Global within-site variance in soil solution nitrogen and hydraulic conductivity are correlated with clay content.

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Abstract

Nutrient fluxes in terrestrial ecosystems are governed by complex biological and physical interactions. Ecologists' mechanistic understanding of these interactions has focused on biological controls including plant uptake and microbial processing. However, ecologists and hydrologists have recently demonstrated that physical controls are also important. Here, we show that within-site spatial variation in soil solution N concentrations is a function of soil clay content across a globally diverse array of field sites. Clay content explained 35% and 53% of the coefficient of variation (CV) in soil solution nitrate (NO_3^-) and dissolved organic nitrogen (DON), respectively. The CV of soil hydraulic conductivity is a similar function of clay content, suggesting that soil hydrology may be a significant mechanism affecting variation in soil solution N. Although vegetation physiognomy and soil C/N ratios are known to affect soil solution N concentrations, neither were significantly related to within-site spatial variation in NO_3^- or DON. However, the spatial variation of NO_3^- and DON was greater in younger forests than in paired older forests. Our data show that the heterogeneity of an important resource, soil solution N, is a predictable function of clay content. Resource heterogeneity, such as that described here for soil solution N, can affect population, community and ecosystem processes.

Keywords: leaching, lysimeter, soil hydrology, resource heterogeneity, soil texture

Introduction

Studies of ecosystem nutrient cycling and retention have traditionally focused on plant and microbial processes (Vitousek and others 1982; Magill and others 1997; Bohlen and others 2001). However, several recent reviews and empirical studies demonstrate that ecosystem losses of nitrate (NO_3^-), dissolved organic nitrogen (DON), and dissolved organic carbon are controlled by complex interactions between biological mechanisms (plant and microbial activity) and physical mechanisms mediated by soil hydrology (e.g, Neff and Asner 2001; Qualls 2000; Lohse and Matson 2005; Asano and others 2006; De Schrijver and others 2007; Dittman and others 2007). At the global scale, the relative importance of biological and physical controls on nutrient cycling has not been evaluated across ecosystems. Moreover, with the exception of several well known examples, the identification of global patterns in terrestrial biogeochemistry is hindered by high chemical and physical variation within soils (e.g., Schimel and others 1994; Raich and Potter 1995; Jobbagy and Jackson 2000).

Variation itself is an important yet often overlooked ecosystem property (Kratz and others 2003). Analyses of ecological variability have provided significant insight into population, community, and ecosystem ecology. For example, studies have shown that cross-scale intraspecific variation in population abundance is predictable (Brown and others 1995), biodiversity can promote community stability (Tilman 1999), and interannual variation in aboveground net primary production is a function of both precipitation variability and potential growth rates (Knapp and Smith 2001). Across ecosystems, variation in properties such as nutrient cycling and productivity is often related to physical attributes including climate and soil (Prentice and others1992; Schimel and others1994; Knapp and Smith 2001).

Nutrient loss through the soil is one important ecosystem property that is affected by interactions between soil hydrology and biogeochemistry (Fisher and others 2004). To measure this property, ecologists routinely sample soil solution nitrogen (N). These data are used to develop ecosystem nutrient budgets and determine potential nutrient pollution of ground and surface waters (Chapin and others 2002). Several reviews have synthesized these measurements, focusing on regional patterns of solute concentration, flux and their controls (Kalbitz and others 2000; Qualls 2000; De Schrijver and others 2007). However, to our knowledge, global cross-ecosystem patterns of variability have not been examined.

Here, we test biologically-based and physically-based hypotheses to explain within-site variability of an important ecosystem resource, soil solution N. Two important biologically-based controls on ecosystem N leaching are vegetation physiognomy and soil C/N ratio. Vegetation physiognomy can affect soil solution N through differences in throughfall and litter quality (e.g, Manderscheid and Matzner 1995; Michalzik and others 2001; De Schrijver and others 2007). Soil C/N ratio is negatively correlated with ecosystem nitrate export (Emmett and others 1998; Lovett and others 2002). Due to the correlations between these variables and soil solution N concentrations, we explored the potential for vegetation physiognomy and C/N ratios to account for within-site variation in soil solution N through the following two hypotheses

1a) Within-site spatial variation of soil solution N is a function of vegetation physiognomy.

1b) Within-site spatial variation of soil solution N peaks at intermediate soil C/N ratios and is lower in soils with narrow (N availability is consistently high with little variation) or wide (rapid immobilization keeps N low with little variation) C/N ratios.

Alternatively, soil hydrologists have demonstrated that physical structure of soil can affect water and solute transport including dissolved N (e.g., Vervoort and others 1999; Jarvis

2007). Recently, Jarvis (2007) developed a conceptual model that describes soil hydrology and solute transport as a function of soil structure. Soil structure refers to the development of soil aggregates; well structured soils have many aggregates whereas poorly structured soils have few aggregates. The model builds upon the general relationship between soil structure and clay content— soils with moderate clay content are well-structured whereas soils with low clay or high clay contents are poorly structured. Accordingly, the model predicts that, as a result of poor structure, soils with low and high clay contents are dominated by homogenous soil hydrology characterized by equilibrium and matrix flow. In contrast, the model predicts that soils with a quantitatively undefined moderate clay content, and thus good structure, are dominated by heterogeneous soil hydrology characterized by non-equilibrium and preferential (bypass) flow. Thus, we hypothesize: 2a) Within-site spatial variation of soil solution N is a function of clay content peaking at moderate clay contents, but not a function of sand or silt content. Because we posit hydrology is a mechanism affecting variation in soil solution N, we further hypothesize: 2b) within-site spatial variation of soil hydrology (as indexed by saturated hydraulic conductivity) is a similar function of clay content.

Methods

Data Retrieval

To test hypotheses 1 and 2a, we searched the peer-reviewed published literature for papers that report mineral soil solution nitrate (NO_3^-) and dissolved organic N (DON) sampled by tension lysimeters, zero tension lysimeters, or centrifuge methods. We selected these two biogeochemicals because they differ in biological availability; NO_3^- is cycled rapidly and widely used by plants and microbes whereas DON is cycled more slowly and is less biologically available (Neff and others 2003). Because hypothesis 2 addresses the relationship between soil solution and soil structure, we did not include data from lysimeters that sampled surface organic soil horizons that overlay mineral soils. However, we did include data from lysimeters that sampled completely organic soils (i.e. peat soils). We also limited our search to non-agricultural systems because agriculture disturbs soil structure and alters N cycling. Similarly, when experiments compared manipulation treatments to untreated controls, we only used data from the controls. When available, we recorded the time since major disturbance such as forest harvest and fire (Appendix). Two papers reported total dissolved inorganic N ($NH_4^+ + NO_3^-$); we included these data with reports of NO_3^- (Lajtha and others 1995; Dijkstra and others 2007). The exclusion of these data did not significantly change our results.

To test hypothesis 2b, we conducted a similar search of the peer-reviewed literature for papers that report saturated hydraulic conductivity (K_s) of surface soils. We selected K_s because this is the most frequently reported soil hydrology variable and the standard for measuring water conductivity due to difficulty in estimating unsaturated conductivity. We executed this search with the same inclusion rules applied to our search for soil solution N data.

