HYDROLOGICAL PROCESSES
Hydrol. Process. **18**, 2713–2725 (2004)
Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/hyp.5577

Regionalization of disturbance-induced nitrogen leakage from mid-Appalachian forests using a linear systems model

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Abstract:

The 'leakage' of nitrate-nitrogen (nitrate-N) to surface waters is a common (but not universal) response of forest ecosystems to both human-induced and natural disturbances. There are several reported examples of the transient leakage of nitrate-N to surface waters from eastern US forests that have sustained outbreaks of defoliating insects, such as the introduced gypsy moth (*Lymantria dispar*) larva. Previous research has suggested that annual nitrate-N leakage from disturbed forests can be modelled using an empirically derived unit nitrogen export response function (UNERF) model. The model represents annual nitrate-N export as a linear deterministic process in both space and time and is analogous to a unit hydrograph. The goal of the present study was to verify and apply a regionalized, lithology-based UNERF model that references the geographic distribution of bedrock class and the timing and extent of gypsy moth defoliation of forests in the non-glaciated highlands of the Chesapeake Bay watershed. Despite an inability to verify the model for most individual watersheds within the study area, the model was able to reproduce the statistical distribution of annual nitrate-N export to streams that comprised our target population. During water year 1991 (the year following peak defoliation) the model results indicated that regional annual nitrate-N export had transiently increased by nearly 1500% from a baseline rate of about 0·1 kg ha^{-1} to a peak value approaching 1·5 kg ha^{-1}. We thus conclude that natural vegetation disturbance is an important mechanism by which dissolved nitrogen is leaked from forested lands to small streams, rivers, and Chesapeake Bay. The present study also illustrates how simple, empirically derived linear systems approaches like the UNERF model can be successfully applied to problems where regionalization is a primary goal. Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS nitrogen; nitrate; forests; disturbance; gypsy moth; modelling; defoliation; regionalization; unit hydrograph; water quality

INTRODUCTION

Understanding and quantifying the loading of nutrients from the land surface to surface waters at the scale of a large complex river basin or entire region is a major challenge for scientists and environmental managers faced with restoring water quality downstream (Wolman, 1971; Smith *et al*., 1987, 1997; Nixon, 1995; Bowen and Valiela, 2001). Nitrogen (N) pollution has been specifically identified as one of the most troublesome water quality problems in the USA (Howarth *et al*., 2002) and globally (Galloway *et al*., 2002), and management strategies and models are needed to target all major N sources within a particular watershed or estuarine system (Driscoll *et al*., 2003). It has been hypothesized that, in heavily forested watersheds, N saturation of N-limited forests from chronically elevated N deposition will eventually lead to sustained 'leakage' of

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Received 1 October 2001
Accepted 27 August 2003

nitrate-N to receiving waters (Aber *et al*., 1989, 1998; Stoddard, 1994). Even in the absence of N saturation, transient nitrate-N leakage from eastern US forests has been shown to be a common (but not universal) response both to harvesting practices (Likens *et al*., 1970, 1978; Bormann and Likens, 1979; Martin *et al*., 1984; Lynch and Corbett, 1991; Dahlgren and Driscoll, 1994; Johnson, 1985; Yeakley *et al*., 2003) and to other natural disturbances, such as outbreaks of defoliating insects (Swank *et al*., 1981; Eshleman *et al*., 1998). Water quality and biogeochemical responses of forest ecosystems to other common natural disturbances, such as outbreaks of pathogens, droughts, tornadoes, hurricanes, floods, and fires (Dale *et al*., 1998; Foster *et al*., 1998) have received far less attention.

Since its introduction into North America in the Boston area in 1869, the gypsy moth (*Lymantria dispar*) larva has gradually moved westward and southward and has become the primary defoliator of deciduous forests in the eastern USA (Doane and McManus, 1981). During 1990, a peak year of gypsy moth activity, nearly 4×10^6 ha of forest in this region were defoliated. Water quality data from five small gauged forested watersheds situated along the path of the gypsy moth's spread within the mid-Atlantic region of the USA indicated that annual nitrate-N leakage from these forests increased rapidly in the years following defoliation, peaked within a period of 1 to 3 years, and then underwent a fairly long decay or recession during a 4–8 year period as fluxes gradually returned to background levels (Eshleman *et al*., 1998). This pattern is qualitatively similar to the pattern of nitrate-N release commonly observed following forest harvesting (Likens *et al*., 1970; Johnson, 1995; Eshleman *et al*., 1998). A subsequent modelling study of the responses of these watersheds to defoliation suggested that multiple partial defoliations of forested watersheds produce rates of annual nitrate-N leakage that are both (1) proportional to the forested area disturbed and (2) additive in time (Eshleman, 2000).

