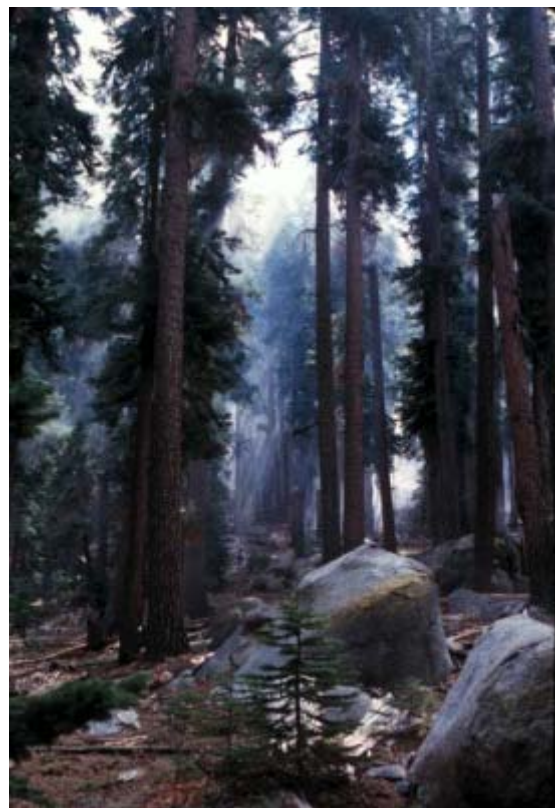


## Why do tree death rates decrease with elevation in the Sierra Nevada?



Because of the great spatial and temporal scales involved, most climatic change research relies on computer models to project possible changes in forest structure, composition, and dynamics. However, another approach is possible: analysis of forest characteristics along natural climatic gradients. Here we examine elevational gradients in the Sierra Nevada, California, and determine whether tree death rates are driven by elevational changes in (1) forest structure, (2) composition, or (3) causes of death.

### Permanent study plots

Permanent study plots were established in the coniferous forest belts of Sequoia National Park and Yosemite National Park. The study plots ranged in elevation from lower treeline (1500 m) to upper treeline (3100 m) and ranged in size from 0.9- to 2.5 hectares. Plot locations were selected to be representative of major forest types along the elevational gradient -- namely, the ponderosa pine-mixed conifer, white fir-mixed conifer, Jeffrey pine, red fir, and western white pine forest types.

In each plot, trees greater than or equal to 1.4 m in height were tagged, mapped, measured for diameter, and identified by species. Every five years the tagged trees were checked for mortality, diameters were re-measured, and new trees (reaching 1.4 m height) were incorporated. For each tree that died, we attempted to determine the possible causes of death. Overall, we have monitored more than 18,000 trees and have recorded 1,813 tree deaths.

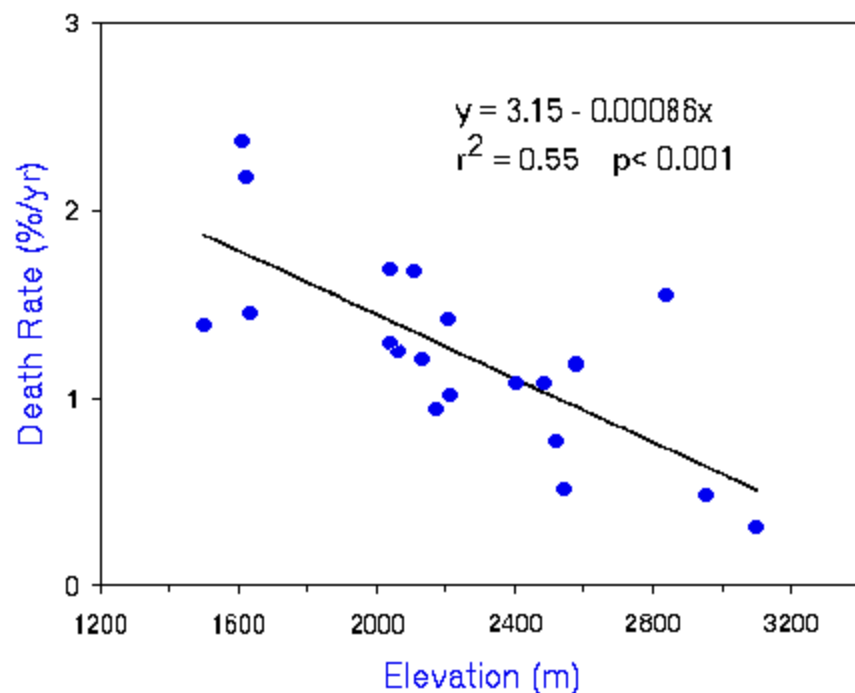
Plot Name	Elevation (m)	Size (ha)	Annual Mortality Checks	Average Annual Tree Density (#/ha)	Species Comprising $\geq 5\%$ of Stand Individuals
YOHO*	1500	1.000	1992-1997	2999	white fir (35%), incense cedar (32%), white pine (26%), ponderosa pine (5%)
BBB	1609	1.000	1993-1997	1213	incense cedar (54%), black oak (24%), white fir (12%), white pine (5%)
CCR	1622	1.125	1992-1997	1891	white fir (46%), incense cedar (30%), black oak (15%), white pine (5%)

