

Available Fuel Dynamics in Nine Contrasting Forest Ecosystems in North America

SOUNG-RYOUL RYU

JIQUAN CHEN

Earth, Ecological and Environmental Science
University of Toledo
Toledo, Ohio 43606, USA

THOMAS R. CROW

North Central Research Station
USDA Forest Service
Grand Rapids, Minnesota 55744, USA

SARI C. SAUNDERS

School of Forest Resources and Environmental Science
Michigan Tech University
Houghton, Michigan 49931, USA

ABSTRACT / Available fuel and its dynamics, both of which affect fire behavior in forest ecosystems, are direct products of

ecosystem production, decomposition, and disturbances. Using published ecosystem models and equations, we developed a simulation model to evaluate the effects of dynamics of aboveground net primary production (ANPP), carbon allocation, residual slash, decomposition, and disturbances (harvesting, tree mortality, and fire frequency) on available fuel (AF; megagrams per hectare). Both the magnitude and the time of maximum ANPP as well as the duration of high productivity condition had a large influence on AF. Productivity and decomposition were two dominant driving factors determining AF. The amount of AF in arid or cold regions would be affected more by climate change than that in other ecosystems. Frequent fire was an effective tool to control the AF, and medium frequency fire produced the most AF. Disturbances increased AF very rapidly in a short period. The results can be used as a basic knowledge to develop a fire management plan under various climate conditions.

Fire is a common disturbance that greatly influences species composition, forest structure, carbon cycling, and nutrient cycling in many forest ecosystems (Dumontte and others 1996, Whittle and others 1997, Thompson and others 2000, Wang and others 2001). Fuel, climate, and topography have been proposed as the three major components to predict fire behavior and ignition (Whelan 1998). Under fire-favorable weather, the role of fuel is likely to be the most important factor determining fire behavior (Bessie and Johnson 1995). The amount of fuel is controlled by vegetation type, decomposition rate, ecosystem productivity, and their interrelationships (Brown and others 1999, Flannigan and others 2000, Cumming 2001, Wang and others 2001, Mickler and others 2002).

The combined effects of fire prevention, fire suppression, timber harvesting, and pest management have altered the patterns of fuel loading (Thompson and others 2000), and climate change will significantly affect the intensity and frequency of fire due to changes in fuel quality and quantity (Stocks and others 1998, Franklin and others 2001). In the United States, fire burned 2.6 million ha from January to September in

the year 2002, more than double the 10-year average area (<http://www.nifc.gov/fireinfo/nfn.html>). The various changes in fire regime are important not only because of the significant effect of fire on management and vegetation but also because of changes in the pattern of the Earth's carbon sequestration (Clark 1990, Overpeck and others 1990, Johnson and Larsen 1991, Stocks and others 1998, Flannigan and others 2000, Franklin and others 2001, He and others 2002). The current forest management paradigm is shifting from a strict focus on fire prevention to accommodation and emulation of the historic fire regime. The primary approach of landscape management is to maintain states of fuel loading similar to those that existed prior to European settlement to achieve sustainable ecosystem management (Boychuk and others 1997). However, a substantial gap remains between the principles of fire accommodation and emulation and their application. A clear understanding of the relationships among fire, weather, fuel, and disturbance across scales is essential.

Available fuel (AF) can be defined as the total dry weight of ground-level fuel per unit area, while potential fuel (PF) is the total biomass per unit area in the system (Whelan 1998). Disturbances can be divided into three types based on the change in available and potential fuel after a disturbance. The first type of disturbance causes an increase in AF without a signifi-

KEY WORDS: Available fuel; Decomposition; Ecosystem productivity; Tree mortality; Fire frequency; Fire intensity; Harvesting

Published online May 12, 2004.

cant change in PF of the system. Examples of this type of disturbance include windthrow and tree death due to insects, acid rain, and disease. The second type is the disturbance transfers potential fuel to AF while consuming both AF and PF (e.g., forest fire). The third type of disturbance increases AF but decreases PF (e.g., harvesting). These disturbance types create differences in fuel quality and quantity (e.g., the amount and ratio of litter and coarse woody debris).

Computer models have been developed to evaluate the effects of forest practices on forest fire because of the difficulties associated with field experiments (Boyчук and others 1997, Karafyllidis and Thanailakis 1997, Peng 2000, Hargrove and others 2000, Thompson and others 2000, Wei and others 2003). Current fire models predict the fuel accumulation pattern, climatic control of fire frequency, and the influence of fuel loads on fires well. However, these detailed models are limited in their capability to simulate at broad spatial and temporal scales and require comprehensive amounts of information (Gardner and others 1999). Studies of landscape-level processes will require a simplified, parameter-scarce approach to modeling the ecosystems within a landscape. It is almost impossible to parameterize a complicated model for a large landscape due to our limited knowledge and data (Levin 1992). Only by using broad-scale simulations under various climate scenarios, can we begin to understand the combined impacts of climate and ecosystem type on the distribution of biomass and subsequent fire regimes at the landscape level.

The primary objective of our study was to evaluate the amount of available fuel under different ecosystem characteristics (e.g., dynamics of aboveground net primary production (ANPP; megagrams per hectare per year, decomposition rates), species characteristics (e.g., carbon allocation, residual slash after harvest), and under alternative disturbance regimes (e.g., mortality rate, fire frequency, and clearcutting) in nine forest ecosystems in North America. We particularly wanted to test what is the most important of these factors in determining the AF among the various ecosystems. By understanding this we will gain insight into important questions in forest fire management, such as; what the most important factor driving forest fire regimes is among (1) elevated CO₂ (related to productivity and decomposition); (2) climate change (related to changes in species composition); and (3) management practices.

Methods

Modeling Overview

Two types of model approaches were used. In the first approach, we varied the values of initial AF, dynam-

ics of ANPP, maximum ANPP, and decomposition rate using the LandNEP model developed by Euskirchen and others (2002), and evaluated the resulting AF dynamics. The second approach used less theoretical input data (i.e., carbon allocation, maximum ANPP, and harvesting) for the various ecosystems. This second approach followed four steps. First, the range of productivity for ecosystems was estimated using PnET-II (Aber and others 1995). The range of decomposition rate was calculated using the equation of Meentemeyer (1978) and evapotranspiration calculated from PnET-II. Second, we represented the dynamics of ANPP using a LandNEP model and a maximum ANPP, estimated from PnET-II output. Third, the amount of carbon flow between dominant carbon pools was determined using published literature (Figure 1). Finally, the AF of each forest ecosystem was estimated for various combinations of ecosystem characteristics (e.g., decomposition and carbon allocation) and disturbances (e.g., harvesting, tree mortality, and fire frequency).

Study Sites

Nine distinct forest ecosystems in the United States were chosen for the study; interior Alaska (AK; *Picea mariana*), H.J. Andrews experimental forest in Oregon (OR; *Pseudotsuga menziesii* and *Tsuga heterophylla*), Sierra National forest in California (CA; *Abies concolor* and *Abies magnifica*), Coconino National Forest in Arizona (AZ; *Pinus ponderosa*), Mark Twain National Forest in Missouri (MO; *Quercus velutina*, *Quercus alba*, *Quercus stellata*, and hickory), Chequamegon National Forest in Wisconsin (WN; *Pinus resinosa* and *Pinus banksiana*), University of Wisconsin Arboretum in Wisconsin (WS; mesic oak-maple, i.e., *Quercus* and *Acer*), Hubbard brook ecosystem study in New Hampshire (NH; northern hardwood i.e. *Acer*, *Fagus*, and *Betula*), and Francis Marion National Forest in South Carolina (SC; *Pinus taeda*) (Harper 1965, Barbour and Billings 1988, Aber and Federer, 1992). Those forest ecosystems represent six of the 13 dominant forest biomes existing in the United States (Barbour and Billings 1978): AK for boreal forest biome, OR for Pacific northwest forest biome, CA for California Upland forest biome, AZ for Southern Rocky Mountain Forest, SC for Southeastern Coastal plain forest biome, and MO, WN, WS, and NH for deciduous forest biome to capture the variety in this biome. Primary climate characteristics for each ecosystem are provided in Table 1.

Model Descriptions

The PnET-II model is a simple, lumped-parameter model of the carbon and water balance of forests (Aber and others 1995). This model is widely used because it

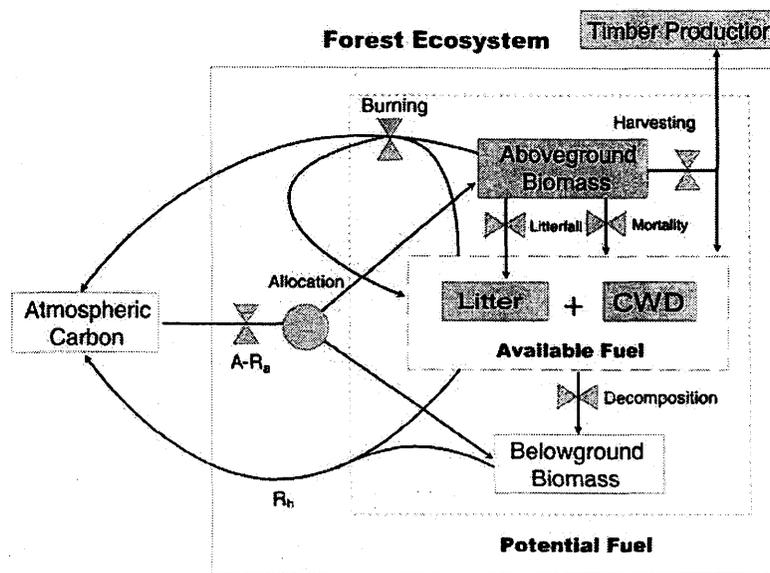


Figure 1. Conceptual model for carbon flow in the forest ecosystem. Carbon pools for the study are indicated as shaded boxes. A , R_a , and R_h stand for total photosynthesis, autotrophic respiration, and heterotrophic respiration, respectively.

has limited parameters and been validated for many forest ecosystems (Aber and others 1996, Jenkins and others 1999). Foliar N content (%), foliage retention year, specific leaf weight (SLW; grams per square meter), and climate (latitude, growth degree days, temperature and precipitation) are key parameters and inputs for predicting ecosystem productivity. The parameter and input values for PnET-II were derived from relevant published literature considering the vegetation (Aber and Federer 1992, Yin 1993, Aber and others 1996, Goodale and others 1998, <http://www.nodc.noaa.gov>) (Table 2). The PnET-II model was run to generate the yearly ANPP for each ecosystem using monthly real temperature and precipitation data of 1951–2000 and modified climate data (multiplying real climate data by 1.05 and 0.95) for each ecosystem to catch the 5% climatic variation (<http://www.nodc.noaa.gov>). The predicted ANPP values from 150 years PnET-II simulation for each ecosystem were similar to expected ranges (Figure 2): published ANPP for AK, OR, CA, AZ, WN, WS, MO, NH, and SC were 0.6–1.5, 6.2–15.0, 4.7–6.5, 2.2–8.4, 6.5–8.3, 8.4–13.71, 6.0, 9–10, and 8.0–9.5 Mg/ha/yr, respectively (Monk and others 1970, Gholz 1982, Barbour and Billings, 1988, Van Cleve and others 1983, McClaugherty and others 1985, Nadelhoffer and others 1985, Kimmins 1987, Aber and Federer 1992, Yin, 1999). We used the predicted ANPP instead of published ANPP, because we tried to estimate the range of productivity and decomposition rate for each ecosystem under various climate conditions. It was hard to compare the published data among ecosystems directly, due to the different meth-

ods used and the variable amount of data available for each ecosystem.