Most state-of-the-art models have not explicitly considered the spatial and temporal dynamics associated with forest vegetation disturbances, their interactions with N deposition, and associated impacts on downstream water quality (Cosby *et al*., 1985; Bicknell *et al*., 1993; Linker *et al*., 1996; Smith *et al*., 1997). Aber *et al*. (2002), however, recently used a lumped model of forest biogeochemical cycles known as PnET-CN to show that elevated nitrate-N losses from watershed 6 at Hubbard Brook Experimental Forest in the 1960s and 1970s could be largely attributed to a significant insect defoliation event in concert with an extreme drought that occurred antecedent to defoliation. Eshleman (2000) earlier showed that a parsimonious, empirical linear systems model could explain large percentages of the temporal variation in annual nitrate-N export from such defoliated watersheds in the years following disturbance. The model—known as the unit nitrogen export response function (UNERF) model—is completely analogous to the unit hydrograph method widely used for describing the characteristics of storm runoff attributable to one unit of excess precipitation onto a watershed. The model treats annual nitrate-N export from disturbed forested watersheds as a linear deterministic process both in space and in time, with the specific model parameters estimated during a deconvolution process (Eshleman, 2000):

$$N_w(t) = \int_0^t U(t-\tau)D_w(\tau)\ \mathrm{d}t + B_w \tag{1}$$

where $N_w(t)$ is the nitrogen export from watershed w in year t, $U(t-\tau)$ is a UNERF, $D_w(\tau)$ is the proportion of forested watershed disturbed in year $\tau(0 \le D_w(\tau) \le 1)$, and B_w is the annual baseline nitrate-N export from watershed w in the absence of disturbance. The term 'unit' is used to represent the nitrate-N export response to a complete disturbance of the watershed (i.e. when 100% of the watershed area is disturbed). The model includes two terms: (1) a convolution of a UNERF with the proportion of the watershed disturbed at time τ, representing the integral response of the watershed to disturbance $N_{w,D}$, and (2) a baseline nitrate-N export response from the watershed without disturbance B_w.

The UNERF model represents the well-known response of a linear system to an 'impulse' (in this case a defoliation event) and is governed by the principles of proportionality and superposition, which allow the responses of the system to partial or multiple impulses to be predicted by convolution once the UNERF is known. The nitrate-N export response model is easily reformulated in the discrete time (annual) domain by incorporating a discrete convolution integral. Essentially, the modelling approach used to describe annual nitrate-N export is analogous to the unit hydrograph method, where the excess precipitation input has been replaced by a disturbance impulse and the unit hydrograph is replaced by the UNERF; the positive baseline nitrate-N export B_w is analogous to a baseflow contribution to runoff in the unit hydrograph method (Eshleman, 2000).

Since forest defoliation outbreaks in a particular year typically occur over relatively large regions, it is appropriate to ask whether the spatio-temporal variations in nitrate-N export from disturbed forested areas can be reasonably described using a regionalized version of the UNERF model. The primary purpose of the present study was to attempt to verify the UNERF modelling approach using data from other gauged (and ungauged) forested watersheds for which both disturbance and annual nitrate-N export time series have been observed or could be estimated. Model verification was attempted on both a watershed-by-watershed basis and through comparison of statistical distributions that represent nitrate-N export from a random sample of low-order streams in the study area. A secondary purpose of the study was to demonstrate a regional application of a UNERF model that references the geographic distributions of bedrock geology and the timing and extent of gypsy moth defoliation over a relatively large region of the eastern USA.

In a previous analysis, the UNERF model was parameterized using data from five intensively monitored forested watersheds in the eastern USA (Eshleman, 2000). Each of these watersheds had been continuously gauged, had a long-term record of streamwater nitrate-N concentration and export data, and had a well-documented history of gypsy moth defoliation. Eshleman *et al*. (2001) used data from 10 ungauged forested watersheds in Shenandoah National Park (SNP; Virginia, USA) to verify a lithology-based UNERF model in which the specific model parameters were found to be differentiable using only three geologic classes (basaltic, granitic, and siliciclastic), and unit nitrate-N export was assumed to decay exponentially from its peak value. Values of model efficiency E (Nash and Sutcliffe, 1970) and r^2, based on comparisons of predictions with estimated annual nitrate-N export rates (computed as the product of a spring baseflow nitrate-N concentration and a long-term runoff value), were found to be relatively high (Eshleman *et al*., 2001). Based on the unexpected, but largely successful, verification of the UNERF model in SNP, it was concluded that lithology can indirectly predict nitrate-N losses from disturbed watersheds where there is a relatively tight coupling between bedrock, soil moisture, and species composition (Eshleman *et al*., 2001). The present analysis makes use of the same lithology-based UNERF model (Figure 1).

