Indicators of Nitrogen Status in California Forests[1]

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Abstract

Indicators of ecosystem nitrogen (N) status are needed for monitoring and for identifying ecosystems that are at risk of becoming N saturated. The N chemistry of a number of plant, soil and hydrologic components were analyzed to assess the N status of mixed conifer forests across an N deposition gradient in the San Bernardino Mountains east of Los Angeles, California. All of the measured parameters at Camp Paivika on the western high-deposition end of the gradient indicated that the forest is N saturated, while forest stands on the eastern end of the gradient are N-limited. On the basis of these and other studies, the following parameters are recommended as indicators for monitoring forest N status: foliar nitrogen:phosphorus (N:P), foliar nitrate (NO_3^-)*, foliar growth response to N fertilization, soil carbon:nitrogen (C:N) ratio,* NO_3^- *in soil extracts or soil solution, and streamwater* NO_3^-*. However, foliar* NO_3^- *levels are more temporally sensitive than the other indicators mentioned, and foliar* NO_3^- *levels vary widely among plant species. Nitrate levels measured in KCl extracts or in soil saturation extracts were as effective as soil solution* NO_3^- *measurements for comparing soil* NO_3^- *concentrations among sites across the N deposition gradient. Extractable* NO_3^- *may be the preferred indicator of soil* NO_3^- *because it can be measured when soils are wet or dry, whereas soil solution cannot easily be obtained from soils with low water content. Elevated N trace gas emissions from soil (nitric oxide [NO] is dominant under the arid conditions of California) seem to be diagnostic of excess soil N, but field measurement of N trace gases (particularly NO) is not routine for most laboratories. Streamwater* NO_3^- *concentration is a highly useful integrative indicator of the net outcome of N cycling processes within a watershed. Temporal trends in streamwater* NO_3^- *are indicative of the N retentiveness of the watershed. Studying a combination of suitable indicators is recommended when evaluating forest N status.*

Introduction

Indicators of ecosystem nitrogen (N) status are needed for monitoring and for identifying ecosystems that are at risk of becoming N saturated. The need for indicators is evidenced by the expanding geographic scope of forested areas over which elevated atmospheric N inputs are expected (Galloway and others 1994). Nitrogen deficiency or limitation is common in northern temperate forests (Vitousek and Howarth 1991), and undisturbed forests are generally considered to be highly conservative of N. However, many recent studies have shown that forests exposed to chronic N deposition often result in nutrient cycling processes that have been significantly altered by excessive inputs of atmospheric N. In many forests the levels of available soil N are in excess of biotic demand, and N losses from these forests can be high (Dise and Wright 1995, Riggan and others 1985). Such forests with available N over and above the biotic and abiotic retention capacities are considered N saturated (Aber and others 1989). Many current and recent studies have focused on the consequences of N deposition and enrichment on natural ecosystems that are adapted to N-limiting conditions. Water quality has deteriorated in many watersheds exposed to N air pollution as a result of high NO_3^- concentrations in streamwater. Although low-to-moderate N deposition may increase productivity, considerable evidence suggests that detrimental environmental effects will ensue in the long-term in forests with high levels of N inputs (Aber 1992).

Nitrogen deposition and ozone concentrations in the South Coast Air Basin (SCAB; Los Angeles, California, and surrounding counties) are among the highest in North America. Montane forests encompassing the SCAB are exposed to high concentrations of ozone and N pollutants (Bytnerowicz and Fenn 1996). Nitrogen and ozone air pollution are also on the rise in the western and southern portions of the extensive Sierra Nevada range, as a result of large urban and agricultural emission sources throughout California (Blanchard and others 1996). The effects

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[1] An abbreviated version of this paper was presented at the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystems, February 5-9, 1996, Riverside, California.

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of N deposition on forests within the SCAB may provide a preview of future scenarios in other western forests as urbanization and fossil fuel consumption continues to increase in western North America. The more extreme cases of air pollution exposure increase the likelihood that signals of air pollution effects will be more clearly discernible above the background variation inherent in natural ecosystems (Lang and others 1982).

