Aboveground Net Primary Production and Leaf-Area Index in Early Postfire Vegetation in Yellowstone National Park
Author(s): Rebecca A. Reed, Mary Ellen Finley, William H. Romme, Monica G. Turner
Source: *Ecosystems*, Vol. 2, No. 1 (Jan. - Feb., 1999), pp. 88-94
Published by: Springer
Stable URL: http://www.jstor.org/stable/3658601
Accessed: 06/08/2011 01:18

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Springer is collaborating with JSTOR to digitize, preserve and extend access to *Ecosystems.*

http://www.jstor.org

Ecosystems (1999) 2: 88–94

ECOSYSTEMS
© 1999 Springer-Verlag

Aboveground Net Primary Production and Leaf-Area Index in Early Postfire Vegetation in Yellowstone National Park

Rebecca A. Reed,[1] Mary Ellen Finley,[2] William H. Romme,[2]* and Monica G. Turner[1]

[1]*Department of Zoology, Birge Hall, University of Wisconsin, Madison, Wisconsin 53706; and* [2]*Department of Biology, Fort Lewis College, Durango, Colorado 81301, USA*

Abstract

Aboveground net primary production (ANPP) and leaf-area index (LAI) of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex Wats.) saplings and aboveground productivity of herbaceous vegetation components were determined 9 years after the 1988 fires in Yellowstone National Park (YNP). Measurements were made in four sites representing a wide range of early postfire vegetation present in YNP, including high-density lodgepole pine, low-density lodgepole pine, and two nonforest stands. LAI of the pine saplings and total ANPP (trees plus herbs) generally increased with increasing sapling density, from 0.002 $m^2\ m^{-2}$ and 0.25 Mg $ha^{-1}\ year^{-1}$ in the infertile nonforest stand (100 pine saplings ha^{-1}) to 1.8 $m^2\ m^{-2}$ and 4.01 Mg $ha^{-1}\ year^{-1}$ in the high-density pine stand (62,800 saplings ha^{-1}). Aboveground herbaceous productivity was not strongly correlated with sapling density, but appeared to be influenced by soil fertility. In the high-density pine stand, tree ANPP and LAI were within the lower range of values reported for similar mature coniferous forests. This finding suggests that at least some ecosystem processes (related to ANPP and LAI) may have nearly recovered after only 9 years of postfire succession, in at least some of the young forests developing after the 1988 Yellowstone fires.

Key words: lodgepole pine; Yellowstone National Park; succession; fire; aboveground net primary production; leaf-area index.

Introduction

The 1988 fires in Yellowstone National Park (YNP), Wyoming, affected more than 250,000 ha, creating a striking mosaic of burn severities across the landscape that is likely to influence ecological processes for decades to come (Christensen and others 1989; Knight and Wallace 1989; Turner and others 1994). Substantial spatial heterogeneity in early postfire succession has been observed in the decade since the fires, resulting largely from spatial variation in fire severity and in the availability of lodgepole pine (*Pinus contorta* var. *latifolia*) seeds in or near the burned area (Anderson and Romme 1991; Tinker and others 1994; Turner and others 1997). Postfire vegetation now includes pine stands ranging from relatively low to extremely high pine sapling density (~ 10,000 to nearly 100,000 stems ha^{-1}) as well as nonforest or marginally forested communities (< 1000 saplings ha^{-1}) in some areas previously characterized by coniferous forest.