CRCR*	1637	1.000	1994-1997	1753	white fir (44%), incense cedar (29%), white pine (18%), ponderosa pine (6%)
SUCR	2033	1.375	1984-1997	749	white fir (55%), incense cedar (20%), white pine (20%)
Swhite fir	2035	0.875	1984-1997	736	white fir (60%), incense cedar (28%), white pine (9%)
Swhite pine	2059	1.125	1984-1997	689	white fir (68%), white pine (22%), incense cedar (9%)
FJeffrey pine	2106	1.000	1984-1997	188	Jeffrey pine (79%), black oak (9%), white fir (8%)
LMCC	2128	1.865	1983-1997	318	white fir (69%), red fir (22%), giant sequoia (7%)
Lgiant sequoia	2170	2.500	1984-1997	434	white fir (76%), red fir (15%), white pine (6%)
Lwhite fir	2207	1.125	1988-1997**	398	white fir (75%), red fir (22%)
Lwhite pine	2210	1.000	1988-1997**	415	white fir (89%), white pine (7%)
LJeffrey pine	2405	1.000	1986-1997**	125	white fir (58%), Jeffrey pine (40%)
SFTR*	2484	1.000	1993-1997	1605	red fir (100%)
WT	2521	1.000	1994-1997	461	red fir (99%)
POFL*	2542	1.000	1995-1997	589	red fir (94%)
PG	2576	1.000	1993-1997	751	red fir (100%)
EI	2838	1.000	1984-1997	35	PIMO (79%), lodgepole pine (21%)
ES	2950	1.000	1984-1997**	60	PIMO (79%), lodgepole pine (10%), Jeffrey pine (10%)
ER	3097	1.125	1985-1997**	87	PIMO (98%)

\* Plots in Yosemite National Park. All other plots are in Sequoia National Park.

\*\* Mortality checks were completed annually for these plots; mortality cause data were taken 1995-1997

