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Temporal fluctuations in throughfall carbon concentrations in a spruce forest

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Abstract

Fluxes of nutrients, energy and ions through forest canopies are spatially and temporally highly heterogeneous and good modelling tools are needed to separate different influential variables. Two important factors affecting the variation in the throughfall fluxes are the amount of precipitation and phytophagous insects in the canopy. In spite of their large abundance, wide distribution and production of large quantities of sugary excreta the role of aphids has not been explored in models of DOC-flux dynamics. We hypothesise that aphids qualify as a crucial factor to better explain the spatial and temporal variability in DOC-fluxes. Here, we build on the available knowledge of aphid population dynamics to explore the relative roles of aphids and precipitation as sources of variability in throughfall fluxes in a mature spruce forest. Peaks in DOC-concentrations usually appeared during June–August and precipitation volumes alone were insufficient to explain DOC-concentrations in throughfall. The developed dynamical model, however, showed a 34% increase in the explained variability in DOC throughfall dynamics if aphids were included. This is the first model, which takes into account the possible influence of sap feeding herbivores on DOC-flux dynamics.
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Keywords: Aphids; Throughfall; Chemistry; Carbon dynamics; Forest

1. Introduction

Fluxes of dissolved organic carbon (DOC), which is a significant component of the C cycle in forest canopies, are spatially and temporally highly heterogeneous (Manderscheid and Matzner, 1995; Carlisle et al., 1966). The most important factors regulating the variation in the throughfall fluxes were proposed to be the amount of rainfall (Lovett et al., 1996) and, more recently, phytophagous insects—predominantly aphids—in the canopy (Stadler and Michalzik, 2000).

Other factors like leaching (Tukey, 1970), leaf physiological activity, senescence, or cuticular weathering by air pollution seem to be of lower importance (Lovett et al., 1996).

Aphids—on spruce it is mainly the genus *Cinara*—are a common component of the canopy. They suck the phloem sap of their host plants and produce large quantities of excreta rich in sugars (honeydew). For example, on 60 years old Norway spruce, quantities of excreted honeydew may range between 30 and 70 kg of fresh mass per year (Eckloff, 1972). Aphids produce several generations per year and their abundance is strongly determined by seasonal fluctuations in temperature, host plant quality, abundance of natural

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enemies and migration (Kidd, 1985; Dixon, 1998; Stadler, 1997, 1998). It was suggested that aphids are key herbivores in coniferous forests and due to their honeydew production strongly influence the flow of energy from the crowns of the trees to the soil (Stadler et al., 1998).

Field and laboratory studies on the trends in DOC-concentrations in throughfall collected beneath aphid infested and uninfested spruce trees (10–15 years old) showed marked spatial and temporal differences (Stadler and Michalzik, 2000). At the beginning of the year some trees in forests are heavily infested while others are uninfested. After dispersal, virtually all trees become infested. For example, in the Waldstein area in Northern Bavaria, Germany, the infestation of Norway spruce by *Cinara pilicornis* (Hartig) shows the following pattern: in spring: 53.2% of all trees are uninfested, 42.6% are infested with up to 100 aphids per m^2 and 4.2% are heavily infested (hot spots: >100 aphids per m^2). After dispersal, almost all of the trees (97.5%) became infested with aphids, however, only in low numbers (Stadler et al., 1998). The correlation between aphid numbers above throughfall samplers and the DOC-concentration in throughfall is highly significant ($r = 0.72$, $n = 30$, $P < 0.001$). In addition, epiphytic micro-organisms thrive better on infested needles and leaves (Stadler and Müller, 1996, 2000), which immobilise nitrogen on the leaves and reduce nutrient concentrations in throughfall (Stadler and Michalzik, 1998). There is a good evidence (Scheurer, 1964; Kidd, 1990) that the abundance and population dynamics of aphids in the upper canopy of conifers is similar to that in the lower canopy with a pronounced peak in abundance during May–June and in some years a second peak in late August–early September.

Thus, given that aphid contribute to the DOC-fluxes in throughfall by means of honeydew production, we hypothesise that the accuracy of predictive models of DOC dynamics could be considerably improved if the temporal variability in DOC throughfall fluxes beneath mature spruce trees is better analysed and linked to patterns in aphid abundance. In order to investigate the potential role of the aphid component in these models, we first analyse the trends and fluctuations in the average DOC-concentrations in throughfall as a function of the amount of precipitations. Then we develop a simple dynamical model with aphids and DOC as

its components and compare the accuracy of its predictions with and without inclusion of the aphid component.

