ÉCOSCIENCE

Double-funneling of trees: Stemflow and root-induced preferential flow[1]

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Abstract: Trees partition rainfall into throughfall and stemflow, resulting in a spatial distribution of nutrient and water fluxes reaching the soil centred on the trunks of trees. Stemflow fluxes of water and nutrients are then funneled preferentially belowground along tree roots and other preferential flow paths, bypassing much of the bulk soil. This double funneling leads to increased soil chemical, biological, and hydrological heterogeneity, which has been shown to persist for decades. In this paper, we review nutrient fluxes of stemflow water for a variety of tree species and climates. The amount of precipitation partitioned by trees to stemflow ranges over more than three orders of magnitude, accounting for 0.07–22% of incident rainfall in a range of precipitation regimes (600–7100 $mm \cdot y^{-1}$). Stemflow fluxes of NO_3^- and K were found to be larger for species with greater stemflow partitioning, regardless of climate type. While stemflow volumes may increase in relation to increasing precipitation, stemflow nutrient concentrations tend to become more dilute. On an annual basis, however, it appears that plant canopy morphology is strongly related to stemflow fluxes for plant-mobile nutrients such as K ($r^2 = 0.64$) and NO_3^- ($r^2 = 0.61$). Root-induced preferential flow provides an additional feedback mechanism in nutrient cycling by which stemflow-derived nutrient fluxes are delivered to the rhizosphere.
Keywords: canopy partitioning, nutrient cycling, preferential flow, soil heterogeneity, stemflow.

Résumé : Les arbres divisent les précipitations en pluviolessivats et en écoulements le long du tronc résultant en une distribution spatiale des nutriments et des flux d'eau au sol centrée sur le tronc des arbres. Les flux d'eau qui s'écoule le long des troncs sont ensuite canalisés préférentiellement en écoulement souterrain le long des racines et dans d'autres réseaux hydrauliques préférentiels, évitant ainsi l'écoulement libre dans le sol. Cette canalisation double de l'écoulement contribue à faire augmenter l'hétérogénéité chimique, biologique et hydrique du sol et il a été démontré que ce phénomène persiste sur plusieurs décennies. Dans cette étude, nous passons en revue les flux de nutriments dans l'eau de ruissellement le long des troncs pour une variété d'espèces d'arbres et de climats. La quantité de précipitation canalisée par les arbres en écoulement le long des troncs varie sur plus de trois ordres de grandeur, représentant entre 0.07 et 22% de la pluie incidente et ce pour une gamme de régimes de précipitation (600–7100 $mm \cdot y^{-1}$). Les flux de NO_3^-, et de K dans l'eau s'écoulant le long des troncs sont plus importants pour les espèces canalisant une plus grande quantité d'eau le long de leurs troncs et ce indépendamment du type de climat. Lorsque les précipitations augmentent, les volumes d'eau s'écoulant le long des troncs sont plus importants mais les concentrations en nutriments deviennent alors plus diluées. Sur une base annuelle cependant, il semble que la morphologie de la canopée des plantes soit fortement liée aux flux de nutriments mobiles tels que K ($r^2 = 0.64$) et NO_3^- ($r^2 = 0.61$) dans l'eau qui s'écoule le long des troncs. Les canaux d'écoulement préférentiels le long des racines procurent un mécanisme de rétroaction supplémentaire grâce auquel les nutriments provenant de l'écoulement le long des troncs sont acheminés vers la rhizosphère.
Mots-clés : canal d'écoulement préférentiel, cyclage de nutriments, écoulement le long du tronc, hétérogénéité du sol, division par la canopée.

Nomenclature: Tutin, 1980; Flora of North America Editorial Committee, 1993.

Introduction

It is well established that deeply rooted trees contribute to greater ecosystem productivity by cycling nutrients from the soil profile to the soil surface via litterfall (Breman & Kessler, 1997), throughfall (Santa Regina & Tarazona, 2000), and stemflow (Parker, 1983; Chang & Matzner, 2000b) and by exploring soil pools inaccessible to more shallow-rooted understory species and crops (Schroth, 1995; Buresh & Tian, 1997). These processes result in a positive feedback between tree functionality and heterogeneity of nutrient stocks and fluxes.

Trees affect a spatial modification of a number of components of the hydrologic cycle. Tree canopies concentrate and channel water and nutrients into zones centred on the trunks of trees. Both the tree canopy and the root system spatially partition water fluxes into distinct pathways, affecting chemical composition and concentrations. As a result of this double funneling, the soil rhizosphere around tree roots is enhanced biologically (Bundt *et al.*, 2001b), hydrologically (Jackson & Wallace, 1999; Burgess *et al.*, 2001), and chemically (Dockersmith, Giardina & Sanford, 1999; Bundt *et al.*, 2001a).

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Aboveground, incident precipitation is redistributed spatially by trees into stemflow (precipitation that has been channeled by leaves and branches and eventually flows down the trunk) and throughfall (precipitation that reaches the ground beneath the canopy and may or may not have made contact with the tree) (Crockford & Richardson, 2000). The chemical composition of precipitation intercepted by the canopy is enhanced by wash-off of dry deposition collected by the canopy and foliar leaching of nutrients into rainwater (Houle *et al.*, 1999; Fan & Hong, 2001). The extent to which dry deposition and foliar leaching enhance the nutrient status of intercepted precipitation is a function of leaf and canopy morphology and nutrient status, as well as regional climatic and environmental conditions.