In the San Bernardino Mountains (SBM) east of Los Angeles, California, a steep air pollution gradient spanning 55 km has been identified, with ozone and N deposition decreasing from west to east (Fenn and Bytnerowicz 1993, Miller and others 1986). Ozone injury to sensitive species has been observed for many years, while more recently the effects of chronic N deposition have also been documented (Fenn and others 1996). A number of nutrient pools and processes have been monitored at sites with high and low N deposition in the SBM to determine the impact of atmospheric N inputs on N cycling.

This paper reviews which nutrient cycling parameters may be useful as indicators of forest N status under the environmental conditions prevalent in California.

Selection Criteria for Indicators of Forest Nitrogen Status

Evaluating forest N status is challenging because N is a major constituent of all life forms and is cycled through a complex web of processes involving many biotic and abiotic mechanisms. Monitoring toxic pollutants or xenobiotics such as heavy metals or pesticides is in many ways a much simpler task. To evaluate the N status of a forest ecosystem, we recommend the use of a small set of reliable indicators that are easy to implement. Although numerous components of the ecosystem could be measured to provide information on forest N status in intensive research studies, the selection of indicators may be limited by practical considerations in monitoring programs. Suggested criteria for selecting suitable indicators for monitoring include the following:

- Accurate measure of site N status
- Lack redundancy
- Lack sensitivity to time of sampling or other environmental factors
- Sufficiently high signal-to-noise ratio
- Relatively standard sampling and analytical methods
- Cost effective (low cost/high information value)
- Definable range of "normal" values
- Clearly identifiable N excess and N deficiency.

Although selected indicators must accurately indicate site N status, evaluations of forest N status may be difficult to establish based on any one indicator. Ecosystem N status should be evaluated with a complementary set of nonredundant indicators so that the relative degree of N limitation, sufficiency, or saturation (excess) may be more firmly established. Vegetation-based indicators of N status are particularly useful because they function as biomonitors and allow site N status to be assessed by plant-environment interactions. Vegetation-based indicators help ensure that interpretations of site N status are biologically relevant. For some indicators, seasonal trends should be monitored to interpret indicator responses.

For sites at risk of N saturation, indicators should be included that can identify when available N exceeds biotic demand. Such indicators typically monitor parameters that are normally at background or low levels in N-limited systems. Sustained high activity levels or concentrations suggest that available N is in excess of biotic demand. Examples of indicators from the literature and from our studies (Fenn and others 1996) that seem to indicate excess plant-available N include foliar accumulation of nitrate (NO_3^-) (Stams and Schipholt 1990) or amino acids (Ohlson and others 1995), elevated emissions of N trace gases from soil (Castro and others 1994, Sitaula and others 1995), high soil solution NO_3^- accompanied by high leachate losses of NO_3^- (Aber and others 1989), and above normal NO_3^- concentrations and fluxes in streamwater (Riggan and others 1985, Stoddard 1994). High levels of nitrate reductase activity (Norby and others 1989) may also be indicative of high NO_3^- availability or elevated atmospheric concentrations of nitric acid vapor (HNO_3). However, in the SBM, concomitant exposure to high ozone concentrations may interfere with enzyme activity, confounding the use of nitrate reductase activity as an indicator of excess N availability (Krywult and others [In press]).

However, the cardinal indicator or manifestation of N saturation in all ecosystem types, including California forests and chaparral, is increased and prolonged NO_3^- loss below the main rooting zone and in streamwater (Dise and Wright 1995). Changes in solution concentrations and fluxes as water passes vertically through forest ecosystems in precipitation, throughfall and stemflow, forest floor percolate, soil solution, surface runoff, and in streamflow have been referred to as solution or water chemistry profiles (Binkley and others 1982, Chorover and others 1994).

The N solution profile in a forest is highly indicative of the N status or degree of N saturation. In N-limited forests, nearly all of the solution N is retained within the vegetation or upper soil layers of the solution profile. However, in N-saturated forests, excess N is transported through the canopy and soil layers and exported mainly as leached NO_3^- and nitrogenous trace gases (Aber 1992).

