Alpine Vegetation Workshop:

Response of Alpine and Subalpine Plant Species to Changes in Atmospheric N Deposition

November 6th – 7th, 2008

Sponsored by National Park Service
and
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WORKSHOP BACKGROUND AND GOALS

It is well known that increased nitrogen (N) supply, for example from atmospheric deposition of oxidized and/or reduced forms of inorganic N, causes some plant species to experience increased growth and abundance. Other species can be out-competed and eventually eliminated from the plant community. This response is especially pronounced in plant communities that have evolved under low N supply and that are dominated by non-woody plant species, including many alpine and subalpine plant communities. Such changes in plant species dominance and distribution can affect species diversity, threaten rare plants, and cause a cascade of ecological effects within the ecosystem. As a consequence of these known patterns of ecological response to N inputs, and because atmospheric N deposition has been high (> 10 to 20 kg N/ha/yr) throughout large areas of central and northern Europe, European scientists have come together to classify plant species found in a wide range of European habitats with respect to their response to changes in N supply (Landholt 1977, Dahl 1998, Ellenberg et al. 1991). A System Analysis method has been used to classify European plants into N supply response classes. It was rooted in the participant approach to group model building. The process developed in an iterative fashion from conceptual diagramming to simulation modeling. Where experimental data were lacking, empirical relationships, or approximations, were used as "best available expert estimate." The ultimate objective was to apply and test ForSAFE, a predictive model for integrated soil chemistry, nitrogen and carbon dynamics (Wallman et al 2005). To the model has been attached a dynamic integrated ground vegetation response model (VEG; Sverdrup et al. 2007). Results of this classification scheme have been used to predict future changes in plant communities, using the For SAFE-VEG model, and to estimate the critical load of N required to prevent further nutrient enrichment impacts and to restore ecological balance (Sverdrup and Warfvinge 1993, Sverdrup et al. 2007). Such work has yielded important data to inform policy discussions regarding N emissions controls in Europe. Comparable data are not presently available for the United States.

A workshop was held at the office of the National Park Service, Air Resources Division (NPS, ARD), in Lakewood, Colorado in November, 2008 to evaluate the feasibility of initiating a similar research effort in the United States. The initial focus was on N effects on alpine and subalpine plant communities. These plant communities were selected because such high-elevation ecosystems are generally quite sensitive to effects from atmospheric deposition of N and sulfur (S), and because many of the plant species found in these ecosystems in the United States are the same as those found in Europe. Funding for this workshop was provided by NPS and the U.S. Environmental Protection Agency (EPA). A small group of scientist who are actively involved in vegetation response research in the alpine and subalpine environments in the United States was invited to participate. The purpose of this report is to summarize the workshop presentations and findings.

Specific Workshop Objectives

1. ***Evaluate existing information, including quantity and scope (geographic, etc.) of information available regarding the response of individual alpine plant species in the U.S. to atmospheric N loading.***
    - N-response data and information for some of the more weedy nitrophilous alpine plant species.

- N-response data and information for some of the rare alpine plant species or those species that tend to be out-competed in response to N-enhanced growth of neighboring nitrophilous species.
- Availability of indicator species in alpine communities for growth enhancement or suppression, including plant groups expected to be most responsive (i.e., lichens, grasses).
- Comparability, with respect to N response, of arctic vs alpine plant species.
- Current state of knowledge regarding the role of mycorrhizal fungi in governing the N response of U.S. alpine plant species.
- Experimental data

2. *Classify U.S. alpine plants into preliminary N loading response classes*

- Evaluate whether U.S. alpine plants can be placed into response classes based on available data.
- Assess transferability from Europe to the U.S. of knowledge regarding alpine plant species growth responses and associated classifications to N loading.
- Evaluate plant group parameters for the European ForSAFE-VEG model and evaluate applicability to U.S. ecosystems and available data.
- Develop preliminary classification for some U.S. alpine plant species regarding response functions for:
    - Average lifespan of individual
    - pH, BC/Al and Ca
    - Nitrogen
    - Water availability
    - Temperature range
    - Light requirements
    - Wind tatter limitation
    - Phosphorus limitation
    - Ungulate grazing preference
    - Rooting depth class
    - Effective shading height

3. *Evaluate effects of climate change*

- Assess whether U.S. alpine plants can be evaluated with respect to their responses to N loading without also considering the effects of a changing climate.
- If climate change must be considered in order to assess U.S. alpine plant responses to changes in atmospheric N loading, determine which aspects of climate change (i.e., temperature, precipitation, growing season, snowpack depth and duration, etc.) must be considered.
- Geographic distribution of knowledge and data regarding alpine plant species responses to N loading and climate change (including N. Rockies, S. Rockies, Cascades, Sierra Nevada, Alaskan ranges).

4. ***Strategize for the future***
    - Outline a series of next steps, required to move the U.S. research community towards an improved capacity to estimate (model) the future response of alpine plant species diversity and relative abundance in response to changing N input (and climate?).

INTRODUCTION AND OVERVIEW

The purpose of the workshop held at the offices of the NPS Air Resources Division, November 6 and 7, 2008 was to bring together a group of subject matter experts in a two-day workshop to agree on a preliminary classification system for alpine/subalpine plant species in the United States with respect to their growth responses to added nitrogen supply. This preliminary system was intended to be based, to the extent practical, on the classification system developed for northern Europe. Workshop participants are listed in Appendix A.

High-elevation plant species in Europe and North America share many commonalities. We invited to the workshop a group of plant ecologists who work in the Rocky Mountains, Cascade Mountains, Sierra Nevada, and Alaska. In addition, one of the principal plant ecologists responsible for the European work was included, along with one of the lead model developers from Sweden. Participants were provided in advance with background information regarding the European classification and modeling efforts. At the workshop, we discussed an analogous classification for U.S. species. It is hoped that this report will provide the foundation for the following: 1) experimental studies to classify the response of important plant species which elude classification based on existing knowledge, 2) process modeling of vegetation community response to changes in atmospheric N loading, 3) estimation of critical loads of atmospheric N deposition to protect against nutrient enrichments effects in U.S. alpine/subalpine plant communities, and 4) development of N response classification systems for other plant communities in the U.S.

One objective of this workshop was to move the scientific research community towards an ability to estimate or model the response of alpine plant communities in the US to changing levels of N input, with a major focus on the effects on species diversity and changes in species relative abundances. In doing this, we recognize that it may not be possible to model future changes in alpine plant communities in response to N, without also considering the effect of climate change (including, but not limited to, temperature and moisture availability).

The workshop agenda is provided in Appendix B. Ellen Porter (NPS,ARD) welcomed the participants and provided a brief overview of the goals of NPS and EPA, the two sponsors of this workshop. Tim Sullivan (E&S Environmental Chemistry, Inc.) outlined the workshop objectives. These introductions were followed by a series of short research presentations, which are described below. The final session of Day 1 involved general discussion of the material presented throughout the day and preliminary development of a classification system for the United States. Day 2 focused mainly on parameterization of a species response matrix for the United States. This was followed by planning for reporting and follow-up.

SYNOPSIS OF WORKSHOP PRESENTATIONS

Estimating Critical Loads for Nitrogen Based on Biodiversity Using a Fully Integrated Dynamic Model, Harald Sverdrup

Professor Harald Sverdrup, Lund University, discussed collaborative work with Dr. Salim Belyazid, Prof. Bengt Nihlgård, Dr. Sabine Braun, Daniel Kurz, and Beat Rihm in regards to dynamic critical loads modeling with ForSAFE-VEG in Sweden and Switzerland. Critical loads estimates are used as input to policy scenarios for all of Europe, including assessments of environmental impacts, timing of events, mitigation cost estimates, and socio-economic benefits. The approach to policy implementation based on critical loads has been to: 1) define environmental thresholds, 2) calculate critical load with an integrated model, 3) establish exceedences, 4) determine sources, and 5) design policy. A map showing critical loads and their exceedences is needed for every protected environment. The ForSAFE-VEG modeling system is currently being used to estimate critical loads for vegetation response. This model is a combination of a previously developed model for predicting tree growth (ForSAFE) with a newly developed model used to incorporate ground vegetation and predict changes in biodiversity in response to environmental conditions and a multitude of stressors (VEG). Figure 1 shows a schematic illustration of the ForSAFE-VEG modeling system.

Parameterization of the model and its functionality were introduced. Management history, in terms of forest management and grazing, is an important component of the model. ForSAFE-VEG was successfully tested at sites that receive a wide range of atmospheric N deposition in Switzerland (30 kg N/ha/yr) and Sweden (2 kg N/ha/yr deposition). Results from various model scenarios considering climate change, acidic deposition, and N addition were presented from two sites in Switzerland and two sites in Sweden.