In general, stemflow has higher nutrient concentrations than throughfall (by up to an order of magnitude [Parker, 1983]), which is in turn more greatly enriched than the incident precipitation. A longer canopy residence time for stemflow water than for throughfall and greater leachability of bark tissue (Levia & Herwitz, 2000) contribute to a chemical concentration gradient of water fluxes in the order: stemflow > throughfall > precipitation. Nevertheless, few studies have explored the relationship between canopy structure and stemflow chemistry (Levia & Frost, 2003).

Belowground, trees further modify water and nutrient cycling by channeling infiltrating water along roots through preferential flow pathways that are formed by means of root action on bulk soil. These root-derived preferential flow pathways result from localized compaction of soil by roots and the addition of root exudates to adjacent soil. These pathways influence water and nutrient fluxes for the active rhizosphere along living roots and along former root channels. Following a rainfall event, the flux of water (volume of water per area per time) passing through these pathways is greater than the water flux through the bulk soil. Nutrient dynamics within root-derived preferential flow pathways are substantially different from that of the bulk soil, as stemflow contributes to higher inorganic nutrient concentrations near the trunk (Koch & Matzner, 1993) and root sloughing and root exudates contribute to elevated organic nutrient concentrations (Bundt *et al.*, 2001b). In addition to root-formed preferential flow pathways, soil macrofauna and swelling and shrinking dynamics of the soil also result in preferential flow pathways that further facilitate both root growth and water flow along roots.

Long-term changes to soil properties resulting from the effects of trees on hydrologic cycling and nutrient cycling pathways have been reported to last decades (Mina, 1967; Bundt *et al.*, 2001a). This increased soil heterogeneity results from the water and nutrient fluxes delivered to localized zones around the trunk as stemflow and then channeled preferentially into and through the soil. The importance of these localized zones of enhanced nutrient status and biological activity as a mechanism for facilitative interaction within the forests and tree-based agroecosystems is highlighted by crop roots growing preferentially within these relatively narrow zones that have been "primed" by trees (van Noordwijk *et al.*, 1991).

The objectives of this paper are to relate the phenotypic and environmental dependencies of (1) the aboveground partitioning of precipitation into stemflow, and the nutrient concentrations and fluxes of stemflow; (2) the belowground funneling of stemflow through preferential flow pathways; and (3) the hydrologic continuity of (1) and (2) in contributing to soil heterogeneity.

Aboveground processes

RAINFALL PARTITIONING TO STEMFLOW

Precipitation intercepted by trees is redistributed by the canopy, resulting in a spatial partitioning of bulk precipitation into throughfall and stemflow. Precipitation that is intercepted by leaves and branches collects in the canopy until it is evaporated back into the atmosphere or gravity overcomes the surface tension of the water, causing it to drip or be routed through the canopy. While the evaporated fraction of intercepted rainfall (termed "interception" in the hydrologic literature) varies by storm and tree species characteristics, it can be significant, ranging to upwards of 30% of precipitation (Rutter *et al.*, 1971).

Water in excess of the leaf or branch water-holding capacity will drip through the canopy as throughfall or will flow from the leaf along the underside of branches towards the trunk or towards the canopy drip line. The quantity of water that a leaf or branch is able to retain on its surface depends upon the leaf or branch morphology and angle. A leaf that has its leaf tip above the petiole will channel water towards twigs and branches; twigs and branches in turn will route water toward the trunk, provided that the branch angle is above horizontal (Crockford & Richardson, 2000). Water that collects in the canopy and is routed toward and eventually down the trunk is considered stemflow. Some water that is routed towards the trunk falls to the ground as throughfall before reaching the trunk due to blockages or discontinuities along flow paths (Crockford & Richardson, 2000). Thus, the throughfall flux near the trunk can be significantly greater than the flux further away from it (Schroth *et al.*, 2001). The relative fractions of intercepted, non-evaporated water partitioned into stemflow and throughfall are determined largely by tree canopy morphology and storm characteristics (*e.g.*, rainfall intensity and wind speed, etc.) (Crockford & Richardson, 2000).

Stand characteristics that influence the spatial partitioning of incident precipitation for a mixed species forest include overall forest canopy structure, individual species canopy storage capacities, and the leaf area index of the stand. Scatena (1990) reported that 50% of stemflow came from 12% of the stems in a mixed species forest. These characteristics also apply to variations between individual species in plantation-type forests and agroforestry systems.

Important species-level characteristics affecting partitioning include branch angle, specific surface roughness of branches and bark (Herwitz, 1987), and leaf morphological characteristics such as shape, size, and convexity or concavity. In natural forests, branch angle tends to be closer to horizontal for upper canopy trees, resulting in less stemflow than for intermediate trees in the canopy, which tend to have a more vertical branch angle (Jordan, 1978).

The amount of stemflow produced by an individual tree varies temporally, as seasonally variable rainfall inten-

sities alter the amount of rainfall partitioned to stemflow (Nagata *et al.*, 2001; Rodrigo & Avila, 2001). Huang, Chen, and Lin (2005) showed that diurnal variations in branch weight (heavier in the morning and lighter in the afternoon) can also affect canopy partitioning, as does increasing branch weight as a result of canopy storage during a storm. Branch angle and branching patterns also exhibit plasticity in response to resource competition (Wilson, 2000; Reynolds & Ford, 2005) and environmental gradients (Kern, Hovenden & Jordan, 2004), though branch angle tends to maximize the effective leaf area of individual branch tiers (Honda & Fisher, 1978). While stemflow partitioning for individual trees clearly varies both within and between rainfall events (Schroth *et al.*, 2001), studies of several species have indicated that the ratio of precipitation to stemflow does not vary significantly between leaves-on and leaves-off vegetative stages (Martinez-Meza & Whitford, 1996; Herwitz & Levia, 1997).