Recommended Indicators in Arid Western Forests

Indicator selection in arid western forests is based on current understanding of N cycling in temperate forest ecosystems and on studies from air pollution gradients in the SBM (Fenn and others 1996) and San Gabriel Mountains (SGM) (Anderson and others 1988, Kiefer 1995, Riggan and others 1985). Valuable indicators of forest N status in the summer-dry conditions that predominate in much of western North America include:

- Soil NO_3^- (in soil solution or in soil extracts)
- Nitrate:ammonium (NO_3^-:NH_4^+) ratios in soil
- Soil carbon:nitrogen (C:N) ratios
- Nitric oxide (NO) emission levels from soil
- N-mineralization and nitrification rates
- Foliar nitrogen:phosphorus (N:P), C:N, and N:cation ratios
- Accumulation of NO_3^- in foliage of understory and overstory species
- Plant response to N fertilization
- Streamwater NO_3^- concentrations and fluxes
- Base saturation and soil pH.

Many of the indicators suggested for arid forests of the western United States have also been demonstrated to be effective in more humid temperate forests as well. However, indicator responses may differ depending on climate and ecosystem characteristics. For example, emission levels of nitric oxide (NO) are good indicators in western forests, while in more humid forests of the eastern U.S. or Europe, studies have shown that nitrous oxide (N_2O) emissions are much greater than NO emissions (Aber and others 1989). Temporal dynamics of streamwater NO_3^- fluxes may also be different in Mediterranean ecosystems (Riggan and others 1985). Nitrate in the soil solution can also build up to high concentrations during the dry season in sites with low or moderate N deposition as soil drying results in low volumes of soil solution with high ionic concentrations (Fenn and others 1996). As with all indicators, data from low-deposition sites or other reference data should be compared for interpreting indicator results.

Characteristics of Recommended Indicators

Soil Nitrate

In strongly N-limited systems, N cycling and plant uptake of N occurs mainly as ammonium (NH_4^+) (Aber 1992). As N saturation develops, plant-available NO_3^- increases in soil. Thus, the NO_3^-:NH_4^+ ratio in soil may be a useful indicator of site N status. Soil NO_3^- but not soil NH_4^+ increased with greater N deposition in the SGM (Kiefer 1995) and SBM (Fenn and others 1996). However, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) trees prefer NO_3^- to NH_4^+ (Griffin and others 1995, Norton and Firestone 1996), contrary to the conventional belief that conifers prefer NH_4^+ (Adams and Attiwill 1982, McFee and Stone 1968). Soil NO_3^- and NH_4^+ can be measured in soil solution or in soil extracts (e.g., saturation or KCl extracts). Obtaining soil solution samples with the widely-used suction lysimeter method (Fernandez and others 1995) from the coarse-textured soils typical for these ecosystems can be very difficult during the dry summer growing season. We found that the soil centrifugation method (Soon and Warren 1993) worked well for obtaining soil solution samples from coarse-textured forest soils with water content near field capacity. However, in our studies in the SBM, NO_3^- levels measured in soil saturation extracts and in KCl extracts were equally effective as soil solution NO_3^- measurements for comparing soil NO_3^- concentrations at sites across the deposition gradient. Soil extracts can be obtained from soils collected at any time, regardless of soil water content or soil texture, and in that regard are probably more practical as an indicator in a monitoring program. Another recent study concluded that KCl extracts performed similarly to suction cup lysimeters in quantifying soil NO_3^- (Djurhuus and Jacobson 1995).

Streamwater Nitrate – a Watershed-Level Indicator

Streamwater ionic flux is a very useful integrator of overall ecosystem integrity and serves as a watershed-level indicator of ecosystem nutrient loss or conservation. Nitrogen saturated watersheds export above-normal amounts of NO_3^- once the capacity for N retention by the biota and soil chemical fixation mechanisms are exceeded (Stoddard 1994). Temporal or seasonal trends in NO_3^- export in streamwater reveal the N retention capacity at the watershed scale and are a consequence of the many nutrient cycling processes occurring within the watershed. A brief and relatively small NO_3^- loss from temperate forest watersheds is expected during the spring water flow from the watershed brought on by snowmelt. During this early spring season water flows are greatest and soil temperatures are still low, and plant and microbial nutrient demand are insufficient to retain all of the dissolved N. However, a state of N saturation is indicated when NO_{3^-} concentrations begin to increase over this “normal” background level and when losses are prolonged. Peak flows in N-enriched California ecosystems seem to occur during major winter storms or during subsequent snowmelt periods when more complete washout of the soil profile occurs (Riggan and others 1985).