2. Materials and methods

2.1. Site description

The data were collected at the Coulissenhieb (50°08′35″N, 11°52′10″E) in the central part of the Fichtelgebirge of Northeastern Bavaria. The experimental plot covers 2.5 ha and carries a 145 years old Norway-spruce (*Picea abies* (L.) Karst.) stand. The annual precipitation in the area is 1100 mm, and the average annual temperature is about 5 °C. The background information on aphid abundance on Norway spruce originates from surveys on young trees, which are only 300 m away from our experimental plot (Stadler et al., 1998). These data should be a good proxy to compare them with the model output for the overall abundance of spruce feeding aphids at this site.

2.2. Sampling of throughfall and chemical analyses

Throughfall was collected every 2 weeks, from 1993 to 1999. Throughfall samplers were $326\,cm^2$ in area. Twenty were placed beneath Norway spruce trees (BN) and 5 in an open area (FN). All samples were filtered through a 0.45-μm cellulose acetate membrane. Dissolved organic carbon was determined as CO_2 after persulphate-UV-oxidation (Foss Heraeus, Liquid TOC).

Fluxes of DOC were standardised to $kg\,ha^{-1}$ per 14 days. The data were first averaged over all sampling sites, then smoothed by using moving averages of length 3, in order to factor out the effects of irregular rainfall. Average values per site (BN and FN) and the corresponding maxima and minima were then calculated.

2.3. The model

Within a year, aphid population dynamics consists of an initial increase in population size, which is typically followed by a steep decline in abundance (Scheurer, 1964; Kidd, 1990; Stadler, 1998). The decline is attributed to migration (Kindlmann and

Dixon, 1996), weather or to the influence of predators. Whatever the causal factor is, it is better correlated with cumulative, rather than with instantaneous density (Kindlmann et al., 2003).

Therefore, we used a specific type of model in order to account for the decline in population numbers, using cumulative density as a factor for modelling the population dynamics of aphids, instead of a logistic equation. Aphid dynamics is then described by the set of differential equations:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = (r - h)x, \qquad x(0) = x_0 \tag{1a}$$

$$\frac{\mathrm{d}h}{\mathrm{d}t} = ax, \qquad h(0) = 0 \tag{1b}$$

where $x(t)$ is the density of aphids at time t; $h(t)$, cumulative density of aphids at time t; a, scaling constant relating aphid cumulative density to its own dynamics; r, maximum potential growth rate of the aphid.

This model was validated against a large set of empirical data (Kindlmann et al., 2003), which it fits very well. Here we used this model for the period May–September, when aphids are actively reproducing and excreting honeydew. During the rest of the year aphids are rare or in hibernation and no honeydew will be produced, which was accounted for in the model.

If aphid honeydew is mainly responsible for the increase in carbon concentration (DOC) in throughfall, then the instantaneous changes in DOC should be proportional to the instantaneous aphid numbers. It is also reasonable to assume an exponential decline, due to washing by rain, in the amount of DOC on the needles, which is proportional to its instantaneous amount and to the instantaneous amount of rain. The dynamics of carbon in honeydew can then be described by

$$\frac{\mathrm{d}C}{\mathrm{d}t} = cx - dCP, \qquad C(0) = C_0 \tag{1c}$$

where C is the amount of DOC on needles; c, rate of aphid honeydew production ($c > 0$ during the season, May–September, and $c = 0$, when aphids are assumed to be absent); d, rate at which honeydew is washed from needles; P, amount of precipitation.

3. Results

3.1. Basic analysis of the data

The smoothed averages (moving averages of length 3) of DOC-fluxes in throughfall for all sampling sites and for individual years are summarised in Fig. 1. The amounts of DOC in rain are consistently lower and less variable than in throughfall. However, although the volumes of throughfall and rain are strongly correlated ($r^2 = 0.92$, $P < 0.001$), there are losses of water during the passage of the canopy, as the slope of the linear relationship was much smaller than one (equal to 0.77). This corresponds to about a 23% loss of rainwater. This loss is probably due to evaporation of some of the rain from the needles. Thus, the larger fluxes of DOC in throughfall relative to rain may not mean that DOC was added to rain in passing through the canopy. DOC-fluxes in throughfall show a clear and consistent pattern (Fig. 1)—a distinct increase in summer and early autumn, weeks 20–40 (May to October), but these tendencies are obscured by other factors, such as the amount of precipitation and its DOC content.

