Landscape Composition in Aspen Woodlands Under Various Modeled Fire Regimes

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Abstract

Quaking aspen (*Populus tremuloides*) is declining across the western United States. Aspen habitats are diverse plant communities in this region and loss of these habitats can cause shifts in biodiversity, productivity, and hydrology across spatial scales. Western aspen occurs on the majority of sites seral to conifer species, and long-term maintenance of these aspen woodlands requires periodic fire. We use field data, remotely sensed data, and fire atlas information to develop a spatially explicit landscape simulation model to assess the effects of current and historic wildfire regimes and prescribed burning programs on landscape vegetation composition in the Owyhee Mountains, Idaho. The model is run in the Tool for Exploratory Landscape Scenario Analyses (TELSA) environment. Model outputs depict the future structural makeup and species composition of the landscape at selected time steps under simulated management scenarios. Under current fire regimes and in the absence of management activities, loss of seral aspen stands will continue to occur. However, a return to historic fire regimes, burning 12–14 percent of the modeled landscape per decade, maintains the majority of aspen stands in early and mid seral woodland stages and minimizes the loss of aspen. A fire rotation of 70–80 years was estimated for the historic fire regime while the current fire regime resulted in a fire rotation of 340–450 years. Implementation of prescribed burning programs, treating aspen and young conifer woodlands according to historic fire occurrence probabilities, are predicted to prevent conifer dominance and loss of aspen stands.

Keywords: Aspen, *Populus tremuloides*, VDDT, TELSA, succession, disturbance, fire regime

Introduction

Region-wide decline of quaking aspen has caused concerns that human alteration of vegetation successional and disturbance dynamics jeopardize the long-term persistence of these woodlands. (Bartos 2001, Kay 1997, Shepperd et al. 2001, Smith and Smith 2005). Aspen are an important component that provides ecosystem diversity in the conifer dominated western mountains. Aspen ecosystems provide a disproportionately diverse array of habitats for flora and fauna for its relatively small area on the landscape (Bartos 2001, Jones 1993, Kay 1997, Winternitz 1980). In the semi-arid western U.S., aspen commonly occurs as a disturbance-dependent species, seral to conifer species (Bartos 2001, Kaye et al. 2005, Smith and Smith, 2005). It is well known that in mixed aspen and conifer stands, periodic fires prevent conifer dominance and possible loss of the aspen stand (Baker 1925, Bartos and Mueggler 1981, DeByle et al. 1987). Although the aspen is a prolific seed producer, the conditions required for successful seed germination and establishment are rare in the American West (Mitton and Grant 1996). Aspen clones in the region reproduce primarily via vegetative suckering and therefore it can be concluded that an aspen clone lost is not likely to re-establish via seed. An example of recent successful establishment of aspen seedlings occurred in response to the severe fires in 1988 in Yellowstone National Park (Romme et al. 2005). All aspen stands are however not seral to conifers. Aspen stands in certain biophysical settings and away from a conifer seed source have been observed to exist as self-regenerating even and uneven aged stands that do not appear to be at risk of

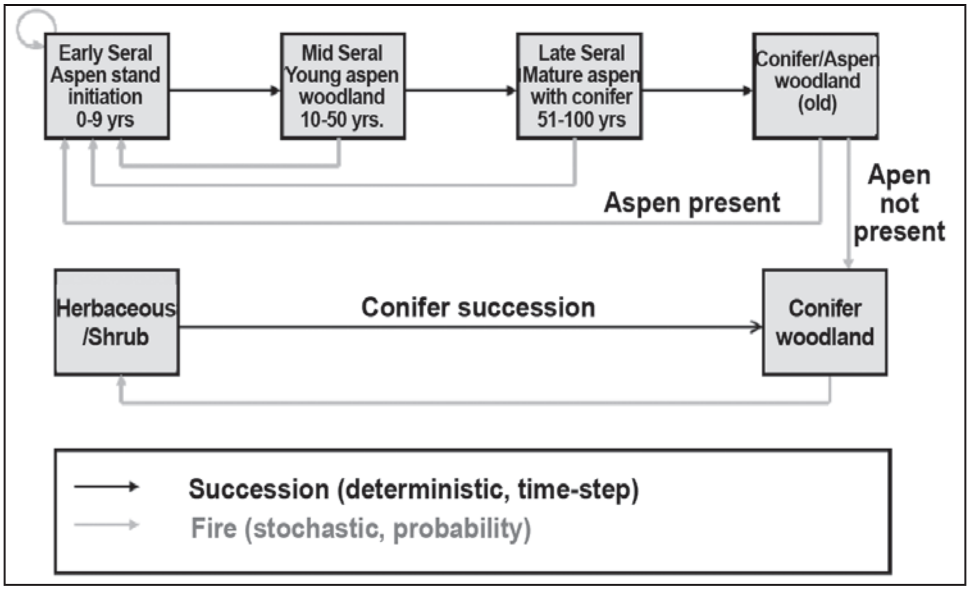

Figure 1—Simplified pathway diagram for upland aspen/conifer communities that served as the conceptual model for vegetation dynamics in the Owyhee Mountains.