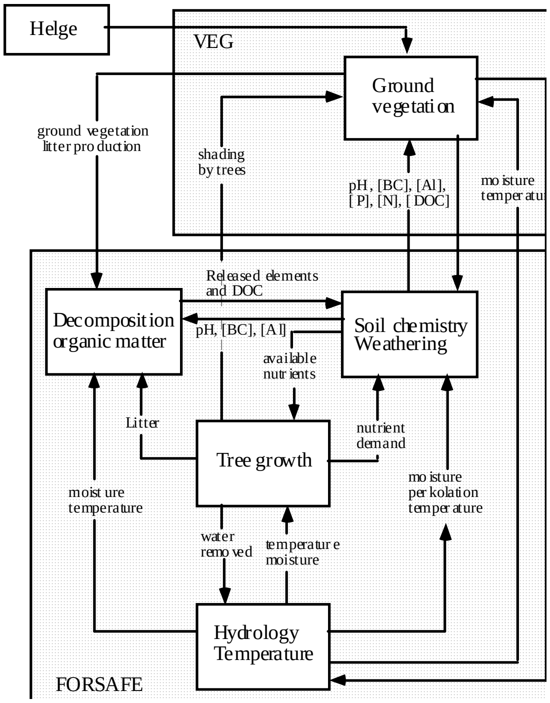

Figure 1. ForSAFE-VEG conceptual diagram.

Several factors are known to have a strong effect on biodiversity, and these are fully coupled in the natural ecosystem, complicating our task considerably. In a forested landscape, these include:

1. Nitrogen
2. Acidity
3. Forest management
4. Climate change

These are assumed to have roughly equal importance for biodiversity, and none can be ignored without significant implications. Any method we use must be able to handle the effect of these factors on biodiversity and must describe their effects on the ecosystem. A full description of

ForSAFE is available in Sverdrup et al. (2007), Belyazid et al (2006, 2007) and in the PhD thesis of Belyazid (2006). The integrated FORSAFE-VEG model includes the following ecosystem components as of April 2008:

1. tree vegetation layer (canopy, stems, roots)
2. ground vegetation layer
3. soil chemistry and geochemical processes
4. soil pools and cycling of nutrients (Ca, Mg, K, P, N) and carbon
5. soil hydrology and energy balance
6. outputs from the system: carbon dioxide, dissolved organic carbon, solution chemistry

In order to synthesize an integrated multiple stress system, ForSAFE-VEG provides simultaneous predictions of ecosystem effects of climate change, soil acidification and eutrophication. It considers the effects of vegetation changes on forest growth and the cycling of cations, acidity, nitrogen and carbon. ForSAFE contains fully mechanistic nitrogen- and carbon-cycle sub-models as well as predictions of forest growth under production management. The ground vegetation composition in a forest or field is determined by a number of **drivers** in the submodel VEG:

1. Soil solution nitrogen activity (kmol m^{-3})
2. *Soil solution phosphorus activity (kmol m^{-3})*
3. Soil chemistry in terms of acidity, antagonists and co-agents: ($[H^+]$, $[BC^{2+}]$, $[Al^{3+}]$)
4. Soil water activity (soil moisture, m^3 water m^{-3} soil)
5. Site soil temperature (^oC), *including wind chill effects (m s^{-1})*
6. Light reaching the ground (micromol photons $m^{-2}s^{-1}$)
7. Grazing by ungulates (moose equivalent units/km^2)
8. *Wind tatter, mechanically damaging soft tissue of plants (m s^{-1})*
9. *Direct effect of gases (SO_x, NO_x, CO_2, O_3)*
10. Forest fire
11. Forest management

Factors in *italics* are not fully activated in the model yet. An important feature of the ForSAFE-VEG model is that the plants have to compete for their share of the available resources and space. The drivers act to give each plant group a competitive strength. Competition is comprised of the following elements, whereby the individual plant groups have feedback on the drivers. Feedbacks affect the individual plant and its neighboring plants:

1. The above-ground competition strategy of the plant group for capturing light and preventing others from getting it depends on plant height and shading capacity.

2. The root competition strategy focuses on capturing water and nutrients, and is also influenced by exposure to soil chemistry (H^+, Al^{3+}, BC^{2+}), expressed through root distribution at different soil depths, in order to take up nutrients competitively.

The competitive strength is the weight each group has when the territory claim assigned to a plant group is determined. The plant group then must use this habitat availability and the passage of time to take that much of the territory. Phosphorus has been conceptualized and only partly parameterized, but still remains to be integrated into the model and the parameterization validated. The plant groups are assumed to be groups of plants with identical responses to all parameters. Indicator plant species are identified for each group. At present we have the ability to consider many tree species as seedlings and as mature trees, in addition to ground vegetation groups. Tree mixes are being integrated at the moment of writing; inter-species tree competition beyond the juvenile stage has not yet been fully integrated into the model.

The ForSAFE-VEG system can at present handle the following ecological functional groups:

1. Trees
2. Shrubs
3. Ground vegetation
    a. Lichens
    b. Mosses
    c. Grasses
    d. Herbs and flowers
    e. Brackens
4. Soil biology
    a. Collemboles
    b. Earthworms
    c. Mollusks and snails
5. Soil functions
    a. Organic matter decomposer bacteria
    b. Organic matter decomposing fungi
    c. Nitrifiers
    d. Denitrifiers
6. *Insects*
    a. Stationary insects of the forest canopy
    b. Insects of dead wood and tree bole habitats
    c. Insects of the soil habitat

Items in *italics* have been conceptually framed in equations, but not yet included in the model. Items in #6 have been framed in equations, but not yet parameterized. For collemboles and earthworms, the coefficients of the equations have been preliminarily parameterized. The normal lettered ones are fully integrated in the model with full environmental responses parameterized and field tested in Sweden, Iceland and Switzerland.

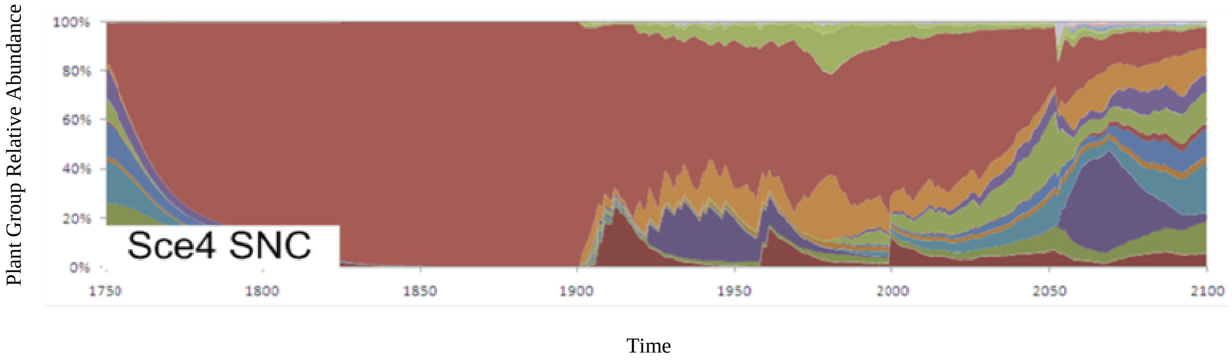

Figure 2. Example of a vegetation output from the model for a Swedish alpine site, for the period 1750-2100, showing combined effects of nitrogen, climate change and air pollution. The different colors represent different plant groups.

Alpine Plants in ForSAFE-VEG, Bengt Nihlgård

Bengt Nihlgård, Lund University, discussed European alpine plant physiology, morphology, and the selection of species for modeling with ForSAFE-VEG. The objective in selecting alpine plants for modeling was to obtain a representative set of species that were common, widely distributed, and responsive to changes in N supply and climatic conditions. General site data and plant specific data inputs were discussed. It was noted that the average age for each species is an important parameter that can be difficult to determine.

Water availability and temperature are more important limiting factors than light availability in alpine regions. Light is not expected to change in the future, but temperature is, causing the subalpine region to move upward and northward. These shifts in plant distributions are expected to bring along shade-tolerant understory species into areas once characterized as "low-alpine". Dwarf shrubs and mosses (e.g. *Salix lanata*, *Salix myrsinifolia*, *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Agrostis capillaries*, and *Hylocomium* mosses) are common on granitic soils in low alpine zones. Many of these species have wide ranges in their tolerance to light availability. The middle-alpine zone is characterized by cold-tolerant forbs such as *Viscaria alpina* and *Antennaria dioica* along with grass species such as *Deschampsia flexuosa* and *Nardus stricta*, all of which have wide light ranges. High-alpine zones are mostly comprised of lichens with some mosses and a few scattered grasses and cold tolerant forbs (e.g. *Saxifraga* species, *Ranunculus glacialis*). High-alpine species were not included in the Swedish model application.

