Maintenance of ecosystem nitrogen limitation by ephemeral forest disturbance: An assessment using MODIS, Hyperion, and Landsat ETM+

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[1] Ephemeral disturbances, such as non-lethal insect defoliations and crown damage from meteorological events, can significantly affect the delivery of ecosystem services by helping maintain nitrogen (N) limitation in temperate forest ecosystems. However, the impacts of these disturbances are difficult to observe across the broad-scales at which they affect ecosystem function. Using remotely sensed measures and field data, we find support for the hypothesis that ephemeral disturbances help maintain landscape-wide ecosystem N limitation. Specifically, a phenology-based defoliation index derived from daily MODIS satellite imagery predicts three ecosystem responses from oak-dominated forested watersheds: elevated stream water N export ($R^2 = 0.48$), decreased foliar N ($R^2 = 0.69$, assessed with Hyperion imagery), and reduced vegetation growth vigor ($R^2 = 0.49$, assessed with Landsat ETM+ imagery). The results indicate that ephemeral disturbances and other forest stressors may sustain N limitation by reducing the ability of trees to compete for – and retain– soil available N.

[2] Ecosystem scientists have obtained some support for this outcome through experimental potted plant [Hunter, 2001; Frost and Hunter, 2004, 2007], and isotope tracer approaches [Christenson et al., 2002], as well as through N budgets calculated from fortuitous stream-water sampling during disturbance events [Eshleman et al., 1998; Lovett et al., 2002; Houlton et al., 2003; Eshleman et al., 2004; Townsend et al., 2004; Lewis and Likens, 2007]. Yet, these plot and small watershed scale studies are necessarily limited in their ability to help identify how and to what extent ephemeral disturbances can maintain ecosystem N limitation across large landscapes. Designing studies to bridge this critical gap in understanding is greatly complicated by the fact that ephemeral disturbances are stochastic in their occurrence and manifest themselves through subtle changes across broad geographic areas.

[3] Satellite-based remote sensing measurements—with large geographic scope and capacity for repeated and consistent observations—present an ideal opportunity for assessing the ecosystem impacts of ephemeral disturbances. Indeed, remote sensing has long been used to map the spatial pattern of ephemeral disturbances [Ciesla et al., 1989; Radoloff et al., 1999; Millward and Kraft, 2004]. Recently, Townsend et al. [2004] showed that change-vector statistics calculated from multiple years of Landsat imagery can be used to predict the variability in stream water N export caused by one ephemeral disturbance: defoliation by the larvae of the gypsy moth (Lymantria dispar L.). Such an approach highlights the potential utility of using remote sensing to not only map the intensity of ephemeral disturbances, but also assess the impact of these disturbances upon nutrient cycling.

[4] Our study advances this potential of remote sensing in two ways. First, we apply a phenology-based method, developed from MODIS imagery immediately before and during the disturbance event that is capable of mapping the intensity of an ephemeral disturbance (K. M. de Beurs and P. A. Townsend, unpublished manuscript, 2007). This method represents an alternative to existing remote sensing approaches that use multiple years of remote sensing data, with one year assumed to be a spatially-even, undisturbed “reference condition” – an assumption that is difficult or impossible to satisfy in forests at differing successional stages and constantly undergoing recurring and differing forms of disturbance. Second, we use single-date imagery collected from NASA’s Landsat and Hyperion sensors during the growing season following a disturbance event...
to directly measure the nutrient cycling legacy of disturbance. This direct measurement builds on and improves the regression-based approach used by Townsend et al. [2004] to predict stream-water N export from remote sensing data in two ways: (1) unlike stream-water measurements that are highly variable seasonally and spatially (e.g., amongst different forest types, land-use histories, and topography [Aber et al., 2003]), direct measurement requires little to no field calibration and may be immediately transferable to all temperate forest systems, (2) direct measurement is capable of assessing ecosystem response in terms of plant N demand, the factor thought to ultimately control ecosystem N limitation [Aber et al., 1998].

6 These two advances in remote sensing techniques enable us to identify how one pervasive but ultimately transient disturbance, defoliation by gypsy moth in the early summer of 2000, may contribute to the maintenance of ecosystem N-limited within an oak-dominated (Quercus spp.) forested landscape in western Maryland and south central Pennsylvania, USA. Townsend et al. [2004] has documented that watersheds experiencing more intense defoliation in 2000 had larger stream water loss of N in 2001, presumably due to large leaching losses of N from the plant-soil system [Swank et al., 1981; Eshleman et al., 1998]. Thus, we hypothesize that increased defoliation will not only relate to increased stream water loss of N, but also cause the growth of trees to become more N limited, as assessed by reduced foliar N and less vigorous growth in the growing season following disturbance.