We are interested in how the variability and spatial pattern of early postfire successional vegetation across the Yellowstone landscape may influence ecosystem processes related to energy flow and biogeochemistry. We also are interested in how quickly these processes may return to their predistur-

Received 7 April 1998; accepted 1 December 1998.
*Corresponding author; e-mail romme_fortlewis.edu

Table 1. Characteristics of Study Sites Where Aboveground Net Primary Production and Leaf-Area Index Were Measured in 1997 in Yellowstone National Park[a]

Study Site	Elevation (m)	Substrate	Lodgepole Pine Density (Stems ha^{-1})	Sapling Height (m) in 1997: Mean	(SE)	*n*	Dominant Herbaceous and Shrub Species	UTM Coordinates and Date of Sampling
Infertile nonforest (Pitchstone)	2570	Rhyolite	100	0.62	(0.06)	10	*Epilobium angustifolium* *Carex rossii*	527050E, 4899400N 26 July 1997
Fertile Nonforest (Mt. Washburn)	2560	Andesite	1000	0.44	(0.09)	10	*Epilobium angustifolium* *Trisetum spicatum*	543400E, 4962900N 28 July 1997
Low-density pine forest (Pitchstone)	2560	Rhyolite	20,100	0.42	(0.08)	10	*Epilobium angustifolium* *Carex rossii*	527600E, 4899300N 26 July 1997
High-density pine forest (Mt. Haynes)	2070	Rhyolite	62,800	0.89	(0.12)	10	*Calamagrostis rubescens* *Spirea betulifolia*	505550E, 4943650N 30 July 1997

[a]*Each site was burned by crown fires in 1988; UTM, Universal Transverse Mercator.*

bance characteristics. In this report, we begin to address these general questions by examining the variation in aboveground net primary production (ANPP) and leaf-area index (LAI) of tree (lodgepole pine) and herbaceous components in successional stands 9 years after the fires. ANPP measures the cumulative new biomass generated over a given period and is a fundamental ecosystem property often used to compare ecosystems (Carpenter 1998). Leaf area (typically expressed as LAI, that is, leaf area per unit ground surface area) influences rates of two fundamental ecosystem processes—primary productivity and transpiration—and is commonly used in ecosystem models [for example, Forest-BGC (Running and Coughlan 1988) and FIRE-BGC (Keane and others 1996)]. Disturbances cause reductions in leaf area that cause simultaneous reductions in transpiration and photosynthesis and increases in stream flow (Helvey and others 1976; Gholz and others 1985; Davis 1987, 1993; Keane and others 1996).

This study had three specific objectives. The first was to address two hypotheses: (a) that total ANPP would primarily reflect variation in tree sapling density, increasing as sapling density increased from nonforest to high-density pine stands; and (b) that herbaceous ANPP would be inversely related to tree ANPP across all sites because of competition between tree saplings and herbaceous plants. Our second objective was to quantify differences in tree LAI across a range of sapling densities. Thirdly, we compared our measured ANPP and LAI with values in the literature to determine how close these 9-year-old postfire stands in YNP have come to developing ANPP and LAI characteristic of mature coniferous forests.

Study Area and Methods

Yellowstone encompasses 9000 km^2 in the northwest corner of Wyoming and is primarily a high, forested plateau. The 1988 Yellowstone fires affected about 45% (400,000 ha) of this area (Despain and others 1989). Fires of this scale have occurred in YNP in the past, most recently in the early 1700s (Romme and Despain 1989). Approximately 80% of the park is covered with coniferous forests dominated by lodgepole pine (Despain 1991). Our study focused on the subalpine forested plateau that covers most of Yellowstone and supports extensive lodgepole pine forests. The climate is generally cool with relatively moist springs and dry summers (Martner 1986). The two most important environmental gradients controlling vegetation on the plateau relate to elevation and geological substrate (Despain 1991), with moisture generally increasing with elevation and soil fertility lower on rhyolite than on andesite and detrital substrates.