Determination of Variation

Several methods are available to measure variation in ecological data (Fraterrigo and Rusak 2008). We used the coefficient of variation (CV) of the mean (CV = 100*1 standard deviation/mean) to standardize and compare within-site spatial variation across studies. The CV has a long history of use in studies of ecosystem variability (e.g., Whittaker and others 1979, Knapp and Smith 2001). Because the CV standardizes for the mean and is a dimensionless number, it permits comparison of variation across ratio scale data with different units and means (Fraterrigo and Rusak 2008). Although the CV can be sensitive to low mean values, we found no correlation between mean soil solution concentrations of NO_3^- and DON or rates of K_s and their respective CVs. Calculation of the CV requires the following information: the mean and standard deviation (SD) *or* the mean, standard error (SE) and sample size. We collected these data from tables and figures. We could not include many reports of soil solution N in our analysis because they did not contain these data, or the data were presented in figures that were too small to interpret (e.g., Carnol and others 1997).

Spatial variability in ecosystem properties can be scale dependent (Collins and Smith 2006) and the papers in our analyses sampled a wide range of spatial scales. Replicate plot sizes ranged from 1-5000m^2; total treatment areas ranged from 6-75,000m^2 (Appendix). However, it was rarely possible to determine the distance between lysimeters within plots or treatments. In a majority of reports, lysimeters were randomly located within plots. Thus, we made no evaluation of spatial scale on soil solution N CVs.

We required spatial means and errors. Thus, we carefully considered how means and errors were derived in each paper. For example, we could not use data that calculated a mean and error by first averaging replicates within each sample time and then averaging across sample times (e.g., a monthly mean). However, we could use data that were derived from multiple sample times but first averaged across-time within a replicate and then multiple replicates' cross-time means were averaged (i.e., a spatial mean).

Several papers reported the spatial mean and error (SE or SD) for multiple time points (e.g, months, seasons, years). In these cases we used the mean CV of the time points in our analysis by calculating the average CV across time. In two of these papers, the standard error was greater than the mean for a particular point in time. We eliminated these time points from calculation of the CV because they do not significantly differ from zero and it was not clear from the methods whether near-zero means resulted from values near detection limits or from missing data assigned a zero concentration value (no water collected in the lysimeter; Johnson and others 2001; Brenner and others 2006). This interpretation rule also resulted in the total elimination of NO_3^- data from a third paper where the standard error was greater than the mean on all sample dates and the CV was >200% (Asano and others 2006).

If a paper reported the mean and an error for replicate locations (e.g., mean and errors of subsamples within a replicate), we used the treatment CV (and not multiple CVs for each replicate). Several papers provided mean soil solution N and error for multiple mineral soil depths within a location; in these cases, we determined the CV for each depth and then used the cross-depth mean CV in our analysis.

Determination of Soil Texture

In addition to the CV of soil solution NO_3^-, DON and K_s, we also required percent clay (by mass) of the soil. We obtained percent clay data in one of five ways (ordered in preference): 1. reported in the paper, 2. reported in a previously published paper from the same location, 3. contacted the author, 4. published on the USDA NRCS Web Soil Survey (NRCS 2008; http://websoilsurvey.nrcs.usda.gov/app/), 5. taken as the mean of the reported soil texture class. The fifth clay determination method was clearly the least accurate. However, we only used this method for 11% of our data. When we were forced to use this method, we determined soil texture as follows: if soil texture was reported to be "clay loam" we used 33.75% clay because that is the mean clay content for the clay loam soil texture class which has a range from 27.5-40% clay (NRCS 2008). Soil clay content typically varies with depth; accordingly, we used the depth-weighted mean soil texture to lysimeter depth when possible.

Data Analysis

To evaluate hypothesis 1a ("within-site spatial variation of soil solution N is a function of vegetation physiognomy"), we sorted each report of soil solution NO_3^- and DON into one of seven vegetation physiognomy groups (Conifer; Hardwood-Deciduous; Hardwood-Evergreen; Grassland; Savanna-Shrubland; Mixed Conifer-Deciduous and Heath). Then, using two individual one-way analyses of variance (ANOVA), we independently analyzed the dependent variables NO_3^- CV and DON CV across the between subject factor vegetation physiognomy. We selected the seven physiognomy groups because two have been used to evaluate the effect of vegetation physiognomy on soil solution N concentrations (i.e., Hardwood-Deciduous and Conifer; e.g., Currie and others 1996; De Schrijver and others 2007); the other four groups separated the remaining data between well accepted global biomes (Prentice and others 1992). Although Savanna-Shrubland and Heath are both dominated by a shrub physiognomy, the Savanna Shrubland sites were dominated by nonericaceous species whereas the Heath sites were dominated by ericoids.

To evaluate hypothesis 1b ("within-site spatial variation in soil solution N peaks at intermediate soil C/N ratios") and 2a ("within-site spatial variation in soil solution N is a function of clay content"), we again independently analyzed NO_3^- and DON data. Using Sigmaplot®, we fit the percent clay (x) and CV (y) data to several Gaussian and lognormal functions exhibiting a single maximum. We did not formally select among curve-fitting options because our interest was in determining whether non-linear relationships existed, rather than defining a specific non-linear curve. However, we did examine the residuals of these curves to determine the modeled data's fit throughout the data range. We also examined the relationships between NO_3^- and DON CVs and sand and silt content although these data were not available for seven reports. To evaluate hypothesis 2b, ("within-site spatial variation of soil saturated hydraulic conductivity is a function of clay content”), we fit K_s CVs and percent clay, sand and silt to the same functions we used for NO_3^- and DON.

We used a subset of reports to 1) evaluate the relative magnitude of NO_3^- and DON CVs for cases when lysimeter water was analyzed for both N species, 2) compare the relative magnitude of NO_3^- or DON CVs between young or recently harvested forests and paired older forests and 3) compare the relative magnitude of NO_3^- or DON CVs between unmanipulated controls and paired N addition treatments (Appendix). Twenty-five reports analyzed lysimeter water for both NO_3^- and DON. Nine reports compared NO_3^- and four reports compared DON between young or recently harvested forests and older forests on the same soils. Four reports compared NO_3^- and four reports compared DON between unmanipulated controls and paired mineral N addition treatments on the same soils. We used paired t-tests to make all of these comparisons. We also used a majority of reports to search for a general effect of time since major disturbance across all reports (i.e., forest harvest, fire or cessation of cropping; Appendix).

The distributions of data did not significantly differ from the normal distribution and variance was not significantly different between groups (t-tests and ANOVA). Sample sizes in analyses of variance for vegetation physiognomy were not equal. However, equal sample sizes are not required for single-factor ANOVA although they do diminish statistical power (Zar 1997).

Results

We found 37 papers that met our requirements for soil solution N data. These papers included a total of 100 independent reports of NO_3^- (62) and DON (38) representing different soils and vegetation physiognomies. Geographically, our data set includes representatives from Africa, Asia, Europe, North America, and South America. Ecologically, these data are distributed across forest, grassland and wetland biomes from the tropics to the sub-arctic. However, there was no effect of vegetation physiognomy or soil C/N ratios on NO_3^- or DON CVs (data not shown). Although not included in our hypotheses, we also found no effect of time since disturbance, or total C or total N on soil solution N CVs.