Maximum, median, and minimum values were estimated from the predicted 150 ANPP values for each ecosystem with PnET-II. Then, they were used as scalar factors in LandNEP model for studying subsequent calculation of ANPP dynamics (Euskirchen and others 2002). We estimated the scalar factor, which is a maximum ANPP in practice, from PnET-II, because the PnET-II model assumes the full use of light, which is maximum growth condition (Aber and Federer 1992). The LandNEP model represented by the three-parameter Weibull function:

$$P = \frac{\gamma}{\beta} \times \left(\frac{\text{age} - \alpha}{\beta} \right)^{\gamma-1} \times e \left[- \left(\frac{\text{age} - \alpha}{\beta} \right)^{\gamma} \right] \quad (1)$$

$$\text{ANPP} = \frac{P - \text{Min}(P)}{\text{Max}(P) - \text{Min}(P)} \times \lambda$$

was used to describe the dynamics of ANPP in the forest ecosystems, where P , α , β , γ , λ , $\text{Max}(P)$, and $\text{Min}(P)$ were probability, location parameter ($\alpha \leq \text{age} < \infty$, otherwise $\text{age} = 0$), scale parameter, shape parameter, scalar factor, maximum of P , and minimum of P ($= 0$), respectively (Euskirchen and others 2002). When we evaluated the effects, for various ecosystems, of magnitude in ANPP, decomposition, and disturbance on AF and its dynamics, α , β , and γ were held at 12, 80, and 2, respectively, to exclude the effect of different NEP patterns among ecosystems.

To estimate the AF at the ecosystem level, the amount of ANPP was partitioned among the several

Table 1. Maximum and minimum temperatures and precipitation values for forest ecosystems^a

Ecosystem	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
AK												
Max temp (°C)	4.3	3.8	5.1	13.3	27.1	24.2	28.3	28.4	19.2	14	-2.9	5.7
Min temp (°C)	-40.7	-32.1	-30.1	-23.1	-6.8	-9.1	3.3	2.7	-1.1	-27.4	-29.3	-40.4
Precipitation (cm)	1.6	0.4	0.4	7.6	1.0	2.0	6.5	7.8	1.0	1.3	0.1	0.6
OR												
Max temp (°C)	4.4	9.5	13.7	18.5	23.7	27.3	30.8	28.6	23.0	14.2	6.2	13.5
Min temp (°C)	-0.9	-1.1	0.8	3.2	5.5	7.8	9.4	8.4	3.8	1.5	0.2	1.3
Precipitation (cm)	24.2	18.4	14.4	13.4	7.5	6.0	2.5	2.5	5.5	11.3	23.8	47.8
CA												
Max temp (°C)	13.1	16.8	19.8	23.9	28.2	32.5	36.1	36.0	32.9	26.5	18.3	13.0
Min temp (°C)	4.3	6.1	7.8	9.6	13.2	16.3	19.2	18.8	16.4	11.5	6.2	3.2
Precipitation (cm)	7.3	6.9	6.2	1.9	1.2	1.3	0.1	0.0	0.2	2.2	2.1	3.6
AZ												
Max temp (°C)	6.4	8.2	10.7	14.4	19.9	25.4	27.7	26.5	23.3	18.3	11.0	6.5
Min temp (°C)	-10.3	-8.9	-7.3	-5.6	-2.4	1.8	5.6	5.7	0.8	-4.1	-8.4	-10.9
Precipitation (cm)	7.1	7.3	6.6	3.1	3.2	2.0	3.3	7.7	3.4	4.1	2.5	3.1
MO												
Max temp (°C)	4.7	9.6	13.5	19.1	24.1	28.2	30.7	30.4	26.0	21.0	11.9	6.7
Min temp (°C)	-5.5	-2.6	0.8	5.7	12.1	16.4	19.0	18.0	12.8	7.1	0.5	-4.0
Precipitation (cm)	8.0	7.7	7.9	4.6	4.8	4.6	7.1	3.6	3.9	7.2	5.6	28.4
WN												
Max temp (°C)	-5.0	-2.6	3.9	11.4	19.5	23.8	26.4	25.0	15.9	13.2	2.5	-4.0
Min temp (°C)	-14.9	-11.6	-4.1	4.9	11.4	14.2	13.1	10.0	2.2	2.2	-4.1	-3.1
Precipitation (cm)	4.2	1.8	5.8	4.3	7.9	8.4	10.8	9.2	6.1	4.7	25.1	10.7
WS												
Max temp (°C)	-3.2	0.7	6.5	13.2	20.8	26.1	27.2	26.5	22.2	16.1	6.0	-0.1
Min temp (°C)	-11.9	-7.8	-3.4	1.6	8.4	13.5	15.6	14.8	10.1	4.2	-2.3	-8.1
Precipitation (cm)	3.7	2.8	5.8	7.5	9.0	14.6	8.5	9.1	10.9	11.6	5.6	10.5
NH												
Max temp (°C)	-4.8	-3.3	0.9	7.8	15.6	20.5	21.8	21	16.2	10.3	2.7	-1.9
Min temp (°C)	-13.8	-12.5	-7.7	-1.5	4.9	10.4	12.6	11.9	7.3	1.5	-4.2	-9.6
Precipitation (cm)	14.2	8.6	12.4	13.9	10.5	8.3	14.1	12.9	13.3	11.3	13.6	10.6
SC												
Max temp (°C)	15.3	16.7	19.8	23.9	27.9	29.9	32.4	31.8	28.9	25.3	19.7	16.7
Min temp (°C)	4.7	5.6	8.4	12.9	17.6	21.2	23.1	22.4	19.5	13.8	8.5	6.1
Precipitation (cm)	12.9	7.5	8.5	6.8	6.1	11.3	16.2	15.9	11.7	10.0	8.3	4.4

^aAverage of 1991–2000 (<http://www.nodc.noaa.gov>). Ecosystem initials are AK, interior Alaska; OR, H.J. Andrews Experimental Forest; CA, Sierra National Forest; AZ, Coconino National Forest; NH, Hubbard Brook Ecosystem Study; WN, Chequamegon National Forest; WS, University of Wisconsin Arboretum; MO, Mark Twain National Forest; and SC, Francis Marion National Forest.

distinct carbon pools in terrestrial ecosystems: aboveground biomass, litter, coarse woody debris (CWD), timber production, and belowground biomass (Figure 1). Aboveground biomass was calculated as the sum of ANPP minus the litterfall and materials removed by disturbance events. The sum of the litter pool and the CWD pool comprised AF. Previous studies showed that the proportion of litterfall from ANPP ($F/ANPP$) is 0.28–0.42 (McClougherty and others 1985, Nadelhoffer and others 1985, Yin, 1999, Gower and others 2001) and 0.35 was used as the standard value. Coarse woody material could be divided into stem and branch for the decomposition process. The published proportions of stem, branch, and foliage within the aboveground biomass were 0.6–0.9, 0.05–

0.28, and 0.01–0.12 (Ter-Mikaelian and Korzukhin 1997, Wagner and Ter-Mikaelian 1999), respectively, and 0.75, 0.20 and 0.05 were used as standard values for allocation of aboveground biomass, respectively. Initial foliage and branch pool were 2 and 8 Mg/ha, respectively.

Meentemeyer (1978) reported a simple, general equation to predict the litter decomposition rate (k) using actual evapotranspiration and lignin content. Since the study focus was the effect of climatic on fuel loading and not fuel quality, the lignin concentration was considered a constant value (15.5%), and the evapotranspiration values from the PnET-II runs were plugged into the equation to calculate the k value for each ecosystem. Maximum, median, and minimum k

Table 2. Major variables controlling photosynthesis in PnET-II model and parameter values for each ecosystem^a

Ecosystem	Latitude	LNC (%)	FolReten (yr)	SLWMax (g/m ²)
AK	65	0.70	10	55
OR	44	1.40	6	135
CA	37	1.10	8	143
AZ	35	1.10	3	117
NH	44	2.40	1	58
WN	47	1.14	3	88
WS	44	2.40	1	77
MO	38	1.47	1	63
SC	33	0.98	2	100

^aFrom Aber and Federer (1992), Yin (1993), Boardman and others (1997), Goodale and others (1998). Variable abbreviations are LNC, leaf nitrogen content; FolReten, foliage retention year; and SLWMax, maximum specific leaf weight. Ecosystem initials are as in Figure 2.

values were estimated among the predicted 150 k values for each ecosystem. We used the single negative exponential equation ($X_t = X_0 \cdot e^{-kt}$) (Waring and Running 1998) to assess decomposition of organic matter. The decomposition rate ratios between stem and branch were reported as 1:2–1:9, while those of litter with branch and stem were 2:1–6:1 and 3:1–12:1, respectively (Melillo and others 1982, McLaugherty and others 1985, Nadelhoffer and others 1985, Landsberg and Gower, 1997, Yin 1999). In this study, the k s of branch and stem were 30% and 10% of the k of litter.

Modeling Scenarios

Four scenarios were tested to evaluate the effect of ecosystem characteristics on AF. The first three scenarios used hypothetical ecosystems (Table 3). Scenarios I, II, and III used the hypothetical ecosystems to isolate the effects of productivity, litterfall rate, and initial condition of AF. Scenario I tested the effect of ecosystem dynamics of ANPP on AF. Five hypothetical ecosystems (MM, EH, LL, MH, and ML) were proposed, each having the same cumulative ANPP but different dynamics of ANPP over 300 years (Figure 3). Ecosystems MM, EH, LL, MH, and ML indicate moderate timing and magnitude, early and high magnitude, late and low magnitude, moderate timing and high magnitude, and moderate timing and low magnitude of maximum ANPP, respectively. The dynamics of ANPP for ecosystems MM, EH, and LL peaked at different ages in the order of ecosystem EH, MM, and LL. Ecosystems MM, MH, and ML had different magnitudes of maximum ANPP during succession. Ecosystem MH had the highest maximum ANPP, followed by MM and then ML. These hypothetical ecosystems represented the various

patterns of ecosystem growth due to differing climates and vegetation types.

Ecosystems MM, EH, LL, MH, and ML were designed to compare fast and steady growth ecosystems. Ecosystems EH and MH grew more at early stages than ecosystems LL and ML, respectively, but grew less than LL and ML at later stages. Ecosystems LL and ML grew more steadily than EH and MH, respectively. The dynamics of ANPP for ecosystem MM were moderate compared to other ecosystems. We evaluated the AF dynamics at these five ecosystems with and without clear-cutting (50 years rotation stem only harvesting).

The amount of annual biomass transferring from ANPP to the AF (F/ANPP) depends on the characteristics of woody vegetation. The effects of five levels (Table 3 and Figure 4a) of F/ANPP on AF were studied at a hypothetical ecosystem (scenario II). The effect of the amount of residual slash after disturbance (initial AF; Mg/ha) was tested using four levels (Table 3 and Figure 4b) of initial AF (scenario III). Initial AF was divided into foliage and branch pools in the model. The effects of various decomposition rates on AF were also studied at nine study ecosystems using the maximum, median, and minimum decomposition rate calculated from Meentemeyer's equation (1978) with 150 years run of PnET-II output (Table 3 and Figures 2 and 5; scenario IV).