2. Data and Methods

7 From the synoptic survey of Townsend et al. [2004], we use stream water and remote sensing data from twenty-three randomly-selected first-order watersheds within the fourth-order, 161-km² Fifteen Mile Creek watershed located in the Ridge and Valley physiographic province of western Maryland and south central Pennsylvania (39.63°N, 78.46°W). Townsend et al. [2004] made repeated baseflow and stormflow stream water measurements for all forms of N (i.e., nitrate, organic N) during the April 2001 through May 2002 growing season. Here, we use the most integrative measure, flow-weighted mean annual total dissolved N, to describe the spatial pattern of stream water N export. On average, these watersheds are 85% forested (1σ = 12%), with more than 87% (1 σ = 7%), of this forested area made up of deciduous oak-dominated forests prone to periods of drought in the summer and fall. In the absence of disturbance, these watersheds retain most N from N deposition (3 to 6 kg ha⁻¹ yr⁻¹ total inorganic wet N deposition measured at two National Atmospheric Deposition Program monitoring sites within 50 km) and show little signs of N saturation as most N export occurs in during the high flow spring snowmelt period [Townsend et al., 2004]. Townsend et al. [2004] also previously found the influence of edaphic, land use, or topographic factors to be minor relative to the effect of gypsy moth disturbance in driving the spatial variability in stream water N export within our study area.

8 The availability of daily multi-spectral reflectance data from the MODIS sensor makes it well suited to characterize the within-year changes in surface phenology that accompany ephemeral disturbances. Details of this application of MODIS imagery are described in a companion study (K. M. de Beurs and P. A. Townsend, unpublished manuscript, 2007). Briefly, we use two relatively cloud-free version 5 MODIS images (tile h11v5): a pre-defoliation image from 1 May, 2000 (day 135) and a mid-defoliation image from 28 May, 2000 (day 162). We select the red reflectance from the 250 meter MOD09GQK reflectance dataset as well as the SWIR (band 6) reflectance from the 500 meter MOD09GKH dataset and calculate the MODIS defoliation index as the ratio of the normalized difference infrared index (NDII) [Jackson et al., 2004] based on the two image dates (Figure 1). As described in a companion study (K. M. de Beurs and P. A. Townsend, unpublished manuscript, 2007), the NDII is ideal for detecting the effects of insect defoliation because it is sensitive to the large changes in canopy water content that accompany the loss of canopy leaf mass.

9 In addition to the stream water data available from Townsend et al. [2004], we assess the nutrient cycling legacy of the 2000 defoliation event by obtaining measurements of foliar N and vegetation growth vigor derived from Hyperion and Landsat Enhanced Thematic Mapper (ETM+) imagery collected on 24 July, 2001. After pre-processing these images, we mask all pixels classified as non-forest by an existing land cover classification and supervised classifications of the imagery [Vogelmann et al., 2001; Townsend et al., 2003, 2004]. The foliar N measurements are from a previous study that used partial least squares regression to relate first-difference reflectance spectra from 42 Hyperion bands to field measurements of foliar N collected within two weeks of the Hyperion image acquisition [Townsend et al., 2003]. We measure vegetation growth vigor from the Landsat image by calculating the “disturbance index” (DI), an index computed as the z-score normalized brightness Tasseled Cap index minus the sum of the z-score normalized greenness and wetness Tasseled Cap indices [Healey et al., 2005]. While the Landsat DI was originally devised to identify disturbed areas (positive DI) using their characteristic high brightness and low greenness and wetness values, it can also be used to identify areas of vigorous vegetative growth (negative DI values) because these areas tend to have low brightness and high greenness and wetness indices [Healey et al., 2005].

10 A subsequent, albeit less intense, defoliation event occurred prior to acquisition of our 2001 images [Townsend et al., 2004]. Nevertheless, the Hyperion foliar N and Landsat DI were statistically unrelated (regression, p > 0.10) to the MODIS defoliation index calculated for year 2001, indicating that the 2001 defoliation had a negligible impact on our ability to measure ecosystem response using the Landsat and Hyperion imagery.