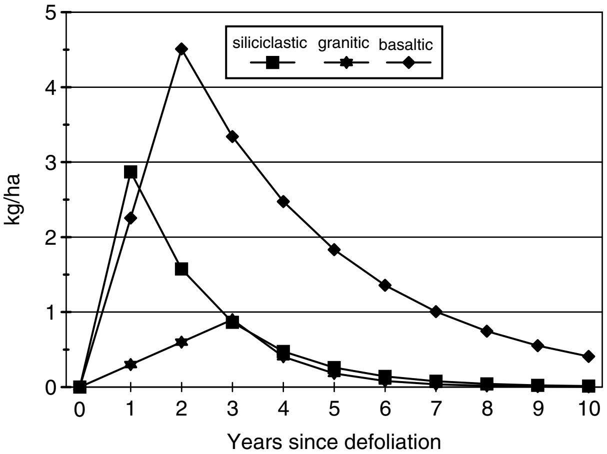

Figure 1. Lithology-based UNERF models for three bedrock classes

STUDY AREA AND TARGET POPULATION

Since one of the purposes of the study was to make regional projections of nitrate-N leakage from forested lands in the eastern USA, it was necessary to define both the target population and the study area rigorously. The target population of interest for this study is comprised of all small (wadeable), minimally disturbed streams draining non-glaciated forested uplands of the Chesapeake Bay watershed. Using data from the US Environmental Protection Agency (USEPA) Mid-Atlantic Highlands Streams Assessment (MAHSA) database (USEPA, 2000), we estimated that the target population comprises approximately 17 800 km of perennial streams; this target population is represented in the database by 53 unique sample stream reaches (hereafter called 'target streams' or 'MAHSA streams') within the study area. Data from the USEPA Multi-Resolution Land Characteristics Consortium (MRLC) national land cover characterization (http://landcover.usgs.gov/natllandcover.html) indicate that the study area is heavily forested; nearly 5×10^6 ha (71%) of the $6{\cdot}96 \times 10^6$ ha study area are classified as forested land (Figure 2). We obtained a preliminary lithologic map from the US Geological Survey (Bruce Johnson, USGS Eastern Mineral Resources Team, personal communication) and classified the primary rocks underlying the study area into five groups: basalt (mafic), granite (felsic), sandstone (siliceous), shale (argillaceous), and limestone (carbonate). For the purposes of this study, we combined the sandstone and shale classes into one siliciclastic group (Figure 3). It should also be noted that, owing to our lack of experience with modelling forested streams in limestone valleys of the study area, roughly 400 000 ha of forest within these valleys (roughly 8% of the total forested area) were not considered part of the present study.

METHODS

The lithology-based UNERF models were tested using stream discharge and streamwater nitrate-N data from 22 gauged forested watersheds located within (or very close to) the study area (Figure 4). All except one of the watersheds (Young Womans Creek, area: 119·8 km^2) were very small (<15 km^2). Although the watersheds were gauged and sampled by different researchers using slightly different field methods (e.g. sampling frequency), we believe that the data are of excellent quality and can provide robust estimates of annual nitrate-N export. We used the linear interpolation scheme described by Eshleman *et al.* (1998) to compute a record of daily nitrate-N export for these watersheds as the product of daily streamflow and an interpolated nitrate-N concentration; monthly and annual (water-year basis) nitrate-N fluxes were computed by summing daily fluxes over appropriate intervals.

Assuming that streamwater nitrate-N concentration measured under spring baseflow conditions is most representative of the annual flow-weighted value, an annual nitrate-N flux was computed for each of the 53 MAHSA streams as the product of the spring nitrate-N concentration (one sample, 1993 or 1994) and the estimated mean runoff value of 0·50 m year^{-1} (Lynch, 1987). Because many of the watersheds had been defoliated several times prior to collecting water-quality data, it was difficult to define baseline annual nitrate-N export B_w values for either the gauged or target streams; therefore, B_w was assumed equal to zero for the purposes of this analysis.

Annual watershed defoliation for the entire study area was based on 2 km gridded digital data obtained from the US Forest Service (USFS) for the period 1975–94 (Sandy Liebhold, USFS, personal communication); these maps were based on a composite of county-level sketch maps drawn from low-altitude overflights of the study area during summer defoliation outbreaks (Liebhold and Elkinton, 1989; Liebhold *et al.*, 1994; images of defoliation can be found on-line at http://www.fs.fed.us/ne/morgantown/4557/gmoth/atlas/). Predictions of annual nitrate-N export for both the gauged and target streams were made by linking the UNERF models to the lithology and defoliation data in a geographic information system (GIS, ArcInfo/ArcView); annual nitrate-N export from each grid cell was computed using the appropriate UNERF model, and annual watershed nitrate-N export was computed as the arithmetic mean of the individual grid cell values. Following model testing using data from the gauged watersheds, we made area-wide estimates of annual nitrate-N export for the 26 year