Study Sites

We conducted this study in late July of 1997 at four sites, each about 1 ha in extent, in YNP (Table 1). These four sites represented four contrasting types of early postfire vegetation: (a) infertile nonforest (Pitchstone Plateau; lodgepole pine sapling density of 100 stems/ha), (b) fertile nonforest (Mount

Table 2. Aboveground Net Primary Production (ANPP) and Leaf-Area Index (LAI, Measured in 1997) in Four 9-Year-Old Stands Developing After the 1988 Yellowstone Fires[a]

Study Site	Aboveground Tree Productivity (Mg ha^{-1} yr^{-1})	Aboveground Herbaceous Productivity (Mg ha^{-1} yr^{-1})	Total ANPP (Mg ha^{-1} yr^{-1})	Proportion Herbaceous	Aboveground Tree LAI (m^2 m^{-2})
Infertile nonforest (Pitchstone)	0.0021 (0.0008–0.0033)	0.2434 (0.1169–0.3700)	0.2455 (0.1177–0.3733)	0.99	0.002
Fertile nonforest (Mt. Washburn)	0.0164 (0.0074–0.0253)	0.7374 (0.5015–0.9732)	0.7537 (0.5089–0.9985)	0.98	0.012
Low-density pine forest (Pitchstone)	0.1431 (0.0563–0.2299)	0.7121 (0.3946–1.0297)	0.8552 (0.4509–1.2596)	0.83	0.138
High-density pine forest (Mt. Haynes)	3.8134 (0.8781–6.7488)	0.1998 (0.0889–0.3108)	4.0133 (0.9670–7.0595)	0.05	1.822

[a]*Numbers are means, with 95% confidence interval in parentheses; mg, metric ton (1,000,000 g).*

Washburn; sapling density of 1000 stems/ha), (c) low-density lodgepole pine (Pitchstone Plateau; sapling density of 20,100 stems/ha), and (d) high-density lodgepole pine (Mount Haynes; sapling density of 62,800 stems/ha). All four sites were fully stocked with trees at the time of the fires in 1988. The fires were stand replacing at all four sites, so the trees for which we measured ANPP and LAI all germinated after 1988.

ANPP Measurements

For field vegetation sampling, we established a 50-m transect through the approximate middle of each study site. We counted the number of postfire lodgepole pine saplings within a 50 × 2-m belt transect along the central transect of the sampling area to determine tree density at the site. The 50-m transect was stratified into five 10-m intervals. Within each interval, we located two 0.25-m^2 quadrats by choosing a distance along the transect at random and then choosing a distance (up to 10 m) away from the transect at random on both the left and the right sides. For herbaceous productivity, we clipped all nontree aboveground biomass within each quadrat and dried and weighed the material. We assumed that this mass represented peak season biomass for all species. The herbaceous samples included small amounts of biomass from low deciduous shrubs (*Vaccinium scoparium* and *Spirea betulifolia*). Ordinarily, the shrub productivity would be separated into wood and foliage components. However, shrubs comprised a very small proportion of the biomass in the stands that we studied, and their woody parts were a very small fraction of total plant biomass. Therefore, the error resulting from their inclusion in the herbaceous samples was minimal.

For woody productivity, we randomly sampled 10 lodgepole pine saplings by selecting the closest sapling to the lower left-hand corner within each sampling quadrat or, if there were no saplings within the quadrat, then the closest to that corner outside the quadrat. We measured the current year's increment in biomass in the 10 sampled trees (as described below), computed an average for the 10, and then multiplied the average value for each component of woody ANPP by the density of trees to obtain an estimate of woody ANPP per hectare. We also computed confidence intervals based on the measured variance in ANPP among the samples within a study site; these confidence intervals (Table 2) do not reflect variance in tree density within a site.