11 We use linear regression to test the hypothesis that higher watershed-mean values of the MODIS defoliation index (independent variable) are predictive of higher stream water N export, lower watershed-mean foliar N, and less vigorous vegetative growth (indicated by higher watershed-mean DI). In our study area, the 30-m² Hyperion and Landsat image pixels tend to be relatively pure forested or non-forested cover types, so we compute averages using only forested pixels in the watershed. On the other hand, we average all MODIS pixels in a watershed because their 250-m² resolution typically causes them to have a mixed,
but still predominately forested cover type. Averaging pixel values within a watershed reduces systematic errors caused by image co-registration and enables us to directly compare data generated at three different resolutions: the 30-m\(^2\) pixel size of the Hyperion and Landsat data, the 250-m\(^2\) pixel size of the MODIS data, and the whole-watershed resolution of the stream water data.

3. Results and Discussion

3.1. Space-Borne Assessment of Nutrient Cycle Response to Ephemeral Disturbance

[12] Consistent with the synoptic survey conducted by Townsend et al. [2004], watersheds identified by the MODIS defoliation index as being heavily defoliated in 2000 had the largest losses of N in stream water in 2001 (Figure 2a). While consistently elevated, stream water loss of N was more variable with increasing defoliation (Figure 2a). This variability may be attributable to watershed differences in species composition, soil microbial activity, watershed topography, or canopy repopulation. In particular, repopulation has received comparatively little study, but may be important as an immediate sink for leaf N mobilized by frass deposition from the defoliating gypsy moths [Frost and Hunter, 2007].

[13] As hypothesized, higher MODIS defoliation index values were predictive of lower foliar N (Figure 2b, R\(^2\) = 0.69) and higher Landsat DI (Figure 2c, R\(^2\) = 0.58), indicating that defoliation in 2000 caused the growth of trees to become more N limited the following year. These strong responses of foliar N and vegetation growth vigor demonstrate considerable potential to directly assess nutrient cycling impacts of ephemeral disturbance from spaceborne platforms. In particular, by linking the coincident spatial variability in foliar N and growth vigor to an ephemeral disturbance in the previous year, our study makes

Figure 1. Conceptual diagram of the MODIS phenology signal in a forest ecosystem. The MODIS defoliation index is calculated as the difference in the normalized difference infrared index (NDII) between an image before defoliation and an image during defoliation (dotted lines) (K. M. de Beurs and P. A. Townsend, unpublished manuscript, 2007).

Figure 2. Watershed-scale ecosystem responses in 2001 to the severity of insect defoliation in 2000. Watershed-mean defoliation intensity is detected by the MODIS Defoliation Index; ecosystem responses are from (a) stream water measurements, (b) watershed-mean foliar N, and (c) watershed-mean disturbance index. Sample sizes differ because several watersheds either had complete stream water data (Figure 2a) or were not within the narrow image swath (7.5 km) of the Hyperion sensor (Figure 2b).
an unique contribution to the growing body of literature concerning the use of hyperspectral analysis of foliar N as a tool to assess plant N demand and ecosystem N status [Wessman et al., 1989; Martin and Aber, 1997; Ollinger et al., 2002; Ollinger and Smith, 2005].

[14] Extension of our remote sensing approach to other systems requires consideration of two key features of our analysis. First, the foliar N map used in our analysis was developed with the benefit of extensive field calibration [Townsend et al., 2004]. While a generalized algorithm for detecting foliar N directly from Hyperion imagery has recently been developed (M. E. Martin et al., unpublished manuscript, 2007), the standard error of prediction of this algorithm is equal to the total range in our data (Figure 2b, range = 0.25%N). Nevertheless, watershed-mean values of foliar N derived from predictions with this generalized algorithm still had a similar – albeit weaker- relation to the MODIS defoliation index ($R^2 = 0.31$, $p = 0.03$, $n = 15$), suggesting that future studies may be able to quickly assess ecosystem response to disturbance through use of foliar N data detected using a generalized algorithm. Second, our study was conducted in a deciduous, oak-dominated forest containing little confounding inter-specific variability in foliar N. In many temperate forest systems, co-occurring tree species can have a range in characteristic foliar N values on the order of 2.25 %N [McNeil et al., 2007]. Thus, investigations in more diverse forest systems will need to explicitly account for the inter-specific variation in foliar N that can easily obscure the 0.25 %N range in foliar N observed in our analysis to correspond to the defoliation in the previous year (Figure 2b).