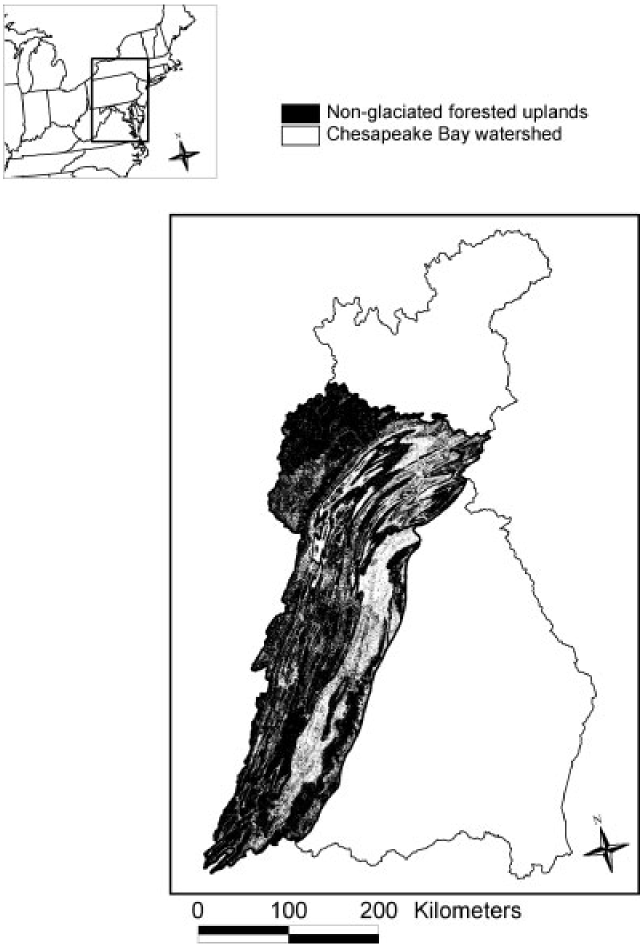

Figure 2. Location of study area comprised of non-glaciated forested uplands in the Chesapeake Bay watershed, USA. Inset: location of study area in the eastern USA

period (1975–2000) using the same linked GIS and modelling approach; we again set B_w equal to zero, a value consistent with our assumptions about the gauged watersheds. It was also necessary to assume that no significant gypsy moth defoliation had occurred in the study area prior to 1975 and after 1994.

RESULTS AND DISCUSSION

With only two exceptions, the defoliation data indicate that the gauged watersheds experienced substantial gypsy moth defoliation during the period from 1976 to 1994; 14 of the watersheds were 100% defoliated in at least one of the years, and six others were at least 75% defoliated. The defoliation data also indicate substantial re-defoliation of the study watersheds, with six of the watersheds apparently experiencing 100% defoliation in three or four different years. With respect to the watersheds of the target streams, defoliation was not nearly as common, nor was it as spatially extensive. Only 27 (51%) of the 53 MAHSA watersheds were 100% defoliated in one or more years, whereas 12 (23%) of the watersheds apparently experienced no significant defoliation at all during the period from 1976 to 1994.

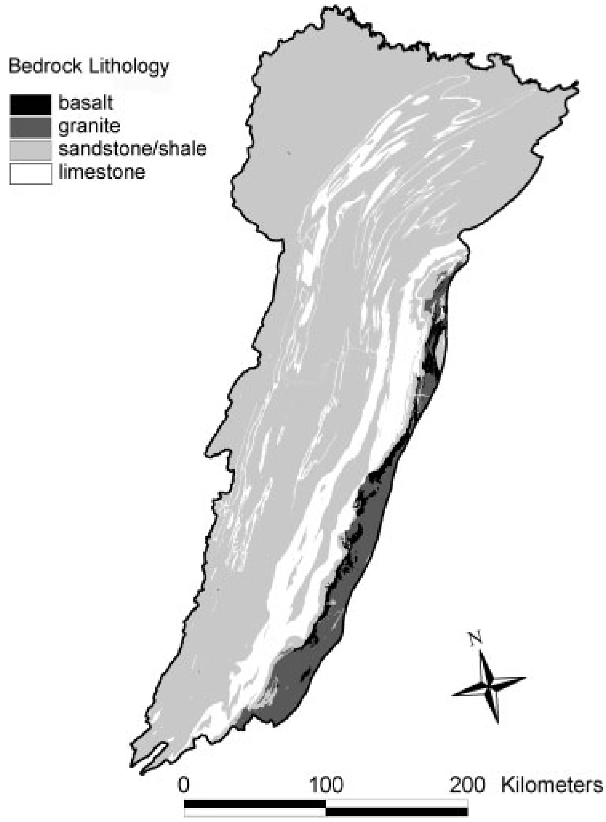

Figure 3. Map showing the spatial distribution of four lithologic classes within the study area

Statistical comparisons of predicted and observed annual nitrate-N export rates for the 22 gauged watersheds indicated few significant linear relationships (Table I). Only three of the individual linear regressions were found to be statistically significant ($\alpha < 0{\cdot}05$), and two of these regressions were found for watersheds actually used in developing the UNERF models (White Oak Run and Paine Run). All three of these watersheds are underlain by siliciclastic bedrock and are located on the Blue Ridge in SNP. The only model verification that produced a positive value of E was found for White Oak Run, suggesting rather limited ability of the model to reproduce the observations (Table I).

It should be noted that the five gauged watersheds used to develop the lithology-based UNERF models were included in the model verification, because the defoliation data used to develop the models were obtained from an independent source from the data used in this verification. The two databases provide very different estimates of the timing, extent, and frequency of gypsy moth defoliation within the individual watersheds. Digital defoliation data obtained specifically for SNP (Dan Hurlbert, SNP, personal communication) did not include information for 1994, whereas the regional USFS database commonly showed extensive defoliation in 1993 that was not present in the SNP database. Observations for the White Oak Run watershed are illustrative of generally poor correspondence between the defoliation records in the two databases, especially for 1990 and 1993 (Figure 5). Since the UNERF model predictions are obviously quite sensitive to the specific disturbance data used in calibration, our results suggest that a large portion of the verification errors may be attributable to the accuracy, precision, and resolution of the regional defoliation database.