rapid decline due to conifer expansion even in the absence of fire (Mueggler 1989, Rogers et al. 2010, Strand et al. 2009). Mortality in these stable aspen stands has however been observed over the past decade (Worall et al. 2008). This mortality has been correlated with rising temperatures and drought in the southwestern U.S. (Huang and Anderegg 2011; van Mantgem and Stephenspn 2007, van Mantgem et al. 2009) potentially caused by hydraulic failure of roots (Anderegg et al. 2012).

Successional rates within pure and mixed aspen stands and interactions with fire and herbivory have been studied at the stand level, however, little work has examined these dynamics across larger landscapes over decades. Computer simulation models may be a means to better understand these dynamics in landscapes where aspen is present. Such landscape level succession/disturbance models have been used for evaluating habitat patterns in forests and woodlands (e.g., Klenner et al., 2000; Bunting et al. 2007) and assessment of fire regimes and management scenarios (Bunting et al. 2007, Franklin et al. 2001, Keane et al. 1997).

In response to the need for better understanding of interactions between aspen/conifer succession and fire regimes across larger landscapes over decadal time scales, we simulated a number of aspen management scenarios using a conceptual state-and-transition model developed for aspen/conifer woodlands (fig. 1, Strand et al. 2009) and the Tool for Exploratory Landscape Scenario Analyses (TELSA, ESSA Technology 2003). We utilized field and remotely sensed data combined with spatially explicit modeling to estimate the effects of current and historic fire regimes on landscape vegetation composition and structure, emphasizing aspen woodland dynamics. Although prescribed fire has been suggested and applied to mitigate the frequent fire events common in the western mountains of the past, with the goal of maintaining and restoring aspen woodlands (Bates et al. 2004, Brown and DeByle 1989, Miller et al. 2005, Shepperd, 2001), little is known about how such management affects the vegetation composition and structure spatially and temporally. We therefore also incorporate prescribed burning scenarios into our modeling runs. In particular, we address the following four research questions: (1) Can we simulate the fire regime that maintained aspen stands prior to Euro-American settlement?; (2) What extent and frequency of fire is required to stabilize the current land cover composition within aspen woodlands?; (3) What is the structural composition of aspen woodlands under historic and current fire occurrence probabilities, and under prescribed burning scenarios?; and (4) What is the effect of fire size on the long-term maintenance of aspen woodlands?

Methods

Site Description

The mountain ranges of the Owyhee Plateau in SW Idaho (116.4° W, 43.0° N) contain vegetation communities representative of many semi-arid mountains of the western U.S.A. We include two study areas in this research: the South Mountain study area encompassing 17,000 ha and the Silver City Range covering 20,000 ha. Western juniper woodlands (*Juniperus occidentalis* ssp. *occidentalis*) and sagebrush (*Artemisia* spp.) steppe dominate the landscape above 1700 m altitude, interspersed with pockets of aspen, mountain shrub species, and meadows. Western juniper is gradually replaced by Douglas-fir (*Pseudotsuga menziesii* ssp. *glauca*) above 1850 m in both mountain ranges. Aspen stands are commonly located on cool northeast facing slopes, in concave snow and moisture accumulation areas. Soils that support aspen include deep fine-loamy and loamy-skeletal mixed pachic or typic cryoborols, rich in organic material with high water-holding capacity (USDA NRCS 1998). In the area, aspen occurs in three distinctly different biophysical settings with different successional trajectories and rates; pure aspen on south-facing aspects above 1900 m, aspen on wet micro sites, and aspen/conifer stands on mountain hillsides (Strand et al., 2009). Areas that support aspen receive 400-1000 mm annual precipitation (Oregon Climate Service 1999) in the form of rain in the spring and fall, and snow during the winter. Summer and early fall are warm and dry with an average high temperature in July of 26.7º C (WRCC 2003).