We found 14 papers that met our requirements for K_s data. These papers included a total of 46 independent reports. Similar to reports of soil solution N, these data were widely distributed both geographically and ecologically (Appendix).

The relationship between clay content and the CVs of soil solution NO_3^-, DON and K_s significantly fit both Gaussian and lognormal distributions (Fig. 1). However, no variable's distribution significantly differed from the normal distribution ($p > 0.2$); thus we display the data as fit by a 4-parameter Gaussian function. Percent clay of the soil accounted for greater than 1/3 of the variation in the CV of mean soil solution NO_3^- and K_s. Peak variation of NO_3^- and DON occurred at ≈12% clay content; peak variation in K_s occurred at a slightly higher clay content—≈15%. Clay accounted for more variation within NO_3^-, DON and K_s CVs than either sand or silt (Table 1).

Considering all data, the magnitude of NO_3^- variation was ≈26% greater than DON. The arithmetic mean CV of NO_3^- and DON were 49.84 % and 39.57%, respectively. Limiting the comparison to NO_3^- and DON CVs from the same samples within reports, NO_3^- CVs were higher. However, the difference in magnitude between NO_3^- and DON CVs was also a function of clay content. At low clay content, NO_3^- CVs were typically greater than DON CVs, whereas at higher clay contents NO_3^- and DON CVs were more similar (Fig 2). Although there was no effect of time since major disturbance across all sites (Appendix), in paired plots both NO_3^- and DON variation were lower in older forests compared to young or recently harvested forests (Fig

3). We found no effect of mineral N additions on NO_3^- or DON CVs ($p > 0.2$; data not shown). However, the sample size ($n = 4$) for mineral N addition comparisons was extremely limited.

Although our hypotheses did not address mean concentrations of NO_3^- and DON, and our data set was not assembled to identify patterns in mean concentrations of soil solution N across sites, we found no correlation between clay content and mean concentrations of soil solution NO_3^- and DON. Similarly, there was no effect of vegetation physiognomy on mean concentrations.

Discussion

For the dataset assembled here, we reject our hypotheses that the coefficient of variation in soil solution N is related to vegetation physiognomy or soil C/N ratios. In contrast, we found significant correlations between clay content and within-site variation of NO_3^-, DON, and K_s. Thus we cannot reject our second hypothesis; clay content, through its impact on hydrology, appears to be an important determinant of within-site variation in soil solution N concentrations. Soil solution N CVs are well-fit by several functions exhibiting a single maximum, suggesting that concentrations are more spatially variable at intermediate clay contents (≈10-15%). Our DON data represent a limited sample size and should be interpreted with caution.

Although we cannot rule out additional mechanisms beyond vegetation physiognomy, soil C/N ratio, total C and total N, the coincident peaks and similar functional relationships between clay and the CVs of K_s, NO_3^- and DON suggest that the mechanistic basis for the clay-NO_3^- CV and clay-DON CV relationships is hydrological. Hydrological controls on variation in soil solution N may ultimately be the result of physical and biological interactions. For example, soil structure may influence the variation in mass flux of water and its transport of soil solution N. In contrast, hydrology may impact the diversity and heterogeneity of the microbial communities that form NO_3^- and DON. Similarly, differences in soil solution N CVs between young and old forests could be the result of physical and biological mechanisms. Harvesting methods physically alter soil structure, which can result in greater soil solution N variation; harvesting also reduces vegetative uptake, which can result in greater soil solution N variation (Guo and others 2004). Nonetheless in our dataset, clay content appears to be working as a proxy for both direct and indirect effects of soil hydrology on soil solution N variation.

That a single variable (clay content) can explain a large portion of the CV in soil solution N is an important discovery. However, a substantial fraction of variation in CVs was not explained by clay. What mechanisms can account for this residual variance? Sand and silt contents explained only a small (although sometimes significant) proportion of the variation in soil solution N CVs and K_s CVs. This affirms, as suggested by Jarvis (2007), that clay plays a greater role affecting soil hydrology than either silt or sand. Vegetation physiognomy can also be ruled out as a dominant control. However, many complex biogenic and physiogenic processes and properties govern heterogeneity in soil structure and hydrology. For example, the abundance of mineral particles > 2mm are not included in soil texture measurements. Similarly, root density and size as well as soil macrofauna can affect soil structure and hydrology (Wilding & Lin 2006). Accordingly, we expect that a significant proportion of the unexplained variation in CVs are due to these site-specific variables that affect soil hydrology but are not explained by clay content. This is particularly likely for K_s and DON which are largely controlled by physical mechanisms (Vervoort and others. 1999; Kalbitz and others 2000).

Chemical mechanisms may also account for the observed relationship between clay content and variation in soil solution N as well as unexplained variation. Soil pH, clay mineralogy and organic matter composition can control the microbial transformation and solid-solution exchange of dissolved N species (De Nobili and others 2002). In particular, DON is a heterogeneous group of molecules that interact with soil solids in different ways. For example, these molecules contain hydrophobic and hydrophilic species (Huygens and others 2008). In particular, interactions between clay mineralogy and NO_3^- and DON may account for unexplained variation in CVs.

In the case of NO_3^-, a significant proportion of the unexplained variation is likely due to its active biological cycling. Many plants and soil microorganisms use NO_3^- as a source of N. In contrast, DON is chemically heterogeneous; a significant fraction of DON is recalcitrant to microbial degradation, and only a small portion of DON is available for direct biological uptake (i.e., amino acids; Chapin and others 2002; Neff and others 2003). Accordingly, NO_3^- turnover is faster than DON turnover and it is probable that the greater biological availability of NO_3^- is responsible for the larger (relative to DON) variation observed for NO_3^- at low clay contents. This interpretation of the relationship between NO_3^- and DON variation is similar to the traditional comparison of biologically reactive chemicals with a conservative tracer (typically Cl^-): molecules that are susceptible to rapid biological cycling have greater variation in mean concentration than tracers. Manderscheid and Matzner (1995) found a strong correlation between Cl^- in throughfall and soil solution, but no correlation between NO_3^- in throughfall and soil solution. Several reviews also indicate that hydrology can control soluble nutrient transport through the soil (Kalbitz and others 2000, Neff and Asner 2001, Qualls 2000). Our interpretation is also consistent with the occurrence of biological hotspots and hot moments of N cycling that increase the heterogeneity of reactive N distribution in the soil (McClain and others 2003). We cannot isolate the mechanism driving the negative exponential relationship between the difference in magnitude of NO_3^- and DON CVs and clay content (Fig 3). Biological mechanisms, physical mechanisms, chemical mechanisms, or their interaction could have resulted in this observation.

Nitrate CVs in our data (range: 0.16-101.54%) were generally within the range reported from single-site studies that were conducted with an objective to characterize spatial variability in soil nitrate concentrations in lysimeter and salt extracted solutions (Robertson and others 1988, CV = 65%; Manderscheid and Matzner 1995, CV = 44.5-75.8%; Rothe and others 2002, CV = 20-129%). One such report from a relatively high-clay soil (19.8%) that did not meet our data inclusion rules found much higher NO_3^- spatial variation (Asano et al. 2006, CV > 200%). These data may reflect an unusually well structured high-clay soil. Although most high-clay soils are poorly structured, exceptions do occur and they might not fit within the patterns observed in our data set. Our lowest NO_3^- CV values (< 1 %) were much lower than these single-site studies because none of them were conducted on extremely high or low clay content soils that we found to be characterized by lower spatial variation.

