

ABOVE-GROUND NET PRIMARY PRODUCTION, LEAF AREA INDEX, AND NITROGEN DYNAMICS IN EARLY POST-FIRE VEGETATION, YELLOWSTONE NATIONAL PARK



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INTRODUCTION

The 1988 fires in Yellowstone National Park (YNP), Wyoming, affected >250,000 ha, creating a striking mosaic of burn severities across the landscape which is likely to influence ecological processes for decades to come (Christensen et al. 1989, Knight and Wallace 1989, Turner et al. 1994). Substantial spatial heterogeneity in early post-fire 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 et al. 1994, Turner et al. 1997). Post-fire vegetation now includes pine stands ranging from relatively low to extremely high pine sapling density (ca 10,000 to nearly 100,000 stems ha⁻¹) as well as non-forest 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 post-fire 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 pre-disturbance characteristics. In this pilot study, we began to address these general questions by examining the variation in above-ground net primary production (ANPP), leaf area index (LAI) of tree (lodgepole pine) and herbaceous components, and rates of nitrogen mineralization and loss in successional stands 9 years after the fires. ANPP measures the cumulative new biomass generated over a given period of time, and is a fundamental ecosystem property often used to compare ecosystems (Carpenter 1998). Leaf area (typically expressed as leaf area index [LAI], i.e., 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 (e.g., Forest-BGC, Running and Coughlan 1988; FIRE-BGC, Keane et al. 1996). Disturbances cause reductions in leaf area that cause simultaneous reductions in transpiration and photosynthesis and increases in

stream flow (Helvey et al. 1976, Gholz et al. 1985, Davis 1987, 1993, Keane et al. 1996).

This study had three specific objectives. The first was to measure ANPP and LAI in stands representing a range of early post-fire vegetation structure. Our second objective was to compare our measured ANPP and LAI with values in the literature to determine how close these 9-year old post-fire stands in YNP have come to developing ANPP and LAI characteristic of mature coniferous forests. Thirdly, we measured nitrogen mineralization and nitrogen loss in stands representing a range of early post-fire vegetation structure. This was a pilot study (Reed et al., submitted), designed in part to test methods and hone our hypotheses for a research proposal to the National Science Foundation which we submitted in December, 1997 (and which was funded in June, 1998).

◆ METHODS

We measured ANPP and LAI in late July of 1997 at four sites, each ca. 1 ha in extent, in Yellowstone National Park. These four sites represented four contrasting types of early post-fire vegetation: (1) infertile non-forest (Pitchstone Plateau; lodgepole pine sapling density of 100 stems/hectare), (2) fertile non-forest (Mount Washburn; sapling density of 1000 stems/hectare), (3) low-density lodgepole pine (Pitchstone Plateau; sapling density of 20,100 stems/hectare), and (4) high-density lodgepole pine (Mount Haynes; sapling density of 62,800 stems/hectare). 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.

We measured nitrogen mineralization during the growing season (May - August) at two sites: (1) high-density lodgepole pine (Mount Haynes; sapling density of 62,800 stems/hectare; the same site in which we measured ANPP and LAI), and (2) infertile non-forest (Mallard Lake site; sapling density < 100 stems/ha). We also collected water from nine first-order ephemeral streams flowing out of small watersheds representing contrasting types of vegetation: (1) non-forest developing after the 1988 fires, (2) low-density pine forest, developing after the 1988 fires, (3) early successional vegetation developing after

the 1996 Pelican fire, and (4) unburned forest having elevation, topography, and substrate similar to the burned watersheds. The streamwater samples were taken late in the snowmelt period (early July), to be analyzed for nitrate concentration.

ANPP and LAI Measurements

For field vegetation sampling, we established a 50 m transect through the approximate middle of each study site. We counted the number of post-fire lodgepole pine saplings within a 50 m x 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-m² quadrats by choosing a distance along the transect at random, then choosing a distance (up to 10 m) away from the transect at random on both the left and right sides. For herbaceous productivity, we clipped all non-tree above-ground biomass within each quadrat, and dried and weighed the material. We assumed that this mass represented peak season biomass for all species.

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 using standard allometric techniques, computed an average for the 10, 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 developed relationships between LAI and dry weight for lodgepole pine saplings for one 10-fascicle sample from each of two trees per site. We averaged the two area/mass ratios derived for each site and averaged the ten total leaf mass samples (from the ten saplings collected per site for the ANPP measurements; new and old leaves calculated separately). The mean tree leaf mass (g) was multiplied by the mean area/mass ratio (cm² g⁻¹) and divided by 10,000 to obtain the mean leaf area per tree (m² tree⁻¹), which was multiplied by site tree density to derive the leaf area per hectare. Herbaceous LAI was not measured because of the diversity of species, leaf shapes, and leaf area/mass relationships among the ground layer species.