Three scenarios were tested to evaluate the effect of various disturbances on AF at the nine ecosystems (Table 3). The effect of alternative mortality rates (scenario V) on AF was tested using three maximum intensities of mortality annually (< 1, < 5, and < 10% of total aboveground biomass) in the nine ecosystems (Frelich and Lorimer 1991) (Table 3). The mortality rate was estimated annually using a random number, and this was multiplied by aboveground biomass to represent the carbon flow from aboveground biomass to AF. We also examined effects of fire frequency (and intensity) on AF at nine ecosystems (scenario VI), and the combined effects of clearcutting, mortality, and fire frequency on AF (scenario VII) in nine ecosystems. For scenario VI, three frequencies of fire were considered (Kasischke and others 1994, Levine and Cofer 1994), (Table 3). Low frequency was a 100-year fire interval with maximum damage on aboveground biomass and AF at 80%. Medium frequency was a 50-year fire interval with 40% and 50% maximum damage on aboveground biomass and AF, respectively, while high frequency was every 10 years, with 5 and 20% maximum damage on aboveground biomass and AF, respectively. The occurrence of fire and the degree of damage were calculated separately using random numbers to represent the uncertainty of fire event and the resultant

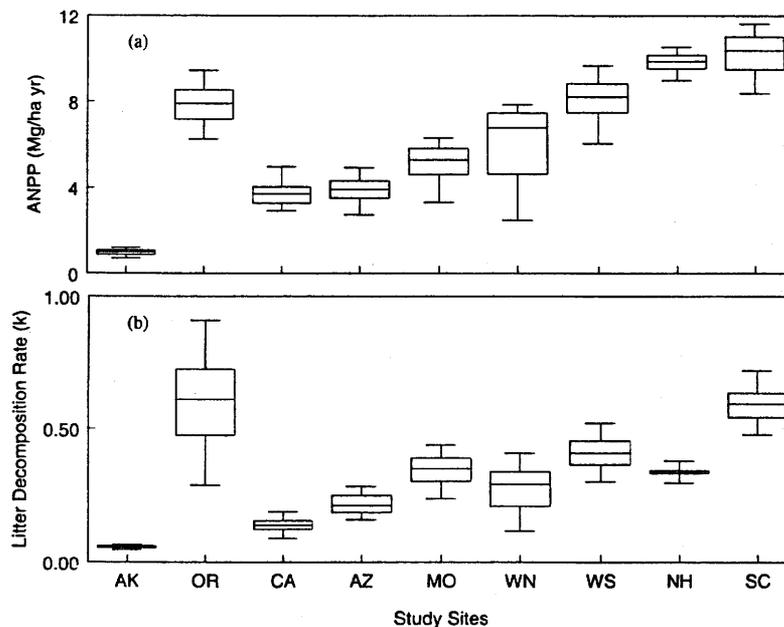


Figure 2. The result of PnET-II model runs for nine study landscapes: (a) The distribution of annual ANPP during 150 simulation years; (b) the distribution of litter decomposition rates during 150 simulation years. In the box and whisker plot, the bottom of the box, middle line, and top of the box indicate the 75th percentiles, median, and 25th percentiles respectively, and the two error bars indicate maximum and minimum values. Ecosystem initials are as in Table 1.

damage. The amount of carbon flow from potential fuel to atmosphere and from aboveground biomass to AF was calculated by multiplying the damage rate by the amounts of aboveground biomass and AF. Scenario VII was designed to mimic and compare two types of management: harvesting with intensive management (HAR) and fire exclusion and protection (FEP). The HAR indicated 50-year rotation harvesting, thinning (high mortality), and frequent prescribed fire (high fire frequency), while FEP indicated fire exclusion (low fire frequency) and effective pest management with low wind damage (low mortality). Clear-cutting was simulated on a 50-year rotation with stem-only harvesting, to leave foliage and branches on the forest floor. In order to evaluate the harvesting effect, it was assumed that harvesting returns the ecosystem age to zero but does not affect the dynamics of ANPP. We wanted to compare the response of ecosystems to the same type of disturbance. Even though we were aware that there was variability in management and responses of ecosystem, we chose 50-year clear-cutting to see the variation in response between ecosystems to a set management regime. The model was run five times for each of scenarios V, VI, and VI. Each run was 300 years and the average value of the five runs was reported. Scenarios I, II, III, and IV were run one time, since there was no variation.

Sensitivity Analysis

Sensitivity analysis was conducted to analyze the sensitivity of AF to changes in model parameters. This

improves understanding of the underlying factors responsible for model behavior (Moorhead and Reynolds 1991). To evaluate the effects of different ecosystem conditions, sensitivity analysis was conducted for AK and SC, which had the lowest and highest rates of productivity and decomposition, respectively. We also considered the effect of clear-cutting by doing sensitivity analysis with and without clear-cutting. We varied F/ANPP, stem/aboveground biomass (AB), foliage/branch biomass, maximum ANPP, litter decomposition rate (k), mortality, fire possibility, and maximum damage by fire to AB and to AF. We reported the percent changes of tested values from standard values and the percent changes of results from standard results for mean AF, maximum (max) AF, and minimum (min) AF per year after running each case 10 times. Sensitivity index was calculated by dividing percent change of the result by percent change of the tested value.

Results

Ecosystem Characteristics and AF

Scenario I. Different dynamics of productivity (ANPP) resulted in various dynamics of AF for the 300-year simulations, even though the cumulative ANPP over 300 years for the five hypothetical ecosystems was equivalent (scenario I; Table 3 and Figure 3a,b). Maximum ANPP was reached at different ages and had different magnitudes among ecosystems A, EH, and LL. The sum of AF for 300 simulation years was

Table 3. Model parameter inputs for each scenario^a

Characteristics and types	Initial F/AF	Clear-cutting ANPP	Mortality rate	Fire		ANPP Peak		Litter decomposition rate		
				Possibility	Maximum AF damage	Maximum AB damage	Magnitude (Mg/ha)		Year	
Scenario I										
Ecosystem MM	10	0.35	No	0	0	-	-	5	56	0.2
	10	0.35	Yes	0				5	56	0.2
Ecosystem EH	10	0.35	No	0	0	-	-	6.1	68	0.2
	10	0.35	Yes	0	0	-	-	6.1	68	0.2
Ecosystem LL	10	0.35	No	0	0	-	-	4.4	82	0.2
	10	0.35	Yes	0	0	-	-	4.4	82	0.2
Ecosystem MH	10	0.35	No	0	0	-	-	6.1	56	0.2
	10	0.35	Yes	0	0	-	-	6.1	56	0.2
Ecosystem ML	10	0.35	No	0	0	-	-	4.1	56	0.2
	10	0.35	Yes	0	0	-	-	4.1	56	0.2
Scenario II										
Low (L)	10	0.1	No	0	0	-	-	6	68	0.2
Medium-low (ML)	10	0.2	No	0	0	-	-	6	68	0.2
Medium (M)	10	0.3	No	0	0	-	-	6	68	0.2
Medium-high (MH)	10	0.4	No	0	0	-	-	6	68	0.2
High (H)	10	0.5	No	0	0	-	-	6	68	0.2
Scenario III										
Low (L)	5	0.35	No	0	0	-	-	6	68	0.2
Medium-low (ML)	10	0.35	No	0	0	-	-	6	68	0.2
Medium-high (MH)	15	0.35	No	0	0	-	-	6	68	0.2
High (H)	20	0.35	No	0	0	-	-	6	68	0.2
Scenario IV										
Minimum (Min)	10	0.35	No	0	0	-	-	Median	68	Minimum
Median (Med)	10	0.35	No	0	0	-	-	Median	68	Median
Maximum (Max)	10	0.35	No	0	0	-	-	Median	68	Maximum
Scenario V										
Low (L)	10	0.35	No	0.01	0	-	-	Median	68	Median
Medium (M)	10	0.35	No	0.05	0	-	-	Median	68	Median
High (H)	10	0.35	No	0.10	0	-	-	Median	68	Median
Scenario VI										
Low (L)	10	0.35	No	0	0.01	0.8	0.8	Median	68	Median
Medium (M)	10	0.35	No	0	0.02	0.5	0.4	Median	68	Median
High (H)	10	0.35	No	0	0.10	0.2	0.05	Median	68	Median
Scenario VII										
FEP	10	0.35	No	0.01	0.01	0.8	0.8	Median	68	Median
HAR	10	0.35	Yes	0.10	0.10	0.2	0.05	Median	68	Median

^aScenario I: ecosystem ANPP dynamics; scenario II: alternative F/ANPP rate; scenario III: various amounts of residual slash; Scenario IV: alternative decomposition rate. Minimum, median, and maximum indicate the values calculated from PnET-II (see Figure 2 for details).

largest at ecosystem EH (1267 Mg/ha) compared to ecosystem MM (1239 Mg/ha) and LL (1218 Mg/ha). Among ecosystems MM, EH, and LL, the ANPP was largest in ecosystem EH until year 86, MM until year 94, and LL from year 93 (Figure 3a), while AF was largest in ecosystem EH until year 94, MM until year 105, and LL from year 106 (Figure 3b). The results showed that high productivity at a young age generated more fuel and that a lag time existed between ANPP dynamics and AF dynamics. However, the different timing of maximum ANPP did not much affect the total AF for 300 years. Among ecosystems MM, MH, and ML, the maximum ANPP was of the same magnitude but at

different ages. The sum of AF for 300 years was largest at ecosystem MH (1277 Mg/ha) versus ecosystem MM (1239 Mg/ha) and ecosystem ML (1180 Mg/ha). The differences among ecosystems were larger in this situation than those differences among ecosystems MM, EH, and LL, but were less than 0.4 Mg/ha/yr. Among ecosystems MM, MH, and ML, the ANPP was largest in ecosystem MH until year 150 and in ecosystem ML from year 151, while the AF was largest in ecosystem MH until year 183 and in ecosystem ML from year 183 (Figure 3a). The results also indicated the relationship of high productivity to high AF and the existence of lag time between ANPP dynamics and AF dynamics. The

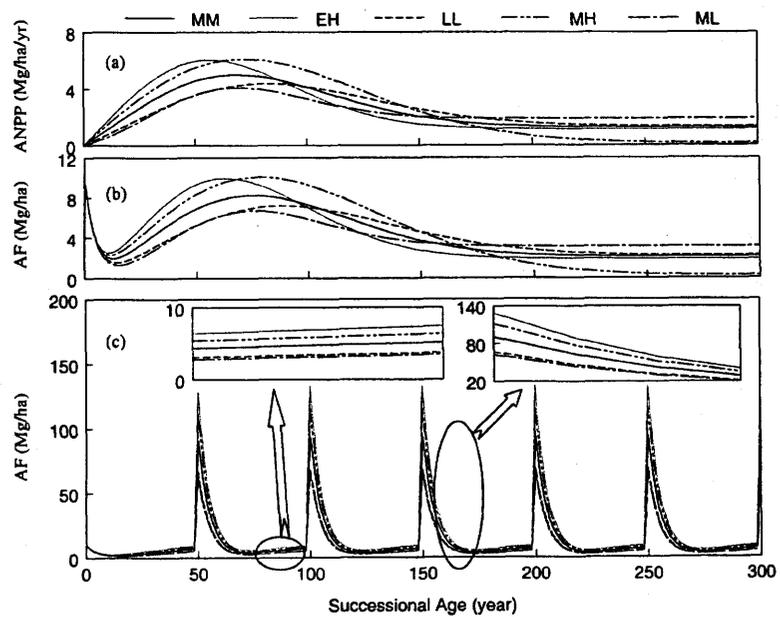


Figure 3. The effect of dynamics of ANPP on available fuel (AF; Mg/ha) (scenario I): (a) ANPP during simulation for five ecosystems; (b) AF under the "no disturbance" condition; and (c) AF under 50-year rotation clearcutting. The two small panels above panel c are enlargements of the pattern in panel c. See Table 3 for parameter values for each run.

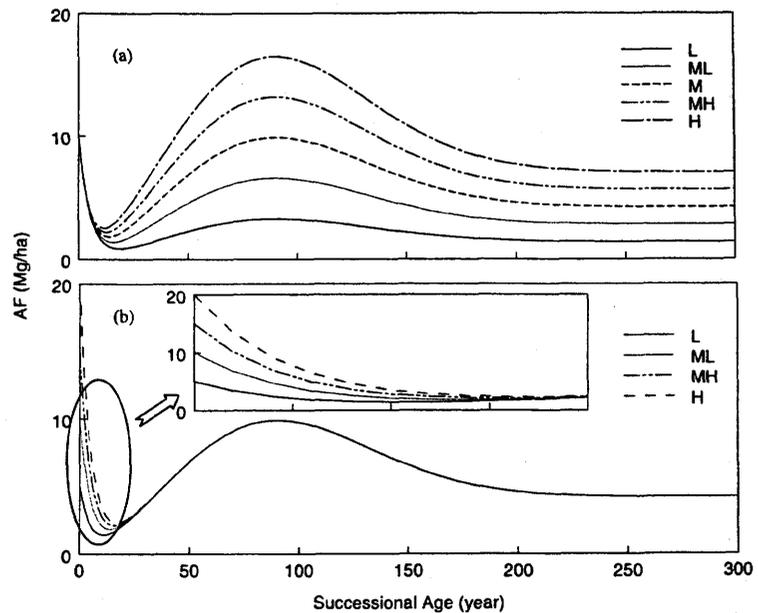


Figure 4. The effect of (a) carbon allocation (scenario II) and (b) initial fuel (scenario III) on available fuel (AF; Mg/ha). See Table 3 for a list of parameter values for each run.

lag time was larger in the later situation than the former. Based on our knowledge of the relationship between ANPP and AF, we applied clear-cutting on a 50-year rotation and expected more AF from ecosystems that had higher productivity before harvesting. Both the sum of ANPP and the AF before year 50 were, from largest to smallest, in the order of ecosystem EH, MH, MM, LL, and ML (Figure 3c). Maximum AF (Mg/

ha) values under clear-cutting conditions during 300 simulation years were 132.7, 115.5, 97.3, 69.1, and 65.0 for ecosystems EH, MH, MM, LL, and ML, respectively (Figure 3c).