For each tree sampled, we measured the length of the stem in 1997 (to the tip of the terminal bud) and in 1996 (the base of the current year's growth), as well as the radius of the woody portion of the base of the tree in 1997 and 1996 (indicated by most recent complete ring). The formula for the volume of a cone was used to compute volume of the stem in 1996 and in 1997; the difference in these two volumes is the current year's increment of stem wood. We also measured the total radius (bark + wood) of the base of the tree in 1997 and used the volume of a cone to calculate the total stem volume. The volume of bark was calculated by the difference between the total stem volume in 1997 and the total wood volume in 1997. For each branch, we also measured the length in 1996 and in 1997, as well as

the radius of the woody portion of the base. The volume of branch wood in 1997 was calculated using the formula for a cone; it was then assumed that the proportion of total wood volume added in this current year is the same in the branches as in the boles. Dividing the new wood volume by the total stem volume gave us the new wood fraction; similarly, dividing the bark volume by the total stem volume gave us the bark fraction. These fractions were then used to calculate the mass of bark and new wood from the measured total stem dry masses. The total bark mass was divided by 3 (the estimated number of years over which the current bark was formed) to estimate the current year's bark production. Finally, we clipped off all of the current year's needles and dried and weighed them. The older wood and needles were dried and weighed to obtain their contribution to the total tree mass.

Our estimates of herbaceous, woody, and total ANPP were underestimates for the year. In late July 1997, the trees had not yet completed their radial growth and their new leaves were not yet fully expanded. In addition, some of the herbaceous species reached their peak season biomass either earlier or later than the sampling date. However, since all four sites were sampled within a few days of each other (Table 1), we can reasonably compare ANPP in late July among the four sites.

LAI Measurements

We developed relationships between LAI and dry weight for lodgepole pine saplings for one 10-fascicle sample from each of two trees per site by using the following procedure. First, the exterior surface area of each fascicle was calculated (assuming a fascicle is two cones oriented end to end) by using its length and diameter measured in the middle of the fascicle (subtracting the bases of the cones). Next, the interior surface area of each fascicle was determined (that is, the area exposed if the two needles were pulled apart) by using its length and intermediate diameter and implementing the formula two times the area of a triangle. We summed the exterior and interior surface areas of each fascicle to obtain the total surface area. The total surface area for all 10 fascicles in the 10-needle sample was summed, and the total 10-fascicle sample surface area was divided by the measured mass of that sample to obtain the area–mass ratio. We averaged the two area–mass ratios derived for each site and averaged the 10 total leaf-mass samples (from the 10 saplings collected per site for the ANPP measurements; new and old leaves calculated separately). The mean tree leaf mass (grams) was multiplied by the mean area–mass ratio ($cm^2\ g^{-1}$) and divided by 10,000 to obtain the mean leaf area per tree ($m^2\ tree^{-1}$), which was multiplied by site tree density to derive the leaf area per hectare. Total lodgepole pine LAI for the site equaled the $LAI_{new\ leaves} + LAI_{old\ leaves}$. Herbaceous LAI was not measured because of the diversity of species, leaf shapes, and leaf area–mass relationships among the ground-layer species. Therefore, the LAI values presented in this report refer to the tree component only.

Results

Aboveground lodgepole pine sapling productivity was lowest in the infertile nonforest stand (0.002 Mg $ha^{-1}\ year^{-1}$), greater in the fertile nonforest stand (0.016 Mg $ha^{-1}\ year^{-1}$), greater yet in the low-density pine stand (0.143 Mg $ha^{-1}\ year^{-1}$), and greatest in the high-density pine stand (3.813 Mg $ha^{-1}\ year^{-1}$) (Table 2). Aboveground herbaceous productivity was approximately 0.20 Mg $ha^{-1}\ year^{-1}$ in the infertile nonforest and the high-density pine stands and approximately 0.70 Mg $ha^{-1}\ year^{-1}$ in both the fertile nonforest and low-density pine stands (Table 2). Total (tree + herbaceous) ANPP was lowest in the infertile nonforest stand (~0.25 Mg $ha^{-1}\ year^{-1}$), comparable in the fertile nonforest and low-density pine stands (~0.80 Mg $ha^{-1}\ year^{-1}$), and greatest in the high-density pine stand (~4.00 Mg $ha^{-1}\ year^{-1}$) (Table 2). Herbaceous species comprised 98%–99% of the total ANPP in both nonforest stands, 83% in the low-density pine stand, and 5% in the high-density pine stand (Table 2).