## What are the project's results?

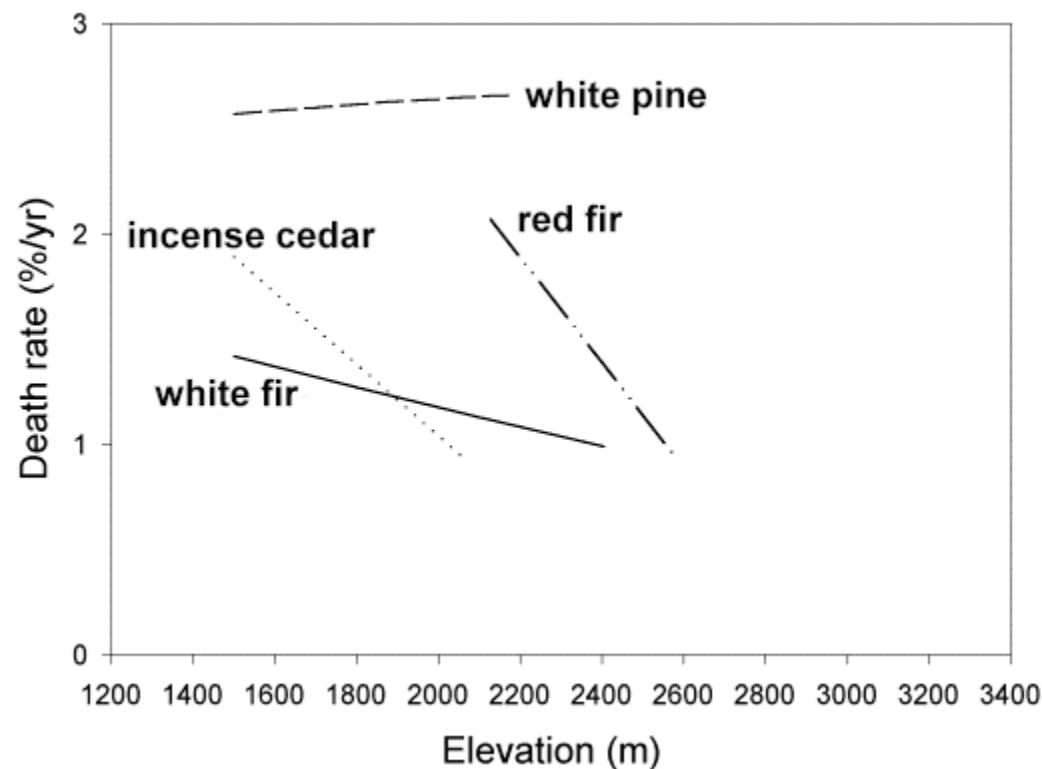


Overall tree death rate decreased significantly with elevation ( $r^2 = 0.55$ ;  $p < 0.001$ )

### Death rate relative to species composition

Linear regression techniques were used to examine elevational trends in death rates within individual species (species inclusion required 50 individuals in at least five plots). Species meeting these criteria were white fir, red fir, incense cedar, and white pine.

Death rates decreased with elevation for three of the four species examined, though none of the slopes were significant at  $p < 0.05$ . When fit with a common slope, however, death rate decreases in these three species became significant ( $p < 0.05$ ). Within two study plots white pine experienced a recent outbreak of white pine blister rust, an introduced pathogen. When outbreak years were excluded from analysis, death rates for white pine also decreased with elevation.



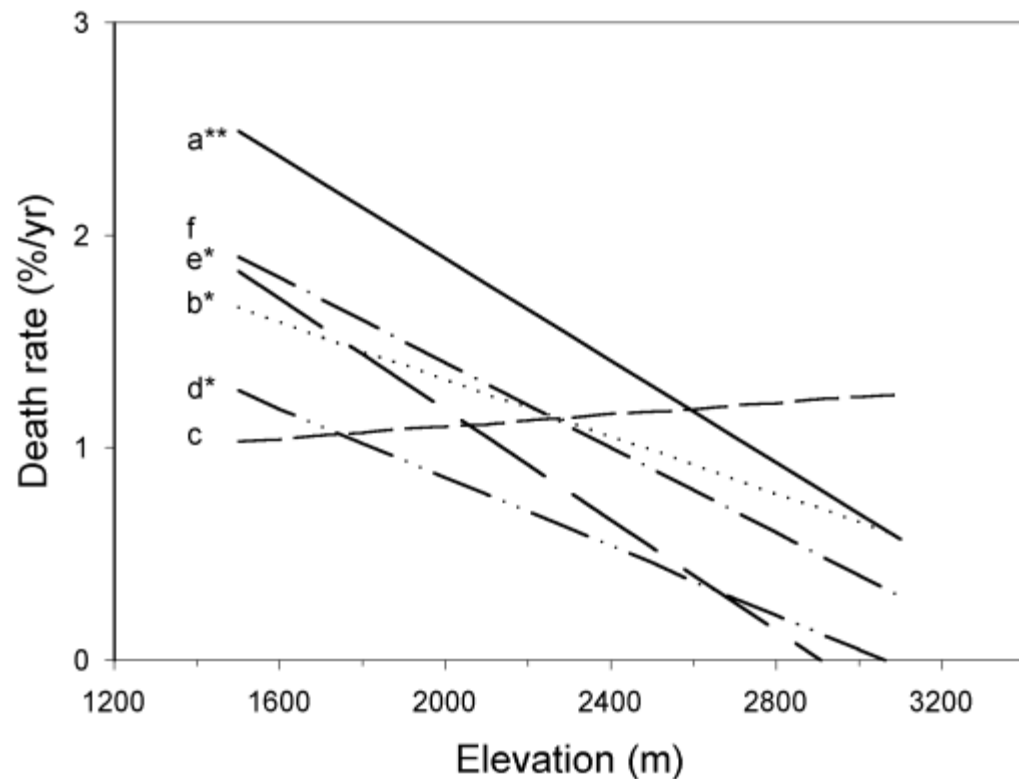
Tree death rates relative to elevation and species.