Model simulations that include consideration of climate change generally specify increases in temperature according to the Intergovernmental Panel on Climate Change (IPCC). Temperature requirements for growth are highly variable among alpine plant species. All species must be adapted to low temperature in the winter, but be able to tolerate relatively high temperature in the summer. High and middle-alpine lichens (*Cladonia*) and mosses (*Hylocomium* and *Sphagum*) are assumed to grow at temperatures between -2.5 ^{o}C and 15 ^{o}C. The grasses *Festuca ovina* and *Nardus stricta* have similar temperature tolerance ranges, with slightly higher optimum temperatures. Low-alpine zone plant species (e.g. *Vaccinium* spp., *Calluna vulgaris*) have slightly higher minimum temperatures (-1.0 ^{o}C) for growth. Subalpine species such as *Betula* shrubs; *Agrostis, Deschampsia, Poa* and *Millum* grasses; and *Epilobium, Geraium, Rubus, Trientalis, Trifolium* and *Urtica* forbs are classified with temperature ranges from 0-20 ^{o}C, with optimum temperatures in the range of 10-15 ^{o}C. *Aconitum lycoctonum* is given a narrower temperature range (2-10 ^{o}C) since it is restricted to the boreal region in its distribution. Average wind speed is transformed as a cooling effect on the temperature parameter.

Water availability for plant species in ForSAFE-VEG is dependent on plant rooting depth and the volumetric soil moisture content. Lichens (*Cladonia* spp. and *Lycopodium alpinum*) can withstand drought conditions for an extended period of time and do not function well in wet soils. Drought-tolerant alpine species, such as *Lotus corniculatus* and *Antennaria diocan* were considered in the model as well. *Empetrum*, *Calluna*, and *Vaccinium* have wide ranges in tolerance to soil moisture. The forb species *Aconitum lycoctonum* and *Matteuccia struthiopteris* demand moist soils and can withstand nearly saturated conditions.

There is considerable variation in the extent of browsing among alpine plant species. Mammals prefer *Epilobium* and *Salix*, while *Betula* has developed an herbivore repellent. Many plants, including *Betula*, are susceptible to insect attack, but this is not considered in the current version of the model. Browsing sensitivity in ForSAFE-VEG is organized into classes from "avoided" to "strongly favored". Sheep and elk grazing in alpine zones will need to be considered in U.S. alpine modeling efforts with ForSAFE-VEG.

Model assumptions concerning the below-ground environment include: 1) Plant species compete for nitrogen and phosphorus, although phosphorus is not yet represented in the model, 2) differences in the availability of base cations and soil acidity favor different plant species, 3) root depth is important for nutrient uptake and competition among plant species, and 4) soil microbiology and soil vertebrates are considered to be of secondary importance for plants and are not yet included in the model.

The BC/Al ratio and soil pH are used to provide an estimate of acidity impacts on nutrient uptake. These parameters may be of lesser importance in alpine environments in the United States, as compared with northern Europe because of differences in the amount of soil acidification that has occurred. There are other potentially important differences between alpine environments in the United States and northern Europe. For example, the climate in the Rocky Mountains is more variable than in Scandinavia and is home to many more plant species, including endemics. *Alpine Plants of North America*, by Nicholls (2002), was suggested by Bengt as a good reference for ecological data on herbs and flowering alpine plants in the United States.

The Effect of Warming and Nitrogen on the Composition of the Alpine Tundra in Niwot Ridge, CO, Isabel Ashton

Isabel Ashton, NPS, discussed collaborative work with Katharine Suding and William Bowman on plant-soil thresholds to N supply and the effects of climate change on alpine plant communities in the northeastern Colorado Rocky Mountains. Artificial N enrichment studies were performed with slow release fertilizer at 16 kg/ha/yr from 2001 to 2008. Warming was simulated using open-topped chambers to increase summer air temperature by 1.0 ^{o}C and soil temperature by 0.5 ^{o}C. Changes in plant species abundance were used as a metric for determining response. Generally, N addition caused a decline in the abundance of *Acomastylis rossii*, which resulted in an increase in *Deschampsia caespitosa* and decreased alpine plant diversity.

The majority of the alpine plant species showed no response for most manipulative studies. There were fewer positive responders than negative responders to both N addition and warming treatments. Species that consistently increased in abundance with N addition were: *Deschampsia caespitosa* (graminoid), *Trifolium parryi* (forb), and *Lewisia pygmaea* (forb).

Between 31% and 36% of alpine plant species responded negatively to N addition. *Acomastylis rossii* (forb) and *Bistorta vivipara* (forb) showed relatively large negative responses to both N addition and warming. No correlation between plant characteristics (i.e. growth form, height, leaf area) and N response was found.

Responses and Feedbacks of Alpine Plants to Atmospheric N Deposition, Bill Bowman.

Bill Bowman, University of Colorado, discussed field and laboratory research related to alpine plant response to atmospheric N deposition in the Rocky Mountains. Alpine microclimates are a source of considerable variation in N supply across the landscape. Spatial differences in local N deposition provide habitat for plants with differing N requirements. Greenhouse studies have shown that grasses, such as *Calamagrostis*, *Deschampsia*, and *Trisetum* are strong positive responders to N addition and may be useful indicator species. Other potential indicator species include: *Allium geyeri, Artemesia* spp*., Polygonum bistortoides, Campanula rotundifolia, Carex rupestris, Mertensia lanceolata, Oreoxis alpina, Poa* spp*., Potentilla* spp*.,* and *Trisetum spicatum* (Theodose and Bowman 1997, Thomas and Bowman 1998). However, these studies were performed under extremely high (250 kg N/ha/yr) simulated N deposition so their results may not be directly transferable to the field. Abundance of *Acomastylis rossii* in moist alpine meadows at Niwot Ridge has been observed to decrease in conjunction with an increase in *Deschampsia caespitosa* abundance under experimentally elevated N supply. This change in species composition led to substantial increases in N mineralization, nitrification, and subsequent N loss to groundwater (Steltzer and Bowman 1998).

It was suggested that the currently low rates of N cycling at Niwot Ridge will increase with N deposition. Monitoring species response to N additions can provide an indication of N critical loads. This method has resulted in experimental estimates of N critical load that range from 4 to 10 kg N/ha/yr for a dry meadow at Niwot Ridge. Acidification effects appear to be occurring at Niwot Ridge in response to experimental N addition, with decreased soil base saturation, decreased soil pH, and increased soil Al^{3+} availability. It was recommended that gramminoids should be differentiated into grasses and sedges for assessing the results of N additions. If mycorrhizal associations are included in the model, consideration should be given to the fact that sedges (*Carex* spp.) may be non-mycorrhizal.

Developing Lichen-based Critical Loads for Nitrogen Deposition in Western North America, Linda Geiser.

Linda Geiser, USFS, discussed collaborative work with Sarah Jovan, Mark Fenn, Matt Porter, and Doug Glavich in developing N critical loads for epiphytic lichen species in montane forests of the Sierra Nevada, forests of western Oregon and Washington, and the Columbia River Gorge National Scenic Area. Lichen abundance data were used in conjunction with N deposition data to determine critical loads. Three levels of critical load were determined, as follows. First, the level of deposition was estimated which results in the upper end of the distribution of % N in *Letharia vulpine*. This most conservative critical load is termed the “clean site threshold”. Second, the level of deposition which results in a community shift from dominance by N-sensitive lichen species (acidophytes) to N-tolerant lichen species (neutrophytes) was determined. Finally, the level of deposition was determined which results in complete removal of acidophytic lichen species from the vegetation community. The critical load was estimated at 3.9 kg N/ha/yr for epiphytic lichens based on the “clean site threshold” method for the Columbia River Gorge. Lichen-based critical load estimates for the Sierra Nevada ranged from 3.1 kg N/ha/yr (clean site) to 10.2 kg N/ha/yr (acidophyte removal). Under average annual precipitation conditions, total N deposition critical load estimates for western Oregon and Washington forests were determined to range from 4 .0 to 5.2 kg N/ha/yr. Lichen-based critical loads in this region were found to be directly proportional to precipitation. Critical load estimates were generally comparable among study sites regardless of deposition data source, use of differing lichen responses, or sample size.

Mycorrhizal Associations: Connecting Belowground Processes to Aboveground Biodiversity, Katie Becklin

Katie Becklin, University of Missouri, discussed the connection between mycorrhizal colonization and plant growth. A decrease in mycorrhizal infection is generally considered to result in decreased plant fitness. A survey of alpine plants in Montana concluded that 68% were mycorrhizal. Both climate change and N-loading may be responsible for changes in mycorrhizal community structure. This may have direct and indirect effects on above-ground plant community composition. Nitrogen addition is anticipated to cause changes in fungal communities and these changes can, in turn, change the relative abundance of various host plant species. Thus, N deposition can impact above-ground plant biodiversity through its effects on mycorrhizal associations.

Variation in N Uptake Traits Among Co-occurring Alpine Species: Implications for Community-Level Change, Amy Miller

Amy Miller, NPS, discussed variations in N uptake among alpine plant species, based on results from field and laboratory experiments. A variety of forbs, grasses, sedges and rushes were considered. It is expected that, as N deposition increases, soil nitrate availability will also increase. Alpine plant species that respond positively to increases in soil nitrate will increase in abundance at the expense of other species. Overall, the response of alpine plant communities to N enrichment is likely to be complex. The ability of a plant to switch back and forth between ammonium and nitrate uptake (plasticity) may provide a competitive advantage under low N conditions. This plasticity may no longer help the plant to compete under higher N loading, when N is no longer limiting.