Tree LAI was lowest (0.002) in the infertile nonforest stand, an order of magnitude greater (0.012) in the fertile nonforest stand, another order of magnitude greater (0.138) in the low-density pine stand, and still an order of magnitude greater (1.82) in the high-density pine stand (Table 2).

Discussion

This study has documented substantial variation in ANPP and LAI in early postfire successional vegetation. Our first hypothesis—that total ANPP would primarily reflect variation in tree sapling density—was generally supported (Table 2), although the difference in total ANPP between two of the stands (the fertile nonforest stand and the low-density pine stand) was not significant (see below). ANPP in the tree component clearly increased as sapling density increased from the nonforest stands to the high-density pine stand. With each order of magnitude increase in sapling density, we observed an order of magnitude increase in tree ANPP, until the step between the low-density and the high-density pine

Table 3. Aboveground Net Primary Productivity (ANPP) and Leaf-Area Index (LAI, Tree Component Only) in Mature Coniferous Forests Similar to Those of Yellowstone National Park

Forest Type	Tree LAI (m^2 Leaf m^2 Ground)	Tree ANPP (mg ha yr^{-1})	References
Lodgepole pine, southeastern Wyoming (75- to 240-year-old stands, 420–14640 stems/ha)	4.5–9.9	0.8–3.0	Pearson and others 1984, 1987
Lodgepole pine, southeastern Wyoming (23- to 117-year-old stands)	1.8–4.6	—	Binkley and others 1995
Lodgepole pine, northern Colorado (71- to 77-year-old stands, 1600–8600 stems/ha)	4.5–14.0	—	Moir and Francis 1972
Lodgepole pine, northern Utah (67- to 134-year-old stands, 208–6300 stems/ha)	2.0–5.0	—	Jack and Long 1991
Lodgepole pine, interior British Columbia (22-year-old stands, 3500–109,000 stems/ha)	2.3–13.4	—	Keane and Weetman 1987
Jack pine, north central Wisconsin (51- to 61-year-old stands, 640–960 trees/ha)	1.2–2.4	2.9–5.1	Fassnacht and Gower 1997
Red pine, north-central Wisconsin (67- to 75-year-old stands, 816–1008 trees/ha)	3.1–3.4	3.9–5.1	Fassnacht and Gower 1997
Scots pine, East Anglia, U.K. (32- to 59-year-old stands, 398–1560 stems/ha)	2.3–4.2	—	Mencuccini and Grace 1996
Evergreen boreal coniferous forests, Canada and Siberia	2–10	0.92–7.19	Box and others 1989
Nine-year-old lodgepole pine stands, Yellowstone National Park (100–62,800 stems/ha)	0.002–1.8	0.002–3.8	This study

stands. Here, while the stem density increased by only a factor of 3, the tree ANPP increased by another order of magnitude. The exceptionally high tree ANPP in the high-density pine stand probably was due not only to the high density of saplings, but also to the greater average size of saplings and a longer growing season on this lowest elevation site (Table 1).

While tree ANPP generally followed the trend in sapling density, herbaceous ANPP showed no simple pattern. As expressed in our second hypothesis, we expected a straightforward trade-off between herbaceous and tree sapling growth, such that herbaceous productivity would decrease as tree productivity increased. However, this hypothesis was rejected. Herbaceous ANPP was comparable in the infertile nonforest and high-density pine stands, suggesting that, even under the intensively competitive environment presented by high pine densities, herbaceous productivity can be maintained at levels comparable to those exhibited in some other postfire stands. Herbaceous ANPP was also comparable in the fertile nonforest stand and in the low-density pine stand, suggesting that even a 20-fold increase in sapling density was not necessarily detrimental to the productivity of herbaceous species.