Soil texture, and clay content in particular, have proven to be a useful proxy for hydrology and robust predictor of global ecological and hydrological properties including soil carbon storage (Jobbagy and Jackson 2000), plant resource limitation (Paruelo and others 1999), dominant vegetation physiognomy (Prentice and others 1992) and water storage (Saxton and others 1986). Our results extend soil texture's utility to describe ecosystem resource heterogeneity. Soil N availability can limit both plant and microbial growth in terrestrial ecosystems (Kaye and Hart 1997), so our data have important implications for variation in plant and microbial activity across sites. For example, spatial heterogeneity of soil resources has recently been proposed to explain why net N mineralization is a good predictor of plant-available N in some ecosystems, and a poor predictor of plant-available N in other ecosystems (Schimel and Bennett 2004). Our data add to this new component of soil N cycling theory by showing that soil solution N will be more patchy, or spatially heterogeneous, in sites with intermediate clay content. In these ecosystems, we would expect a diverse array of soil microsites that enable both oxidative (e.g. nitrification) and reductive (e.g. denitrification) microbial processes to occur in different soil patches (Schimel and Bennett 2004). In contrast, soils with very high or low clay content will have less spatial variation in soil solution N, which would lead to decreased heterogeneity in microbial processes.

Resource heterogeneity can shape ecosystems' productivity, diversity, function and structure (e.g., Hutchings and others 2003; Maestre and Reynolds 2007). These processes operate across scales from physiology (Jackson and Caldwell 1996) to ecosystems (Anderson and others 2004). For example, spatial variation in soil solution N can control population, community and ecosystem structure as well as function (Sulkava and Huhta 1998; Ettema and Wardle 2002; Anderson and others 2004). Our data should encourage further testing of resource heterogeneity hypotheses in natural systems without manipulation.

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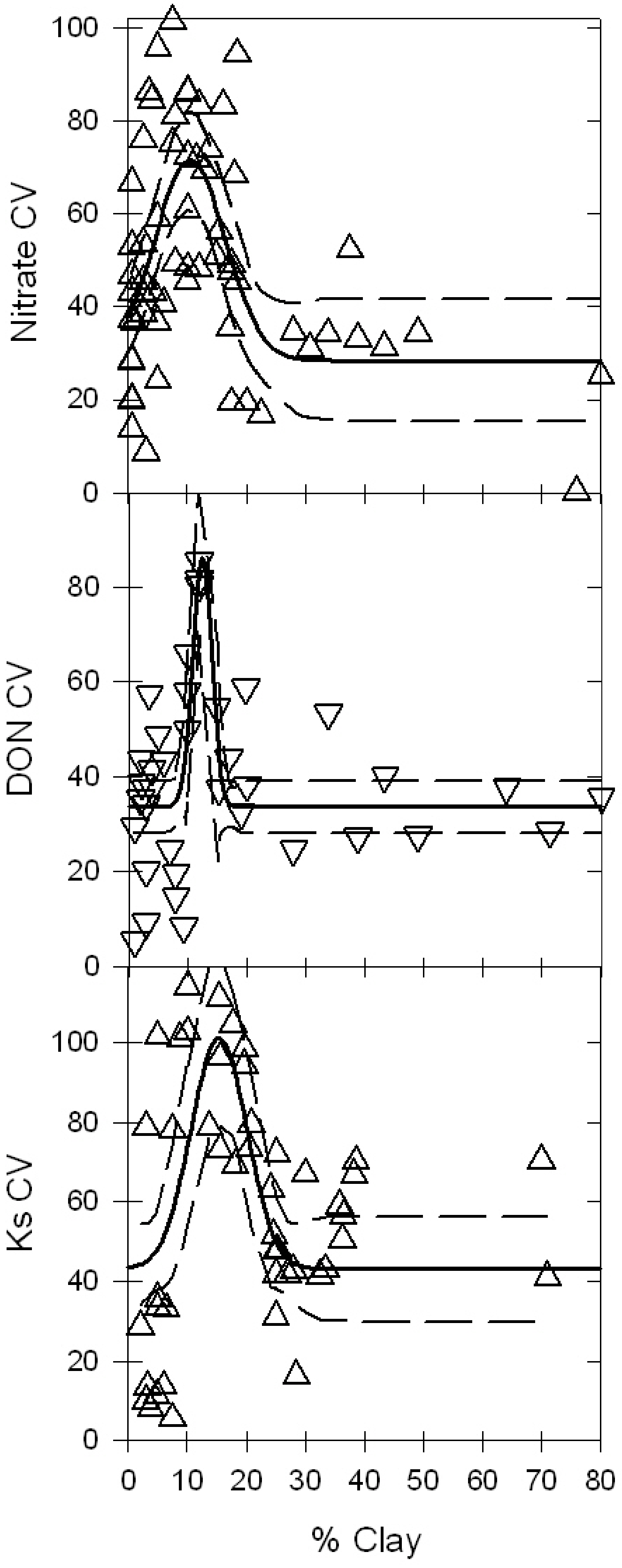
Nitrate CV
0
20
40
60
80
100
DON CV
0
20
40
60
80
Ks CV
0
20
40
60
80
100
0
10
20
30
40
50
60
70
80
% Clay

618

Figure1. Nitrate (NO_3^-), dissolved organic N (DON) and K_s (soil saturated hydraulic conductivity) coefficients of variation and corresponding clay contents. Each triangle represents an independent report. The bold, solid lines correspond to modeled data from a 4 parameter Gaussian function $y = y_o + ae\left[-0.5\left(\frac{x - x_o}{b}\right)^2\right]$. Nitrate, $r^2 = 0.35$, $p < 0.0001$; DON, $r^2 = 0.53$, $p < 0.0001$; K_s $r^2 = 0.39$, $p = 0.0001$. The smaller dashed lines represent the 95% and 5% confidence intervals of the regression modeled data.