CHEMICAL ENHANCEMENT OF STEMFLOW

As the tree canopy partitions rainfall into stemflow, the intercepted water washes off nutrients that were deposited in the canopy by dry atmospheric deposition or animal droppings. Dry and wet deposition of nutrients from the atmosphere is determined by regional environmental and climatic conditions and is generally much greater for N and S in or near industrialized areas, while Na deposition is high near oceans (Parker, 1983).

Incident precipitation interacts chemically with the leaves, branches, and trunk of the tree due to the concentration gradients between the precipitation and the plant parts. The direction of the concentration gradient with respect to the water/tree interface determines if the nutrient concentrations of intercepted water are enriched via foliar leaching or diminished via foliar uptake. Fan and Hong (2001) found foliar exchange reactions to control stemflow and throughfall concentrations for most solutes when compared with the processes of atmospheric deposition and wash-off.

Dilute nutrient concentrations in precipitation imply that foliar leaching is much more common than foliar uptake. Foliar leaching of cations from plant tissue is driven by exchange reactions with rainfall-supplied hydrogen ions (Fan & Hong, 2001). These H^+ ions more easily displace those nutrients that are mobile within the plant. Thus K, a mobile nutrient in plants, is more easily leached to stemflow than Ca, which is incorporated into cell walls. Foliar uptake occurs when lower elemental concentrations are found in plant tissue than in rainfall. In addition, epiphytic plants and lichens contribute to uptake of nutrients from intercepted rainfall (Houle *et al.*, 1999).

Climatic factors that influence chemical composition of stemflow for an individual tree for a single storm include the amount of stemflow generated during the storm (a function of rainfall intensity and wind speed) and the duration of the dry period preceding the storm (Mina, 1967). Further, stemflow nutrient concentrations vary within a storm, generally decreasing with increasing cumulative rainfall (Koichiro *et al.*, 2001; Schroth *et al.*, 2001).

Canopy architecture and leaf morphology also affect the chemical concentrations of stemflow water. Augusto and Ranger (2001) report that harvest of atmospheric deposition is more efficient for conifers than for hardwoods, while intercepted water may become more enriched due to canopy features that increase residence time of water in the canopy, such as leaf concavity and shallow branch angle (Levia & Herwitz, 2000). Older trees of the same species tend to have greater trunk surface roughness, resulting in less stemflow due to increased storage capacity (Houle *et al.*, 1999; Levia & Frost, 2003). In addition, rough-barked species show higher nutrient concentrations than smooth-barked species (Parker, 1983).

STEMFLOW FLUXES OF WATER AND NUTRIENTS

We conducted a review of stemflow water chemistry and fluxes for a variety of tree species in a range of environments and rainfall regimes to determine the extent to which tree canopies influence (1) the flux of nutrients delivered to the base of trees via stemflow and (2) chemical enrichment of stemflow water with respect to rainfall. Studies included in the comparative analysis were those that considered stemflow volumes and nutrient concentrations on an annual basis; they include a variety of tree species growing under a wide range of precipitation regimes (600–7100 mm·y^{-1}), in both temperate and tropical climates (Table I).

The percentage of rainfall partitioned to stemflow (SF%) integrates the canopy architectural and climatological factors influencing rainfall partitioning. SF% was determined as the percentage of incident rainfall delivered as stemflow on a volumetric basis as follows:

$$SF\% = \frac{SF}{PPT} \times 100$$

where SF is the volume of stemflow on a per hectare of forest basis and PPT is the volume of rainfall per hectare of open area. SF% ranges from 0.07% to 22% for published data included in the present study (Table I).

Several other parameters have been employed to represent the stemflow volumes and nutrient fluxes of individual trees. These include the funneling ratio (Herwitz, 1986a), which relates the amount of stemflow generated for the basal area of the tree to the bulk precipitation of an equivalent area, and the stem area index (Price & Watters, 1989), which relates the bark surface area (trunk circumference times trunk length) to the land surface area. However, the data presented in the majority of the reviewed studies did not allow for the determination of these parameters.

Species effects on stemflow nutrient fluxes were compared for NO_3^-, Ca, Mg, and K. Studies indicating anthropogenic factors strongly affecting atmospheric deposition of specific nutrients were not included in the corresponding comparisons. Several studies also report organic nutrient concentrations (DOC, DON, organic phosphorus) and micronutrient concentrations (Cu, Zn, Mn, Fe) in stemflow water. Because organic and micronutrients are less commonly reported in the stemflow literature, a comparative analysis across species was not possible. Instead, data on organic and micronutrients are summarized at the end of this section.

Canopy partitioning of incident rainfall exerts a strong influence on nutrient fluxes delivered via stemflow.

TABLE I. Tree species-author key with canopy stemflow partitioning and precipitation regime.