Substrate and soil characteristics appeared to influence productivity, especially of the herbaceous component, although our sample size was limited. Herbaceous ANPP was significantly greater in the nonforest stand on fertile andesite than in the nonforest stand on infertile rhyolite at comparable elevations, and total ANPP on the fertile nonforest site was comparable to total ANPP in the low-density pine stand (which is on an infertile substrate). This latter finding suggests that, during the early stages of succession, areas recovering as herbaceous vegetation can be as productive as areas recovering as forest.

Not surprisingly, tree LAI followed closely the variation in tree sapling density among the four stands. With order-of-magnitude increases in sapling density, we saw order-of-magnitude increases in tree LAI. What was surprising, however, was that leaf area in the high-density pine stand had reached the lower range of values reported in the literature for similar mature coniferous forests (Table 3). ANPP in the high-density pine stand also was well within the lower range of values reported for mature forests (Table 3). This would indicate that at least some ecosystem processes (related to ANPP and LAI) in at least some of Yellowstone's young pine forests have recovered or nearly recovered to prefire conditions after only 9 years. We hasten to emphasize that this statement applies only to high-density young pine forests at lower elevations, such

as the stand sampled in this study, and that even these forests are obviously different from mature forests in terms of tree size, standing crop, and other important ecosystem characteristics. Moreover, much of the burned area in Yellowstone is covered by lower-density pine stands and nonforest stands, where LAI and ANPP are substantially lower than in mature forests. Nevertheless, it is interesting and surprising to find that, on at least some sites and with some initial densities of pine saplings, functional properties related to LAI and ANPP are recovering remarkably fast from the severe disturbance caused by the 1988 fires.

Understanding the implications of landscape heterogeneity and disturbance dynamics for ecosystem processes remains an important challenge (Schimel and others 1997), and predicting broad-scale patterns of ecosystem processes requires understanding the variability within and among ecosystems (Zak and others 1989; Walley and others 1996). Little is known about the long-term implications of a fire-generated landscape mosaic for ecosystem processes, and strong links between pattern and process at broad scales have yet to be documented for natural ecosystems. The significant variation in ANPP and LAI that we observed in four contrasting stands of early postfire vegetation suggests substantial variation in at least some parameters of ecosystem function across the postfire Yellowstone landscape. The differences in ANPP and LAI between the nonforest stands and those developing new forests are likely to persist for many decades. However, the differences between the low-density and high-density pine stands may diminish over time as both kinds of forests form closed canopies. Pearson and colleagues (1984) reported similar LAIs in two mature lodgepole pine stands that grew on similar soils but differed greatly in tree density (2217 vs 14640 trees/ha) and suggested that LAI is controlled more by site water balance than by forest structure in mature stands. Similarly, Jack and Long (1991) found no significant trend in LAI as tree density increased from 200 to 6300 trees/ha. Keane and Weetman (1987), however, found a substantial reduction in LAI in extremely dense stands (> 80000 trees/ha). Continuing, long-term studies of infrequent "natural experiments" like the 1988 Yellowstone fires can contribute to our general understanding of ecosystem structure and function at broad scales.

ACKNOWLEDGMENTS

We thank our 1997 summer field crew (Yvonne Corcoran, Cindy Gordon, Zac Harlow, Erin Lehmer, Chris Mitchell, Matt Romme, and Michael Stevens) for their hard work and diligence. This research was funded by the US Department of Agriculture, National Research Initiative Competitive Grants Program, Forest/Range/Crop/Aquatic Ecosystems Program (grant 95–37101–1689), and by the National Science Foundation, Ecology and Ecosystem Studies Programs (grant DEB9806440). Housing and logistical support were provided by the University of Wyoming–National Park Service Research Center. The Yellowstone Center for Resources and the Yellowstone Ranger Division furnished assistance throughout the field season. The senior author was supported in part by a Guyer Postdoctoral Research Fellowship from the Department of Zoology, University of Wisconsin–Madison.

REFERENCES

Anderson JA, Romme WH. 1991. Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone fires. Int J Wildland Fire 1:119–24.