Another reason for the poor degree of correspondence between the predicted and observed nitrate-N export rates is undoubtedly due to the relatively short record lengths for many of the watersheds. Nine of the

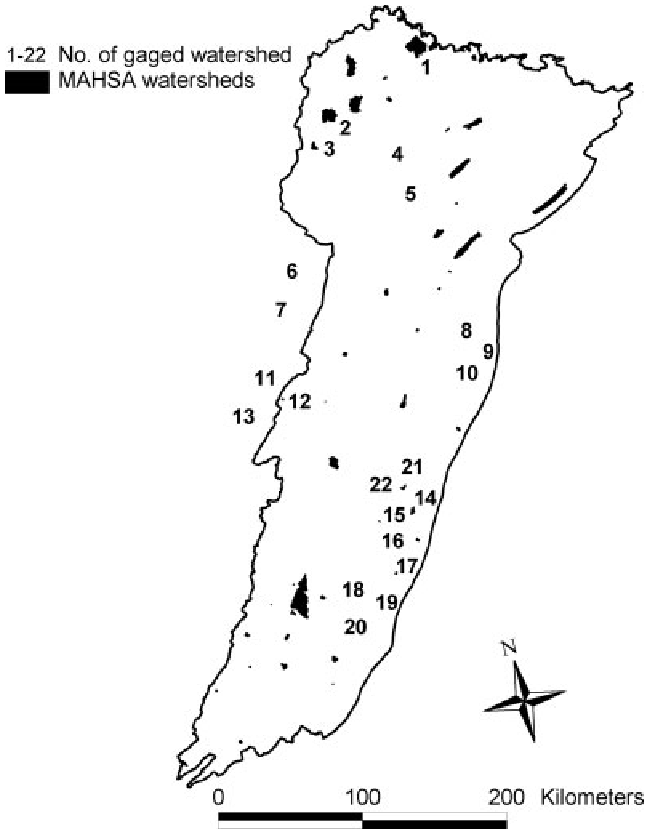

Figure 4. Map showing locations of 22 gauged forested watersheds and 53 MAHSA watersheds within the study area. Note: watersheds 6, 7, 11, and 13 are located just outside the study area boundary, but were included in our analysis

gauged watersheds had record lengths shorter than 7 years and only six watersheds had record lengths longer than 10 years (Table I). Interestingly, the three watersheds that produced significant regressions had record lengths of 17, 17, and 9 years. The results of the study thus underline the need for long temporal records of observations from gauged watersheds that can be used to identify and quantify water quality responses to disturbances and management actions.

A linear regression of the predicted and estimated annual nitrate-N export rates for the 53 MAHSA streams produced no statistically significant ($\alpha < 0{\cdot}05$) linear relationship either (Figure 6). However, when stratified by physiographic region, we obtained a statistically significant ($\alpha = 0{\cdot}008$; $r^2 = 0{\cdot}79$), but highly biased, linear regression for the seven target streams located within the Blue Ridge physiographic region. Regressions for the Ridge and Valley and Appalachian Plateau target streams produced no statistically significant ($\alpha < 0{\cdot}05$) relationships, however (Figure 6).

Results from a comparison of cumulative frequency distributions of annual nitrate-N export (1993 or 1994) derived from the MAHSA watersheds (using the appropriate weighting factors to extrapolate to the target population) are shown in Figure 7. Most importantly, the median value for the distribution corresponding to the estimated nitrate-N export using one index sample (0·36 kg ha^{-1}) is within 30% of the median of the distribution based on the UNERF model (0·28 kg ha^{-1}), suggesting no appreciable model bias. The model also adequately reproduces the lower tail of the observed distribution, but the upper tails show some deviation, although the variation is less than a factor of two. Figure 7 also shows a cumulative frequency distribution based on predicted values for all forested pixels (not including forests on limestone) in the study area for 1993

Table I. Gauged watersheds in the study area that were used in UNERF model verification.[a] Statistical results (r^2, E) from the verification tests are also shown

Watershed name, state[b]	No.[c]	Rock type (%)			Years of data	r^2	E
		Basaltic	Granitic	Siliciclastic			
Young Womans Creek, PA	1	0·0	0·0	100·0	1978–95	0·15	−6·5
Roberts Run, PA	2	0·0	0·0	100·0	1989–95[d]	0·11	−6·2
Stone Run, PA	3	0·0	0·0	100·0	1989–94[d]	0·01	−28·3
Benner Run, PA	4	0·0	0·0	100·0	1989–95[d]	0·51	−2·1
Leading Ridge One, PA	5	0·0	0·0	100·0	1978–93	0·05	−627·8
Baldwin Creek, PA	6	0·0	0·0	100·0	1989–95[d]	0·22	−0·7
Linn Run, PA	7	0·0	0·0	100·0	1989–95[d]	0·02	−5·7
Hunting Creek, MD	8	30·2	69·8	0·0	1983–91	0·07	−5·2
Bear Branch, MD	9	2·0	0·0	98·0	1991–93	0·02	−5·9
Hauver Branch, MD	10	96·3	0·1	3·5	1983–94	0·00	−2·4
Alexander Run, MD	11	0·0	0·0	100·0	1991–94	0·04	−2·9
Upper Big Run, MD	12	0·0	0·0	100·0	1990–2000	0·28	−2·0
Herrington Run tributary, MD	13	0·0	0·0	100·0	1992–97	0·26	−1·8
Piney River, VA	14	70·0	30·0	0·0	1988–96	0·42	−2·3
North Fork of Dry Run, VA	15	0·0	100·0	0·0	1988–95	0·00	−2·1
Old Rag, VA	16	0·0	100·0	0·0	1984–92	0·11	−81·1
Staunton River, VA	17	0·0	100·0	0·0	1988–96	0·05	−3·1
Deep Run, VA	18	0·0	0·0	100·0	1978–95	0·56[e]	−130·7
White Oak Run, VA	19	0·0	0·0	100·0	1978–95	0·67[e]	0·51
Paine Run, VA	20	0·0	0·0	100·0	1988–95	0·51[e]	−1·4
Mill Run, VA	21	0·0	0·0	100·0	1991–93	0·99	−449·8
Shelter Run, VA	22	0·0	0·0	100·0	1984–94	0·01	−730·7