Species or ecosystem	Common name	SF%	Location	PPT (mm·y⁻¹)	Study
Eschweilera spp.	Jarana (Brazil), Kakeralli (Guyana)	0.07	Brazil	2262	[1]
Bixa orellana	Annatto, Arnatto	0.38	Brazil	2262	[1]
Pinus sylvestris	Scots pine	0.45	Spain	1254	[2]
Quercus spp.	Oak spp.	0.50	Mexico	974	[3]
Pinus pseudostrobus	Pino blanco, False Weymouth pine	0.60	Mexico	974	[3]
Oenocarpus bacaba	Bacaba or Turu palm	0.66	Brazil	2262	[1]
Pinus resinosa	Red pine	0.70	Canada	nd*	[4]
Cerrado (Native savanna)	Mixed species	0.83	Brazil	1656	[5]
Eucalyptus melanophloia	Silverleaf ironbark	0.84	Australia	718	[6]
Nothofagus betuloides	Ouchpaya, Roble colorado	1.41	Chile	7111	[7]
Rain forest with low abundance of ectomycorrhizal trees	Mixed species	1.48	Cameroon	5370	[8]
Larix laricina	Larch, Tamarack	1.60	Canada	nd	[5]
Eucalyptus mixed cross	Eucalyptus	1.62	Congo	1502	[9]
Lithocarpus–Castanopsis association with bryophytes	Stone oak, zhui shu	1.96	China	2165	[10]
Nothofagus dombey	False beech	2.00	Chile	1982	[11]
Quercus copeyensis (old growth rain forest)	White oak	2.23	Costa Rica	2830	[12]
Rain forest with high abundance of ectomycorrhizal trees	Mixed species	2.24	Cameroon	5370	[8]
Picea rubens	Red spruce	2.30	Canada	nd	[4]
Quercus ilex	Montane Holm oak	2.66	Spain	1275	[13]
Lithocarpus–Castanopsis association without bryophytes	Stone oak, Zhui shu	2.77	China	2165	[14]
Bertholletia excelsa	Brazil nut	2.83	Brazil	2262	[1]
Abies balsamea	Balsam fir	3.50	Canada	nd	[4]
Theobroma grandiflorum	Cupuaçu	3.71	Brazil	2262	[1]
Betula papyrifera	White birch, Paper birch	3.90	Canada	nd	[4]
Fagus sylvatica	Beech	5.21	Germany	691	[15]
Pinus strobus	White pine	5.30	Canada	nd	[4]
Acer rubrum	Red maple	5.60	Canada	nd	[4]
Populus grandidentata	Largetooth or Canadian aspen	6.10	Canada	nd	[4]
Picea glauca	White spruce	6.40	Canada	nd	[4]
Fagus sylvatica	Beech	6.47	Spain	1465	[2]
Laurel forest	Mixed species	6.88	Canary Islands	625	[16]
Bactris gasipaes	Peach palm (managed for fruit)	9.00	Brazil	2262	[1]
Nothofagus pumilio	Lenga	9.02	Chile	5332	[17]
Quercus copeyensis (early successional forest)	White oak	16.07	Costa Rica	2900	[12]
Quercus copeyensis (mid- successional forest)	White oak	16.55	Costa Rica	2900	[12]
Vismia spp.	Vismia (fallow species)	20.00	Brazil	2262	[1]
Pinus radiate	Monterey Pine	22.00	Chile	1982	[11]

PPT = mean annual precipitation; SF% is the stemflow partitioning as a percentage of incident precipitation; *nd = not determined.

[1] Schroth *et al.*, 2001; [2] Santa Regina & Tarazona, 2000; [3] Silva & Rodriguez, 2001; [4] Mahendrappa, 1974; [5] Lilienfein & Wilcke, 2004; [6] Prebble & Stirk, 1980; [7] Oyarzún *et al*., 2004; [8] Chuyong, Newbery & Songw, 2004; [9] Laclau *et al*., 2003; [10] Liu, Fox & Xu, 2003; [11] Uyttendaele & Iroume, 2002; [12] Holscher *et al.,* 2003; [13] Rodrigo, Avila & Roda, 2003; [14] Liu, Fox & Xu, 2002; [15] Chang & Matzner, 2000a; [16] Aboal *et al*., 2002; [17] Godoy, Oyarzun & Bahamondes, 1999.

Comparing fluxes across a range of tree species and rainfall regimes shows larger stemflow fluxes of NO_3^- and K for species with greater stemflow partitioning, regardless of climate type (Figures 1a and b). In contrast, Ca and Mg showed an indeterminate relationship with stemflow partitioning (Figures 1c and d).

The SF% parameter (representing the stemflow partitioning factors described previously) accounts for at least 61% of NO_3^- stemflow flux variability for trees in locations not strongly affected by anthropogenic nitrogen sources (*e.g.*, industrial activity or large-scale agriculture). Similarly,