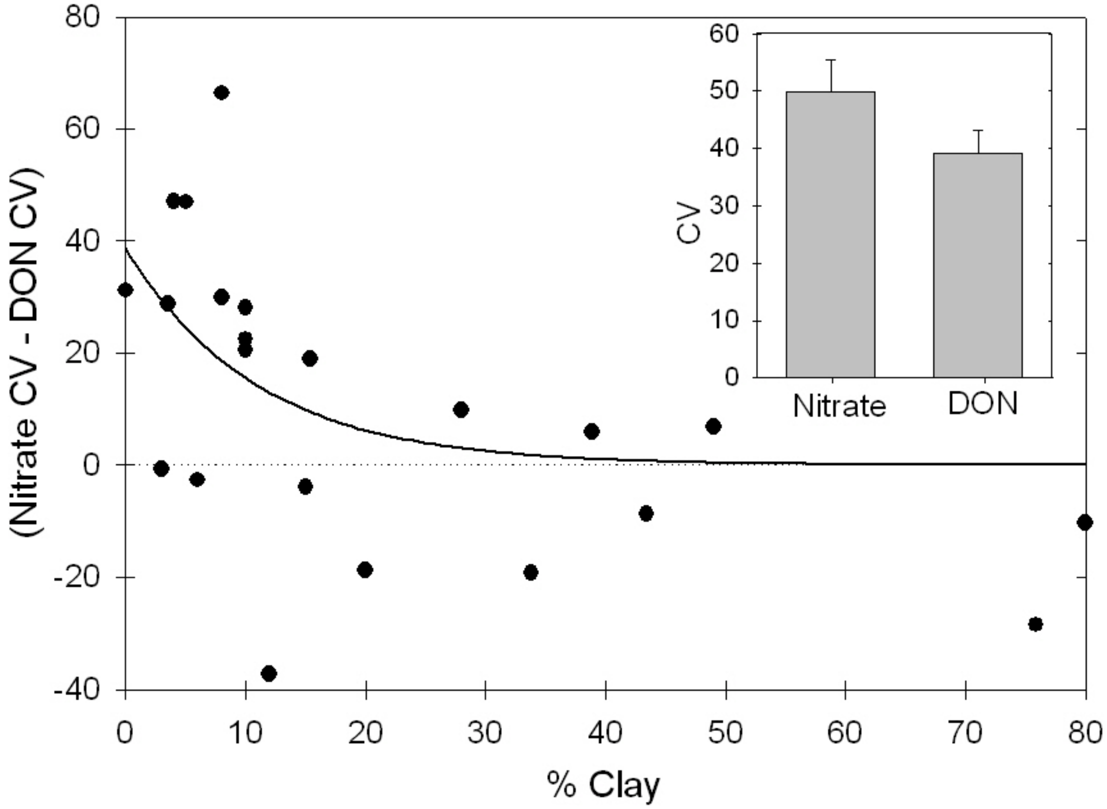

Figure 2. Inset: Mean (se) nitrate and DON CVs from the same lysimeters within reports (paired t-test n = 23; p = 0.072). However, the difference in magnitude of variation was a function of clay content. On the y-axis, zero corresponds to no difference between nitrate and DON CVs. The bold curve represents modeled data from the exponential function $y = ae^{-bx}$ ($r^2 = 0.30$; p = 0.007).

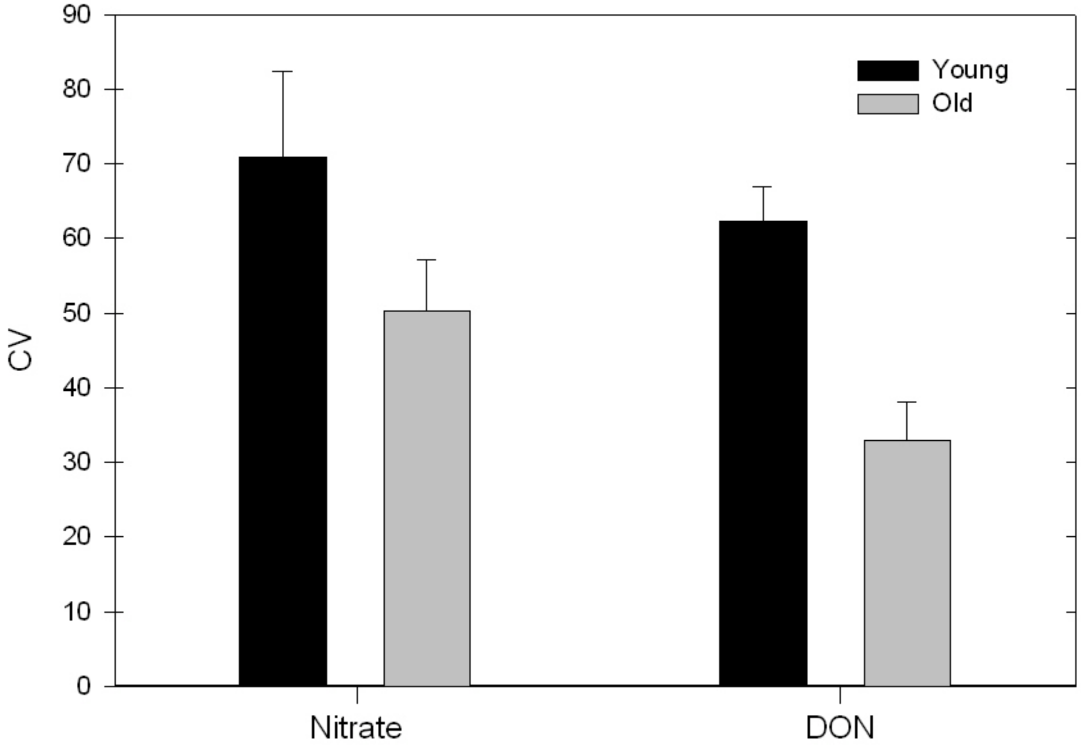

Figure 3. Paired comparison of nitrate and DON CVs (mean, se) from reports that compared soil solution N between young or recently harvested forests and old forests (paired t-test; nitrate n = 8, p = 0.033; DON n = 4; p = 0.038).

	Nitrate CV	DON CV	Saturated Hydraulic Conductivity CV
% Sand	r^2 = 0.03 (p =.6365)	r^2 = 0.15 (p = 0.1706)	r^2 = 0.29 (p = 0.0028)
% Silt	r^2 = 0.13 (p = 0.0522)	r^2 = 0.08 (p = .4367)	r^2 = 0.23 (p = 0.0133)
% Clay	r^2 = 0.35 (p < 0.0001)	r^2 = 0.53 (p < 0.0001)	r^2 = 0.39 (p = 0.0001)

Table 1. Four Parameter Gaussian function fit to soil texture and coefficient of variation (CV) data. See Figure 2 caption for equation.