Scenarios II and III. When the productivity and decomposition conditions were the same, the proportion of litterfall to ANPP ($F/ANPP$) was a critical factor determining the amount of AF. We changed $F/ANPP$

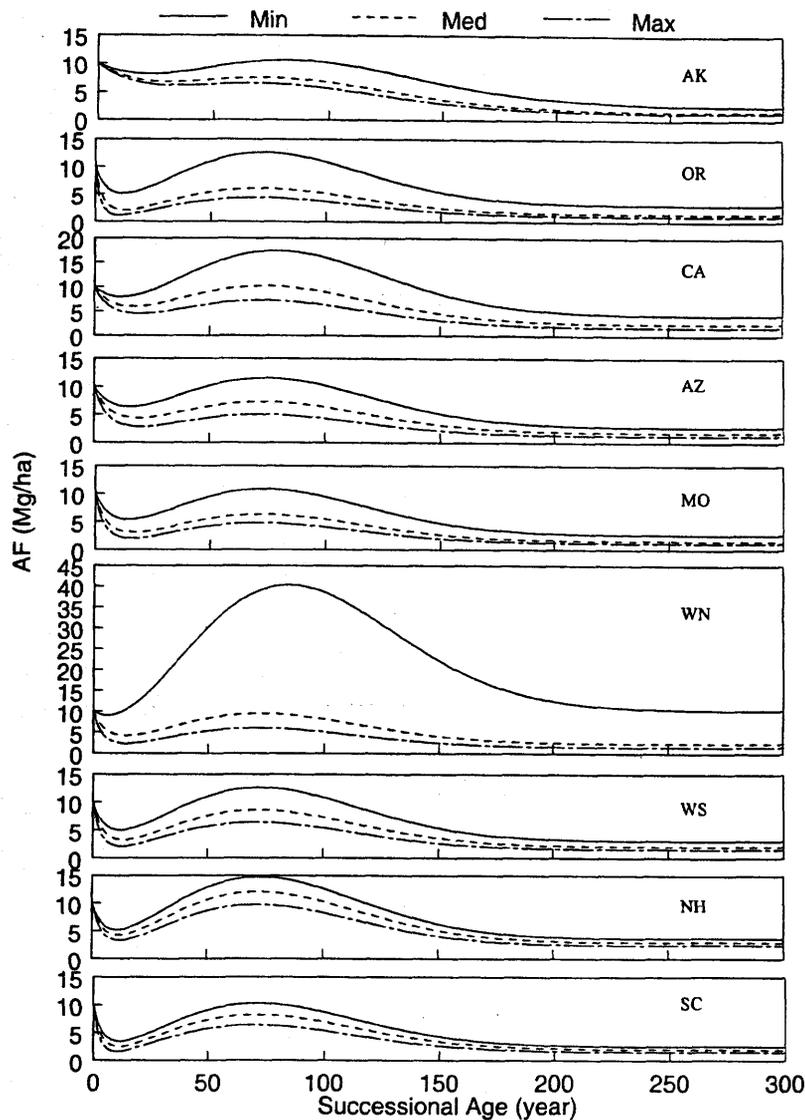


Figure 5. The effect of three levels of decomposition rate on available fuel (AF; Mg/ha) at nine study landscapes (scenario IV). See Table 3 for a list of parameter values for each run. Ecosystem initials are as in Table 1.

from 0.1 to 0.5 with five levels at a hypothetical ecosystem and observed a larger AF with a higher F/ANPP ratio (scenario II). There was less than a 1 Mg/ha difference in AF over the initial 10 years, among F/ANPP conditions from 0.1 to 0.5 (Figure 4a). The maximum difference in AF between F/ANPP ratios of 0.1 and 0.5 was 13.2 Mg/ha (Figure 4a), and the difference was > 400% of the smaller AF. When we changed the amount of initial AF, we found the difference in AF between various conditions got smaller (scenario III). The AF difference between the highest and lowest initial AF conditions resulted in less than a 1 Mg/ha after 25 years (Figure 4b).

Scenario IV. To evaluate the sole effect of decomposition on AF, we estimated the ranges of rates of litter decomposition for nine ecosystems using the equation of Meentemeyer (1978). The results demonstrated an impact of decomposition rate on the AF throughout the simulation period for the nine study ecosystems (Table 3 and Figure 5). AF was less than 10 Mg/ha at all ecosystems except NH throughout the simulations under median and maximum decomposition rates. NH had less than 10 Mg/ha only with a maximum decomposition rate. It was noteworthy that studied ecosystems showed similar amount of AF during simulation under high decomposition rates, although there was a large difference in pro-

Table 5. AF dynamics under various mortality conditions (refer to 3 for details) at nine study ecosystems

Ecosystem ^a	Mortality	Maximum AF	Year of Maximum AF	Total AF
AK	low	25.0 (0.66)	297.5 (2.68)	4902.7 (87.88)
	mid	38.4 (0.63)	184.9 (11.16)	8366.0 (53.46)
	high	41.1 (0.50)	145.5 (6.15)	9004.8 (19.75)
OR	low	32.6 (1.60)	173.8 (37.14)	6389.5 (65.45)
	mid	64.5 (4.30)	112.4 (16.32)	10159.7 (52.55)
	high	76.1 (2.95)	102.1 (8.43)	10573.8 (26.36)
CA	low	50.1 (1.85)	250.3 (28.13)	10007.4 (262.35)
	mid	88.8 (2.35)	151.5 (13.83)	17241.9 (90.66)
	high	97.6 (2.30)	130.3 (9.71)	18273.0 (47.34)
AZ	low	38.6 (1.08)	235.8 (40.38)	7791.2 (148.99)
	mid	72.6 (2.71)	141.1 (13.95)	13117.6 (62.24)
	high	80.0 (2.31)	121.6 (6.24)	13791.6 (28.33)
MO	low	34.4 (1.90)	194.8 (39.44)	6935.8 (164.24)
	mid	67.3 (2.37)	123.0 (13.11)	11371.2 (57.05)
	high	76.3 (2.70)	110.5 (11.44)	11834.4 (35.82)
WN	low	51.1 (1.20)	209.4 (32.31)	10335.4 (249.59)
	mid	99.9 (4.48)	137.0 (15.43)	17220.8 (59.44)
	high	111.0 (3.55)	116.6 (8.50)	18016.3 (32.39)
WS	low	51.4 (2.38)	217.8 (35.33)	10442.3 (368.30)
	mid	98.6 (3.34)	134.1 (10.29)	17188.8 (107.68)
	high	112.8 (2.99)	112.5 (11.86)	17988.8 (45.15)
NH	low	63.4 (2.85)	199.0 (46.69)	12883.2 (152.29)
	mid	127.3 (6.29)	128.3 (10.08)	21059.6 (91.85)
	high	144.8 (4.54)	109.9 (13.82)	22066.9 (40.53)
SC	low	43.5 (1.57)	179.0 (40.46)	8508.3 (157.93)
	mid	88.3 (3.81)	117.3 (12.85)	13779.3 (76.13)
	high	100.9 (4.08)	105.0 (9.24)	14336.9 (20.04)

^aEcosystem initials are as in Table 1.

ductivity. Small changes in decomposition rate at AK boreal forest, resulted in relatively large variation in AF. For example, the 0.01 change in litter decomposition rate at AK (the difference between median and maximum litter decomposition rate) resulted in a difference of 177 Mg/ha in total AF over 300 simulation years, while a 0.39 difference in k values for OR generated only a 257 Mg/ha difference in total AF over 300 simulation years. The 80 Mg difference in total AF over 300 years was a remarkably small difference between AK and OR considering the eightfold difference in maximum ANPP and 39-fold difference in k value. Different decomposition rates induced different AF peak times; e.g., the AF peak times of WN Min and Med conditions were years 84 and 72, respectively (Figure 5). The minimum decomposition rate produced the largest AF among the three decomposition levels. WN showed the largest difference in AF between minimum and median decomposition rates, because WN had a very low minimum decomposition rate (0.06) and a large difference between minimum and median decomposition rates (0.23).

Disturbances and AF

Scenario V. Higher mortality rate resulted in higher AF at the early stage but the lower mortality condition

produced higher AF at the late stage of the simulation (Table 5 and Figure 6). As the mortality rate increased, the maximum AF during simulation as well as the sum of AF during simulation increased. It was very interesting that the maximum AF (and sum of AF during simulations) had a positive linear relationship with maximum ANPP and had a positive non linear relationship with decomposition rate (Figure 7). This indicated that high decomposition rates decreased AF even though ecosystems with high decomposition rates had high productivity (Figure 2). OR showed the second lowest total AF due to having the highest decomposition rate. AK showed the lowest maximum AF and sum of AF during simulation because of low productivity (Table 5). Even though NH did not have the highest productivity, it showed highest maximum AF and sum of AF over simulation (Table 5 and Figure 6). Maximum AF occurred later when the decomposition rate was smaller (Table 5 and Figure 2).

Scenario VI. Low and median fire frequency generated high fluctuations of AF and the fluctuation started after 100 years (Table 3, Figure 8). NH had the largest difference between highest and lowest average AF (10.5 Mg/ha), while CA showed the smallest difference (3.2 Mg/ha). When dividing the difference of the highest

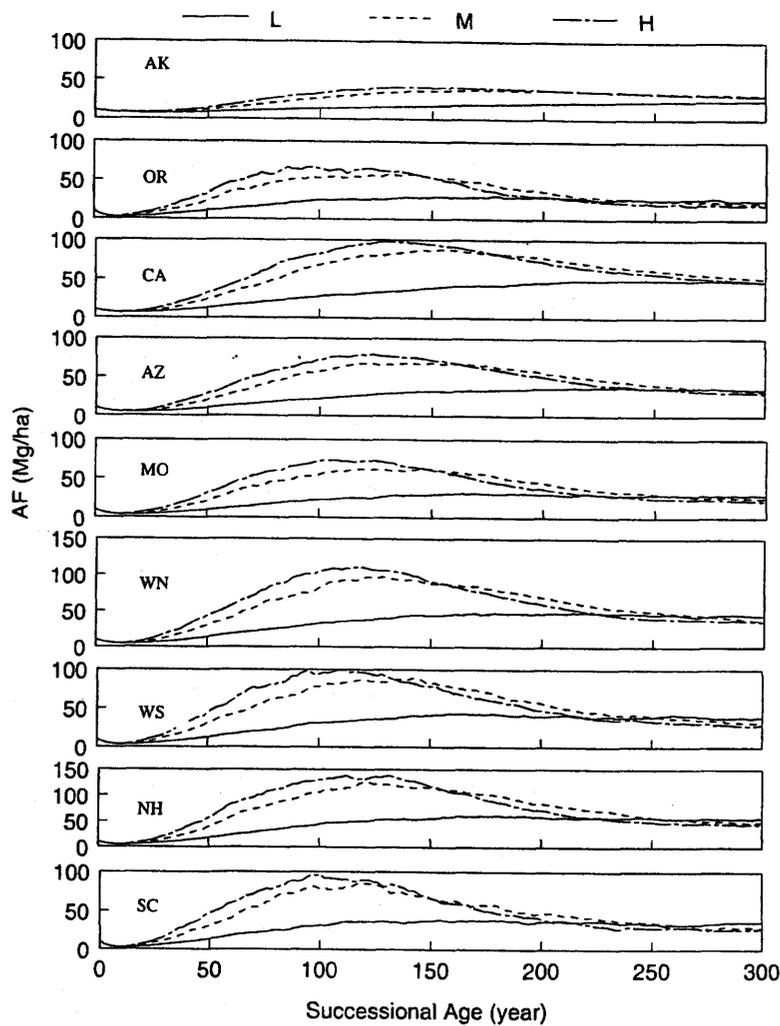


Figure 6. The effect of three levels of mortality rate on available fuel (AF; Mg/ha) at nine study ecosystems (scenario V). See Table 3 for a list of values for these parameters for each run. Ecosystem initials are as in Table 1.

and lowest AF average by lowest AF average, the percent increase was over 80% at AZ and SC, over 60% at AK and NH, and lower than 40% in CA. During the second half of the simulation (151–300 years), the average of AF was lowest under the high fire frequency condition, but, unexpectedly, medium fire frequency exhibited the highest AF average at OR, CA, AZ, WS, and NH. Days with < 20 Mg/ha AF was smallest under medium fire frequency except AK and OR (Figure 9). Low fire frequency had smallest days of < 20 Mg/ha AF at AK and OR, but the difference between low and medium fire frequency was less than 2%. Medium fire frequency induced highest possibility of having > 60 Mg/ha AF at all ecosystems except SC (Figure 9). Because of high productivity in SC, low fire frequency had highest possibility of having > 60 Mg/ha AF. NH had highest possibility of having > 40 Mg/ha AF because of second

highest productivity but moderate decomposition rate (Figure 9).