SF% describes 64% of the variability in K stemflow flux. Interestingly, normalizing the fluxes by the annual rainfall amount did not improve the correlations between nutrient fluxes and stemflow partitioning, nor the significance of the relationships. That is, more precipitation does not imply larger stemflow fluxes for these plant-mobile nutrients; rather, increased precipitation generally results in larger volumes of more dilute stemflow. Therefore, canopy characteristics appear to be the most important factor in determining fluxes of plant-mobile nutrients delivered in stemflow waters. Stemflow fluxes of Ca and Mg, which are
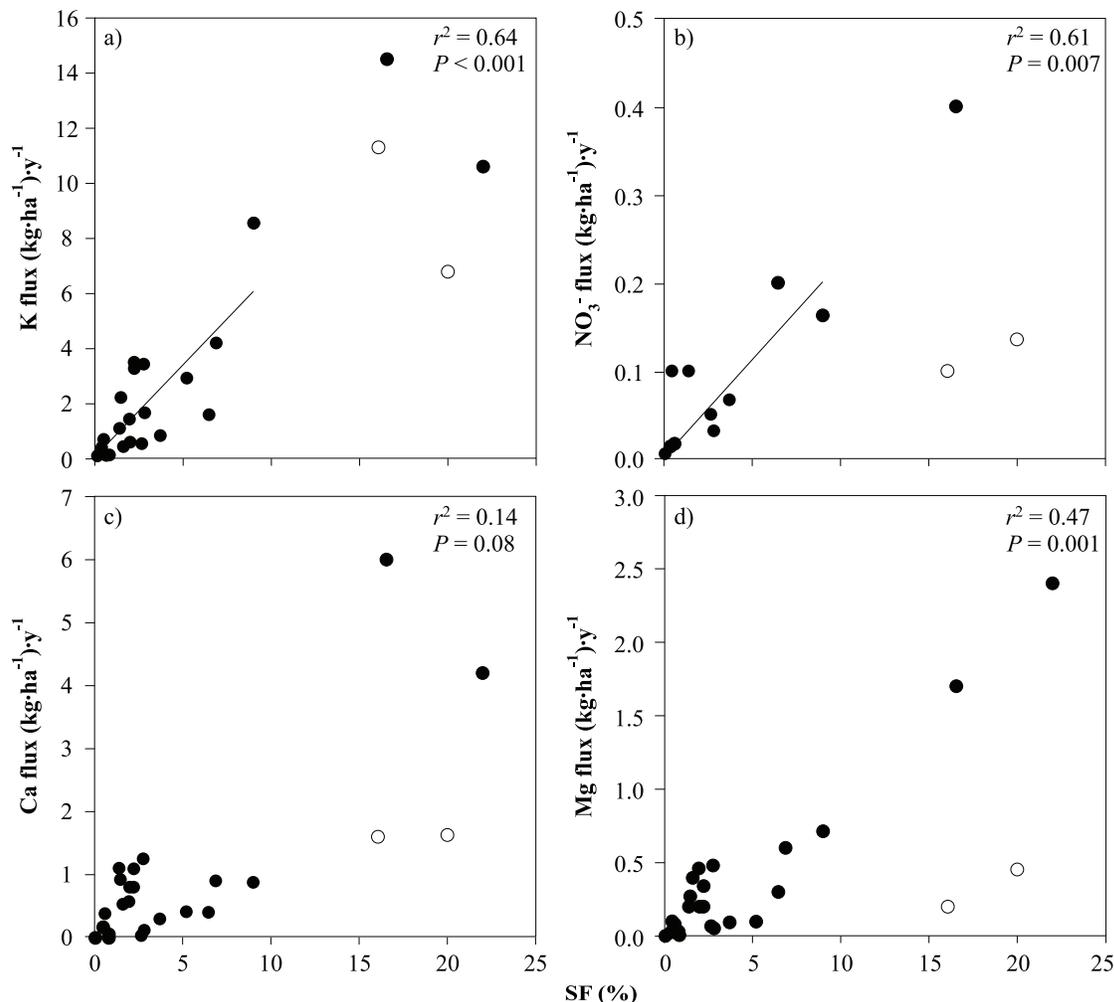
FIGURE 1. Stemflow nutrient fluxes *versus* canopy stemflow partitioning (SF%) (closed circles), the percentage of incident precipitation delivered to base of tree as stemflow. Open circles indicate stemflow fluxes of young, closed canopy secondary forest vegetation described in Schroth *et al.* (2001) and Holscher *et al.* (2003). For all nutrients, the Pearson's r^2 and *P*-values were determined for SF% values of < 10 to avoid bias due to large leverage of the high values. SF% described more than half of the variation ($r^2 > 0.5$) in stemflow nutrient fluxes for nutrients that are more mobile within plants (K and NO_3^-, Figures 1a and b, respectively).

not mobile in plants (Broyer & Stout, 1959), did not exhibit a strong relationship with stemflow partitioning (SF%).

The form in which nutrients are cycled (*e.g.*, organic *versus* inorganic) is important in determining subsequent plant nutrient availability. Considering organic nutrient concentrations in stemflow water, Moreno, Gallardo, and Bussotti (2001) reported dissolved organic carbon (DOC) stemflow concentrations for *Quercus pyrenaica* ranging from 71.8 to 123 $mg \cdot L^{-1}$, while concentrations in rainfall ranged from 5.9 to 7.1 $mg \cdot L^{-1}$. DOC concentrations in throughfall were intermediary to stemflow and rainfall, at 9.9 to 23.5 $mg \cdot L^{-1}$ (Moreno, Gallardo & Bussotti, 2001). Mahendrappa (1974) reported soluble organic carbon stemflow concentrations ranging from 13.74 $mg \cdot L^{-1}$ (white birch, *Betula papyrifera*) to 129.91 $mg \cdot L^{-1}$ (larch, *Larix laricina*). Comparing stemflow DOC concentrations with rainfall DOC concentrations (where reported) shows stemflow water to be enriched by 703–2372% relative to rainfall (Table II). In addition to DOC, stemflow water contains high concentrations of particulate organic matter (POM)

(Parker, 1983). Both DOC and POM are highly enriched with organically bonded nutrients, such as N, P, and S.

Dissolved organic nitrogen (DON) concentration in stemflow water of several temperate species was reported to range from 0.27 to 1.39 $mg \cdot L^{-1}$ (Mahendrappa, 1974; Chang & Matzner, 2000a), and from 0.21 to 1.04 $mg \cdot L^{-1}$ for a variety of tropical forest and fruit species (Schroth *et al.*, 2001). For all reviewed species, the DON enrichment of stemflow water concentration ranged from 233% to 1155% compared to precipitation (Table III). While stemflow DON fluxes delivered to zones of preferential flow would certainly contribute to the significant fraction of N that is lost from forests as DON (Perakis & Hedin, 2002), watershed exports of stemflow-derived DON remain understudied. Stemflow water has also been shown to be enriched in organic phosphorus. Schroth *et al.* (2001) reported organic phosphorus concentrations in stemflow water to range from 10 to 14 $\mu g \cdot L^{-1}$, an enrichment over incident precipitation of 500 to 3600%.

Micronutrients are also concentrated in stemflow water, although both foliar leaching and foliar uptake are pos-

TABLE II. Effect of stemflow partitioning on dissolved organic carbon (DOC) concentration in stemflow water and as percent enrichment with respect to throughfall and rainfall DOC concentrations.