Field Data Collection

A total of 82 aspen clones along elevational and succesional gradients were sampled across the study areas. Site characteristics were recorded: slope, elevation, aspect, and Universal Transverse Mercator (UTM) coordinates. We further collected stand characteristics: canopy cover of aspen and conifers in the crown and below 2-m height, increment cores from the five tallest mature aspen and conifer trees (thought to be among the oldest), stem counts of aspen and conifers in three height classes (< 2 m, 2 m up to 75 percent of the stand height, and trees taller than 75 percent of the stand height). The increment cores were mounted and sanded, and the annual growth rings counted in a stereo-microscope for the age estimate. Faint annual rings in aspen were stained with phloroglucinol solution before ring counting (Patterson 1959).

Model Requirements and Assumptions

TELSA (Essa Technology 2003) is a spatially explicit landscape dynamics model environment, allowing the user to explore the effect of natural and anthropogenic disturbances on landscape composition. Input data to this model include potential natural plant communities, initial vegetation types and structural stages, along with natural and anthropogenic disturbance agents and pathways. Succession is treated as a deterministic variable with a constant pre-determined time period between successional states.

Successional rates in upland aspen stands are based on models developed by Strand et al. (2009). They discovered that the successional development in upland aspen/conifer woodlands on the Owyhee Plateau can be characterized with a positive exponential function where the proportion conifer in the stand is fit against time since conifers were introduced to the stand:

$$f(t) = A\ e^{kt}\ (0 < f(t) < 1) \quad (1)$$

where f(t) is the proportional cover of conifers in the aspen stand (e.g. conifer cover divided by total cover of all tree species), which is close to 0 at $t = 0$ and approaches 1 at complete conifer dominance, and the constant k represents the successional rate. The best model estimate ($R^2 = 0.63$, F=114.4, p<0.001) was:

$$f(t) = 0.0177\ e^{0.0315*t}\ 0 < f(t) < 1 \quad (2)$$

where the model constant A = 0.0177 and successional rate k = 0.0315. Time since the initiation of conifer establishment was the only variable that significantly affected the successional rate in this data set although environmental variables such as terrain attributes, soil and climate data were included in model development (Strand et al. 2009). This model was developed using only upland aspen/conifer stands, and does not apply to aspen in riparian areas nor

Table 1—Areas of mapped cover types within the South Mountain and Silver City Range study sites on the Owyhee Plateau in SW Idaho

Cover type	South Mountain Area (ha)	Silver City Range Area (ha)
Aspen woodland (pure aspen)	496	236
Aspen/Douglas-fir woodland	1371	2002
Aspen/Western juniper woodland	745	527
Bare/Rock	2	72
Ceanothus/Mesic shrub	299	365
Douglas-fir	298	923
Juniper woodland/Low sage open	1635	787
Juniper woodland/Low sage closed	1056	141
Juniper woodland/Mountain big sage open	4062	3321
Juniper woodland/Mountain big sage closed	3451	1259
Curlleaf mountain-mahogany	227	1983
Low sagebrush steppe	1335	2343
Mountain big sagebrush steppe	1729	5992
Wet meadow	42	189

areas around meadows and springs. An exponential increase in the conifer dominance occurs 50–60 years after conifers were initiated to the aspen stand, as prolific conifer seed production and spread begins (see Strand et al. 2009). This exponential increase in conifer dominance marks the transition of mid seral aspen into late seral aspen (fig. 1).

In TELSA, disturbance is treated as a stochastic variable driven by user-defined probabilities. This stochastic component in landscape models results in many possible landscape configurations given the same input variables, allowing the range of variability in landscape composition to be explored statistically.

Spatially explicit simulations in TELSA require information in the form of GIS data layers (digital maps) of the study area. Each landscape unit in the map must be classified hierarchically in a potential vegetation type (PVT), current cover type, and current structural class. PVTs are groupings of habitat types or ecological sites with similar overstory composition in the absence of a disturbance and similar environmental requirements. For the sagebrush steppe/juniper woodlands we employed the PVT classification developed by Bunting et al. (2007) in the same general study area. As mentioned earlier, aspen woodlands are potentially present in three PVTs (Strand et al. 2009): pure aspen, aspen/western juniper, and aspen/Douglas-fir.

In the simulation, aspen stands on pure aspen PVTs represent stands that can be expected to self-regenerate and persist as uneven aged aspen stands for decades into the future. Over time, aspen on aspen/western juniper and aspen/Douglas-fir PVTs become outcompeted by western juniper and Douglas-fir, respectively, and in the absence of a disturbance within a certain time period will permanently convert to pure conifer stands (Wall et al. 2001, Strand et al. 2009). Aspen/conifer stands that burn prior to permanent conversion to conifer stands are assumed to return to stand initiation aspen stands (fig. 1).