[a] Watersheds 6, 7, 11, and 13 are located slightly outside the study area boundary, but were included because they are otherwise similar to watersheds in the study area.
[b] Data for watersheds shown in bold were used in development of the lithologically based UNERF models (Figure 1).
[c] Refers to location on study area map (Figure 4).
[d] Data for 1991 water year were not available.
[e] Regression x-coefficient significant at 0·05 level.
[f] Value of $E > 0$ indicates that the model is more predictive than the mean value of the observations.

and 1994. The median of this distribution (0·22 kg ha^{-1}) is nearly identical to the median of the predicted distribution for the target population based on the 53 MAHSA watersheds, confirming that the 53 target stream samples provide a comparable characterization of the regional-scale water quality response to defoliation.

Predicted area-wide estimates of annual nitrate-N export suggest a fairly dramatic transient response to defoliation, particularly during the late 1980s and early 1990s as gypsy moth defoliation encompassed a larger portion of the study area (Figure 8). Gypsy moth defoliation peaked three times during the 26 year period: in 1978, 1981, and 1990, with the latter peak causing the most extensive damage. Whereas the 1978 and 1981 peaks involved less than 20% of the forested area in the region, the 1990 peak in activity affected 43·8% of these forests. The model predicts that area-wide annual average nitrate-N export from forests in this region increased 15-fold from a rate of 0·1 kg ha^{-1} in 1975 to a rate of about 1·5 kg ha^{-1} in 1991; as defoliation declined in the early 1990s, the model suggests that average annual nitrate-N export declined exponentially from its 1991 peak to an estimated value in 2000 that is very close to the initial value predicted for 1975. Over the entire study period, the region-wide annual nitrate-N export averaged 0·5 kg ha^{-1}, a value that is actually much lower than values reported for forested watersheds in the Chesapeake Bay region by other sources. DeWalle and Pionke (1994), for example, estimated a mean value for 25 streams as 2·1 kg ha^{-1}, and Linker *et al*. (1996) have assumed for modelling purposes that forests generate a load of 4·3 kg ha^{-1} of

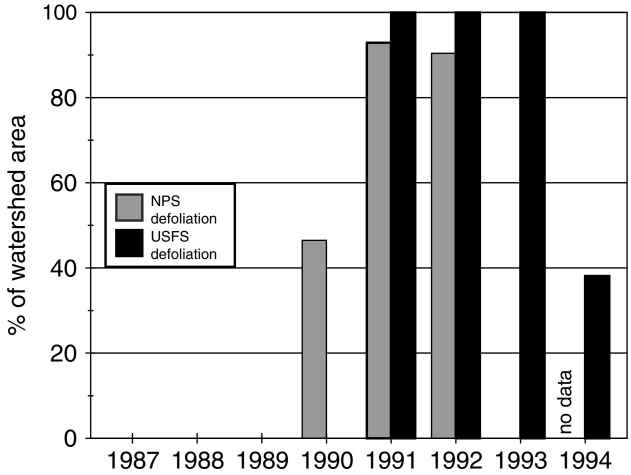

Figure 5. Comparison of two estimates of gypsy moth defoliation in the White Oak Run, Virginia, watershed during the period 1987–94. NPS defoliation data courtesy of Dan Hurlbert and USFS defoliation data courtesy of Sandy Liebhold

