominance of nitrate over ammonium in soil water, and (3) strong evidence that ground vegetation recovery is an important N sink. However, the correlation between vegetation data and nitrate leaching varied between treatments in a way suggesting that additional N sinks, other than leaching and uptake in vegetation, were important and that immobilization in dead below-ground tree biomass was the most likely candidate. Other important findings were that nitrate leaching rates in storm-felled 0 and V treatments were at the high end of reported estimates for Sweden and other Nordic countries, and that leaching was markedly elevated in storm-felled stands previously subjected to repeated fertilization. High precipitation and decades of high N deposition at the site probably contributed to the generally high leaching levels. This study demonstrated that previous treatments can influence N fluxes after disturbances in several ways, with the principal influence on net N mineralization being modified by treatment influences on ground vegetation recovery and species composition, including amounts and composition of deadwood remaining in the soil following disturbance. Vegetation feedback on leaching depended on the type of fertilization, with the N-free V treatment stimulating rapid vegetation control of leaching and the IF treatment reducing vegetation recovery.

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CRediT authorship contribution statement

Bengt A. Olsson: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Funding acquisition, Visualization. **Johan Bergholm:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – review & editing. **Ghasem Alavi:** Methodology, Software, Formal analysis, Investigation, Writing – review & editing. **Tryggve Persson:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120422.

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