Plant and Community Responses to Climate Warming, Nitrogen Deposition, and Herbivory in Subalpine Meadows, Zac German

Zac German, Colorado State University, discussed experimental work regarding subalpine meadow plant community response to climate warming, N deposition, and herbivory at the Rocky Mountain Biological Laboratory in Gothic, CO. Artificial N enrichment studies were performed with dissolved ammonium nitrate at 90.0 kg N/ha/yr. Warming was simulated using open-topped chambers to increase summer air temperature by 2.0 to 3.0 ^{o}C and soil temperature by 1.5 to 2 ^{o}C. Grazing was simulated by clipping. Plant response was determined through a variety of metrics including: flowering phenology, flower/fruit number, percent species aerial coverage, species architecture, species productivity, stomatal conductance, fluorescence, and leaf nitrogen content. No consistent season-long trends were observed and most of the responses were small and differed by species, site, and growth phase.

N Loading in High Latitudes: Examples from Alaska, Svalbard, and Northern England, Jeff Welker.

Jeff Welker, University of Alaska - Anchorage, discussed collaborative work with Rachel Lehmkuhl regarding to N loading in high latitude regions of the world including; Alaska, Svalbard, Norway, and northern England. High latitude systems are typically nutrient limited and increases in atmospherically derived nutrients may result in an increase in CO_2 release to the atmosphere. Of the areas examined, nitrogen and sulfur deposition was lowest in Alaska. The eastern Arctic site (Svalbard) exhibited large fluctuations in N and S deposition. These trends were not observed in the western Arctic site (Alaska). N and S deposition in northern England are similar to the lowest values found in the Rocky Mountains. Available data suggest that shrub abundance is increasing and tree line is moving north and to higher elevations at northern latitudes worldwide. There was some discussion about the possibility of considering arctic systems separately from alpine systems to the south in the contiguous United States for the purpose of assessing the effects of N supply and climate change on plant species composition. It was agreed that combining arctic with alpine would be appropriate.

Estimating Critical Loads for Nitrogen Based on Biodiversity: Setting Plant Parameters, Harald Sverdrup.

Harald Sverdrup discussed collaborative work with Salim Belyazid and Bengt Nihlgård regarding FORSAFE-VEG model function and parameter requirements for estimating critical loads. A variety of ecosystem components are considered in the model. These include trees, shrubs, ground vegetation, soil biology and soil function. ForSAFE-VEG requires input data for plant characteristics (height, rooting depth, etc.) and habitat requirements such as nitrogen, moisture, light, temperature and others (See Appendix C for a complete list). Many of these parameters are represented by a response curve which is defined by the levels at which the parameter initiates growth (K_{min}), promotes growth (K_{top}), retards growth (K_{max}), and eliminates the species (K_{end}) (Figure 3).

Environmental parameters used to drive changes in biodiversity in the model are:

- Available soil nutrients:
    - Nitrogen
    - Base cations
      Phosphorus (not yet included)
- Soil chemistry
- Climate:
    - Site temperature
    - Soil moisture
    - Wind tatter
- Light to ground, as influenced by vegetative shading

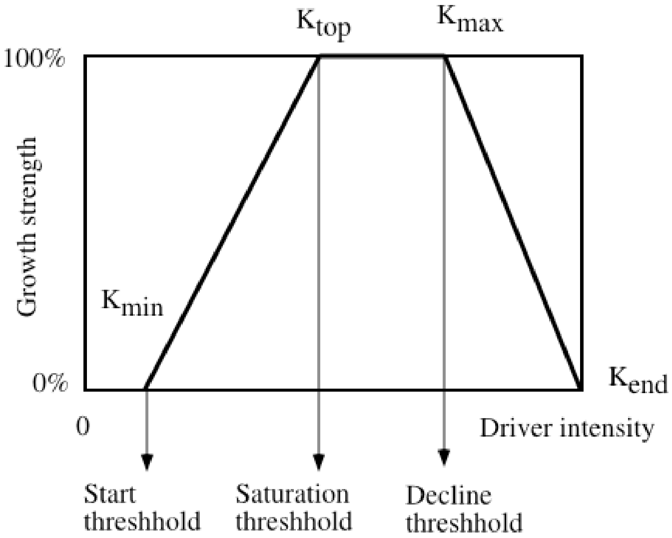

Figure 3. Schematic representation of the influence of environmental parameters on vegetative growth strength.

- Plant competition strategy variables:
  - Mutual shading
  - Root distribution
  - Grazing deterrence by taste
- Grazing and browsing by animals
- Forest/grass fires and disasters
- Forest management, thinning, harvest, planting, clearing

Work Session 1: Establishing an American Alpine Plant List and Setting Parameters in ForSAFE-VEG, Harald Sverdrup

The group began working on generating a list of alpine plant species that are known to occur in the United States and that have already been parameterized during European modeling efforts. This initial American alpine/subalpine plant list was comprised of several classes of plants including: lichens (epiphytic and ground), mosses, ericaceous shrubs, grasses, sedges, ferns and brackens, herbs and forbs, and trees. After selecting plants that co-occur in the U.S. and in Europe, the group began adding species that are unique to alpine zones in the U.S. The goal was to add species that are relatively abundant and for which reasonable response data are available. In addition, it was considered important to include some rare species that are expected to be responsive to changes in N and climate even if experimental response data are not available. A representative list of alpine plant species that occur in the U.S. was established during this work session. It included both native and non-native species, and also a few species that might be expected to expand into the alpine zone with climate warming.

Work Session 2: Parameterizing the American Alpine Plant List

Plant species that were carried over from the European list were already fully parameterized for model application in Europe. For the initial classification work here, it will be assumed that these species exhibit characteristics in Europe that are consistent with their American counterparts. However, some of these characteristics were modified where there were known discrepancies. Harold Sverdrup provided further details and guidance in regards to setting parameters required by ForSAFE-VEG for modeling purposes and the group parameterized the American plant list to the best of their ability with available data. It was agreed that the workshop participants would finish parameterizing the list after the workshop was completed. Discussion arose in regards to incorporating mycorrhizae into the model. Adding mycorrhizal associations as a separate component in ForSAFE-VEG would be considerably more work than incorporating them through modification of existing parameters (e.g. rooting depth, temperature tolerance) if the plant is known to be mycorrhizal. It would useful to consider other benefits of mycorrhizae such as disease resistance as well. Katie Becklin offered to draft a conceptual methodology for incorporating mycorrhizae into ForSAFE-VEG.

Other points of discussion during Work Session 2 included:

- Engleman spruce and mountain hemlock were chosen as representative subalpine tree species. There was not enough data to distinguish characteristics among all of the potential indicator subalpine tree species.
- Lichens were separated into epiphytic and ground lichens.
- It was noted that water response for epiphytic lichens would be different from ground lichens.
- It was decided that shading height, rooting depth, and browsing preference do not apply to epiphytic lichens.
- Linda Geiser has good N response data for lichens and agreed to provide it after the workshop.
- Maximum and minimum temperature for each species can sometimes be derived from maps of plant distribution and spatial temperature data. However, detailed species distribution maps are generally not available, and the available temperature data are relatively coarse. Optimum values can be selected from existing European data and professional judgment.
- A method to informally validate ForSAFE-VEG is to run the model iteratively to get a good fit at a data-rich site (i.e., Niwot Ridge), and then take it to another site and run it there to see if the general responses are similar.
- Linda Geiser suggested that each plant should be characterized with the ecoregion(s) in which it can be found and agreed to provide a map showing the boundaries of the Taiga/Tundra, Northwestern Forested Mountains, and Marine West Coast Forest ecoregions to be used for classification.
- Tim Sullivan noted that modeling with ForSAFE-VEG should be framed as a hybrid decision support/process-based effort.
- ForSAFE-VEG requires input parameters that have not been well-studied in experimental work in the United States. These include temperature tolerances, light requirements and response, and generation time. Based on available knowledge and data, inferences can be made concerning these parameters, but more work focused on these response functions would be helpful.

WORKSHOP SUMMARY STATEMENTS AND RECOMMENDATIONS

There was consensus that more research and data collection will be required to develop adequate input data for modeling alpine plant biodiversity with ForSAFE-VEG in the United States. A list of recommendations regarding experimentation was generated, as follows:

- Continue research on projects that are already underway.
- Older studies should be revisited; much can be learned from comparing historic datasets with newly collected data. In some cases, the occurrence and/or abundance of some species may already have changed in response to changes in N loading and/or climate.
- New project proposals should involve a minimum of three years of experimental treatment. Important changes are often not evident during the first one or two years.
- The dose of added N addition should generally vary between about 1 and 10 kg N/ha/yr, with a focus on a range of 1 to 5 kg N/ha/yr. Many past projects have added N in amounts that greatly exceed expected levels of atmospheric deposition at high elevation and high latitude sites in the United States. Although these projects have provided useful data, it is difficult to use the results from such studies to predict plant responses at lower, more realistic, N loadings. Therefore, studies that incorporate N loading at levels representative of the landscapes in the United States are now needed.
- When interpreting results of N addition experiments, researchers should also take into consideration the ambient deposition loading at the site.
- Experimental N addition should mimic natural N deposition to the extent possible in both timing and form.
- NPS Inventory and Monitoring (I&M) field staff should be made aware of this project and the data needs for model implementation.
- Data collection should largely focus on:
    - Soils data: C-N ratio, pH, texture, base saturation, mineral soil chemistry, total N, total digestion analysis of the mineral substrate, CEC
    - Management history (especially grazing)
    - Atmospheric deposition.