In order to factor out the influence of DOC in rain the differences in their concentrations in throughfall and rain were plotted indicating that there is a peak in the concentration of DOC in June–August (Fig. 2). One exception is 1996, with a large distinct peak early in April–May. This, however, is associated with extremely low rainfall during spring (February–April) of that year (Fig. 3). Thus, when the chemical content of rainwater is factored out, two things become apparent. First, a lot of DOC was added to the throughfall in summer, when aphid numbers are usually high on Norway spruce (see Scheurer, 1964; Stadler, 1998; Kidd, 1990 for typical aphid dynamics). Second, the amount of rain strongly influences the concentration/fluxes.

A similar conclusion about the influence of the quantity of rain can be drawn from the correlation coefficients between bi-weekly amounts of rainfall and concentrations of DOC, which are shown for the years 1994–1999 and for spring, summer and autumn (Table 1). The correlations for DOC in spring and autumn in Table 1 are negative, whereas there is either no or positive correlation for DOC in most years in summer (Table 1). If there were no other factor than rainfall, the correlation would be negative: lots of
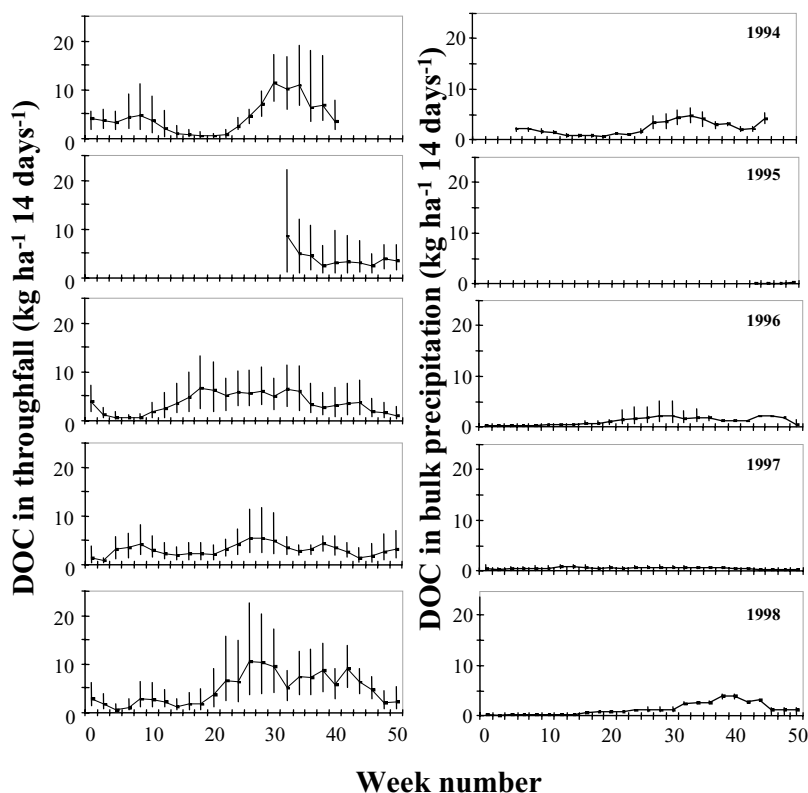
Fig. 1. Fluxes (±range) of DOC in throughfall (kg ha^{-1} per 14 days) collected beneath the canopy of Norway spruce (left) and in bulk precipitation (right) from 1994 to 1998.

rain translates into a low concentration of the corresponding substance in the throughfall, due to dilution effects. Thus, the absence of a negative correlation for DOC in most years, and especially in summer, means

that there are factors other than rainfall affecting its concentration in throughfall.

However, the above only suggests that when aphids are abundant the DOC content of throughfall is in-

Table 1
Correlation coefficients between volumes of rainfall collected in 2-week intervals and concentrations of DOC separated for different years, and between volumes of rainfall and concentrations of DOC separated for seasons

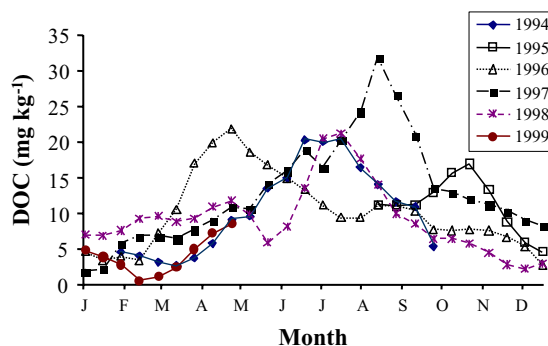| Year/season	DOC-concentration
1994	0.51
1995	0.93
1996	0.49
1997	0.67
1998	0.62
1999	−0.19
Spring	−0.30
Summer	0.26
Autumn	−0.40