Each landscape unit is characterized by its PVT, but also by the current cover and structure. The current cover map represents the vegetation currently present on the ground and includes the climax vegetation classes represented by the PVTs with the addition of seral cover types such as grasslands, shrublands, and young woodlands. The structural classes within aspen succession include: stand initiation aspen, young aspen woodlands, mature aspen woodlands, aspen woodlands with conifers, and conifer woodlands. We used input GIS layers previously developed for the Owyhee Plateau by Strand (2007) depicting the PVT, current vegetation and structural stages, see table 1 for landscape distribution of cover types and table 2 and figure 2 for distribution of PVTs.

Table 2—Areas of mapped potential vegetation types (PVT) within the study area

Cover type	Silver City South Mountain Area (ha)	Range Area (ha)
Aspen woodland	496	236
Aspen/Douglas-fir woodland	1669	2925
Aspen/Western juniper woodland	745 5	27
Bare/Rock	2 7	2
Ceanothus/Mesic shrub	299	365
Juniper woodland/Low sage	4028	3272
Juniper woodland/Mountain big sage	9240	10571
Curlleaf mountain-mahogany	227	1983
Wet meadow	42	189

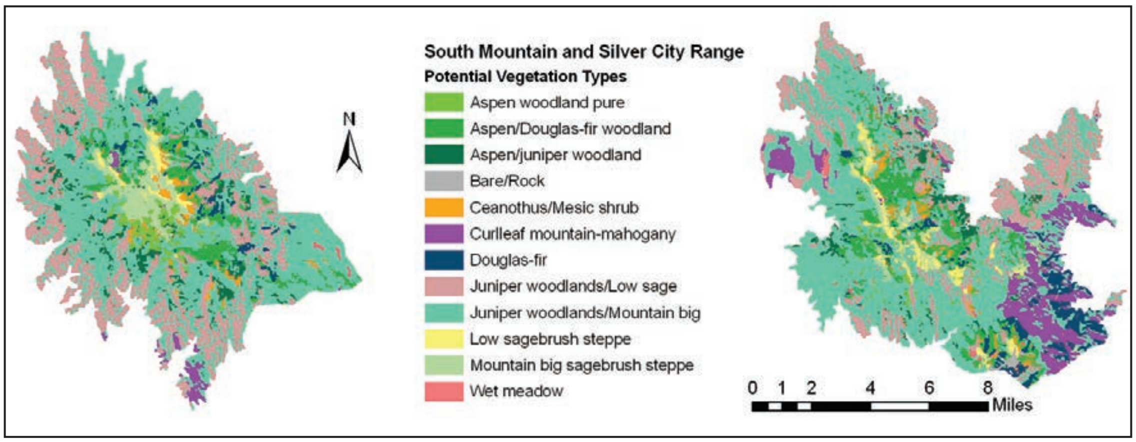

Figure 2—Potential vegetation maps of the South Mountain (left) and the Silver City (right) 856 areas of the Owyhee Mountains in SW Idaho.

In general, we make the assumption that PVTs are static, and consequently a landscape unit occupied by a PVT at the beginning of the simulation will stay within that PVT throughout the simulation. The land cover and structural vegetation stage within the landscape unit may change via the successional time step or revert to an earlier seral stage via disturbance (i.e. fire). This static view of PVT works well in most ecosystems within reasonable time periods. In the aspen ecosystem, however, this static view is limited for two reasons. First, aspen has been observed to expand into adjacent areas with low canopy cover such as grasslands and sagebrush steppe. Such expansion of aspen clones was observed during field assessments during this study and has also been reported by other researchers (Manier and Laven 2001). Expansion of aspen could not be incorporated directly in the TELSA simulations, but upper limits of aspen expansion were estimated based on expansion rates and the length of currently available aspen/sagebrush edge. The rate of aspen expansion into adjacent cover types, was estimated by recording the decrease of aspen stem age along four transects perpendicular to the aspen/sagebrush steppe ecotone during the 2006 field season in the nearby Jarbidge Mountains. The four transects show similar expansion rates of approximately 0.5 m per year (20 m expansion in 40 years). We assume here that the aspen expansion rates are similar in the Jarbidge and Owyhee Mountains, because the two mountain ranges are located at similar latitudes and span similar altitudes. Second, it is currently not known how long and under what conditions an aspen clone can persist after conifers dominate a site. It has been suggested that aspen clones can be sustained for decades in the absence of mature ramets maintained only by transient suckers

(Despain 1990). This hypothesis has not yet been tested (Hessl 2002); and we assume here that old mixed aspen/conifer stands permanently transition to conifer stands 120 years after aspen regeneration has diminished due to conifer dominance within a stand (Strand et al., 2009). In such stands we do not expect a fire event to return the landscape unit to young aspen woodland but rather to young conifer woodlands, resulting in permanent loss of aspen within the landscape unit (fig. 1).