The workshop group judged that it is not practical to quantify the effects of N unless consideration is given to climate change. The most important aspects of climate to be considered are:

- Long term changes in temperature, but with attention paid to the following aspects:
    - Beginning/end of snow season, which can be derived from soil temperature data.
    - Temperature: minimum, maximum, and average daily temperature during the growing season; PRISM may help with this.
    - Maximum snow depth; lacking this information, the relative change in snow depth at one location can be suitable even if it may not be the maximum snow depth for the site.
- Changes in available moisture. Soil moisture can be measured, but can also be modeled using soil texture.

The workshop participants believed that it was possible now to make a first cut at classifying alpine plant species in the United States, based on their response to N and climate. This was done to a first approximation as part of the workshop. Additional work is needed. Workshop participants judged that, after identifying data gaps, it would possible to develop a more robust classification scheme after an estimated three years of data collection. European data regarding N response is helpful since many of the alpine plants found in Europe are also found in the United States. The European data will also be helpful in the model validation process.

Historic land management is an important component of ForSAFE-VEG model function. Grazing intensities will need to be measured or estimated for modeled sites, along with other historical land use data.

Niwot Ridge, CO has been the most intensively studied site in the United States in terms of alpine plant response to N addition. More data are needed at other U.S. alpine sites, including at research sites in the Sierra Nevada, Cascade Mountains, and Northern Alaska. The NPS networks should be made aware of the data needs and objectives of this research effort. The group recommends that Niwot Ridge could be used as an effective model test site for assessing the feasibility of estimating critical loads for nitrogen based on ground vegetation responses.

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APPENDIX A. WORKSHOP ATTENDEES

Workshop Participants
Harald Sverdrup, Lund University
Bengt Nihlgård, Lund University
Bill Bowman, University of Colorado
Linda Geiser, U.S. Forest Service
Zac German, Colorado State University
Regina Rochefort, National Park Service, North Cascades National Park
Isabel Ashton, National Park Service
Katie Becklin, University of Missouri
Todd McDonnell, E&S
Tim Sullivan, E&S
Amy Miller, National Park Service, Southwest Alaska Network
Ellen Porter, National Park Service, Air Resources Division

Phone Participants
Jeff Welker, University of Alaska, Anchorage
Elizabeth Waddell, National Park Service, Pacific West Region
Pamela Padgett, U.S. Forest Service

Technical Assistant
Carl Axel Sverdrup, Natural Science Programme, Lund Katedralskola, Lund, Sweden

APPENDIX B. AGENDA

Alpine Vegetation Workshop: Response of Alpine and Subalpine Plant Species to Changes in Atmospheric N Deposition

Sponsored by National Park Service and U.S. Environmental Protection Agency

National Park Service
Room 440, Academy Place
7333 W. Jefferson Avenue, Lakewood, CO

Thursday, November 6, 2008

9:00 Welcome – Ellen Porter, on behalf of NPS and EPA
9:15 Description of workshop objectives – Tim Sullivan
9:30 Outline of ForSAFE-VEG and description of ongoing efforts in Europe – Harald Sverdrup
10:00 Break
10:30 Alpine plants in ForSAFE-VEG – Bengt Nihlgård
11:00 Variation in N uptake traits among co-occurring alpine species: implications for community-level change - Amy Miller
11.20 Mycorrhizal associations: Connecting belowground processes with aboveground biodiversity - Katie Becklin
11.40 Developing lichen-based critical loads for nitrogen deposition in western North America - Linda Geiser
12:00 Break for lunch
13:00 N loading to Arctic and alpine plant communities in Alaska: Comparison to other Arctic locations and variation across plant communities, elevation, and geographic location - Jeff Welker (via speaker phone)
13:20 Responses and feedbacks of alpine plants to atmospheric N deposition - Bill Bowman
14.00 Plant and community responses to climate warming, nitrogen deposition, and herbivory in subalpine meadow communities - Zac German
14:20 The effect of warming and nitrogen on the composition of the alpine tundra in Niwot Ridge, CO – Isabel Ashton
14.40 Break
15:00 Setting parameters combining quantitative and qualitative data and expert judgment - Harald Sverdrup
15.10 Workshop sweat session I:
Building the American list: the European plant list; what can be transferred to the North American list - Introduction by Harald Sverdrup
16:15 General discussion and preliminary classification of U.S. alpine plant species – ALL

Friday, November 7, 2008

9:00 Workshop sweat session II:
Parameterization work on the American list – Facilitated by Harald Sverdrup
11:45 Break for lunch
13:00 Workshop sweat session III:

Parameterization work on the American list and discussion – Facilitated by Harald Sverdrup
14:30 Plans for report preparation and follow-up – Tim Sullivan
15:00 Adjourn

Workshop facilitated by:
E&S Environmental Chemistry, Inc.
P.O. Box 609
Corvallis, OR 97339
(541) 758-5777
www.ESenvironmental.com

APPENDIX C – PLANT CHARACTERISTICS REQUIRED BY FORSAFE-VEG

Delay Time

The delay time (DT) is expressed in years. It reflects the time a competitor must wait until the incumbent will leave the habitat. The delay time is generally estimated as something between the average generation time and the average population age. Average population age is probably from 1/2 to 1/3 of the plant lifespan. The minimum population age is 1 yr. (Picture a population of dafodils; suddenly, geranium has now come into strength to take 10 places among the dafodils, now it does not occupy any of the space. How long must the geraniums wait on average for those 10 slots to be physically free of dafodil occupants ?)

Nitrogen Response

The N response is made up of a promoting component and a retarding component.

Promoting is done according to class. It reflects the N deposition at which growth of the species begins to be promoted. Classes are defined as follows:

1 = requires very little N (<1 kg N/ha yr),
2= requires small amounts of N (2 kg N/ha yr),
3= intermediate (4 kg N/ha yr),
4= substantial need (8 kg N/ha yr),
5= needs a lot (>12 kg N/ha yr)

For lichens, the data are based on the actual experimental response curves in kg N/ha yr. Retarding is also done according to class:

1 = retarded by little N,
2= retarded by some N,
3 = not retarded at all, or limited to less than 20% impact from excessive N supply compared with maximum growth.

The promoting function is:

$$f(N+) = a_0 * [N]^{w+} / (k_+ + [N]^{w+})$$

Higher values of a_0 increases promotion, k+ how late it kicks in, w+ sets the steepness of the curve.

The retarding function is:

$$f(N-) = k_- / (k_- + [N]^{w-})$$

Higher values of k- gives very little retarding, smaller values will have a large retarding effect, w_- sets the steepness of the curve

Soil Acidity (kph)

The limit given reflects the soil pH at which the plant growth strength declines by 20% or more in response to low pH. A proxy is to set the pH at which the plant starts to disaapear from a location; typically this would be set at 50% effect on the response curve. Using the approach described by Sverderup and Warfvinge (1993), this can be used to set the k(BC/Al) coefficient.

$$f(BC/Al) = BC/Al / (k_{BC/Al} + BC/Al)$$

Lower k values implies a high tolerance to aluminum, high values indicates high sensitivity to aluminum

$$f(pH) = 1/(1 + k_{pH} * [H^{+}])$$

Soil Moisture

Promotion in response to water availability (expressed as minimum amount [Wmin]) is done by class:

1 = tolerates very dry conditions and occasional complete drying (<0.05 m^3/m^3 soil)
2 = dry conditions (0.05-0.1 m^3/m^3 soil)
3= normal soil conditions (0.15-0.2 m^3/m^3 soil)
4 = moist conditions (0.2-0.3 m^3/m^3 soil)
5 = wet conditions (0.3-0.4 m^3/m^3 soil)

Saturation (Wtop) and maximum amount of soil water tolerated (Wmax) are done by the same classes as above.

Temperature

The temperature envelope is done by degrees centigrade (^{o}C) assessed as:

Tmin: lowest annual average temperature at which this plant can germinate;
T<u>top</u>: temperature at which further increase of temperature does not give more promotion;
Tmax: annual average temperature at which the plant no longer thrives due to excessive heat.