Nitrate Data

Source	Location	Texture Determination	%Sand	% Silt	% Clay	CV (%)	Sampling Method	# lysimeters / Replicate/ Depth	Replicates	approximate total sample times	depth	dominant vegetation
Adamson (1998)	United Kingdom	Mean Text. Class (Peat)	Peat	Peat	Peat	36.64	T	1	6	78	10 & 50 cm mean	Heath
Bohlen et al. (2004)	NY, USA	Author Contacted/ WSS	32.1	55.9	12	83.20	O&T Mean	4	3	27	15 & 40 cm mean	Hardwood-Deciduous
Borken et al. (2004)	Solling, Germany	Borken & Beese (2002)	14	58	28	34.6	T	4	3	12	10cm	Conifer
Borken et al. (2004)	Solling, Germany	Borken & Beese (2002)	39	46	15	50.86	T	4	3	13	10cm	Conifer
Brenner et al. (2006)	AK, USA	WSS	15.05	77	8	49.45	T	5, 4	3	20	12 & 40 cm mean	Hardwood-Deciduous
Brenner et al. (2006)	AK, USA	WSS	15.05	77	8	81.01	T	5, 4	3	20	12 & 40 cm mean	Conifer
De Schrijver et al. (2008)	Belgium	Author contacted	>90	5-9	<5	42.58	T	3	4	12	100 cm	Hardwood-Deciduous
De Schrijver et al. (2008)	Belgium	Author contacted	>90	5-9	<5	45.50	T	3	2	12	100 cm	Conifer
De Schrijver et al. (2008)	Belgium	Author contacted	>90	5-9	<5	53.76	T	3	2	12	100 cm	Conifer
De Schrijver et al. (2008)	Belgium	Author contacted	>90	5-9	<5	76.09	T	3	2	12	25cm	Heath
De Schrijver et al. (2008)	Belgium	Author contacted	>90	5-9	<5	38.46	T	3	2	12	25cm	Heath
Dijkstra et al. (2007)	MN, USA	Author contacted	94	2.5	3.5	86.16	T	1	12	20	100cm	Grassland
Dittman et al. (2007)	NY, USA	Mean Text. Class (Sandy Loam)	65	25	10	72.45	O	1	2	145	22.5cm, 44.5cm mean	Conifer
Dittman et al. (2007)	NY, USA	Mean Text. Class (Sandy Loam)	65	25	10	85.96	O	1	3	145	22.5cm, 44.5cm mean	Hardwood-Deciduous
Dittman et al. (2007)	NY, USA	Mean Text. Class (Sandy Loam)	65	25	10	86.31	O	1	3	145	22.5cm, 44.5cm mean	Hardwood-Deciduous
Fang et al. (2008)*	Zhaoqing, China	Author contacted	36.8	29.4	33.8	34.12	O	2	3	24	20cm	Hardwood-Evergreen (young growth)
Fang et al. (2008)*	Zhaoqing, China	Author contacted	22.1	34.5	43.4	31.26	O	2	3	24	20cm	Hardwood-Evergreen (old growth)
Fisk et al. (2002)*	MI, USA	Reported	63	32	4	84.57	T	8	3	30	100cm	Hardwood-Deciduous (old growth)
Fisk et al. (2002)*	MI, USA	Reported	70	25	5	95.78	T	8	3	30	100cm	Hardwood-Deciduous (young growth)
Hagedorn et al. (2001)†	Switzerland	Reported	5	46	49	34.38	T	1	5	>20	5cm	Conifer
Holloway and Dahlgren (2001)	CA, USA	Mean Text. Class (Sandy Loam)	65	25	10	48.35	C	1	3	12	30-60cm	Savanna-Shrub
Holloway and Dahlgren (2001)	CA, USA	Mean Text. Class (Silt Loam)	25	67.5	13.75	73.85	C	1	3	12	30-60cm	Savanna-Shrub
Hope (2009)*	BC, Canada	Reported	64.67	30.97	4.27	42.94	T	6	3	~24	50-60cm	Conifer
Huygens et al. (2008)	Chile	Huygens et al. (2007)	71	23	6	40.64	T	1	4	na	10, 50, 100 cm mean	Hardwood-Evergreen
Johnson et al. (2001)	NV, USA	Author Contacted/ Mean Text. Class (Sand)	92.5	7.5	5	59.16	T	1	6	4	15 and 30 mean	Conifer
Jones and Willett (2006)	United Kingdom	Author Contacted	19	69	12	48.19	C	1	6	na	A horizon	Hardwood-Deciduous
Jones and Willett (2006)	United Kingdom	Author Contacted	44	36	20	19.34	C	1	6	na	A horizon	Hardwood-Deciduous
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	20.12	O	4	2	>10	50cm	Grassland
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	28.28	O	4	2	>10	50cm	Savanna-Shrub
Lajtha et al. (1995)*	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	43.07	O	4	2	>10	50cm	Mixed Hardwood-Deciduous (young growth)
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	53.04	O	4	2	>10	50cm	Conifer
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	19.74	O	4	2	>10	50cm	Mixed Hardwood-Deciduous
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	66.60	O	4	2	>10	50cm	Hardwood-Deciduous
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	46.61	O	4	2	>10	50cm	Hardwood-Deciduous
Lajtha et al. (1995)*	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	37.42	O	4	2	>10	50cm	Mixed Hardwood-Deciduous (old growth)
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	13.78	O	4	2	>10	50cm	Hardwood-Deciduous
Lajtha et al. (1995)	MA, USA	Author Contacted/ Seely & Lajtha 1997	90	10	<1	28.46	O	4	2	>10	50cm	Hardwood-Deciduous
Lajtha et al. (2005)	OR, USA	Reported	na	na	13	69.28	T	5	3	na	30 & 100 cm mean	Conifer
Lohse and Matson (2005)†	HA, USA	WSS	31.5	31	37.5	52.29	T	2	4	>20	47cm	Hardwood-Evergreen (300 year old soil)
Lohse and Matson (2005)†	HA, USA	WSS	48.6	34.1	17.3	35.50	T	2	4	>20	28cm	Hardwood-Evergreen (4.1my old soil)
Marques and Ranger (1997)*	France	Reported	38.3	50.67	11.6	71.88	O	1	4	32	15, 30, 60 mean	Conifer
Marques and Ranger (1997)	France	Reported	45.25	38.73	16.025	83.25	O	1	4	32	15, 30, 60 mean	Conifer
Marques and Ranger (1997)*	France	Reported	44.33	35.08	18.05	68.35	O	1	4	32	15, 30, 60, mean	Conifer
McLaughlin and Phillips (2006)*	ME, USA	Author Contacted/ Mean Text. Class (Loamy Sand)	80	15	7.5	75.00	T	2	4	21	25 cm & 50cm mean	Conifer (old growth)
McLaughlin and Phillips (2006)*	ME, USA	Author Contacted/Mean Text. Class (Loamy Sand)	80	15	7.5	101.54	T	2	8	21	25 cm & 50cm mean	Conifer (young growth)
Mitchell et al. (2001)	NY, USA	WSS/ Mitchell et al. (2003)	37.5	38.75	17.5	47.64	T	3-4	3	>10	15cm & 50cm mean	Hardwood-Deciduous
Mitchell et al. (2001)	NY, USA	WSS/ Mitchell et al. (2003)	92.5	7.5	5	36.79	T	3-4	3	>10	15cm & 50cm mean	Hardwood-Deciduous
Mitchell et al. (2001)	NY, USA	WSS/ Mitchell et al. (2003)	65	25	10	60.92	T	3-4	3	>10	15cm & 50cm mean	Hardwood-Deciduous
Mobley, Richter et al. (Unpublished)	SC, USA	Richter et al. (1994)	67.6	17	15.4	56.25	O	12	1	19	7.5cm	Hardwood-Deciduous
Murphy et al. (2006)*	NV, USA	Author Contacted/ Mean Text. Class (Loam)	37.5	38.75	17.5	49.05	T	1	4	3 years	30cm	Conifer
Neill et al. (2006)*	Brazil	Reported	na	na	30.75	31.09	T	1	5	>20	30cm & 100cm mean	Hardwood-Evergreen
Rothe et al. (2002)	Germany	Kreutzer and Weiss (1998)	29.02	47.01	18.45	45.33	T	1	10	48	20, 40, 100cm	Hardwood-Deciduous
Rothe et al. (2002)	Germany	Kreutzer and Weiss (1998)	29.02	47.01	18.45	94.33	T	1	10	48	20, 40, 100cm	Conifer
Schroth et al. (2000)	Brazil	Reported	na	na	80	25.30	T	1	6	13	10cm & 60cm mean	Hardwood-Evergreen
Schwendenmann and Veldkamp (2005)	Costa Rica	Reported	na	na	75.86	0.16	T	4	4	>20	20, 40, 75, 150, 250 350 cm mean	Hardwood-Evergreen
Silva et al. (2005)	OK, USA	Reported	50	27.5	22.5	16.67	T	2	2	23	50cm	Grassland
Silva et al. (2005)	OK, USA	Reported	45	35.5	17.5	19.35	T	2	2	23	50cm	Hardwood-Deciduous
Silva et al. (2005)	OK, USA	Reported	80	10	10	45.45	T	2	2	23	50cm	Grassland
Silva et al. (2005)	OK, USA	Reported	87.5	7.5	5	24.12	T	2	2	23	50cm	Hardwood-Deciduous
Strahm et al. (2005)*	WA, USA	Author contacted	16.42	44.72	38.86	33.16	T	1	4	>10	100 cm	Conifer
Zak et al. (2004)	MI, USA	Author contacted	84	13	3	8.62	T	4	3	22	75cm	Hardwood-Deciduous