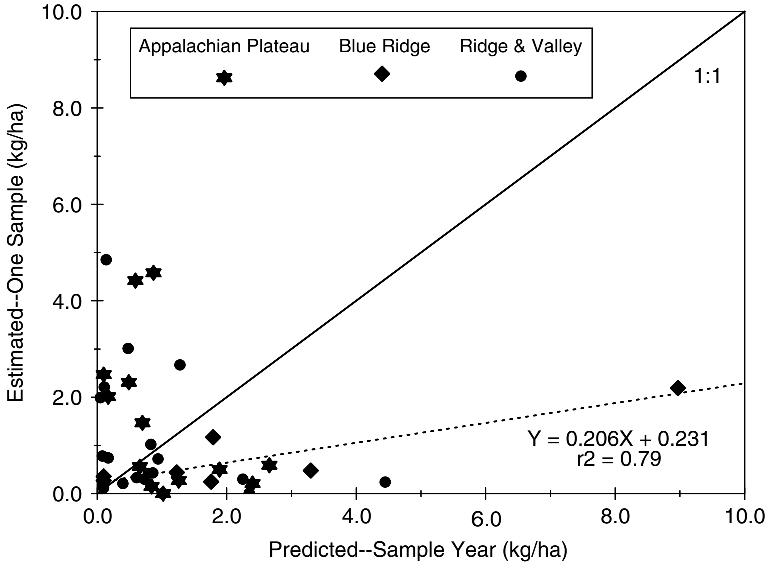

Figure 6. Scatter diagram of estimated and predicted annual nitrate-N export values (1993–94) for 53 target streams in three physiographic regions. Statistical relationship between estimated and predicted annual nitrate-N export for seven Blue Ridge streams is also shown

nitrate-N in an average year. It is interesting that even the predicted peak value for 1991 (following extensive defoliation) is less than the average values based on the other studies. This result underlines a potential danger in extrapolating short-term results from gauged watersheds without consideration of the geographic representativeness of the individual sites and the temporal representativeness of the available records.

With the exception of three gauged streams located on the Blue Ridge in SNP (two of which were used during model development) and the seven target streams within the Blue Ridge physiographic province, the results of the study produced no statistically significant correspondence between observed (or estimated) and predicted annual nitrate-N export rates. This result underscores a potentially serious problem in applying the model to individual watersheds. The relatively greater correspondence between observed and predicted

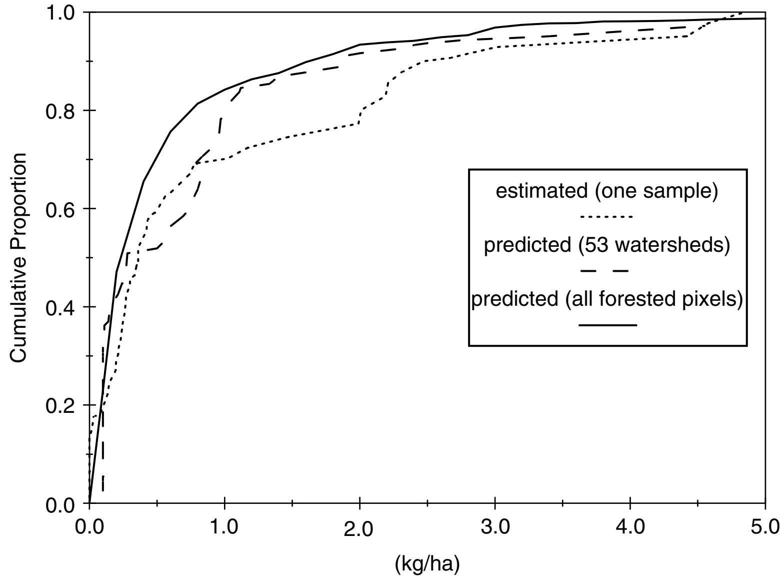

Figure 7. Observed and predicted cumulative frequency distribution of annual nitrate-N export (1993–95) for the target population of streams based on the MAHSA sample. A cumulative frequency distribution based on all forested pixels in the study area is also shown. All distributions truncated above 5 kg ha^{-1}

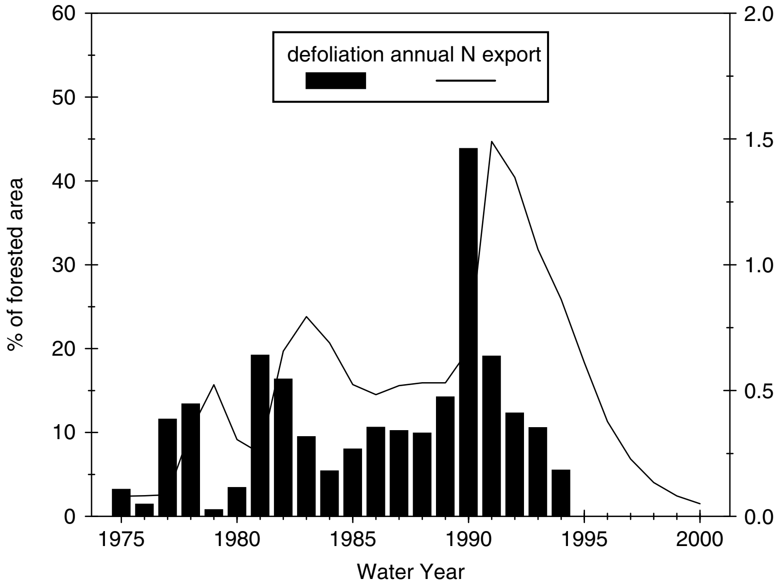

Figure 8. Annual gypsy moth defoliation and predicted nitrate-N export for the study area for the period 1975–2000

nitrate-N fluxes from Blue Ridge watersheds is consistent with the fact that predictions for these sites were based on application of three different UNERF models, one for each of the three lithologic classes (Figure 1). Conversely, predictions for watersheds located in the Ridge and Valley and Appalachian Plateau provinces were made using one UNERF developed from data from two watersheds underlain by siliciclastic bedrock. Predictions for these streams could potentially be improved through development of separate UNERF models for other lithologic classes (e.g. sandstone, shale, etc.). Alternately, UNERF models could perhaps be developed for specific forest vegetation types, rather than lithologic classes, especially given the preference of the gypsy moth for defoliating particular tree species, such as the oaks (*Quercus* sp.).