Light

Light response is done by class:

1= very shade tolerant (dense closed canopy)	(<100 µmole photones/m^2/s)
2 = shade tolerant (closed deciduous canopy lighting)	(300 µmole photones/m^2/s)
3 = normal open forest ground lighting	(600 µmole photones/m^2/s)
4 = light demanding	(1200 µmole photones/m^2/s)
5 = requires unimpeded straight sunlight	(3500 µmole photones/m^2/s)

Light saturation is done by minimum (Lmin) and maximum (Lmax) classes. For larger plants with dominating shapes, distinction must sometimes be made between the parameters in the seedling stage and the parameters in the grown large plant stage (cf., *Lupinus notkatensis*).

Effective Height

Effective shading height is done by meters (m). Shading reduces the light available to neighbors. It is not necessarily the same as the plant total height. Trees form a separate level above the ground vegetation. Tree seedlings are expressed as having a standard height of 0.25 m, and treated as ground vegetation for the first 3 years.

Rooting Depth

Roots are done by rooting depth classes:

0 = no roots, roots in air
1 = shallow roots (0-0.1 m)
2 = intermediate roots (0-0.3 m)
3 = deep roots (>0.4 m)

Phosphorus Response

Phosphorus response (kP) is done by class:

1 = requires very little phosphorus,
2 = normal demand,
3 = needs a lot for growth

Browsing Preference

Browsing preference (kG) is done by food palatability classification:

32 = Highly desirable food
9 = Good; generally browsed on
2.3 = Acceptable
0.7 = Avoided, but will be consumed when other food resources are scarce
0 = Inedible or toxic; never eaten

The model browsing input unit is expressed as international moose units (IMU); 1 IMU is equal to 4 deer, 6 sheep, or 24 hares. Browsing depends on ungulate density multiplied by a browsing preference function; the output reflects the fraction of the available biomass of each plant eaten.

Wind Effects

Wind resistance (wind) is a mechanical factor that relates to whether the plant is mechanically affected by wind or not (flag tatter effect). The classes used are:

0 = no wind effect,
0.5 = wind resistant,
1 = wind sensitive
2 = wind intolerant

The wind chill effect is treated separately as a part of shifting the local ambient temperature at the plant site.

APPENDIX D
PRELIMINARY CLASSIFICATION OF U.S. ALPINE AND SUBALPINE PLANTS[1]

The spreadsheet in this appendix lists plant species known to occur in the alpine and/or subalpine environment in the United States for which adequate data were available to set preliminary parameter values for applying the ForSAFE-VEG model. Parameter values were based on European studies on those species found in both Europe and the United States, and based on data and knowledge of the workshop participants. Appendix C gives descriptions of the variables included in this spreadsheet.

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[1] Preliminary classifications based on data developed in Europe for species that are common to both Europe and North America, and on data and insights provided by workshop participants.

		Delay Time	Nitrogen Response					Soil Acidity			Soil Moisture			Temperature			Light		Effective Height	Rooting Depth	Phosphorus Response	Browsing Preference	Wind Effects
Growth Form	**Latin name**	**years**	**a0**	**k+**	**w+**	**k-**	**w-**	**kbc/al**	**kbc**	**kph**	**Wmin**	**Wtop**	**Wmax**	**Tmin**	**Ttop**	**Tmax**	**Lmin**	**Lmax**	**h(m)**	**z**	**kP**	**kG**	**Wind**
Lichens Epiphytic	Latharia vulpina	15	1	0.05	1	5	2	0.1	0	1500	0.05	0.2	0.4	-2.5	5.5	13.5	1200	2000		0	1	0	2
Lichens Epiphytic	Xanthoria polycarpa	0.5	1	5	1	1000	0	50	0	750000	0.05	0.2	0.4	-2.5	5.5	13.5	600	2000		0	1	0	1
Lichens Epiphytic	Alectoria sarmentosa	15	1	0.05	1	10	2	1	0	15000	0.17	0.25	0.4	-2.5	5.5	13.5	1200	2000		0	1	0	2
Lichens Epiphytic	Hypogymnia Imshaugii	15	1	0.05	1	10	2	0.1	0	1500	0.05	0.15	0.4	-2.5	5.5	13.5	600	1200		0	1	0	1
Lichens Ground	Cladonia chlorophea	15	1	0.1	1	0.1	2	0.05	0	900	0.1	0.3	0.4	-2.5	5.5	13.5	600	2000	0.05	1	1	0	1
Lichens Ground	Sphaerophorus globosis	15	1	0.005	1	0.005	3	0.1	0	1500	0.3	0.3	0.4	-2.5	5.5	13.5	300	1200	0.05	1	1	0	1
Lichens Ground	Parmelia saxatilis	15	1	0.3	1	10	2	0.1	0	1500	0.1	0.3	0.4	-2.5	5.5	13.5	300	2000	0.01	1	1	0	1
Lichens Ground	Cladonia bellidiflora	15	1	0.01	1	0.05	2	0.07	0	1050	0.01	0.3	0.4	-2.5	5.5	13.5	600	2000	0.05	1	1	0	1
Lichens Ground	Cladonia norwegicus	20	1	0.01	1	0.003	3	0.07	0	1050	-0.2	0.05	0.25	-2.5	5.5	13.5	500	2500	0.05	0	0.1	0.7	1
Mosses	Hylocomium mosses	20	1	0.03	1	1000	0	0.07	150000	1050	0.05	0.15	0.35	-1	7	15	100	2500	0.02	0	3	0	0
Mosses	Dicranum fuscescens								0											0			
Mosses	Aulacomnium palustre								0											0			
Mosses	Calliergon sarmentosum								0											0			
Mosses	Ceratodon purpureus								0											0			
Mosses	Racomitrium mosses	30	1	0.1	1	1000	0	0.07	150000	1050	0.2	0.5	0.35	-2	5	13.5	175	700	0.05	0	0	0	0
Mosses	Mnium mosses	20	1	0.3	2	1000	0	0.4	0	6000	0.15	0.25	0.6	0	8	16	50	2500	0.02	0	3	0	0
Mosses	Polytrichum juniperinum	20	1	0.03	1	0.1	1	0.6	0	90000	-0.10	0.15	0.50	0	8	15	100	2500	0.03	0	2	0.0	0
Mosses	Sphagnum mosses	20	1	0.03	1	0.1	3	0.01	150000	150	0.40	0.60	1.00	-1	7	15	100	2500	0.02	0	1	0.0	0
Ericaccous Shrubs	Arctostaphylos alpina	15	1	0.01	1	0.1	2	50	0	750000	0.05	0.25	0.40	-1.6	2.3	8	300	1200	0.10	1	1	0.7	0.5
Ericaccous Shrubs	Ledum palustre	10	1	0.03	1	0.5	2	100	150000	1500000	0.10	0.25	0.40	-1.6	4	12	300	1200	0.20	2	1	0.0	0.5
Ericaccous Shrubs	Empetrum nigrum	15	1.6	0.03	1	0.003	3	0.2	0	3000	-0.2	0.1	0.4	-1.5	6.5	14	500	5000	0.1	1	1	0	0.5
Ericaccous Shrubs	Vaccinium myrtillus	10	1.6	0.1	1	0.1	3	0.1	0	1500	-0.1	0.15	0.5	-1.5	5	11	100	2000	0.3	1	1	2.3	0.5
Ericaccous Shrubs	Vaccinium vitis-idea	15	1.6	0.03	1	0.003	3	0.35	0	5250	-0.2	0.1	0.45	-1.5	4.5	10.5	500	4000	0.15	1	1	0.7	0.5
Ericaccous Shrubs	Myrica gale	10	1	1	2	1000	0	0.8	0	12000	0.25	0.35	0.6	3	7	18	1500	4000	0.6	2	1	0.67	0.5
Ericaccous Shrubs	Rhododendron sp	10	1	0.03	2	1000	0	0.2	150000	3000	0.25	0.35	0.50	-1	5	9	1000	3500	0.50	2	1	0.0	0.5
Ericaccous Shrubs	Rubus idaeus	5	1	1	2	1000	0	1	0	15000	0.15	0.25	0.4	2	10	18	1500	5000	0.8	2	3	9	1
Ericaccous Shrubs	Salix lanata	30	1	0.5	1	0.1	3	1	0	9000	0.15	0.35	0.6	-2	2	6	1000	4000	1.2	3	1	2.3	0.5
Ericaccous Shrubs	Salix_phylicifolia	50	1	0.5	2	1000	0	0.1	0	1500	0.2	0.5	0.9	2	10	18	150	800	1	2	1	9	0.5
Ericaccous Shrubs	Vaccinium uliginosum	10	1	0.02	1	0.1	2	0.15	0	2000	0.1	0.25	0.6	-1.6	6.8	15	600	1200	0.25	1		2.3	0.5
Ericaccous Shrubs	Phyllodoce empetriformes	15	1								0.1	0.25	0.4				600	3500	0.2	1		2.3	0.5
Ericaccous Shrubs	Phyllodoce glanduliflora	15	1								0.1	0.25	0.4				600	1200	0.2	1		2.3	0.5
Ericaccous Shrubs	Cassiope mertensiana	15	1								0.1	0.25	0.4				600	1200	0.2	1		2.3	
Sedges	Carex bigelowii	5	1	0.03	1	1000	0	0.45	150000	60000	0.1	0.25	0.3	-1.6	3.5	7	600	1200	0.1	2	1	0.7	1
Sedges	Carex rupestris	5	1	0.03	1	1000	0	50	0	750000	0.05	0.15	0.2	-1.6	3.5	7	600	1200	0.07	1	1	0.7	0.5
Sedges	Carex scopulorum	5	1	0.01	1	1000	0	100	75000	1500000	0.25	0.3	0.4	2.9	9.6	12	600	1200	0.1	2	3	32	1
Sedges	Carex nigricans	5	1											-1.6	3.5	7			0.1				
Sedges	Carex spectabilis	5	1											-1.6	3.5	7			0.2				
Sedges	Carex breweri	5	1											-1.6	3.5	7			0.1				
Sedges	Carex engelmanni	5	1											-1.6	3.5	7			0.1				
Sedges	Eriophorum angustifolium	5	1	0.01	1	1000	0	0.04	150000	250	0.1	0.25	0.4	-1.6	3.5	7	600	1200	0.6	2	2	0.7	1
Sedges	Eriophorum scheuchzeri	5	1	0.03	1	2000	1	60	0	900000	0.05	0.2	0.3	-1.6	3.5	7	600	1200	0.6	2	2	0.7	1
Sedges	Eriophorum vaginatum	10	1	0.01	1	1000	0	0.1	75000	1200	0.25	0.3	0.5	-1.6	3.5	7	600	1200	0.6	2	2	0.7	1
Sedges	Kobresia myosuroides	10	1	0.01	1	0.1	2	50		750000	0.05	0.1	0.2	-1.6	3.5	7	1200	3500	0.1	1	1	0.7	0.5
Sedges	Luzula spicata	3	1	0.01	1	1000	0	0.3	30000	3000	0.05	0.2	0.3	-1.6	3.5	7	1200	3500	0.1	1	1	0.7	0.5
Sedges	Juncus parryi	3	1	0.2	1	1	2	5	150000	75000	0.25	0.4	0.3	-1.6	3.5	7			0.1	2			0.5
Sedges	Juncus drummondii	3	1	0.15	1	1	2	10	75000	150000	0.25	0.4	0.4	-1.6	3.5	7			0.2	2			0.5