ABCO = white fir, ABMA = red fir, CADE = incense cedar, and PILA = white pine.

### Death rate relative to population size structure

Linear regression techniques were used to examine elevational trends in death rates relative to stem size (low elevation plots have proportionally more small trees, which tend to have higher death rates, than high elevation plots). Six diameter size classes of trees were established: 0-10, 10-20, 20-40, 40-60, 60-100, and >100 cm.

Death rates decreased significantly with elevation in four of six size classes ( $p < 0.01$  to  $p < 0.05$ ). One high-elevation plot had only six trees in the 20-40 cm size class, and three of these were killed in a single avalanche. When this plot is removed from analysis, death rate decreases with elevation in the 20-40 cm size class, though non-significantly.



Tree death rates relative to elevation and tree size class.

The size classes, in cm dbh, are a = 0-10, b = 10-20, c = 20-40, d = 40-60, e = 60-100, and f > or = 100.

\*  $p < 0.05$ ; \*\*  $p < 0.01$ .

### Death rate relative to stand density

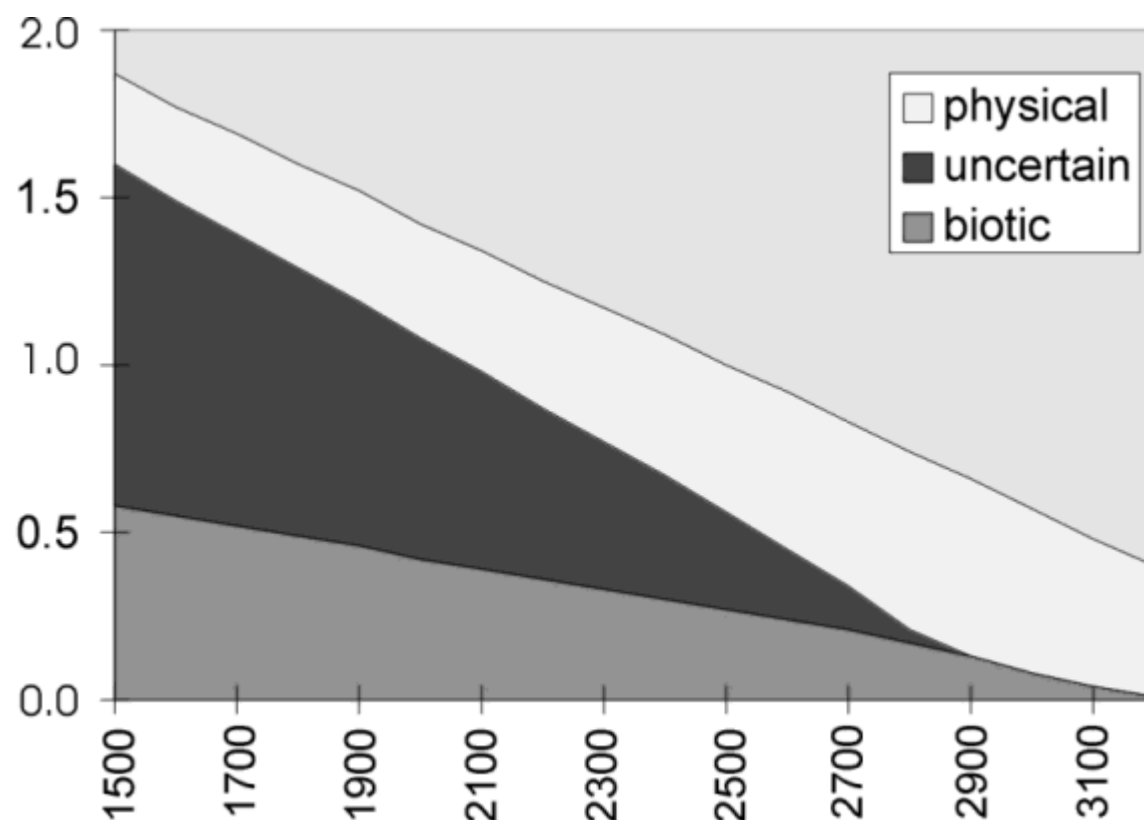
To determine whether elevational changes in stand density drive death rates (low elevation stands being more dense than high elevation stands), we compared regressions of death rate on elevation alone and on stand density alone, and performed multiple regressions using both independent variables.