Fig. 2. Temporal pattern of the differences in DOC-concentrations in throughfall and bulk precipitation from 1994 to 1999.
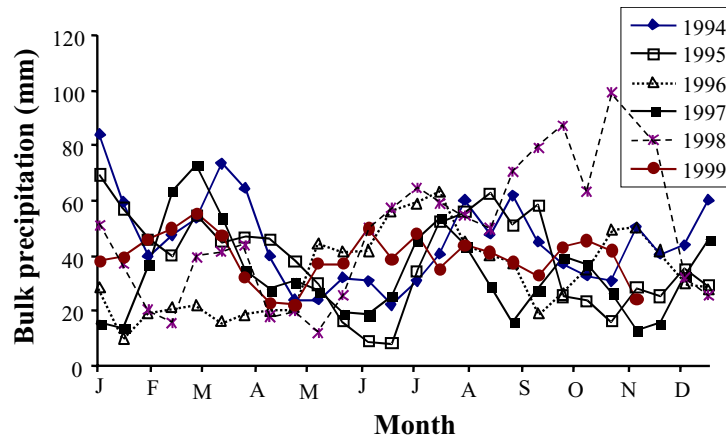
Fig. 3. Monthly averages of bulk precipitation (mm) collected from 1994 to 1999.

creased, which is in line with findings from small trees (Stadler et al., 1998). Our model now describes the dynamics of DOC to explain larger patterns.

3.2. Fitting the model to empirical data

The model was fitted to data for the years 1996–1998, for which both the quantities of rainfall and throughfall, and the concentrations of DOC were available. The difference in the average DOC-concentration in throughfall and bulk precipitation was used to factor out the DOC in rainwater. It was assumed that the abiotic parameters affecting DOC-fluxes, C_0 and d, were the same each year,

whereas the biotic parameters, aphid abundance and rate of honeydew production, x_0, r, a and c, were not.

The trends in aphid abundance predicted by the model are illustrated in Fig. 4. They are qualitatively similar to those actually recorded in the field for species like *Cinara piceae* or *C. pilicornis* on Norway spruce (Scheurer, 1964; Stadler, 1998).

The fit of the model to the empirical data on DOC dynamics in the 3 years is remarkable (see Fig. 5). It explains 74–78% of the variability in 1997 and 1998.

Fig. 4. Seasonal changes in aphid abundance from 1996 to 1998 predicted by the model (1).

Table 2
Parameters of model (1)—constraints of model parameters, residual sums of squares (RSS) and R^2 values (R^2 value explains the amount of variability explained by the model)

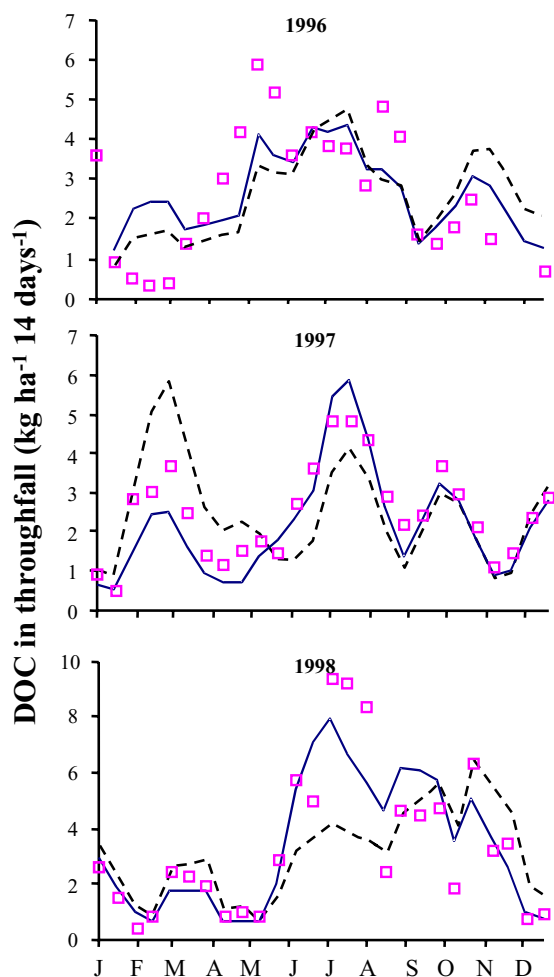| Parameter	Constraint		1996	1997	1998
	Lower	Upper			
c_0			7.27	7.27	7.27
d			0.017	0.017	0.017
x_0	0	100	0.053	23.92	31.32
r	3	20	20.00	15.72	8.624
a	0	1	0.124	0.102	0.043
c	0	1	0.08	0.287	0.207
Model with aphids					
RSS			51.60	8.86	39.05
R^2			0.32	0.74	0.78
Model without aphids					
RSS			68.54	23.26	106.22
R^2			0.10	0.32	0.39

Fig. 5. Dynamics of DOC-fluxes in throughfall from 1996 to 1998 in a mature Norway spruce stand. Dots are empirical throughfall data corrected for bulk precipitation; continuous line is the prediction of model (1) when aphids are included; dotted line, when aphids are excluded.