[15] We have provided an appealing framework for using remote sensing data to assess the within-year phenological variability associated with differing magnitudes of an ephemeral disturbance as well as directly measure its impact upon the cycling of carbon and nitrogen within temperate forest systems (Figure 2). While the results presented here are best interpreted generally (i.e., as defoliation increased, foliar N and growth vigor decreased), our ongoing work indicates that remote sensing measures may also be used to quantify the magnitude of disturbance (e.g., in terms of kg ha$^{-1}$ yr$^{-1}$ of defoliation) and measure its affect upon the N content (as opposed to %N) of vegetation canopies (P.A. Townsend et al., unpublished manuscript, 2007). Accordingly, we suggest that technical advances focused on increasing the precision of these remote sensing measurements may provide a general capacity to perform basic assessments of ecosystem nutrient budgets from space-borne platforms.

3.2. Evidence for Maintenance of Ecosystem N Limitation by Defoliation

[16] Initially, we interpreted the relationships shown in Figure 2 as follows: (1) following defoliation, soil microbes quickly convert frass and greenfall organic N to nitrate [Christenson et al., 2002; Frost and Hunter, 2007], (2) mobile nitrate is leached or “flushed” [Creed et al., 1996] to stream waters during high flow periods of stormflow and spring snowmelt in 2001 (Figure 2a), and (3) leaching loss of N directly led to a condition of nutrient limited growth in trees in the following growing season, as evidenced by lower foliar N (Figure 2b) and reduced growth vigor (Figure 2c). We also considered that nutrient limited growth could be reinforced by diminished allocation of N to leaves in response to herbivory [Frost and Hunter, 2007]. Overall, this causal explanation is consistent with findings from Townsend et al. [2004], who not only observed that most of the N export occurred during high flow periods, but also did not observe significant evidence of defoliation-induced loss of organic N to stream water. Nevertheless, upon closer examination of our results (Figure 2), we suspected that this causal explanation may be incomplete.

[17] In particular, it is striking that much of the foliar N (Figure 2b) and Landsat DI (Figure 2c) response is observed in watersheds with a MODIS defoliation index below 1.0. Logical consideration of the MODIS defoliation index (Figure 1) suggests that variability below 1.0 may be driven by non-disturbance related factors that influence canopy water content, such as access to soil water. In fact, this interpretation of the MODIS defoliation index is consistent with field and Landsat data from a companion study showing that watersheds with MODIS defoliation index values below 1.0 had little defoliation (K. M. de Beurs and P. A. Townsend, unpublished manuscript, 2007). Thus, as an extension of our initial causal explanation, we suggest that the connections among the vernal phenology of canopy water content, annual aboveground net primary productivity (ANPP), and ecosystem N retention merit a more careful consideration. For undefoliated watersheds in our study, we hypothesize that in comparison to drought-stressed watersheds (case B in Figure 1), forests with more water available in the spring (i.e., Case A in Figure 1) likely have relatively higher ANPP, and a greater supply of carbon resources to compete with microbes for organic and inorganic soil N [Schimel and Bennett, 2004]. Such an enhanced competitive ability would not only reduce leaching of N to streamwater (Figure 2a), but also increase foliar N (Figure 2b) and growth vigor (Figure 2c). Likewise, defoliation serves to greatly diminish ANPP by reducing the foliar resources invested toward photosynthesis (i.e., Case C in Figure 1). We suggest that further testing of this hypothesis promises to not only help elucidate the poorly understood connections among vegetation phenology and the cycling of N in forested ecosystems, but also could make a valuable contribution to a growing view of the active role played by plants in cycling and retaining N resources [Hobbie, 1992; Schimel and Bennett, 2004; Chapman et al., 2006].

4. Conclusions

[18] We present a multi-faceted remote-sensing approach to obtain a landscape-scale perspective on the nutrient cycling legacy of an ephemeral disturbance. Our results indicate that insect defoliation leads to three conditions that help maintain N limitation in this oak-dominated temperate forest: transient stream water losses of N, a reduction of foliar N, and diminished vegetation growth vigor. Interestingly, interpretation of the phenology-based MODIS defoliation index suggests that factors such as drought-stress could lead to these same three conditions. Thus, we hypothesize that any reduction in ANPP –be it through moderate effects (e.g., drought-stress) or the more severe effects of defoliation- could leave a legacy that exacerbates N limitation in this system.
Given these findings, it follows that this exacerbated N limitation may ultimately cause forests stressed by drought, insect defoliation or other ephemeral disturbances to be more susceptible to mortality (i.e., less resilient) in the face of subsequent diseases, disturbances, and climatic change. While the short time interval of this current study precludes testing this hypothesis, our study indicates that the growing remote sensing data record –especially from the current and future generations of high spatial resolution, hyper-temporal (MODIS), and hyperspectral (Hyperion) instruments– can provide an invaluable source of data for understanding the long-term nutrient cycling legacy of ephemeral disturbances.

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References