Monitoring streamwater NO_3^- dynamics throughout the hydrologic year will provide the most information on watershed N processing and losses. However, with an understanding of the temporal dynamics of streamwater chemistry within a given set of environmental conditions and ecotypes, sampling windows may be identified when NO_3^- in streamwater is indicative of above-normal N losses or N saturation. For example, high streamwater NO_3^- concentrations during the summer when the terrestrial and aquatic biota are normally capable of retaining available N may suggest an N-saturated condition. When the objective is to compare annual N inputs and outputs for a watershed, streamwater flow volumes and NO_3^- concentrations should be measured.

Soil C:N Ratio

The soil C:N ratio is a useful indicator of N enrichment in forests. Soil C:N ratio is less temporally and environmentally sensitive than other indicators, such as NO_3^-

levels in soil and foliage, nitrate reductase activity, amino acid concentrations in foliage, trace gas emissions from soil, and streamwater NO_3^- concentrations. The relative stability of soil C:N enhances the utility of this indicator and reduces the odds of fluctuating environmental conditions or nutrient cycling processes confounding interpretation of indicator results. However, the fire history of monitored sites must be considered when implementing any N status indicator (Chorover and others 1994), including C:N ratio. Percent C and N losses from burned plant material are highly similar (Raison and others 1985), and soil C:N ratios appear to be little changed after fire (Carreira and others 1994, Raison 1979). However, total C and N pools can change dramatically in burned sites (Raison 1979), suggesting the need for caution when monitoring sites have burned recently.

Foliar Nitrate

Nitrate is stored in the vacuole (Granstedt and Huffaker 1982) but does not accumulate in foliage until the growth requirements for N are satisfied (Zhen and Leigh 1990) and the capacity for NO_3^- assimilation is exceeded (Lee and others 1986). Nitrate accumulation in plants can be a very useful indicator of N excess because NO_3^- does not accumulate in foliage unless plant demand for N has been met. Nitrate concentrations in foliage of pine, oak and fern were much higher at an N-saturated site compared to an N-limited site in the SBM (Fenn and others 1996). Nitrate accumulation was especially high in bracken fern (*Pteridium aquilinum* var. *pubescens* Underw.), a species that has been shown to accumulate NO_3^- under conditions of high N deposition (Stams and Schipholt 1990).

Amino acid levels in foliage may also be an effective indicator of N status or storage of excess available N (Ericsson and others 1993, Ohlson and others 1995), but this has not yet been investigated in western forests. However, amino acid analysis is not likely to be routine for many plant and soil analysis laboratories.

Foliar Nutrient Ratios

Foliar nutrient ratios are often more reliable and informative indicators of plant nutrient status than nutrient concentration alone (Ericsson and others 1993, Hüttl 1990, Mohren 1986, Zinke 1980). In three separate studies, foliar N:P ratio has been found to increase with increasing N deposition in the mountains of southern California (Fenn and others 1996, Poth and others 1991, Zinke 1980). Foliar C:N ratio is also a useful indicator of site N status (Fenn and others 1996). Nitrogen:cation ratios in foliage have not been sufficiently tested as N status indicators in California but may also be useful indicators of N status or of nutrient imbalances (Hüttl 1990).

Elaborate nutritional diagnosis systems have been developed based on a suite of nutrient ratios. The Diagnosis and Recommendation Integrated System (DRIS) is an example of a widely used system in agriculture (Walworth and Sumner 1987), which has also been applied to a number of forest species (Binkley and others 1995, Riiters and others 1992, Shumway and Chappell 1995). DRIS uses nutrient ratios in high-productivity sites as a guide to optimum ratios that could be achieved through fertilization of less productive sites. Before DRIS can be used for a particular plant species, however, DRIS “norms” have to be determined for that species based on nutrient data from a large survey of the species in question (Needham and others 1990). DRIS norms have not been developed for ponderosa pine or most other western forest species; but if they are developed, DRIS could prove to be a very effective tool for evaluating site N status and for identifying other nutrients that may be limiting or in excess. This could be particularly useful in cases where excess N may induce deficiencies of other nutrients (Houdijk and Roelofs 1993, Mohren and others 1986, Schulze 1989).