		Delay Time	Nitrogen Response					Soil Acidity			Soil Moisture			Temperature			Light		Effective Height	Rooting Depth	Phosphorus Response	Browsing Preference	Wind Effects
Growth Form	**Latin name**	**years**	**a0**	**k+**	**w+**	**k-**	**w-**	**kbc/al**	**kbc**	**kph**	**Wmin**	**Wtop**	**Wmax**	**Tmin**	**Ttop**	**Tmax**	**Lmin**	**Lmax**	**h(m)**	**z**	**kP**	**kG**	**Wind**
Sedges	Carex vaginata	7	1	0.1	1	1000	0	0.3	0	3000	0.1	0.4	0.7	1	9	17	10	500	0.3	3	1	9	0.5
Grasses	Poa alpina	2	1	0.1	1	1000	0	20	150000	300000	0.1	0.2	0.3	-1.6	7	15	600	1200	0.15	2	1		1
Grasses	Poa arctica	2	1	0.1	1	1000	0	20	0	300000	0.1	0.2	0.3	-1.6	7	15	600	1200	0.15	2	3		1
Grasses	Calamagrostis canadensis	3	1	0.1	1	1000	0	0.3	150000	3000	0.2	0.3	0.4	-1.6	7	15	300	1200	1.5	2	3	2.00	1
Grasses	Trisetum spicatum	4	1	0.03	1	1000	0	0.6	150000	6000	0.1	0.25	0.35	-1.6	7	15	600	1200	0.15	1.5	1	0	1
Grasses	Festuca brachyphylla	2	1	0.03	1	1000	0	0.7	0	7500	0.1	0.2	0.3	-1.6	7	15	600	1200	0.07	1	3	2.3	1
Grasses	Alopecurus pratensis	5	1	20	2	1000	0	1.2	0	7500	0.2	0.15	0.8	5	13	20	200	1000	0.5	2	1	2.3	1
Grasses	Agrostis capillaris	10	1	0.5	2	1000	0	0.2	0	3000	0.05	0.15	0.5	3	11	19	750	4000	0.25	2	3	2.3	1
Grasses	Deschampsia caespitosa	5	1	0.5	2	1000	0	0.2	0	3000	0.15	0.35	0.6	3	11	19	1000	5000	0.35	2	3	0	1
Grasses	Festuca vivipara	10	1.4	0.02	2	10	1	0.1	0	1500	-0.1	0.2	0.6	3	11	19	200	1000	0.1	1	30	9	1
Grasses	Festuca ovina	10	1.4	0.02	2	10	1	0.1	0	1500	-0.25	0.05	0.25	3	11	19	1500	5000	0.1	1	30	0.67	1
Grasses	Lolium perenne	5	1	20	2	1000	0	2	0	30000	0.1	0.4	0.6	5	13	21	200	1100	0.5	2	3	9	1
Grasses	Stipa	10	1	0.5	2	1000	0	50	0	75000	-0.2	0.1	0.4	3	19	35	300	1200	0.8	3	1	0.67	1
Grasses	Poa pratensis	5	1	20	2	1000	0	50	0	75000	0.1	0.4	0.5	4	12	25	250	1000	0.5	3	10	9	1
Grasses	Poa glauca	5	1	10	2	1000	0	10	0	150000	0.1	0.4	0.5	1	9	17	250	1000	0.4	3	3	9	1
Grasses	Poa nemoralis	5	1	5	2	1000	0	8	0	120000	0.05	0.1	0.2	2	10	20	1250	5000	0.4	2	3	9	1
Fern allies	Selaginella densa																						
Ferns	Lycopodium annotinum	5	1	0.01	2	0.003	1	0.6	0	9000	0.15	0.35	0.60	-1	7	15	150	2500	0.15	1	1	0.0	0.5
Ferns	Blechnum spicant	20	1	0.05	2	3	1	0.6	0	9000	0.15	0.35	0.50	3	11	19	100	2000	0.15	1	1	0.0	0.5
Ferns	Athyrium filix-femina	20	1	0.05	2	5	1	1	0	20800	0.15	0.35	0.50	-1	7	15	150	2500	0.40	2	1	0.0	0.5
Ferns	Dryopteris austriaca	20	1	0.5	2	1000	0	2	0	30000	0.1	0.3	0.5	3	11	19	150	2500	0.4	2	1	2.3	1
Ferns	Pteridium aquilinum	20	1	0.5	2	1000	0	12	0	180000	0.05	0.2	0.3	2	8	18	750	3250	0.5	2	1	0	0.5
Forbs and herbs	Mertensia lanceolata	3		0.1	2	10	1	0.3	0	3000	0.1	0.2	0.5				300	1200	0.2	2	30	9	1.5
Forbs and herbs	Geum rossii	5		0.03	2	0.05	1	0.4	75000	5000	0.1	0.2	0.4	-1.6	6	12	300	1200	0.1	1	1	2.3	1
Forbs and herbs	Trifolium dasyphyllum	5		200	0	0.3	1	0.3	0	3000	0.1	0.2	0.25				450	1200	0.05	1	30	9	0.5
Forbs and herbs	Antennaria alpina	10		0.01	2	1000	0				0.1	0.2	0.3				600	1200	0.1	2	3	2.3	0.5
Forbs and herbs	Arenaria fendleri	3		0.01	2	10	1				0.05	0.2	0.3				600	1200	0.1	2	1	2.3	0.5
Forbs and herbs	Artemesia scopulorum	6		0.1	2	10	1				0.1	0.4	0.4				300	1200	0.1	2	3	2.3	0.5
Forbs and herbs	Bistorta bistortoides	5		0.1	2	10	1				0.1	0.4	0.5				600	1200	0.15	2	1	9	1
Forbs and herbs	Bistorta vivipara	10		0.1	2	10	1				0.1	0.4	0.4				300	1200	0.1	2	3	2.3	1
Forbs and herbs	Campanula rotundifolia	2		0.5	2	10	1	0.2	150000	1500	0.1	0.3	0.4	4	10	14	300	1200	0.1	2	3	2.3	1.5
Forbs and herbs	Castilleja occidentalis	10		0.1	2	0.1	1				0.1	0.3	0.3				600	3500	0.2	1	3	2.3	1
Forbs and herbs	Cerastium arvense	3		0.1	2	10	1				0.2	0.3	0.3	5.1	12.1	16	600	1200	0.1	2	3	2.3	0.5
Forbs and herbs	Erigeron simplex	10		0.1	2	10	1				0.2	0.3	0.3				600	1200	0.15	2		2.3	0.5
Forbs and herbs	Lewisia pygmaea	4		0.1	2	10	1				0.1	0.3	0.35	2.9	8	12	300	1200	0.05	2		2.3	0.5
Forbs and herbs	Lloydia serotina	4		0.1	2	0.3	1	300	0	3000000	0.1	0.3	0.35				600	1200	0.1	2	1	2.3	0.5
Forbs and herbs	Minuartia obtusiloba	6		0.1	2	10	1				0.05	0.2	0.35				600	1200	0.05	1	30	2.3	0.5
Forbs and herbs	Potentilla diversifolia	3		0.5	2	10	1	500	150000	7500000	0.1	0.3	0.35	-1	5.1	9	300	1200	0.1	2	3	2.3	0.5
Forbs and herbs	Sedum lanceolatum	10		0.01	2	0.1	1				0.05	0.2	0.35	-1	5.1	9	600	1200	0.1	1	3	2.3	0.5
Forbs and herbs	Silene acaulis	15		0.1	2	0.3	1	0.35	150000	5000	0.05	0.2	0.4	-1.6	4	8	600	3500	0.05	1	30	2.3	0.5
Forbs and herbs	Trifolium parryi	4		200	0	0.1	1	1.3	1.3	19500	0.1	0.3	0.35	5	15	25	300	1200	0.05	1	30	9	0.5
Forbs and herbs	Caltha leptosepala	1		0.01	2	10	1	100	150000	1500000	0.2	0.3	0.3	-1.6	5.1	10	600	1200	0.1	2	30	2.3	0.5
Forbs and herbs	Oreostemma alpigenum	5									0.2	0.3	0.35									9	1
Forbs and herbs	Aconitum lycotonum	2	1	1	2	1000		0.5	0	7500	0.25	0.55	0.9	2	6	10	1000	5000	0.3	3	1	0	1
Forbs and herbs	Allium ursinium	1	1	1	2	1000		2	0	30000	0.25	0.2	0.6	4	12	20	250	5000	0.2	2	30	9	1
Forbs and herbs	Anemone nemorosa	4	1	1	2	1000		0.5	0	7500	0.2	0.3	0.4	2	10	18	250	1500	0.1	1	3	0.7	1