Scenario VII. FEP produced a higher sum of AF over the 300 year simulations than did HAR (Figure 10). Especially after year 100, FEP had higher AF than HAR over 70% of the time for the nine ecosystems, and HAR had higher AF for only a few years after harvesting. Because harvesting produced a lot of AF within a short period of time, AF in HAR fluctuated more than that in FEP. FEP generally had more days of > 20 Mg/ha AF than HAR during the simulation (Figure 11). However, WN and NH had twice as many days of < 20 Mg/ha under FEP than under HAR. The reason for this was not clear. Both ecosystems had moderate decomposition rates (5th and 6th highest) among study ecosystems. The period during which the ecosystems had > 60 Mg/ha AF was more than twice as long under FEP than

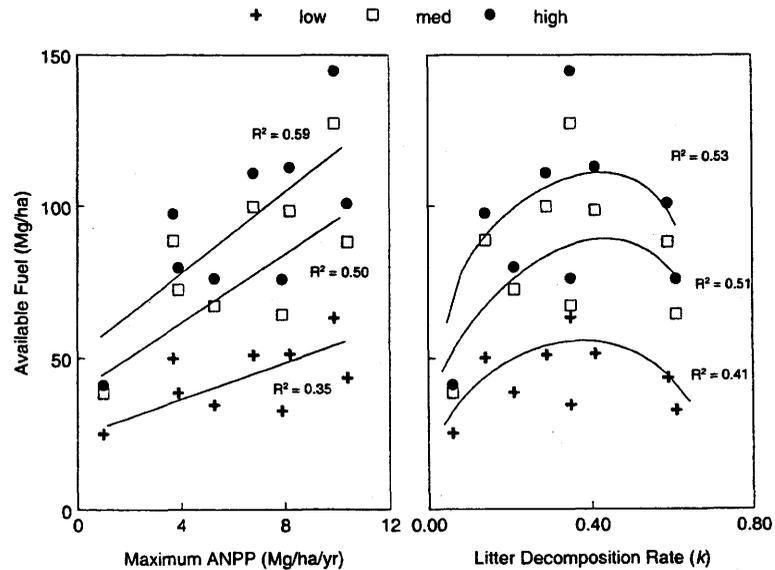


Figure 7. The relationship between average available fuel (Mg/ha) over the 300-year simulation and maximum ANPP (Mg/ha/yr) and litter decomposition rate. The AF values are an average of 10 runs.

under HAR (Figure 11). It was interesting that CA, WN, and WS had 20–40 Mg/ha AF over 65% of simulation days under HAR conditions and had < 20 Mg/ha AF for fewer than 25% of days. This was a higher rate than other ecosystems at the same condition.

Sensitivity Analysis

The model was most sensitive to changes in ANPP and decomposition rate among input parameters under clearcutting and non-harvesting conditions (Table 4). Sensitivity of the model was not always similar between the low and high productivity ecosystems. The low productivity ecosystem (AK) had a higher sensitivity index (SI) over the range of change in decomposition under clear-cutting conditions than under nonharvesting conditions. In contrast, a high productivity ecosystem (SC) had higher SI over the maximum ANPP change and was less sensitive to the decomposition rate under harvesting condition than under nonharvesting condition. These results indicated the combined effect of productivity, decomposition, and harvesting on AF. Even though the percent change was the same for two ecosystems, the amount of slash input after harvesting varied due to different standard values.

Two ecosystems, AK and SC, became more sensitive to the maximum mortality rate and less sensitive to fire possibility under clear-cutting than nonharvesting, because clear-cutting reverted the ecosystem to a young stage, with high productivity and low aboveground biomass. Even though maximum mortality and fire possibility exhibited lower SIs than other ecosystem characteristics, the mean percent change in AF was largest for

these characteristics, because the range of variability was a lot larger than for other variables examined.

Discussion

Ecosystem Characteristics and AF

Four scenarios were applied here to evaluate the effect of ecosystem characteristics on the dynamics of AF (Table 3). We predicted that the pattern of change in AF dynamics and the total amount of AF would change according to the dynamics of ANPP. The AF dynamics that resulted from various ANPP dynamics (scenario I) suggested that the timing, magnitude, and duration of the maximum ANPP are critical factors determining the amount of AF (Figure 3). This indicates that high productivity and high carbon allocation to the litterfall generates more AF. The result also suggests that climate would modify the dynamics of AF change due to changes in species composition and increased CO₂. Our results thus broaden the implications of numerous recent studies suggesting that climate change will directly affect the amount and pattern of forest ecosystem productivity due to increased CO₂ (Aber and others 1995, Pan and others 1998, King and others 1997, Noormets and others 2001, Wang and Curtis 2001), or changes in vegetation composition (He and others 2002, Iversen and Prasad, 2002).

The carbon allocation pattern (F/ANPP) also influenced the AF but had a relatively minor effect early in succession, when production in the ecosystem is lim-

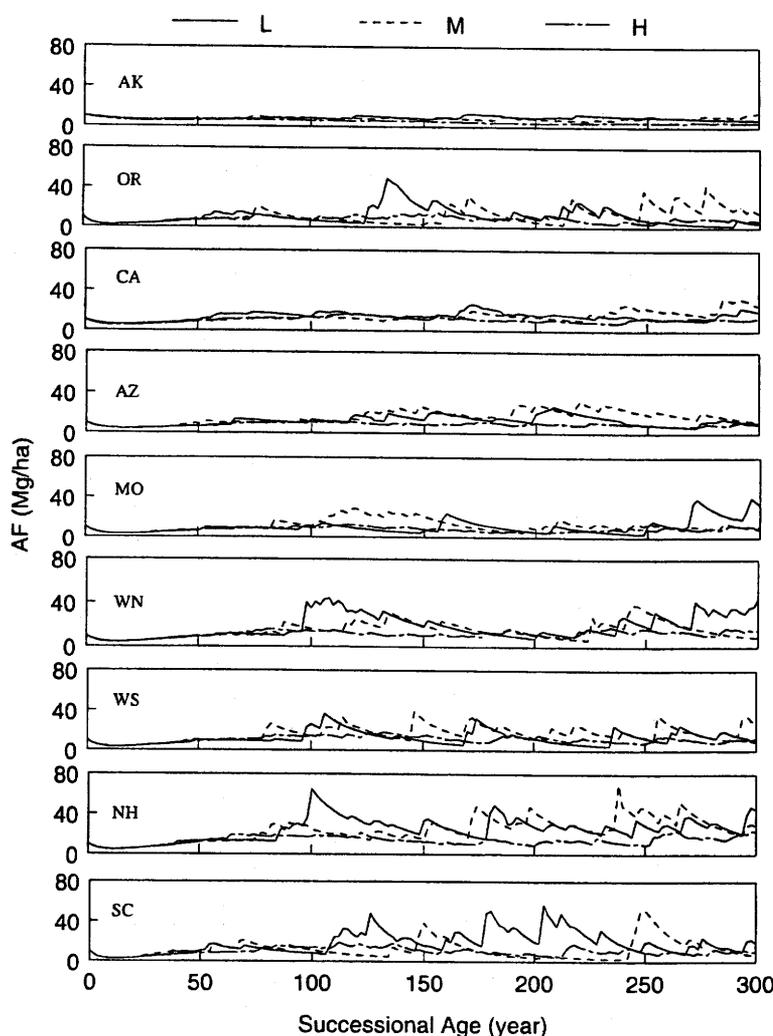


Figure 8. The effect of three levels of fire frequency and intensity on available fuel (Mg/ha) at nine study ecosystems (scenario VI). See Table 3 for a list of values for these parameters for each run. Ecosystem initials are as in Table 1.

ited. AF at the early stage of succession was significantly affected by the initial AF (Figure 4). The results imply that changes in carbon allocation patterns after climate change would not greatly affect young stands much, but that we need to pay attention to the amount of fuel after harvesting or disturbance (Norby and others 1987, Noormets and others 2001).

In an ecosystem with a slow decomposition rate (e.g., AK), a small change in decomposition rate produced a large change in AF; AF accumulates even in these conditions of low productivity because of the low decomposition rate (Figure 5). This suggests that the amount of AF would change drastically in arid or cold regions with even moderate, regional-scale climate change. Sensitivity analysis also demonstrated that decomposition rate had a larger effect on AF than other factors such as carbon allocation, mortality rate, and fire pos-

sibility (Table 4). Decomposition rate will be affected by climate change, since climate change alters temperature, precipitation, and species composition (and chemical property of litter).

Our results, showing the effect of dynamics of ANPP, carbon allocation, and decomposition on dynamics of AF, imply that a heterogeneous landscape structure will produce heterogeneous fuel distributions, because a landscape is composed of various ecosystems with alternative production, patterns of carbon allocation, and decomposition rates. Moreover, the results insist that fuel management will need a special attention on ecosystem adjacency as well as within ecosystem. The quantity and connectivity of fuel are key factors determining the rate of fire spread, intensity and frequency (Miller and Urban 2000).