Binkley D, Smith FW, Son Y. 1995. Nutrient supply and declines in leaf area and production in lodgepole pine. Can J For Res 25:621–8.

Box EO, Holben BN, Kalb V. 1989. Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO_2 flux. Vegetatio 80:71–89.

Carpenter SR. 1998. Ecosystem Ecology. In: Dodson SI, Allen TFH, Carpenter SR, Ives AR, Jeanne RL, Kitchell JF, Langston NE, Turner MG. Ecology. New York: Oxford University Press. p 123–61.

Christensen NE, Agee JK, Brussard PF. 1989. Interpreting the Yellowstone fires of 1988. BioScience 39:678–85.

Davis EA. 1987. Chaparral conversion to increase streamflow in Arizona: sequential treatments extend duration of nitrate loss to stream water. For Sci 33:89–103.

Davis EA. 1993. Chaparral control in mosaic pattern increased streamflow and mitigated nitrate loss in Arizona. Wat Resour Bull 29:391–9.

Despain DG. 1991. Yellowstone vegetation: consequences of environment and history in a natural setting. Boulder (CO): Robert Rinehart.

Despain D, Rodman A, Schullery P, Shovic H. 1989. Burned area survey of Yellowstone National Park: the fires of 1988. Yellowstone National Park (WY): Division of Research and Geographic Information Systems Laboratory; unpublished report.

Fassnacht KS, Gower ST. 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Can J For Res 27:1058–67.

Gholz HL, Hawk GM, Campbell A, Cromack K Jr. 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Can J For Res 15:400–9.

Helvey JD, Tiedemann AR, Fowler WB. 1976. Some climatic and hydrologic effects of wildfire in Washington State. In: Proceedings of the tall timbers fire ecology conference (1974), 15: 201–22.

Jack SB, Long JN. 1991. Response of leaf area index to density for two contrasting tree species. Can J For Res 21:1760–4.

Keane RE, Ryan KC, Running SW. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological processes model FIRE-BGC. Tree Physiol 16:319–32.

Keane MG, Weetman GF. 1987. Leaf area–sapwood cross-sectional area relationships in repressed stands of lodgepole pine. Can J For Res 17:205–9.

Knight DH, Wallace LL. 1989. The Yellowstone fires: issues in landscape ecology. BioScience 39:700–6.

Martner BE. 1986. Wyoming climate atlas. Lincoln: University of Nebraska Press.

Mencuccini M, Grace J. 1996. Hydraulic conductance, light interception, and needle nutrient concentration in Scots pine stands and their relations with net primary productivity. Tree Physiol 16:459–68.

Moir WH, Francis R. 1972. Foliage biomass and surface area in three *Pinus contorta* plots in Colorado. For Sci 18:41–5.

Pearson JA, Fahey TJ, Knight DH. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Can J For Res 14:259–65.

Pearson JA, Knight DH, Fahey TJ. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. Ecology 68:1966–73.

Romme WH, Despain DG. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39:695–9.

Running SW, Coughlan JC. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol Modell 42:125–54.

Schimel DS, VEMAP participants, Braswell BH. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecol Monogr 67:251–71.

Tinker DB, Romme WH, Hargrove WW, Gardner RH, Turner MG. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Can J For Res 24:897–903.

Turner MG, Hargrove WW, Gardner RH, Romme WH. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J Vegetat Sci 5:731–42.

Turner MG, Romme WH, Gardner RH, Hargrove WW. 1997. Effects of fire size and pattern on early postfire succession in subalpine forests of Yellowstone National Park, Wyoming. Ecol Monogr 67:411–33.

Walley FL, Van Kessle C, Pennock DJ. 1996. Landscape-scale variability of N mineralization in forest soils. Soil Biol Biochem 28:383–91.

Zak DR, Host GE, Pregitzer KS. 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern Lower Michigan. Can J For Res 19:1521–6.