		Delay Time	Nitrogen Response					Soil Acidity			Soil Moisture			Temperature			Light		Effective Height	Rooting Depth	Phosphorus Response	Browsing Preference	Wind Effects
Growth Form	**Latin name**	**years**	**a0**	**k+**	**w+**	**k-**	**w-**	**kbc/al**	**kbc**	**kph**	**Wmin**	**Wtop**	**Wmax**	**Tmin**	**Ttop**	**Tmax**	**Lmin**	**Lmax**	**h(m)**	**z**	**kP**	**kG**	**Wind**
Forbs and herbs	Antennaria diocia	5	1	0.01	2	1000	0	0.1	0	1500	0.05	0.1	0.2	0	6	12	2000	5500	0.01	1	1	0	0.5
Forbs and herbs	Arnica montana	8	1	1	2	1000	0	0.7	0	1000	0.1	0.25	0.3	3	10	12	1500	3000	0.2	1	1	9	1
Forbs and herbs	Epilobium augustifolium	5	1	1	2	1000	0	2	0	30000	0.15	0.2	0.3	0	8	20	1750	5500	0.8	2	3	32	2
Forbs and herbs	Geranium robertianum	3	1	1	2	1000	0	6	0	90000	0.15	0.25	0.40	-1	7	16	500	3000	0.15	1	2	9.0	1
Forbs and herbs	Galium bifolium	3	1	5	2	1000	0	1.2	0	18000	0.2	0.5	0.7	3	11	19	50	1000	0.15	1	1	0.7	2
Forbs and herbs	Luzula luzuloides	5	1	0.03	2	0.1	1	0.3	0	3000	0.10	0.25	0.40	0	8	16	375	3000	0.2	1	1	0.7	1
Forbs and herbs	Equisetum hyemale	15	1	0.05	2	3	1	12	0	200000	0.20	0.25	0.60	0	8	16	375	3000	0.30	2	1	0.0	2
Forbs and herbs	Equisetum sylvaticum	15	1	0.05	2	3	1	0.3	0	3000	0.20	0.40	0.60	2	10	18	375	3000	0.30	2	1	0.7	1
Forbs and herbs	Circaea alpina	5	1	1	2	10	1	12	0	200000	0.15	0.25	0.50	3	11	19	500	3000	0.20	1.5	1	0.7	1
Forbs and herbs	Ranunculus	5	1	0.1	2	10	1	6	0	90000	0.15	0.25	0.30	-1	4	7	1250	300	0.20	0	2	0.7	0.5
Forbs and herbs	Dryas octopetala	30	1	0.1	1	1000	0	2	0	30000	0.05	0.25	0.6	-1.5	6.5	18	250	1000	0.07	3	0	0.7	0.5
Forbs and herbs	Equisetum pratense	10	1	0.5	2	1000	0	0.5	0	7500	0.1	0.35	0.6	0	8	16	10	500	0.2	3	1	0.67	1
Forbs and herbs	Trientalis europaea	2	1	0.5	2	10	1	0.2	0	3000	0.1	0.2	0.4	2	10	18	250	3000	0.15	1	1	0.67	1
Forbs and herbs	Trifolium repens	5	1	1	0	1000	0	1.3	0	19500	0.2	0.35	0.4	5	15	25	1250	5500	0.3	2	1	32	2
Forbs and herbs	Lupinus nootkatensis seedlings	1	1	0.1	1	1000	0	6	0	90000	0.05	0.15	0.4	0	6	12	250	1500	0.2	2	3	9	2
Forbs and herbs	Lupinus nootkatensis	20	1	1	0	1000	0	6	0	90000	0.1	0.25	0.4	0	6	12	250	1500	0.8	2	3	2.3	0.5
Forbs and herbs	Urtica dioica	5	1	5	2	1000	0	10	0	150000	0.15	0.25	0.45	2	10	20	500	5000	0.8	1	3	0	2
Trees and bushes	Alnus incana	30	1	0	0	1000	0	6	0	90000	0.20	0.30	1.00	0	8	16	500	3500	0.10	3	1	0.7	1
Trees and bushes	Alnus viridis	30	1	0	0	1000	0	1.2	0	12000	0.20	0.30	1.00	-1	7	17	1200	5000	0.10	3	1	0.7	1
Trees and bushes	Larix lyallii	60	1	0.05	2	3	1	0.6	0	9000	0.15	0.25	0.50	-1	7	15	800	2700	0.10	3	1	9.0	1
Trees and bushes	Picea engelmannii	60	1	0.01	2	3	1	0.32	0	4500	0.15	0.25	0.50	-1	7	15	400	1700	0.10	3	1	0.7	1
Trees and bushes	Pinus albicaulis	80	1	0.01	2	0.1	1	0.32	0	4500	0.15	0.25	0.50	4	12	20	1000	2600	0.10	3	1	0.7	1
Trees and bushes	Populus tremuloides	40	1	0.01	2	3	1	0.6	0	9000	0.10	0.20	0.50	3	11	19	1200	3500	0.10	3	1	9.0	1
Trees and bushes	Prunus pensylvanica	20	1	0.05	2	3	1	0.25	0	3500	0.15	0.25	0.50				600	2600	0.10	3	2	32.0	1
Trees and bushes	Sambucus racemosa	8	1	0.5	2	1000	0	0.4	0	6000	0.15	0.25	0.50	5	13	21	1200	5000	0.10	2	3	32.0	1
Trees and bushes	Sorbus sitchensis	20	1	0.05	2	0.1	1	0.6	0	90000	0.15	0.25	0.50	4	12	20	800	4000	0.10	3	3	9.0	1
Trees and bushes	Sorbus aurucaria	20	1	0.1	2	1	1	0.24	0	3400	0.15	0.25	0.40	-1	7	12	900	1200	0.40	3	2	9.0	1
Trees and bushes	Betula nana	7	1	0.01	2	3	1	0.6	75000	9000	0.2	0.35	0.5	-1.9	2.4	8	600	1200	0.6	3	3	0.7	1
Trees and bushes	Salix glauca	30	1	0.1	2	3	1	100	150000	1500000	0.1	0.2	0.4	-1.6	16.2	22	600	1200	0.65	2	3	32	1
Trees and bushes	Picea engelmannii	15	1	0.05	2	1	1	0.15	0	1800	0.1	0.2	0.4	0.5	9	14	600	1200	0.25	1	3	0	1
Trees and bushes	Picea glauca	15	1	0.05	2	3	1	0.2	150000	1500	0.1	0.2	0.4	0.7	9	15	600	1200	0.25	1	3	0	2
Trees and bushes	Tsuga mertensiana	15	1	0.1	2	3	1	0.25	0	3500	0.2	0.35	0.45	2.9	9.6	16	450	1000	0.25	2	30	0.7	2
Trees and bushes	Abies lasiocarpa	15	1			3	1	0.35	0	5000							600	1200	0.25	2	3	2.3	2
Trees and bushes	Pinus albicaulis	15	1			3	1	0.35	0	5000							600	1200	0.25	3	3	2.3	2