It was noteworthy that the amount of initial AF was a dominant factor deciding the amount of AF at the early

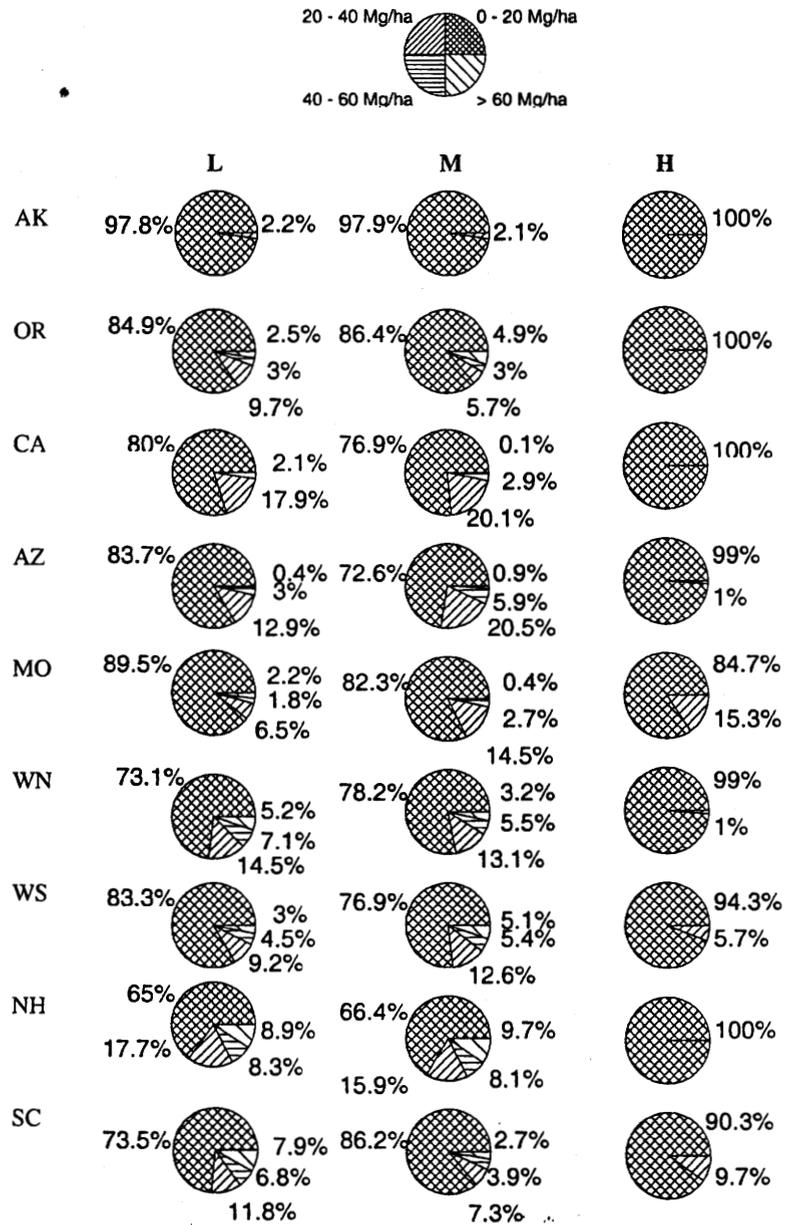


Figure 9. The effect of three levels of fire frequency and intensity on available fuel (AF; Mg/ha). The distribution of annual AF was shown after five runs. See Table 3 for a list of values for these parameters for each run (scenario VI). Ecosystem initials are as in Table 1.

age of succession, while the effects of productivity and F/ANPP dominated at the later period of an ecosystem's development. Decomposition influenced AF throughout simulation. Thus, fuel management strategies must be specific not only to an ecosystem but also to the successional stage of that system. Different processes must be monitored (and manipulated) over the development of a stand to predict adequately the fuel load. The development of management policies that are highly dynamic in space and in time poses a challenge to regional planners. It

is especially important to develop a fuel management plan with an understanding of the relationships between productivity, carbon allocation, and decomposition rate on AF under expected conditions of climate change. Our results suggest that the boreal ecosystem will be affected most among our study ecosystems by climate change, but the degree depends on the variation in productivity and decomposition because of altered climate. SC will be affected least by changes in climatic conditions, due to its high decomposition rate.

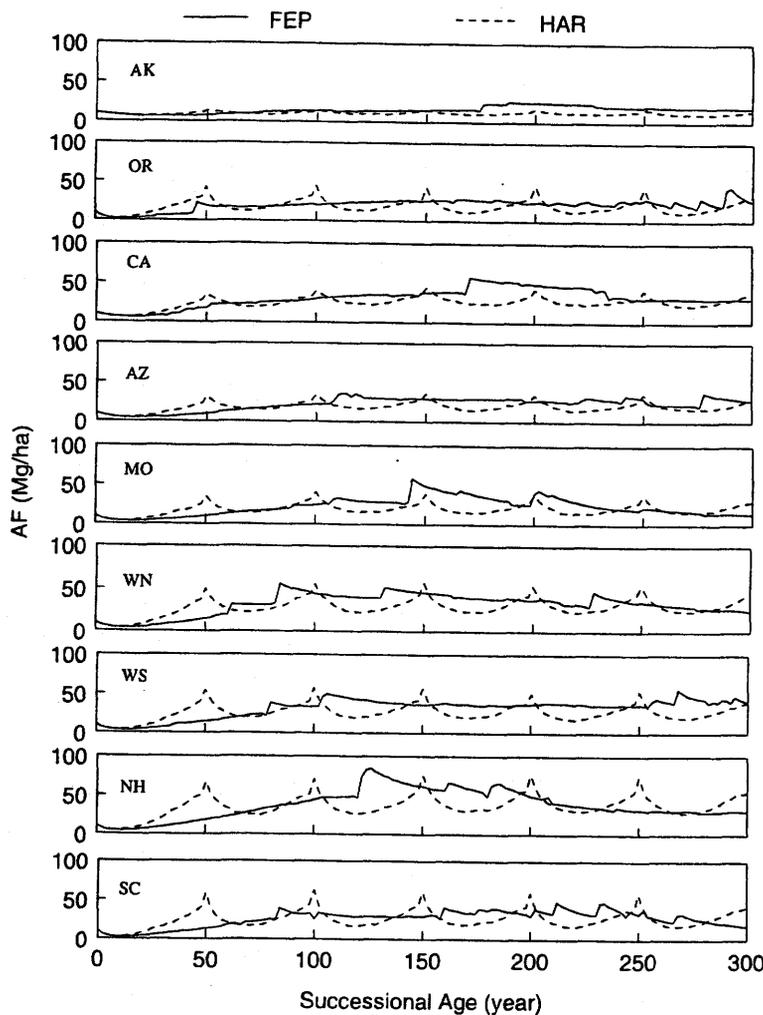


Figure 10. The effect of two management strategies on available fuel (AF; Mg/ha) (scenario VII) at nine study ecosystems. HAR indicates harvesting with intensive management, while FEP is fire exclusion and protection. See Table 3 for a list of values for these parameters for each run. Ecosystem initials are as in Table 1.

Disturbances and AF

Many researchers reported that tree mortality would increase with climate change due to increases in insects, diseases, or natural disasters (Masters and others 1998, Venier and others 1998, Aamlid and others 2000, Abrams and others 2001, Wilf and other 2001). Tree mortality rate is closely related to fuel quality because it determines the proportion of woody material within AF. Because it takes more time to decompose and to ignite woody debris than leaf litter, the amount of woody debris is an important factor influencing fire behavior (Bond and Wilgen 1996, Whelan 1998, DeBano and others 1998). In our work, the peak and the sum of AF were higher under high mortality conditions not only because of the high biomass input, but also because of the composition of the biomass input. Subsequent research could indicate that a high decompo-

sition rate can efficiently reduce the AF; e.g., creating low AF in OR and SC, which had high productivity and decomposition rate under various mortality conditions (Table 5 and Figure 7).

As expected, lower fire frequencies generated larger AF fluctuations. Additionally, AF increased after fire, providing a good source of fuel for future fire ignitions. Vazquez and Moreno (2001) reported that fire burned more often in places that have already experienced fire in central Spain. Historically four of our study ecosystems (AZ, MO, NH, and SC) have short fire intervals (Schmidt and others 2002). The sum of AF increased more than 60% over the 300-year simulations at AZ, NH, and SC, when fire interval was changed from short (10 years) to long (100 years). This implies an efficient controlling effect of frequent fire on AF. Proper use of prescribed fire could provide an effective tool for man-

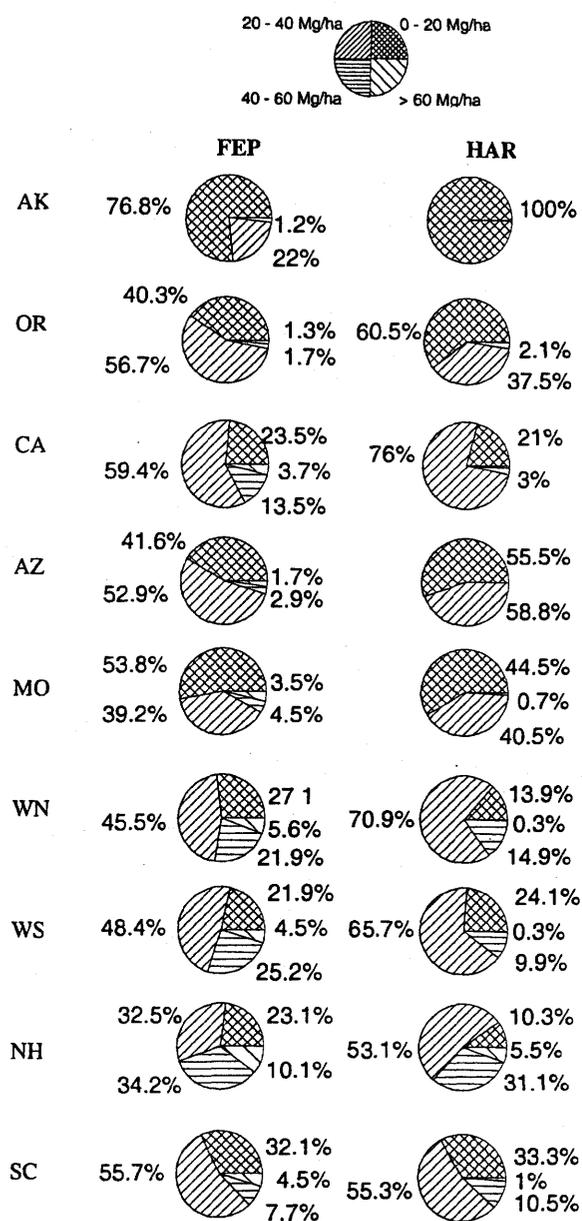


Figure 11. The effect of two management strategies on available fuel (AF; Mg/ha) (scenario VII) at 9 study ecosystems. The distribution of available fuel was shown after five runs for each condition. HAR indicates harvesting with intensive management, while FEP is fire exclusion and protection. See Table 3 for a list of values for these parameters for each run. Ecosystem initials are as in Table 1.

agement of AF. Our results indicated higher fuel load under moderate fire intensity (medium fire frequency). Because moderate fire has the ability to transfer biomass from aboveground biomass to AF (by killing

trees), medium fire frequency resulted in higher fuel load than other fire frequencies (Figure 9). This suggests that we should avoid medium frequency fire to prevent catastrophic fire. Ecosystems with high productivity and moderate decomposition rate, such as NH, had the highest possibility of having a large fuel load (Figure 2). Our result implies that we would have large fuel load if higher atmospheric CO₂ produced more biomass without changing decomposition rate much. We believe that the model would be more realistic if we could consider the effect of fire on ecosystem productivity. However, this is currently not possible due to the limited data available for various ecosystems.

The results of scenario VII demonstrated that high fire frequency, such as prescribed fire, could control the AF effectively. Even though harvesting with intensive management (HAR) had high fuel input from aboveground biomass due to high tree mortality and slash from harvesting, HAR had less AF than fire exclusion and protection (FEP) due to the AF reduction by frequency fire (Cain and others 1998, Stephens 1998), (Figure 10). However, managers must be cautious in using prescribed fire to control fuel loading. Although prescribed fire can reduce the risk of catastrophic fire, it may influence carbon sequestration (e.g., reducing carbon stock in a forest ecosystem), biogeochemical cycling (e.g., decrease the nitrogen pool in the soil or increase nitrogen availability in soil), and habitat fragmentation (e.g., increase edge) (Schlesinger and Gill 1980, Dumontet and others 1997, Whittle and others 1997, Boerner and others 2000, Brais and others 2000, Cochrane 2001). Our results indicated that CA, WN, and WS would have higher fuel load under intensive management than other ecosystems. This was due to a combined effect of model variables and suggested the possibility of large fire with intensive management of these ecosystems. Every disturbance event increased AF remarkably in a short period of time but productivity and decomposition had influence throughout the simulation. Furthermore, disturbances had larger influence on AF in short temporal scale than other factors because of high variability in disturbance regimes.