Appendix 1. Sampling method abbreviations: T = tensions lysimeters, O = Zero tension lysimeters and C = centrifuge.
Texture Determination Abbreviation: WSS = Web Soil Survey (see literature cited)
na = not available

* = report used in young vs. old forest paired comparison; Hope (2009); Murphy et al. (2006), Neill et al. (2006) and Strahm et al. (2005) paired sites were harvested immediately prior to data collection and thus not included in clay-CV regression.
† = report used in paired N addition comparison

DON Data

Castellano Kaye Appendix

Source	Location	Texture Determination	%Sand	% Silt	% Clay	CV (%)	Sampling Method	# lysimeters / Replicate/ Depth	Replicates	approximate sample times	lysimeter depth	dominant vegetation
Adamson et al. (1998)	United Kingdom	Mean Text. Class (Peat)	Peat	Peat	Peat	5.46	T	1	6	26	10 & 50 cm mean	Heath
Asano et al. (2006)	OR, USA	WSS	27.65	52.55	19.80	58.76	T	1	19	15	50cm	Conifer
Borken et al. (2004)	Solling, Germany	Borken & Beese (2002)	27	54	19	32.35	T	4	3	10	10cm	Hardwood-Deciduous
Borken et al. (2004)	Solling, Germany	Borken & Beese (2002)	14	58	28	24.72	T	4	3	6	10cm	Conifer
Borken et al. (2004)	Solling, Germany	Borken & Beese (2002)	39	46	15	54.7	T	4	3	12	10cm	Conifer
Borken et al. (2004)	Unterlüß, Germany	Borken & Beese (2002)	77	16	7	24.73	T	4	3	8	10cm	Hardwood-Deciduous
Borken et al. (2004)	Unterlüß, Germany	Borken & Beese (2002)	74	23	3	34.1	T	4	3	8	10cm	Conifer
Borken et al. (2004)	Unterlüß, Germany	Borken & Beese (2002)	81	16	3	20.18	T	4	3	8	10cm	Conifer
Brenner et al. (2006)	AK, USA	WSS	15.05	77.00	8.00	19.50	T	5,4	3	20	13 & 40 cm mean	Hardwood-Deciduous
Brenner et al. (2006)	AK, USA	WSS	15.05	77.00	8.00	14.63	T	5,4	3	20	14 & 40 cm mean	Conifer
Currie et al. (1996)†	MA, USA	WSS/ Author Contacted	68.00	16.70	12.00	80.27	T	5	1	14	60cm	Conifer
Currie et al. (1996)†	MA, USA	WSS/ Author Contacted	68.00	16.70	12.00	81.63	T	5	1	14	60cm	Hardwood-Deciduous
Dijkstra et al. (2007)	MN, USA	Author contacted	94.00	2.50	3.50	57.4	T	1	12	20	60cm	Grassland
Dittman et al. (2007)	NY, USA	Mean Text. Class (Sandy Loam)	65.00	25.00	10.00	49.98	O	1	2	145	22.5cm, 44.5cm mean	Conifer
Dittman et al. (2007)	NY, USA	Mean Text. Class (Sandy Loam)	65.00	25.00	10.00	57.88	O	1	3	145	22.5cm, 44.5cm mean	Hardwood-Deciduous
Dittman et al. (2007)	NY, USA	Mean Text. Class (Sandy Loam)	65.00	25.00	10.00	65.72	O	1	3	145	22.5cm, 44.5cm mean	Hardwood-Deciduous
Fang et al. (2008)*	Zhaoqing, China	Author contacted	36.80	29.40	33.80	53.29	O	2	3	24	20cm	Hardwood-Evergreen (young growth)
Fang et al. (2008)*	Zhaoqing, China	Author contacted	22.10	34.50	43.40	39.97	O	2	3	24	20cm	Hardwood-Evergreen (old growth)
Fisk et al. (2002)*	MI, USA	Reported	63.00	32.00	4.00	37.44	T	8	3	30	30	Hardwood-Deciduous (old growth)
Fisk et al. (2002)*	MI, USA	Reported	70.00	25.00	5.00	48.82	T	8	3	30	30	Hardwood-Deciduous (young growth)
Hagedorn et al. (2001)†	Switzerland	Reported	5.00	46.00	49.00	27.50	T	1	5	>20	5cm	Conifer
Huygens et al. (2008)	Chile	Huygens et al. (2007)	71.00	23.00	6.00	43.32	T	1	4	na	10, 50, 100 cm mean	Hardwood-Evergreen
Jones and Willett (2006)	United Kingdom	Author contacted	19.00	69.00	12.00	85.40	C	1	6	na	A horizon	Hardwood-Deciduous
Jones and Willett (2006)	United Kingdom	Author contacted	44.00	36.00	20.00	38.10	C	1	6	na	A horizon	Hardwood-Deciduous
Kaiser and Guggenberger (2005)	Germany	Reported	na	na	17.00	44.06	O&T Mean	8	3	2	25-30cm & 90cm mean	Hardwood-Deciduous
Lilienfein et al. (2004)	CA, USA	Dickson & Crocker (1953)	40.30	57.59	2.11	43.77	T	1	5	8	mean 10cm, 40, 150 cm	Conifer
Lilienfein et al. (2004)	CA, USA	Dickson & Crocker (1953)	42.10	55.76	2.14	38.58	T	1	6	8	mean 10cm, 40, 150 cm	Conifer
Lilienfein et al. (2004)	CA, USA	Dickson & Crocker (1953)	45.70	50.36	3.94	41.62	T	1	5	8	mean 16cm, 40, 150 cm	Conifer
Lilienfein et al. (2004)	CA, USA	Dickson & Crocker (1953)	44.60	53.40	2.00	35.23	T	1	5	8	mean 20cm, 40, 150 cm	Conifer
Mobley, Richter et al. (Unpublished)	SC, USA	Richter et al. (1994)	67.60	17.00	15.40	37.33	O		12	19	7.5cm	Hardwood-Deciduous
Park and Matzner (2003)	Germany	Eusterhues et al. (2005)	na	na	9.40	8.33	T	1	3	46	20cm	Hardwood-Deciduous
Qualls and Richardson (2003)	FL, USA	Mean Text. Class (Peat)	Peat	Peat	Peat	29.50	O	1	>10	3	12.5 & 60 mean	Grassland
Schroth et al. (2002)	Brazil	Reported	na	na	80.00	35.58	T	1	6	13	10cm & 60cm mean	Hardwood-Evergreen
Schrumpf et al. (2006)*	Tanzania	Author Contacted	16.00	19.88	64.10	37.70	T	3	3	>50	15, 30, 100 mean	Hardwood-Evergreen
Schwendenmann and Veldkamp (2005)	Costa Rica	Reported	na	na	71.38	28.61	T	4	4	>20	20, 40, 75, 150, 250 350 cm mean	Hardwood-Evergreen
Strahm et al. (2005)*	WA, USA	Author contacted	16.42	44.72	38.86	27.28	T	1	4	>10	100 cm	Conifer
Zak et al. (2004)	MI, USA	Author contacted	84.00	13.00	3.00	9.30	T	4	3	22	75cm	Hardwood-Deciduous