Elevation and stand density were negatively correlated ( $r^2 = 0.50$ ;  $p < 0.001$ ) suggesting that declining death rate with elevation might be due to declining stand densities. However, elevation alone explains more of the variance in tree death rate ( $r^2 = 0.55$ ;  $p < 0.001$ ) than stand density alone ( $r^2 = 0.18$ ;  $p = 0.064$ ). In multiple regression analysis, elevation was the stronger correlate of death rate ( $p=0.001$  for elevation versus  $p=0.38$  for stand density).

### Death rate relative to factors associated with death

To determine whether factors associated with tree death drive changes in death rates with elevation, we regressed death rate on elevation for three broad death factor categories: physical (uprooting, breaking, or being crushed), biotic (insects and pathogens), and unknown (most likely biotic).

Death by physical factors increased slightly and non-significantly with elevation. In contrast, death associated with biotic factors decreased dramatically and significantly with elevation ( $r^2 = 0.35$ ;  $p < 0.01$ ), as did death by unknown causes ( $r^2 = 0.56$ ;  $p < 0.001$ ).



Tree death rates relative to elevation and factors associated with death.

*Physical* = tree uprooted, broken or was crushed.

*Biotic* = tree was killed by insects or pathogens.

*Uncertain* = factors are most likely biotic, but not known with certainty.

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## What are the implications for global warming?

Declines in tree death rate with elevation are independent of changes in stand structure and composition and appear to be related to biotic (insects and pathogens) and unknown (most likely biotic) factors. Death rate declines may be driven by (1) reduced insect and pathogen activity with declining temperature at higher elevations, or (2) decreased length/severity of summer drought stress at higher elevations, hence lower susceptibility of trees to biotic causes of death. If these findings hold in other forest types and regions, they suggest a potential tree death rate increase in the face of global warming.

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Photo of PI

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## **Selected Publications:**

**Fullmer, D. G., R. R. Rogers, J. D. Manley, and N. L. Stephenson.** 1996. Restoration as a component of ecosystem management for giant sequoia groves in California. Pages 109-115 in D. L. Peterson and C. V. Klimas (eds.), *The Role of Restoration in Ecosystem Management*. Society for Ecological Restoration, Madison, Wisconsin.

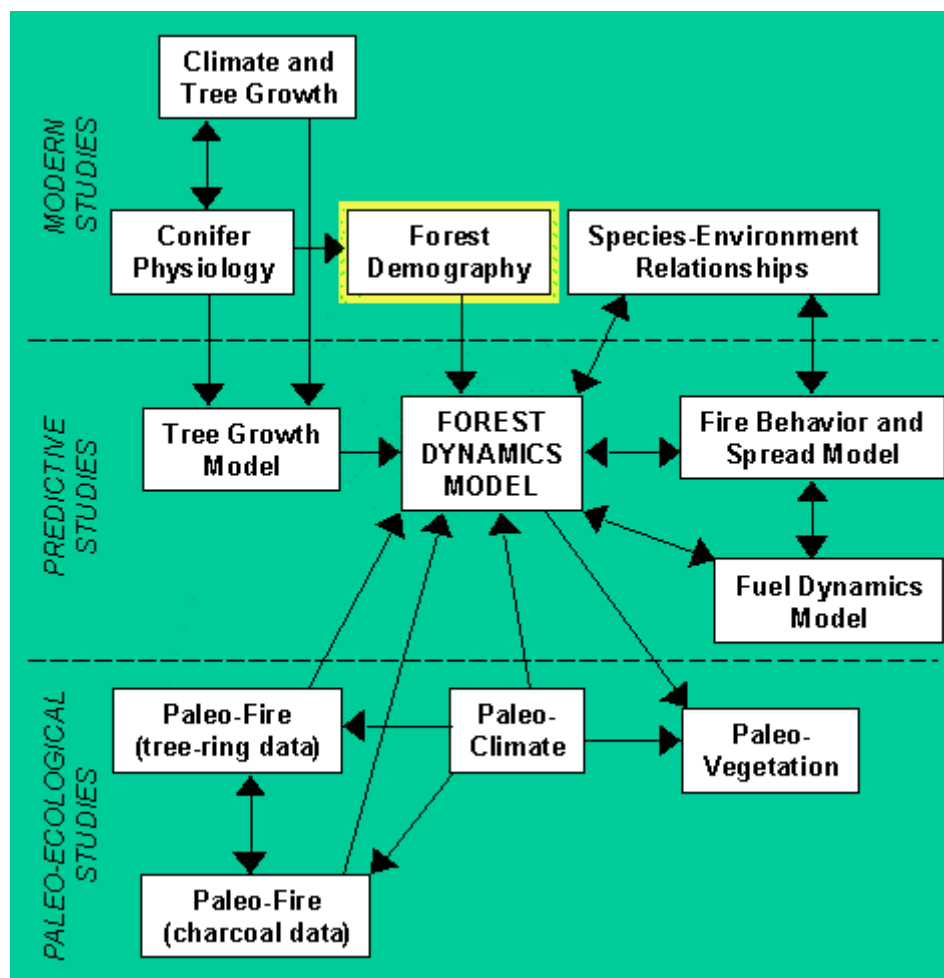
**Parsons, D. J., D. M. Graber, and N. L. Stephenson.** 1990. Planning for global climate change research -- an example from Sequoia and Kings Canyon National Parks. *The George Wright Forum* 6(4):1-9.