Plant Response to Fertilization

Studies of plant response to N amendment treatments is an effective technique for evaluating site N status, although this requires treatment application and subsequent comparisons of untreated control plants and fertilizer-treated plants. Vector analysis is a simple, but elegant, graphical technique by which tree N status can be determined from physiological responses to fertilization under field conditions (Haase and Rose 1995, Timmer and Stone 1978, Weetman and Fournier 1982). Fertilization of individual trees with N before the growing season followed by end-of-season analysis of tree response in terms of foliar biomass, N content, and N concentration (vector analysis) can provide clear indications of the N status of forest trees. The value of the fertilization / vector analysis method, however, is that field grown trees can be used to biomonitor and interpret site N status — at least for the selected tree species. Vector analysis studies in the SBM and SGM suggest that ponderosa and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) trees in stands with N deposition from ca. 6 to 16 kg ha^{-1} yr^{-1} are N deficient, while N was not limiting at sites with more than 30 kg ha^{-1} yr^{-1}, (Kiefer and Fenn [In press]).

Nitrogen Mineralization and Nitrification

In N-enriched sites, N-mineralization and nitrification rates are usually increased (Aber and others 1989, Van Miegroet and others 1992). Under conditions of excess available N, the need for N conservation is reduced, and canopy N turnover, net N-mineralization and net nitrification increase. Nitrogen mineralization can be measured in situ with the buried bag technique (Pastor and others 1984), or potential N-mineralization and nitrification can be assayed under controlled conditions. Both aerobic and anaerobic assays can be used, although nitrification rates are not determined in anaerobic incubations (Binkley and Hart 1989). The laboratory assays provide information on potential net N-mineralization and nitrification rates, which are measures of the soil capacity to supply N, while eliminating confounding environmental influences on soil N cycling. Assays performed under standard conditions allow for comparisons of soil N status for different sites and remove site environmental constraints (e.g., temperature and moisture limitations) that are constantly changing. N mineralization rates were higher in sites with greater N deposition in the SBM and SGM in southern California (Fenn and others 1996, Kiefer 1995).

Fluxes of N Trace Gases

Fluxes of trace gases from soil often increase with greater soil N supply (Castro and others 1994, Sitaula and others 1995). In forests in eastern North America and in Europe, N_2O emissions appear to be much greater than NO emissions (Aber 1992), although NO fluxes are frequently not measured. In California soils, NO fluxes are typically much greater than N_2O fluxes (Anderson and others 1988, Davidson 1993). NO emissions were much higher in a high deposition site compared to a low deposition site in the SBM (Fenn and others 1996). Nitric oxide appears to be diagnostic of excess available soil N in western coarse-textured soils. A major drawback of NO as an indicator of soil N status is the specialized equipment required to measure NO. Under conditions where N_2O emissions are sufficiently high (finer textured soils with more than 60 percent water-filled pore space) (Davidson 1993), simple flux chambers could be installed on the forest floor and headspace samples collected, transported to the laboratory, and N_2O quantified via gas chromatography. Although N trace gas fluxes seem to be indicative of soil N status, other indicators may be easier to implement for the general plant and soil chemical analysis laboratory.

Soil pH and Base Saturation

Decreased base saturation and soil pH in forests with high N inputs does not prove cause and effect because other stand development factors can also cause soil acidification and decreased base cation levels in soil. However, if other indicators provide evidence of N saturation, decreasing base saturation and soil pH may provide supporting data of the effects of N enrichment. Decreased base saturation is a result of cation leaching as counter-balancing ions for leached NO_3^-. In the SBM soils in sites with high N deposition had lower base saturation and pH than soil in sites with low N deposition (Fenn and others 1996).

Summary

To assess the N status of a forest ecosystem several reliable and complementary indicators should be selected. Under the arid conditions of much of the western U.S., recommended indicators include the following:

- NO_3^- concentrations in soil and foliage
- Foliar nutrient ratios such as N:P
- Soil C:N
- Streamwater NO_3^- concentrations and fluxes
- Plant response to N fertilization or vector analysis.

The N status of a forest ecosystem can also be assessed in the context of solution chemistry profiles that consider the sequential processing of N in precipitation, throughfall and stemflow, forest floor percolate, soil solution, surface runoff, and streamflow. Nitrogen mineralization and nitrification rates and trace gas fluxes from soil (especially NO) are also potentially useful indicators of N status. With further research, amino acid levels in foliage and the Diagnosis and Recommendation Integrated System (DRIS) method could also be used in evaluating site N status. However, DRIS norms would need to be developed for the particular plant species.

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