The lack of agreement between the predictions and the observations from individual watersheds may also be partially explained by the quality and spatial resolution of the regional defoliation data that are inputs to the model. Eshleman *et al*. (2001) found surprisingly good agreement between predicted and estimated annual nitrate-N export for a group of ungauged Blue Ridge streams in SNP, despite the fact that annual export was computed using the same 'one sample' technique as in the present analysis. Another major difference between these two analyses is with respect to the quality and spatial resolution of the defoliation data. In the case of the SNP analysis, it was possible to use a detailed, 30 m $\times$ 30 m gridded digital defoliation map for the park for each year of the study. However, in the current regional study, the 2 km $\times$ 2 km gridded data provided a 4400-fold reduction in data resolution that may be unsuitable as input to models of small watersheds that may encompass only a few defoliation pixels. The defoliation data used in the present regional study also appear to contain a number of substantial errors (i.e. biases) associated with field data collection, especially with respect to measuring and classifying defoliation from county-based aerial surveys, and extrapolating the observations to the county, state, and regional scale. For example, the database includes many examples where gypsy moth defoliation in a particular year stopped abruptly at political borders, a telltale sign that the data from certain states and counties may be biased for one or more reasons. Other errors, falling under the general heading of 'locational accuracy' (Burrough and McDonnell, 1998), may also be a significant component of the regional defoliation database. For these reasons, Townsend *et al*. (2004) suggested that satellite imagery is far better suited for characterizing insect defoliation over large areas, because it is automated, repeatable, and not subject to errors associated with human interpretation of aerial photographs or sketch maps drawn during aircraft surveys.

In contrast to the predictions for the individual watersheds, the UNERF model provided quite satisfactory predictions of the distributions of annual nitrate-N export based on computations for samples of streams representing the entire study area. The problem of regionalization, i.e. making estimates, projections and forecasts for populations of systems within a region for which little empirical data may exist, is now a central focus of both hydrology and environmental assessment (Small and Sutton, 1986; Hornberger *et al*., 1987; Eshleman *et al*., 1988, 1995; Herlihy *et al*., 1991). Many of these published studies have demonstrated the utility of comparing statistical distributions of predictions and observations, rather than values from individual sites. Since the specific goal of regionalization is to provide an unbiased description or prediction across a large region, the importance of accurate predictions for individual sites is subordinated by the need to provide satisfactory predictions of central tendency and variance (Hornberger *et al*., 1987). The results from this study thus provide another example of the challenges associated with predicting ecosystem responses at both local and regional scales with a common modelling approach.

CONCLUSIONS

A modelling study of the effects of gypsy moth defoliation on non-glaciated, upland forests in the Chesapeake Bay watershed suggests region-wide occurrence of dramatic transient increases in nitrate-N leakage to small streams. Despite an inability to verify our UNERF model for most individual watersheds within the study area, the model was able to reproduce the statistical distribution of annual nitrate-N export to streams that comprised our target population. During water year 1991 (the year following peak defoliation) the model results indicated that regional annual nitrate-N export had transiently increased by nearly 1500% from a baseline rate of about 0·1 kg ha^{-1} to a peak value approaching 1·5 kg ha^{-1}. Consistent with other recent studies of nitrate-N leakage from forests in the northeastern and southeastern USA (Aber *et al*., 2002; Yeakley *et al*., 2003), our results suggest that natural vegetation disturbance is an important mechanism by which dissolved N can be leaked from forested lands to small streams, rivers, and Chesapeake Bay. Whereas other studies (e.g.

Lovett *et al*., 2002) have obviously provided far greater insight into the hydrobiogeochemical mechanisms by which nitrate-N is leaked from forests following disturbance, the present study suggests that simple empirically derived linear systems approaches, like the UNERF model, can be successfully applied to problems where regionalization is a primary goal.

ACKNOWLEDGEMENTS

We gratefully acknowledge the following researchers who provided field data from the 22 gauged watersheds that were used in this analysis: Owen Bricker, David Clow, Dave DeWalle, James Galloway, Jim Lynch, and Ray Morgan. We also thank Sandy Liebhold for making the USFS digital defoliation data available to us. Bruce Johnson provided us with a draft digital lithologic map of the Chesapeake Bay watershed that allowed us to apply the regional water quality model. We acknowledge support for the study by the Electric Power Research Institute (no. WO5304-02) and by a STAR (Science to Achieve Results) Program grant (no. CR826110-01-0) from the USEPA. Although the research described in this article has been funded in part by the USEPA through a grant to the University of Maryland Center for Environmental Science, it has not been subjected to the USEPA's required peer and policy review and, therefore, does not necessarily reflect the views of the USEPA and no official endorsement should be inferred. This paper is scientific contribution no. 3768 from the University of Maryland Center for Environmental Science.

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