- Parsons, D. J., N. L. Stephenson, D. M. Graber, and A. M. Esperanza.** 1993. Understanding the effects of climatic change on the ecosystems of the Sierra Nevada. *Bull. Ecol. Soc. Am.* 74:384-385 (abstract).
- Stephenson, N. L.** 1992. What do "wet" and "dry" really mean to vegetation? *Bull. Ecol. Soc. Am.* 73(2):355-356 (abstract).
- Stephenson, N. L.** 1994. Effects of two millennia of changing climate and fire regimes on giant sequoia populations. Page 63 *in* Ecosystem Management and Restoration for the 21st Century, 21st annual Natural Areas Conference, Palm Beach Gardens, Florida (abstract).
- Stephenson, N. L.** 1994. Long-term dynamics of sequoia populations: implications for managing a pioneer species. Pages 56-63 *in* P. S. Aune, ed., Proceedings of the Conference, Giant Sequoias: Their Place in the Ecosystem and Society. USDA Forest Service Gen. Tech. Rep. PSW-GTR-151.
- Stephenson, N. L.** 1996. Ecology and management of giant sequoia groves. Pages 1431-1467 *in* Sierra Nevada Ecosystem Project: Final Report to Congress, vol. II, Assessments and Scientific Basis for Management Options. Centers for Water and Wildland Resources, University of California, Davis.
- Stephenson, N. L.** In press. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.*
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- Stephenson, N. L., and A. Demetry.** 1995. Estimating ages of giant sequoias. *Can. J. For. Res.* 25:223-233.
- Stephenson, N. L., and D. J. Parsons.** 1993. A research program to predict the effects of climatic change on the Sierra Nevada. Pages 93-109 *in* S. D. Veirs, T. J. Stohlgren, and C. Schonewald-Cox (eds.), Proceedings 4th Conference on Research in California's National Parks. Transactions and Proceedings NPS/NRUC/NRTP-93/9, USDI National Park Service, Washington, D. C.
- Stephenson, N. L., D. J. Parsons, and T. W. Swetnam.** 1991. Restoring natural fire to the sequoia - mixed conifer forest: should intense fire play a role? *Proc. Tall Timb. Fire Ecol. Conf.* 17:321-337.
- Stephenson, N. L., L. S. Mutch, A. J. Das, V. G. Pile, C. I. Dickard, and P. E. Moore.** 1998. Why do tree death rates decrease with elevation in the Sierra Nevada? Abstracts, Annual meeting of the Ecological Society of America, p. 219 (abstract).
- Stephenson, N. L., J. J. Battles, and J. S. Ansley.** In review. Effects of fire and fire exclusion on forest pattern in the Sierra Nevada,



California, USA. Submitted to Canadian Journal of Forest Research.

**Urban, D. L., C. Miller, N. L. Stephenson, and P. N. Halpin.** Submitted. Forest pattern in Sierran landscapes: the physical template. Submitted to Landscape Ecology.



[Return to Start Page](#)