The fit in 1996 is weaker (only 35% of the variability is explained), due to the poor fit early in the season (February–March). This is probably due to the extremely low amount of rainfall during this period (Fig. 3).

When the aphid component of the model is not included, i.e. $x_0 = 0$, then in all years the fit is poor (Fig. 5), the residual sums of squares is much larger and the model explains only 10–39% of the variability in the data (Table 2).

4. Discussion

Amount of precipitation, forest type and leaf area are thought to affect throughfall fluxes and chemistry (Lovett et al., 1996). Additionally, throughfall contain leachates and material deposited on the surface of leaves and washed off by rain (Hoffman et al., 1980). Thus, internal cycling processes and external events may affect the chemical content of throughfall. Implicit in this is the belief that canopies basically act like ion exchangers, especially under H^+ and NH_4^+ deposition. The rare modelling efforts were concentrated mainly on the dynamics of DOC in the soil (Kucharik et al., 2001; Neff and Asner, 2001) or in water ecosystems (Meyer et al., 1998; Reche et al., 2000).

The effects of insects living in the canopies of trees has received much less attention most likely because it is difficult to follow the rise and fall in their numbers at the tops of mature trees. However, there is strong evidence that folivores and sap sucking insects increase the leaching of ions and the nutrient transfer to the litter layer (Carlisle et al., 1966; Seastedt and Crossley, 1984; for a review see Schowalter et al., 1986; Schowalter, 2000). The feeding damage of aphids is usually less spectacular than that of folivores. However, the drain of nutrients may be considerable. Aphids of the genus *Cinara* may substantially affect DOC-fluxes as they excrete 400–700 kg of honeydew ha^{-1} per year in mature coniferous forests (Zwölfer, 1952; Zoebelein, 1954). Carlisle et al. (1966) showed for the size class up to 200 μm an annual input of particulate organic carbon (POC) in throughfall of $227\,kg\,C\,ha^{-1}$, including a carbohydrate input of $89\,kg\,ha^{-1}$. These carbohydrates contained melezitose, which is mainly present in honeydew produced by aphids. Guggenberger and Zech (1994) reported for a study site only some 7 km away from ours an annual flux of carbohydrates of $70\,kg\,ha^{-1}$, and that the throughfall was rich in hexose-C and deoxysugars from April until September. They attributed this to microorganisms on the needles. Although epiphytic microorganisms undoubtedly play an important role in the cycling of nutrients in tree canopies (Stadler and Michalzik, 1998) a more likely source of the carbohydrates and hexose-C in throughfall is aphids. Different species of tree dwelling aphids may show somewhat different population dynamics, vertical movements within the canopy and dependence on

specific weather conditions (Dixon, 1998), but it is likely that their seasonal dynamics are good indicators of DOC-fluxes in forested ecosystems.

It could be argued that the order of improvement achieved by including aphid abundance in the model (1) was not large enough bearing in mind the increase in the number of parameters. However, it is clear from Fig. 5 that in all years the prediction based only on rainfall consistently underestimated the observed trends.

As data on aphid population dynamics necessary for a direct verification of our model are not available for mature trees, we have—strictly speaking—only shown that there exists a component X positively contributing to the DOC contents in throughfall, and that the dynamics of this component is similar to that in Fig. 4. We believe this component is aphids rather than plant specific factors for two reasons: (1) it has been clearly demonstrated that aphids contribute significantly to the amount of DOC in throughfall even at low densities (Stadler and Müller, 1996, 2000; Stadler and Michalzik, 1998, 2000); (2) it is unlikely that other factors, such as leaching would show the wide temporal fluctuations shown in Fig. 5, which is, however, so characteristic for aphids. Our inability to prove directly that the component X is aphids argues for the necessity to study their seasonal abundance in canopies of mature trees and thus shows directions for further research.

This is the first model, which takes into account the possible influence of sap feeding herbivores on DOC-flux dynamics. Our analysis suggests that aphids in mature coniferous forests can act as a major source of variability in carbon throughfall fluxes, which otherwise would remain obscured and indicates the necessity to include information on aphid population dynamics in models of DOC-flux dynamics in forest canopies.

Acknowledgements

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