Nitrogen Mineralization and Streamwater Nitrate

We measured rates of nitrogen mineralization during the growing season by driving twenty 2-inch PVC tubes into the ground at each study site, and placing a resin bag at the base of the tube. During the 4-month period that the resin bag was in the tube, it sequestered nitrate and ammonium ions released within the soil core lying above it in the tube. At the end of the 4-month incubation period, we removed the resin bags and returned them to the laboratory for standard chemical analysis.

Streamwater samples were frozen until they could be returned to a standard water chemistry lab for determination of nitrate concentrations.

◆ RESULTS

ANPP and LAI

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

Tree LAI was lowest (0.002) in the infertile non-forest stand, an order of magnitude greater (0.012) in the fertile non-forest 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 1).

Table 1. Above-ground net primary production and leaf area index (measured in 1997) in four 9-year-old stands developing after the 1988 Yellowstone fires. Numbers are means, with 95% confidence interval in parentheses.

| Study site | Above-ground Tree Productivity ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) | Above-ground Herbaceous Productivity ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) | Total Above-ground NPP ($\text{Mg ha}^{-1} \text{ yr}^{-1}$) | Proportion herbaceous | Above-ground Tree LAI ($\text{m}^2 \text{ m}^{-2}$) |
|---------------------------------------|--|--|--|-----------------------|---|
| Infertile Non-forest (Pitchatone) | 0.0021 (0.0008-0.0033) | 0.2434 (0.1169-0.3700) | 0.2455 (0.1177-0.3733) | 0.99 | 0.002 |
| Fertile Non-forest (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 (Pitchatone) | 0.1431 (0.0563-0.2299) | 0.7121 (0.3346-1.0297) | 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 |

Nitrogen Mineralization and Streamwater Nitrate

The nitrogen mineralization rate was higher in the non-forest site than in the high-density pine stand: $2.59 \text{ vs } 1.23 \text{ mg N / kg soil / day}$ (Table 2). Streamwater nitrate concentrations were extremely low ($0.04 - 0.12 \text{ mg / l}$) in all nine streams sampled, and there were no consistent patterns in nitrate concentration with respect to watershed vegetation.

Table 2. Nitrogen Mineralization Rates in contrasting sites (both of which burned in 1988) from May 18 - September 20, 1997.

| Site | mg N / kg soil / day |
|---|----------------------|
| High-density lodgepole pine (Mt Haynes) | 1.23 |
| Non-forest (Mallard Lake trail) | 2.59 |

◆ DISCUSSION

This study documented substantial variation in ANPP and LAI in early post-fire successional vegetation. Total above-ground net primary productivity generally reflected variation in tree sapling density, although the difference in total ANPP between two of the stands (the fertile non-forest stand and the low-density pine stand) was not significant. ANPP in the tree component clearly increased as sapling density increased from the non-forest 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- and high-density pine 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.

While tree ANPP generally followed the trend in sapling density, herbaceous ANPP showed no simple pattern. Herbaceous ANPP was comparable in the infertile non-forest 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 post-fire stands. Herbaceous ANPP was also comparable in the fertile non-forest stand and in the low-density pine stand, suggesting that a even a 20-fold increase in sapling density was not necessarily detrimental to the productivity of herbaceous species. This latter finding also 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 leaf area index 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 and ANPP in the high-density pine stand had reached the lower range of values reported in the literature for similar mature coniferous forests (e.g., Pearson et al. 1984, 1987, Binkley et al. 1995). 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 pre-fire conditions after only 9 years.

The lower rate of nitrogen mineralization in the high-density pine stand compared with the non-forest site may be a consequence of more rapid nitrogen uptake by the vegetation in the high-density pine stand. Our ANPP measurements indicated that this was a very productive stand, potentially capable of absorbing nitrogen almost as quickly as it is released into the soil solution. In contrast, the non-forest stand had far lower plant biomass, and probably lower ANPP (though we did not measure it). Our findings with regard to nitrogen mineralization rates in two contrasting kinds of vegetation following the 1988 fires suggests that there may be important differences across the landscape in biogeochemical processes, but additional sampling is needed.

The extremely low nitrate concentrations in streamwater flowing out of burned watersheds was surprising. We expected to see a significant loss of nitrogen from the recently burned Pelican site (1 year post-fire) and possibly from the watersheds burned in 1988 that still had relatively low biomass and ANPP (e.g., non-forest and low-density pine stands). However, nitrate loss in all of the burned watersheds was not significantly different from loss in unburned watersheds, and nitrogen export was extremely low in all watersheds. Many of the substrates in Yellowstone have extremely low amounts of nitrogen, and vascular plants and microbes apparently have extremely efficient mechanisms for capturing and sequestering nitrogen. Even a major disturbance, like the fires of 1988 or the Pelican fire in 1996, does not lead to large losses of this limiting nutrient.

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