Model Validation

Validation of this model will only be possible as long-term datasets become available for different forest ecosystems. No datasets were available that included long-term (i.e., up to 300 years) dynamics of AF under different initial conditions and the multiple scenarios of management and disturbance that we studied. Monitoring efforts that are undertaken in national forests in the context of adaptive management experiments

Table 4. Sensitivity of model output (available fuel, Mg/ha) to changes in parameter values under conditions of nonharvesting and clear-cutting (50-year rotation) in AK and SC^a

Standard Value	Tested			Mean		Max		Min	
	Value	% Change	Ecosystem	% Change	SI	% Change	SI	% Change	SI
Nonharvesting									
Ecosystem characteristics									
Maximum ANPP (Mg/ha/yr) = 1	0.8	-20	AK	-13.5	0.68	-10.3	0.52	12.8	-0.64
	1.2	20		25.5	1.28	30.7	1.54	39.3	1.97
Maximum ANPP (Mg/ha/yr) = 10.4	8.3	-20	SC	-18.8	0.94	-15.9	0.8	-12	0.6
	12.5	20		10.6	0.53	-7	-0.35	7.6	0.38
Litter decomposition rate = 0.06	0.05	-20	AK	14.5	-0.73	12.5	-0.63	16.6	-0.83
	0.07	20		-2.6	-0.13	4.8	0.24	11	0.55
Litter decomposition rate = 0.59	0.48	-20	SC	23.7	-1.19	-15.7	0.79	30.6	-1.53
	0.71	20		-16.4	-0.82	-23.2	-1.16	-18.6	-0.93
Species characteristic									
F/ANPP = 0.35	0.3	-14	AK	0.5	-0.04	-0.2	0.01	0.5	-0.04
			SC	5.2	-0.37	5.4	-0.39	-9.5	0.68
	0.4	14	AK	-0.1	-0.01	-2.6	-0.19	17.5	1.25
			SC	-5.9	-0.42	-10.6	-0.76	9.4	0.67
Stem/AB = 0.75	0.7	-7	AK	-7.5	1.07	-11.2	1.6	-17.8	2.54
			SC	-3	0.43	6.1	-0.87	-0.4	0.05
	0.8	7	AK	-0.7	-0.1	1.9	0.27	0.8	0.12
			SC	0.3	0.04	13.2	1.89	-4.1	-0.59
Foliage litter/branch = 0.25	0.1	-60	AK	-1.7	0.03	-2.8	0.05	16.2	-0.27
			SC	-4.7	0.08	-29.8	0.5	10.7	-0.18
	0.4	60	AK	-3.7	-0.06	-0.8	-0.01	2.3	0.04
			SC	-2.5	-0.04	-1.9	-0.03	-7	-0.12
Disturbance Regimes									
Maximum Damage of Fire									
Maximum mortality (%) = 1	5	500	AK	39.9	0.08	38.5	0.08	26.2	0.05
			SC	40.3	0.08	-24.4	-0.05	3.3	0.01
	10	1000	AK	51.5	0.05	54.6	0.05	8.9	0.01
			SC	46.5	0.05	-29.3	-0.03	13.8	0.01
Fire possibility = 0.01	0.03	300	AK	-22.2	-0.07	-12.3	-0.04	-35.4	-0.12
			SC	-16.6	-0.06	-0.9	0.00	-15.6	-0.05
	0.05	500	AK	-44.4	-0.09	-24.3	-0.05	-57.4	-0.11
			SC	-16.2	-0.03	-3.6	-0.01	-13.0	-0.03
On AB (%) = 80	60	-25	AK	-7.7	0.31	-15.2	0.61	-5.0	0.20
			SC	-5.7	0.23	-27.9	1.12	-3.3	0.13
	70	-13	AK	-3.1	0.24	-3.0	0.23	30.6	-2.36
			SC	-6.4	0.49	-30.2	2.32	0.4	-0.03
On AF (%) = 80	60	-25	AK	5.2	-0.21	0.6	-0.02	33.5	-1.34
			SC	-4.3	0.17	-34.0	1.36	-1.2	0.05
	70	-13	AK	5.2	-0.40	10.0	-0.77	22.5	-1.73
			SC	1.4	-0.11	-10.9	0.84	0.4	-0.03
Clear-cutting									
Ecosystem Characteristics									
Maximum ANPP (Mg/ha/yr) = 1	0.8	-20	AK	-17.9	0.89	-21.6	1.08	0.1	0.00
	1.2	20		18.1	0.90	18.9	0.94	66.2	3.31
Maximum ANPP (Mg/ha/yr) = 10.4	8.3	-20	SC	-21.4	1.07	-23.4	1.17	-7.7	0.38
	12.5	20		18.1	0.91	18.3	0.91	16.2	0.81
Litter decomposition rate = 0.06	0.05	-20	AK	15.5	-0.78	14.3	-0.72	50.7	-2.54
	0.07	20		-14.1	-0.71	-13.2	-0.66	-2.6	-0.13
Litter decomposition rate = 0.59	0.48	-20	SC	19.5	-0.97	6.0	-0.30	29.2	-1.46
	0.71	20		-16.3	-0.81	5.7	0.29	-15.1	-0.75
Species Characteristic									
F/ANPP = 0.35	0.3	-14	AK	-1.6	0.11	1.2	-0.08	9.0	-0.65
			SC	0.5	-0.03	4.4	-0.31	-10.3	0.73
	0.4	14	AK	-1.6	-0.11	-0.7	-0.05	4.7	0.34

Table 4. (Continued)

Standard Value	Tested		Ecosystem	Mean		Max		Min	
	Value	% Change		% Change	SI	% Change	SI	% Change	SI
Stem/AB = 0.75	0.7	-7	SC	-5.9	-0.42	-10.4	-0.75	6.9	0.49
			AK	4.8	-0.68	5	-0.72	11.2	-1.61
	0.8	7	SC	-0.6	0.09	6.6	-0.94	1.3	-0.18
			AK	-3.6	-0.51	-9.4	-1.34	11.4	1.63
Foliage litter/branch = 0.25	0.1	-60	SC	-5.1	0.73	-10.8	-1.54	3	0.43
			AK	5.2	-0.09	1.8	-0.03	10.9	-0.18
	0.4	60	SC	2.2	-0.04	-3.9	0.06	-1.3	0.02
			AK	-2.4	-0.04	-2.9	-0.05	7.4	0.12
			SC	-10.5	-0.18	-1.4	-0.02	-11.1	-0.18
Disturbance Regimes									
Maximum Damage of Fire									
Maximum mortality (%) = 1	5	500	AK	45.8	0.09	48.0	0.10	41.4	0.08
			SC	66.6	0.13	10.4	0.02	6.7	0.01
	10	1000	AK	81.8	0.08	80.8	0.08	71.4	0.07
			SC	121.4	0.12	18.8	0.02	19.9	0.02
Fire possibility = 0.01	0.03	300	AK	-16.9	-0.06	-6.1	-0.02	-38.0	-0.13
			SC	4.3	0.01	3.7	0.01	-15.5	-0.05
	0.05	500	AK	-25.2	-0.05	-8.7	-0.02	-60.6	-0.12
			SC	13.8	0.03	17.1	0.03	-12.2	-0.02
On AB (%) = 80	60	-25	AK	-1.9	0.08	-2.2	0.09	7.7	-0.31
			SC	0.2	-0.01	0.8	-0.03	-0.4	0.02
	70	-13	AK	-4.4	0.34	-4.0	0.31	2.9	-0.22
			SC	-2.8	0.22	-1.8	0.14	-5.7	0.44
On AF (%) = 80	60	-25	AK	2.9	-0.12	0.5	-0.02	39.3	-1.57
			SC	-1.4	0.06	5.9	-0.24	4.2	-0.17
	70	-13	AK	0.5	-0.04	-2.9	0.22	17.5	-1.35
			SC	9.0	-0.69	-3.7	0.28	5.1	-0.40

*Refer to Table 1 for details. Reported values for available fuel are the averages, from 10 runs, of the 300-yr (simulation) mean (mean), maximum (max), and minimum (min). Sensitivity index (SI) is the ratio of the percent change in model predictions to the percent change in the input value. Symbols are: ANPP, aboveground net primary production (Mg/ha/yr); AF, available fuel (Mg/ha); and AB, aboveground biomass (Mg/ha).

could greatly contribute to the ability to validate and refine models of forest ecosystem dynamics.

The model has limitations because we do not know precisely several important parameters; e.g., the dynamics of ANPP for each ecosystem, relationships between disturbance and productivity, biomass consumption of fire events, and the true nature of relationships between decomposition rates of litter and woody material. However, the results of our study were consistent with our general knowledge of factors such as fuel load differences under various fire frequencies, the effects of prescribed fire, and fuel load and decomposition rate. By using a PnET and LandNEP model, we could evaluate the variability of AF, but we would be able to predict fuel load more precisely by refining PnET and LandNEP parameters. To show the model's ability we compared the average AF of scenario VI and VII with published forest floor biomass. Vogt and others (1986) reported mean forest floor biomass for the world's forests, in which warm temperate forest, cold temperate broadleaf deciduous, cold temperate needleleaf ever-

green, and boreal needleleaf evergreen were reported as 11.5–20.0, 32.2 (3.9), 44.6 (4.3), and 44.7 (6.0) Mg/ha (standard errors in parentheses), respectively. Our results showed 2.8–45.8 Mg/ha for the AK, boreal needleleaf forest, and 5.7–59.0 for the WN, cold temperate needleleaf forest. Northern hardwood, NH, had 4.3–168.0 Mg/ha. The other six ecosystems demonstrated 6.1–175.0 Mg/ha. AF for temperate forest was mostly < 20 Mg/ha (Figures 9 and 11). AF of AK was a lot smaller than published data, because the simulation was only 300 years and the ecosystem has a very slow turnover. Our results showed high variation in the AF than published forest floor biomass data, because our results reflects various effects of disturbances on AF.

Conclusion

The goal of this study was to demonstrate the possibility of using a simple, generic model to present AF dynamics under various ecosystems and disturbance regimes. Our results revealed that the magnitude and

the point in time of maximum ANPP, as well as the duration of the high productivity condition, had large influences on AF. The model showed that frequent fire reduced AF effectively and that medium frequency fire produced the largest AF. Ecosystems that historically experience frequent fire tend to show large difference in AF between low and high fire frequency. The magnitude and dynamics of productivity and decomposition rate affected AF more strongly than did species characteristics and disturbances. Productivity and decomposition were also closely related to disturbance regimes because of their influence on biomass and productivity. Our study suggested that AF in arid or cold regions would be affected more by climate change than would AF in other regions. Disturbances increased AF very rapidly during a short period. In a short temporal scale, disturbances had a larger influence on AF than other factors because of the high variability in disturbance regimes. Species characteristics had the least effect on AF among studied factors, but species characteristics have a close relationship with productivity and decomposition rate. Further research is needed to evaluate those detailed relationships.

The simple model we presented clearly showed different responses of ecosystems to the various disturbances and ecosystem characteristics. However, we believe that to be able to predict fire behavior at the landscape level, future work must focus on building the capabilities of the model to be spatially-explicit and to represent relationships between fire and productivity, mortality, and fire ignition due to accumulated fuel.

Acknowledgements

This publication was supported by the Joint Fire Science Program of the USDA Forest Service, North Central Research Station, and University of Toledo. We are thankful for the helpful advice and comments of Dr. Daryl Moorhead, Dr. Yude Pan, Dr. Harbin Li, Dr. Malcolm North, and the LEES Lab of the University of Toledo.