Species	Common name	SF%	SF DOC	TF DOC	RF DOC	SF:TF	SF:RF	Study
				$(mg \cdot L^{-1})$		Enrichment (%)	Enrichment (%)	
Quercus pyrenaica	Pyrenean oak	0.8	168.4	23.5	7.1	716.6	2371.8	[1]
Quercus pyrenaica	Pyrenean oak	0.61	138.4	15.7	6.3	881.5	2196.8	[1]
Larix laricina	Larch, Tamarack	1.6	129.9	nd*	nd	nd	nd	[2]
Abies balsamea	Balsam fir	3.5	90.8	nd	nd	nd	nd	[2]
Pinus resinosa	Red pine	0.7	82.1	nd	nd	nd	nd	[2]
Quercus pyrenaica	Pyrenean oak	0.64	68.2	13.9	5.9	490.6	1155.9	[1]
Picea glauca	White spruce	6.4	65.8	nd	nd	nd	nd	[2]
Quercus pyrenaica	Pyrenean oak	0.95	62.3	9.9	6.4	629.3	973.4	[1]
Picea rubens	Red spruce	2.3	60.6	nd	nd	nd	nd	[2]
Populus grandidentata	Largetooth aspen	6.1	32.3	nd	nd	nd	nd	[2]
Pinus strobus	White pine	5.3	31.6	nd	nd	nd	nd	[2]
Acer rubrum	Red maple	5.6	28.4	nd	nd	nd	nd	[2]
Fagus sylvatica	Beech	5.2	15.8	16.3	2.2	97	703.1	[3]
Betula papyrifera	White or paper birch	3.9	13.7	nd	nd	nd	nd	[2]

SF% is the stemflow (SF) partitioning as a percentage of incident rainfall (RF). TF is throughfall.

*nd = not determined; [1] Moreno, Gallardo & Bussotti, 2001, [2] Mahendrappa, 1974, [3] Chang & Matzner, 2000a.

TABLE III. Effect of stemflow partitioning on dissolved organic nitrogen (DON) concentration in stemflow water and as percent enrichment with respect to rainfall DON concentrations.

Species	Common name	SF%	SF DOC	TF DOC	RF DOC	SF:RF	Study
				$(mg \cdot L^{-1})$		Enrichment (%)	
Larix laricina	Larch, Tamarack	1.60	1.39	nd*	nd	nd	[1]
Abies balsamea	Balsam fir	3.50	1.33	nd	nd	nd	[1]
Eschweilera spp.	Jarana, Kakeralli	0.07	1.04	nd	0.09	1155.6	[2]
Picea glauca	White spruce	6.40	0.94	nd	nd	nd	[1]
Pinus resinosa	Red pine	0.70	0.93	nd	nd	nd	[1]
Fagus sylvatica	Beech	5.21	0.90	1.1	0.29	310.3	[3]
Picea rubens	Red spruce	2.30	0.88	nd	n.d.	nd	[1]
Bixa orellana	Annatto, Arnatto	0.38	0.80	nd	0.09	888.9	[2]
Populus grandidentata	Largetooth aspen	6.10	0.70	nd	nd	nd	[1]
Acer rubrum	Red maple	5.60	0.63	nd	nd	nd	[1]
Bactris gasipaes	Peach palm (fruit)	9.00	0.56	nd	0.09	622.2	[2]
Vismia spp.	Vismia (fallow species)	20.00	0.50	nd	0.09	555.6	[2]
Oenocarpus bacaba	Bacaba palm, Turu palm	0.66	0.49	nd	0.09	544.4	[2]
Bertholletia excelsa	Brazil nut	2.83	0.49	nd	0.09	544.4	[2]
Theobroma grandiflorum	Cupuaçu	3.71	0.48	nd	0.09	533.3	[2]
Pinus strobus	White pine	5.30	0.37	nd	nd	nd	[1]
Betula papyrifera	White or paper birch	3.90	0.27	nd	nd	nd	[1]
Bactris gasipaes	Peach palm (heart of palm)	15.50	0.21	**nd**	**0.09**	**233.3**	**[2]**

SF% is the stemflow (SF) partitioning as a percentage of incident rainfall (RF). TF is throughfall.

*nd = not determined; [1] Mahendrappa, 1974; [2] Schroth et al., 2001; [3] Chang & Matzner, 2000a.

sible outcomes for rainfall that interacts with tree canopies. Silva and Rodriquez (2001) reported pine and oak stemflow concentrations to be enriched with Cu, Fe, Mn, and Zn compared with rainfall concentrations. For an oligotrophic forest, Moreno, Gallardo, and Bussotti (2001) reported stemflow water enrichment in Fe and Mn with respect to rainfall concentrations and a dilution of Zn in stemflow water compared with rainfall, indicating foliar uptake of Zn.

Belowground processes

The spatial redistribution of water to stemflow leads to zones of greater percolation and increased soil water status near the trunk, an effect that has been documented for trees (Ladekarl, 1998) and for crops (Dolan, Dowdy & Lamb, 2001). Stemflow that moves into the soil around the base of a tree has been postulated to be an important mechanism by which trees are able to withstand drought (Martinez-Meza & Whitford,

1996), while abundant precipitation can lead to stemflow-induced localized runoff near the trunk (Herwitz, 1986b).