Appendix 1. Sampling method abbreviations: T = tensions lysimeters, O = Zero tension lysimeters and C = centrifuge.

Texture Determination Abbreviation: WSS = Web Soil Survey (see literature cited)

na = not available

* = report used in young vs. old forest paired comparison; Schrumpf et al. (2006) and Strahm et al. (2005) paired sites were harvested immediately prior to data collection and thus not included in clay-CV regression.

† = report used in paired N addition comparison

Ks Data

Source	Location	Clay Determination	%Sand	% Silt	% Clay	CV (%)	Sampling Method	N	Sampling Location
Buczko et al. (2006)	Germany	Reported	93.70	3.10	3.20	13.39	Ring Infiltrometer	30	Field
Buczko et al. (2006)	Germany	Reported	92.80	3.40	3.80	7.96	Ring Infiltrometer	33	Field
Buczko et al. (2006)	Germany	Reported	91.70	5.40	2.90	9.85	Ring Infiltrometer	33	Field
Buczko et al. (2006)	Germany	Reported	89.00	6.20	4.80	11.33	Ring Infiltrometer	28	Field
Grace et al. (2006)	NC, USA	Mean Texture Class (Clay loam)	32.50	34.25	33.45	42.86	Constant head	11	Lab
Jansson and Johansson (1998)	Switzerland	Reported	17.70	70.40	8.80	100.85	Permeater	0-5	Lab
Johnson et al. (2006)	Brazil	Author Contacted	na	na	32.40	41.32	Infiltrometer	4	Field
Johnson et al. (2006)	Brazil	Author Contacted	na	na	36.40	56.51	Infiltrometer	4	Field
Julia et al. (2004)	Spain	Reported	20.50	31.10	20.50	73.17	Various	120	Various
Julia et al. (2004)	Spain	Reported	5.00	7.00	5.00	101.42	Various	38	Various
Julia et al. (2004)	Spain	Reported	27.00	33.20	27.00	41.67	Various	472	Various
Julia et al. (2004)	Spain	Reported	19.70	30.30	19.70	94.34	Various	200	Various
Julia et al. (2004)	Spain	Reported	24.70	26.80	24.70	51.55	Various	163	Various
Julia et al. (2004)	Spain	Reported	25.20	26.20	25.20	71.94	Various	46	Various
Julia et al. (2004)	Spain	Reported	15.50	27.70	15.50	96.15	Various	182	Various
Julia et al. (2004)	Spain	Reported	20.80	32.00	20.80	79.37	Various	141	Various
Julia et al. (2004)	Spain	Reported	17.70	23.90	17.70	104.53	Various	30	Various
Julia et al. (2004)	Spain	Reported	38.20	25.70	38.20	66.67	Various	98	Various
Julia et al. (2004)	Spain	Reported	35.70	21.50	35.70	58.82	Various	288	Various
Julia et al. (2004)	Spain	Reported	25.00	21.10	25.00	47.62	Various	78	Various
Julia et al. (2004)	Spain	Reported	24.20	21.60	24.20	63.03	Various	408	Various
Julia et al. (2004)	Spain	Reported	15.40	26.60	15.40	111.11	Various	145	Various
Julia et al. (2004)	Spain	Reported	25.00	35.60	25.00	31.06	Various	225	Various
Julia et al. (2004)	Spain	Reported	18.10	30.90	18.10	69.12	Various	39	Various
Julia et al. (2004)	Spain	Reported	19.70	28.10	19.70	98.43	Various	79	Various
Julia et al. (2004)	Spain	Reported	25.40	29.20	25.40	47.85	Various	49	Various
Julia et al. (2004)	Spain	Reported	28.50	37.40	28.50	16.13	Various	37	Various
Li et al. (2007)	China	Mean Sand	92.50	7.50	5.00	35.57	Permeater	4	Field
Li et al. (2007)	China	Mean Texture Class (Loamy Sand)	80.00	15.00	7.50	5.48	Permeater	3	Field
Li et al. (2007)	China	Mean Texture Class (Sandy Loam)	65.00	25.00	10.00	113.95	Permeater	12	Field
Li et al. (2007)	China	Mean Texture Class (Silty Loam)	25.00	67.50	13.75	78.58	Permeater	13	Field
Li et al. (2007)	China	Mean Texture Class (Silty Clay Loam)	10.00	66.25	36.25	50.58	Permeater	3	Field
Malmer (1996)	Malaysia	Clay Mean	22.50	30.00	70.00	70.23	Infiltrometer	10	Field
Malmer (1996)	Malaysia	Sand Mean	92.50	7.50	5.00	33.33	Infiltrometer	10	Field
Neirynck et al. (2000)	Belgium	Reported	10.50	74.00	15.50	72.99	Not available	5-10	Lab
Perkins et al. 2007	GA, USA	Mean Texture Class (Loamy sand)	80.00	15.00	7.50	78.00	Ring Infiltrometer	24	Field
Ramos et al. (2007)	Spain	Reported	70.40	23.10	6.50	33.00	Infiltrometer	6	Field
Schack-Kirchner et al. (2007)	Brazil	Reported	7.00	22.00	71.00	40.89	Falling head	6	Lab
Sheridan et al. (2007)	Australia	Mean Texture Class (Sandy clay & Clay)	30.00	24.00	30.00	66.89	Ring Infiltrometer	27	Field
Xu et al. (2002)	SC, USA	Author Contacted	65.00	25.00	10.00	102.53	Not available	6	Lab
Young et al. (2004)	NV, USA	Reported	95.00	3.00	2.00	28.57	Infiltrometer	na	Field
Young et al. (2004)	NV, USA	Reported	85.00	12.00	3.00	78.75	Infiltrometer	na	Field
Young et al. (2004)	NV, USA	Reported	70.00	24.00	6.00	13.64	Infiltrometer	na	Field
Young et al. (2004)	NV, USA	Reported	47.00	25.00	28.00	42.84	Infiltrometer	na	Field
Young et al. (2004)	NV, USA	Reported	53.00	22.00	25.00	41.67	Infiltrometer	na	Field
Ziegler et al. (2006)	Malaysia	Reported	34.00	27.50	38.50	70.00	Amoozemeter	10	Field

na = not available