References

- Aamlid, D., K. Torseth, K. Venn, A. O. Stuanes, S. Solberg, G. Høyen, N. Christophersen, and E. Framstad. 2000. Changes of forest health in Norwegian boreal forests during 15 years. *Forest Ecology and Management* 127:103–118.
- Aber, J. D., and C. A. Federer. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystem. *Oecologia* 92:463–474.
- Aber, J. D., S. V. Ollinger, C. A. Federer, P. B. Reich, M. L. Goulden, D. W. Kicklighter, J. M. Melillo, and R. G. Lathrop, Jr. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5:207–222.
- Aber, J. D., P. B. Reich, and M. L. Goulden. 1996. Extrapolating leaf CO₂ exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia* 106:257–265.
- Abrams, M. D., C. A. Copenheaver, B. A. Black, and S. van de Gevel. 2001. Dendroecology and climatic impacts for a relict, old-growth, bog forest in the Ridge and Valley Province of central Pennsylvania, U.S.A. *Canadian Journal of Botany* 79(1):58–69.
- Barbour, M. G., and W. D. Billings. 1988. North American terrestrial vegetation. Cambridge, New York, 434 pp.
- Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behaviour in subalpine forests. *Ecology* 76(3):747–762.
- Boerner, R. E. J., S. J. Morris, E. K. Sutherland, and T. F. Hutchinson. 2000. Spatial variability in soil nitrogen dynamics after prescribed burning in Ohio mixed-oak forests. *Landscape Ecology* 15:425–439.
- Bond, W. J., and B. W. van Wilgen. 1996. Fire and Plants. Chapman & Hall, New York, 263 pp.
- Boychuk, D., A. H. Perera, M. T. Ter-Mikaelian, D. L. Martell, and C. Li. 1997. Modelling the effect of spatial scale and correlated fire disturbances on forest age distribution. *Ecological Modelling* 95:145–164.
- Brais, S., P. David, and R. Ouimet. 2000. Impacts of wild fire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. *Forest Ecology and Management* 137:231–243.
- Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14:513–532.
- Cain, M. D., T. B. Wigley, and D. J. Reed. 1998. Prescribed fire effects on structure in uneven-aged stands of loblolly and shortleaf pines. *Wildlife Society Bulletin* 26(2):209–219.
- Clark, J. S. 1990. Fire and climate change during the last 750 yr in Northwestern Minnesota. *Ecological Monographs* 60:135–159.
- Cochrane, M. A. 2001. Synergistic interactions between habitat fragmentation and fire in evergreen tropical forests. *Conservation Biology* 15:1515–1521.
- Cumming, S. G. 2001. Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn?. *Ecological Applications* 11:97–110.
- DeBano, L. F., D. G. Neary, and P. F. Ffolliott. 1998. Fire's effects on ecosystems. John Wiley & Sons, New York, 333 pp.
- Dumontet, S., H. Diné, A. Scopa, A. Mazzatura, and A. Saracino. 1996. Post-fire soil microbial biomass and nutrient content of a pine forest soil from a dunal Mediterranean environment. *Soil Biological Biochemistry* 28(10/11):1467–1475.
- Euskirchen, E. S., J. Chen, H. Li, E. J. Gustafson, and T. R. Crow. 2002. Modeling landscape net ecosystem productivity (LandNEP) under alternative management regimes. *Ecological Modelling* 154:75–91.

- Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest fires. *The Science of the Total Environment* 262:221–229.
- Franklin, J., A. D. Syphard, D. J. Mladenoff, H. S. He, D. K. Simons, R. P. Martin, D. Deutschman, and J. F. O'Leary. 2001. Simulating the effects of different fire regimes on plant functional groups in southern California. *Ecological Modelling* 142:261–283.
- Frelich, L. E., and C. G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper great lakes region. *Ecological Monographs* 61:145–164.
- Gardner, R. H., W. H. Rommer, and M. G. Turner. 1999. Predicting forest fire effect at landscape scales. Pages 163–185 in D. J. Mladenoff and W. L. Baker (eds.), *Spatial modeling of forest landscape change*. Cambridge University Press, Cambridge.
- Gholz, H. L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63(2):469–481.
- Goodale, C. L., J. D. Aber, and E. P. Farrell. 1998. Predicting the relative sensitivity of forest production in Ireland to site quality and climate change. *Climate Research* 10:51–67.
- Gower, S. T., O. Krankina, R. J. Olson, M. Apps, S. Linder, and C. Wang. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecological Applications* 11(5):1395–1411.
- Hargrove, W. W., R. H. Gardner, M. G. Turner, W. H. Romme, and D. G. Despain. 2000. Simulating fire patterns in heterogeneous landscapes. *Ecological Modelling* 135:243–263.
- Harper, V. L. 1965. *Silvics of forest trees of the United States*. Agricultural Handbook No. 271. USDA Forest Service, Washington DC, 762 pp.
- He, H. S., D. J. Mladenoff, and E. J. Gustafson. 2002. Study of landscape change under forest harvesting and climate warming-induced fire disturbance. *Forest Ecology and Management* 155:257–270.
- Iverson, L. R., and A. M. Prasad. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. *Forest Ecology and Management* 155:205–222.
- Jenkins, J. C., D. W. Kicklighter, S. V. Ollinger, J. D. Aber, and J. M. Melillo. 1999. Sources of variability in net primary production predictions at a regional scale: a comparison using PnET-II and TEM 4.0 in Northeastern US forests. *Ecosystems* 2:555–570.
- Johnson, E. A., and C. P. S. Larsen. 1991. Climate-induced change in fire frequency in the southern Canadian Rockies. *Ecology* 72:194–201.
- Karafyllidis, I., and A. Thanailakis. 1997. A model for predicting forest fire spreading using cellular automata. *Ecological Modelling* 99:87–97.
- Kasischke, E. S., K. P. O'Neill, N. F. F. French, L. L. Bourgeau-Chavez. 1994. Controls on patterns of biomass burning in Alaskan boreal forests. Pages 173–196 in E. S. Kasischke and B. J. Stocks (eds.), *Fire, climate change, and carbon cycling in the boreal forest*. Springer-Verlag, New York.
- Kimmins. 1987. *Forest ecology*. Macmillan, Company, New York, 531 pp.
- King, A. W., W. M. Post, and S. D. Wullschlegel. 1997. The potential response of terrestrial carbon storage to changes in climate and atmospheric CO₂. *Climatic Change* 35:199–227.
- Landsberg, J. J., and S. T. Gower. 1997. *Applications of physiological ecology to forest management*. Academic Press, San Diego, 354 pp.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Levine, J. S., and W. R. Cofer, III. 1994. Boreal forest fire emissions and the chemistry of the atmosphere. Pages 31–48 in E. S. Kasischke and B. J. Stocks (eds.), *Fire, climate change, and carbon cycling in the boreal forest*. Springer-Verlag, New York.
- Masters, G. J., V. K. Brown, I. P. Clarke, J. B. Whittaker, and J. A. Hollier. 1998. Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). *Ecological Entomology* 23:45–52.
- McClougherty, C. A., J. Pastor, J. D. Aber, and J. M. Melillo. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology* 66(1):266–275.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465–472.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63(3):621–626.
- Mickler, R. A., T. S. Earnhardt, and J. A. Moore. 2002. Regional estimation of current and future forest biomass. *Environmental Pollution* 16:S7–S16.
- Miller, C., and D. L. Urban. 2000. Connectivity of forest fuels and surface fire regimes. *Landscape Ecology* 15:145–154.
- Monk, C. D., G. I. Child, and S. A. Nicholson. 1970. Biomass, litter and leaf surface area estimates of an oak-hickory forest. *Oikos* 21:138–141.
- Moorhead, D. L., and J. F. Reynolds. 1991. A general model of litter decomposition in the northern Chihuahuan Desert. *Ecological Modelling* 56:197–219.
- Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. *Ecology* 66(4):1377–1390.
- Noormets, A., E. P. McDonald, R. E. Dickson, E. L. Kruger, A. Sober, J. G. Isebrands, and D. F. Karnosky. 2001. The effect of elevated carbon dioxide and ozone on leaf- and branch-level photosynthesis and potential plant-level carbon gain in aspen. *Trees* 15:262–270.
- Norby, R. J., E. G. O'Neill, W. G. Hood, and R. J. Luxmoore. 1987. Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO₂ enrichment. *Tree Physiology* 3:203–210.
- Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343:51–53.
- Pan, Y., J. M. Melillo, A. D. McGuire, D. W. Kicklighter, L. F. Pitelka, K. Hibbard, L. L. Pierce, S. W. Running, D. S. Ojima, W. J. Parton, and D. S. Schimel. 1998. Modeled responses of terrestrial ecosystems to elevated atmospheric CO₂: a comparison of simulations by the biogeochemical

- models of the vegetation/ecosystem modeling and analysis project (VEMAP). *Oecologia* 114:389–404.
- Peng, C. 2000. Understanding the role of forest simulation models in sustainable forest management. *Environmental Impact Assessment Review* 20:481–501.
- Schlesinger, W. H., and D. S. Gill. 1980. Biomass, production, and changes in the availability of light, water, and nutrients during the development of pure stands of the chaparral shrub, *Ceanothus Megacarpus*, after fire. *Ecology* 61:781–789.
- Schmidt, K. M., J. P. Menakis, C. C. Hardy, W. J. Hann, and D. L. Bunnell. 2002. Development of coarse-scale spatial data for wildland fire and fuel management. GTR RMRS-87. USDA Forest Service, Washington, DC.
- Stephens, S. L. 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behaviour in Sierra Nevada mixed-conifer forests. *Forest Ecology and Management* 105:21–35.
- Stocks, B. J., M. A. Fosberg, T. J. Lynham, L. Mearns, B. M. Wotton, Q. Yang, J.-Z. Jin, K. Lawrence, G. R. Hartley, J. A. Mason, and D. W. McKenney. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. *Climate Change* 38:1–13.
- Ter-Mikaelian, M. T., and M. D. Korzukhin. 1997. Biomass equations for sixty-five North American tree species. *Forest Ecology and Management* 97:1–24.
- Thompson, W. A., I. Vertinsky, H. Schreier, and B. A. Blackwell. 2000. Using forest fire hazard modeling in multiple use forest management planning. *Forest Ecology and Management* 134:163–176.
- Van Cleve, K., L. Oliver, R. Schlentner, L. A. Viereck, and C. T. Dyrness. 1983. Productivity and nutrient cycling in taiga forest ecosystems. *Canadian Journal of Forest Research* 13:747–766.
- Vazquez, A., and J. M. Moreno. 2001. Spatial distribution of forest fires in Sierra de Gredos. *Forest Ecology and Management* 147:5–65.
- Venier, L. A., A. A. Hopkin, D. W. McKenney, and Y. Wang. 1998. A spatial, climate-determined risk rating for Scleroderris disease of pines in Ontario. *Canadian Journal of Forest Research* 28(9):1398–1404.
- Vogt, K. A., C. C. Grier, and D. J. Vogt. 1986. Production turnover, and nutrient dynamics of above- and below-ground detritus of world forests. *Advances in Ecological Research* 15:303–377.
- Wagner, R. G., and M. T. Ter-Mikaelian. 1999. Comparison of biomass component equations for four species of northern coniferous tree seedlings. *Annals of Forest Science* 56:193–199.
- Wang, C., S. T. Gower, Y. Wang, H. Zhao, P. Yan, and B. P. Bond-Lamberty. 2001. The influence of fire on carbon distribution and net primary production of boreal *Larix gmelinii* forests in north-eastern China. *Global Change Biology* 7:719–730.
- Wang, X., and P. S. Curtis. 2001. Gender-specific responses of *Populus tremuloides* to atmospheric CO₂ enrichment. *New Phytologist* 150:675–684.
- Waring, R. H., and S. W. Running. 1998. Forest ecosystems. Academic Press, San Diego, 340 pp.
- Wei, K., J. P. Kimmins, and G. Zhou. 2003. Disturbances and the sustainability of long-term site productivity in lodgepole pine forests in the central interior of British Columbia—an ecosystem modeling approach. *Ecological Modelling* 164:239–256.
- Whelan, R. J. 1998. The ecology of fire. Cambridge University Press, Cambridge, 346 pp.
- Whittle, C. A., L. C. Duchesne, and T. Needham. 1997. The impact of broadcast burning and fire severity on species composition and abundance of surface vegetation in a jack pine clear-cut. *Forest Ecology and Management* 94:141–148.
- Wilf, P., C. C. Labandeira, K. R. Johnson, P. D. Coley, and A. D. Cutter. 2001. Insect herbivory, plant defense, and early Cenozoic climate change. *PNAS* 98:6211–6226.
- Yin, X. 1993. Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Canadian Journal of Forest Research* 23:1587–1602.
- Yin, X. 1999. The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. *Oecologia* 121:81–98.