Specht (1957) described the influence of canopy partitioning as creating a "rain-shadow" near the periphery of canopies. He further observed that soil moisture patterns are quickly established in response to rainfall partitioning. A 24-mm rainfall resulted in a change in soil moisture from uniformly near wilting point to highly heterogeneous after 24 h, with soil adjacent to stemflow-receiving areas at or near field capacity, while soil less than 30 cm away remained at wilting point (Specht, 1957). The spatially variable soil moisture recharge was observed following rains occurring in both wet and dry seasons (Specht, 1957), and was attributed to stemflow. The persistence of this spatial variability in soil moisture was noted to be strongly dependent on rates of evapotranspiration (ET) and frequency of rainfall, which remove and replenish moisture in the root-zone, respectively.

Jackson, Wallace, and Ong (2000) also found changes in soil moisture following rain events to be substantially larger in areas near the base of trees than for soil further from trees. This difference was striking during periods of soil water recharge (*i.e.*, periods in which rainfall exceeds ET), in which soil proximal (0.3 m) to trees showed a 45% greater increase in soil moisture than soil 2.5 m from the base of trees (Jackson, Wallace & Ong, 2000). During periods of soil water depletion (*i.e.*, periods in which ET exceeds rainfall), the effect was even greater: increases in soil moisture were found to be 315% larger at 0.3 m from trees compared to 2.5 m from tree bases (Jackson, Wallace & Ong, 2000).

The spatial redistribution of precipitation by tree canopies leads to spatial variability in water and solute fluxes reaching the soil in forests and agroforestry systems. Stemflow-derived nutrient inputs to soil are further channeled into distinct spatial zones, bypassing much of the soil matrix. The impact of growing tree roots on soil creates conduits for the rapid conveyance of stemflow water through preferential flow pathways such as those related to the rhizosphere. The nutrient and water fluxes associated with tree roots lead to distinctive nutrient and microbial dynamics for the rhizosphere compared with the bulk soil. The quantitative and qualitative aspects of flux modifications will be discussed in the following section.

WATER FLUXES AND PREFERENTIAL FLOW PATHWAYS

Preferential flow is the spatially heterogeneous flow of water through soil, under which larger fluxes are found in continuous voids and along structural discontinuities. Root-derived preferential flow pathways are created by growing tree roots that apply compressive forces to the soil combined with the cementing action of substances exuded by roots (Angers & Caron, 1998). These pathways provide a rapid entry point into the soil for stemflow water, both while the roots are present (Mitchell, Ellsworth & Meek, 1995) and after the roots have decomposed (Devitt & Smith, 2002).

In bypassing much of the soil matrix, preferential flow constitutes the most significant field-scale leaching process for mobile nutrients as well as fertilizers and herbicides (Gish, Gimenez & Rawls, 1998). Stemflow can be considered as multiple point sources of water and nutrient inputs within forest ecosystems (Tanaka, Taniguchi & Tsujimura, 1996).

Tree roots result in wider and deeper preferential flow pathways than do roots of annual crops or pasture plants. Yunusa *et al.* (2002) attributed the 51% increase in preferential water flow for a woody treatment compared with a cropped treatment to increases in the number of large pores (> 2 mm) remaining after removal of the woody species. Using rhodamine-B dye, Martinez-Mesa and Whitford (1996) showed deep infiltration of stemflow water along active root networks of desert shrubs. Deep infiltration of stemflow water may be an important localized recharge mechanism for forest species that depend upon deep water, such as the deeply rooted (> 8 m) evergreen forests of the Brazilian Amazon reported by Nepstad *et al.* (1994).

Hydrological continuity between stemflow and soil preferential flow pathways is an important feature of forest ecosystems and agroforestry systems. While the flux of stemflow water is small at the stand scale compared to net precipitation, its contribution to groundwater recharge and therefore net leaching from the plant root zone can be substantial. Using chloride concentrations in stemflow, throughfall, and precipitation as a tracer, Taniguchi, Tsujimura, and Tanaka (1996) showed that for a pine forest with stemflow partitioning (SF%) of 1%, stemflow contributed from 10.9 to 19.1% of total groundwater recharge over the course of their year-long study. Similarly, Chang and Matzner (2000a) found 13.5% of annual infiltration in a beech forest (SF% of 5.2%) occurred within 1 m^2 of the base of trees, an area representing just 3% of the total forest area. However, the effect of varying antecedent moisture content in relation to belowground funneling requires further study.

SOIL HETEROGENEITY

The spatially distinct fluxes of chemically enhanced stemflow water centred on the base of trees leads to enriched microsites that are distinct from the bulk soil. Nutrient availability of soil near or within the rhizosphere is strongly affected by large fluxes of nutrients delivered as seepage of stemflow water. The longevity of tree roots allows time for the establishment of distinctive rhizospheric conditions (Gobran, Clegg & Courchesne, 1998) that persist for years after removal of the tree (Dockersmith, Giardina & Sanford, 1999).

Soil organic C (SOC) concentrations in preferential flow pathways of forest soils were found to be 10–70% higher than in the soil matrix, while increases in soil microbial C were highly correlated with SOC and were also higher (9–92%) within preferential flow pathways than in the soil matrix (Bundt *et al.*, 2001a,b). Further, SOC associated with preferential flow pathways was shown by its isotopic ($\delta^{13}C$) composition to be younger and less humified than SOC of the soil matrix (Bundt *et al.* 2001a). Most of the preferential flow paths that Bundt *et al.* (2001a) detected and analyzed coincided with living or decayed roots. This observation is consistent with the conceptual model of the rhizosphere as being a zone of positive feedbacks resulting in higher nutrient stocks and increased nutrient availabilities.

Nitrogen cycling is enhanced within preferential flow pathways. These pathways exhibit both enhanced denitrification under the reducing conditions of temporary and localized soil saturation following infiltration of stemflow and enhanced net nitrification after drying (Hagedorn *et al.*, 1999). Overall NO_3^- transport was found to be faster in preferential flow pathways than in the bulk soil (Bundt *et al.*, 2001a). Chang and Matzner (2000b) reported NO_3^- seepage at 60 cm depth in soil proximal to stems to be four times that of the bulk soil, NH_4^+ seepage to be five times greater, and DON to be 8.5 times greater. Differences between seepage rates were attributed to stemflow N inputs (Chang & Matzner, 2000b).

In addition to preferential flow pathways along roots, chemical concentration gradients in soil solution have been reported by several authors to be associated with distance to trees. Chang and Matzner (2000a) found soil solution K concentration to decrease with increasing distance from stems. Since K is not a mobile nutrient in soil and can exhibit a depletion zone proximal to the rhizosphere, stemflow replenishment of K to the rhizosphere appears to be an

important internal nutrient cycling mechanism. Additionally, Gobran, Clegg, and Courchesne (1998) argue that higher P and K contents in rhizospheric soil compared to bulk soil reported in a number of studies of forest rhizospheric soil challenge the traditional view of P and K depletion near roots due to rapid uptake and slow diffusion of these nutrients. This discord warrants further research. The higher P and K concentrations that have been observed in rhizospheric soil may be explained by considering the double funneling process of stemflow partitioning of rainfall and transport through preferential flow paths in root channels. Inputs to the rhizosphere via preferential flow pathways of stemflow water that is up to 400 times richer in phosphate than rainfall (Schroth *et al.*, 2001) would certainly contribute to high rhizospheric P concentrations.

Stemflow-induced patterns of soil acidity are well established in the literature (Zinke, 1962; Mina, 1967; Rhoades, 1996). Spatial heterogeneity of cation exchange capacity (CEC) has also been reported for sites where trees concentrate base cations in stemflow. For example, Koch and Matzner (1993) showed soil heterogeneity of pH and CEC to result from beech stemflow, while heterogeneity did not result for spruce as stemflow was not a significant nutrient pathway for the spruce forest analyzed. Differences have also been shown in microbial populations between bulk soil and preferential flow pathway soil for the bacterial genus *Pseudomonas* (Bundt *et al.*, 2001b). Interactions between stemflow fluxes and microbial populations and activities are not well understood, and the implications for nutrient forms and mobility are unknown.

Conclusion

Trees in forests and agroforestry systems redistribute hydrologic and nutrient fluxes to the root zone through a double-funneling process. Trees first partition rainfall into throughfall and stemflow, resulting in a spatial redistribution of nutrient and water fluxes reaching the soil. Organic and inorganic nutrients, including significant quantities of DOC and DON, are delivered in stemflow water. Stemflow fluxes delivered to the soil at the base of trees are further funneled by the trees through preferential belowground flow pathways.

In this paper, we reviewed stemflow nutrient fluxes for a variety of tree species. Stemflow partitioning ranged from 0.07 to 22% of rainfall for a wide range of species and environmental conditions. Tree canopy characteristics that increase the stemflow flux relative to bulk precipitation also increase the magnitude of nutrient fluxes delivered by stemflow water for plant-mobile nutrients NO_3^- and K, but not for Ca and Mg. Similar trends are presumed for other nutrients and micronutrients relative to their mobility within plants, but there are not sufficient data in the literature at present for a comparative analysis.

There is a clear linkage between aboveground and belowground tree effects on hydrology and nutrient cycling in which increases in stemflow fluxes of nutrients and water relative to bulk precipitation also contribute to increases in soil chemical, biological, and hydrological heterogeneity. Deep infiltration of stemflow through preferential flow pathways aids trees in withstanding droughts, while nutrient fluxes delivered in stemflow augment the quantities

of available nutrients in the rhizosphere. This coupling of aboveground and belowground processes represents an important internal nutrient cycling mechanism inherent to forest ecosystems, particularly for K.

FUTURE RESEARCH DIRECTIONS

As stated by Rhoades (1996), "the soil patches found beneath tree canopies are important local and regional nutrient reserves that influence community structure and ecosystem function." Efforts to incorporate the double-funneling phenomenon into the design of managed agroecosystems should consider long-term hydrological effects of trees on soil heterogeneity induced by aboveground spatial partitioning of nutrient and water fluxes. Species that have a high partitioning of precipitation to stemflow have higher nutrient fluxes in stemflow water. Hence, aboveground modification of canopy architecture due to management practices will affect nutrient recycling in stemflow and the subsequent spatial distribution of nutrient fluxes delivered as stemflow.

Several knowledge gaps remain to be explored. In particular, the role of antecedent moisture content in relation to the routing of stemflow fluxes through root-induced preferential flow paths requires further research. Very little is known about the stemflow of standing dead trees and its priming effect on the associated soil. While standing dead trees presumably have much smaller stemflow partitioning than full-canopy live trees, the stemflow concentrations of K and PO_4^{2-} are considerably higher for dead trees than live ones (Fujimoto *et al.*, 1996).

The response of double-funneling processes in relation to ecosystem disturbances also merits investigation. Lower-intensity disturbances that impact the understory are more frequent than severe disturbances that impact the overstory (*e.g.*, frequent light surface fires in forests *versus* infrequent crown fires). Within mixed forests, the understory has also been shown to be important for stemflow generation (Manfroi *et al.*, 2004) and stemflow nutrient fluxes (Price & Watters, 1989). However, the majority of stemflow studies consider dominant trees only. A whole ecosystem perspective is needed that considers stemflow-derived nutrient fluxes to soil for both overstory and understory canopy strata and the response of these processes to disturbance. Future studies should also consider double-funneling as a mechanism by which atmospheric pollution (*e.g.*, acid deposition, mercury and other trace metals) is routed through the biosphere and into the hydrosphere.

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