The current wildfire size distribution was calculated from a fire database provided by the Interior Columbia Basin Ecosystem Management Project (http://www.icbemp.gov/) for the interior Columbia River basin between 1986–1992. The maximum allowable area burned in prescribed fires was set to 1000 ha per year in scenarios that included prescribed fire.

Current wildfire probability of occurrence in each PVT and structural stage was computed from an overlay analysis in a GIS (ESRI 1999–2005) of digital fire atlas data from 1957–2002 and a recently developed landcover map for the Owyhee Plateau (Roth 2004). Historic wildfire probabilities were estimated based on the 40–60 year fire interval suggested by Jones and DeByle (1985a) for aspen woodland with increasing fire probability later in succession where flammable conifers are present. The fire occurrence probability for juniper woodlands at their initiation was derived from the 40–50 year mean fire return interval suggested by Burkhardt and Tisdale (1976). As western juniper woodlands mature, there is a decrease in understory productivity resulting in lower amounts of fine fuels and a reduced ability to carry fire in these older woodlands (Miller et al. 2005, Bunting et al. 2007). For mid- and late seral juniper woodlands, we employed fire occurrence probabilities used by Bunting et al. (2007).

During a TELSA simulation, fires start in random locations according to the assigned disturbance probability. A fire that starts in a landscape unit can spread into an adjacent landscape unit if that unit is eligible for fire disturbance. The size of wildfires and prescribed fires were randomly assigned to each fire based on the pre-defined fire size probability distribution.

Six major assumptions and simplifications relating to aspen ecology and succession are important parts of this model. They are:

1) Aspen reproduction from seed is not included in this model.
2) Aspen are not allowed to spread laterally into other PVTs (e.g. sagebrush).
3) Adjacency between vegetation types does not affect succession.
4) Fire will convert a conifer dominated aspen stand to a young aspen stand regardless of the pre-disturbance conifer cover in the stand, i.e. no legacy effects are considered.
5) Aspen stands are permanently converted to conifer stands 120 years after aspen suckering has ceased due to conifer dominance (i.e. ~230 years after conifer initiation into the stand).
6) Effects of insects, disease, and animal use are not included in this model.

The potential effects of these assumptions and simplifications on model outcome and interpretation are addressed in the Discussion section.

Model Scenarios

To determine whether the assigned model parameters were realistic, we tested the model by subtracting 100 years from the age of each landscape unit followed by a simulation 100 years into the future using assigned successional rates, fire probabilities, and fire size distributions. The actual current landscape composition was then compared to the modeled composition. Future landscape compositions for the two study areas were evaluated at 25, 50, 100 and 200 years from current time. Fire management regimes included:

Scenario 1: Current fire management i.e. suppressed wildfire only.

Scenario 2: Historic wildfire probabilities.

Scenario 3: Historic wildfire probabilities with larger fires.

Scenario 4: Prescribed fire in aspen/conifer woodlands according to historic fire probabilities, no prescribed fire applied in other cover types.

Table 3—The TELSA model requires estimates of the disturbance size distribution as part of the input. This table describes the percent of fires in each size class for the five simulation scenarios. The current wildfire size distribution was estimated from the Interior Columbia Basin Ecosystem Management Project geographic database (ICBEMP 1995)

Scenario	Fire size 0-1 ha	Fire size 1-10 ha	Fire size 10-100 ha	Fire size 100-1000 ha
1	90	5	3	2
2	90	5	3	2
3	50	20	15	15
4	1	4	25	70
5	1	4	25	70

Table 4—This table described the current and historic probability of wildfire occurrence in the major PVTs and structural stages on the Owyhee Plateau

PVT	Structural stage	Current wildfire probability	Historic wildfire probability
Low sagebrush steppe	Grassland	0.00064	0.002
	Low sagebrush steppe	0.00064	0.005
Mtn big sagebrush steppe	Grassland	0.001	0.002
	Mtn big sagebrush steppe	0.001	0.02
Juniper woodlands/Low sagebrush steppe	Grassland	0.00064	0.002
	Low sagebrush steppe	0.00064	0.02
	Stand initiation juniper	0.0008	0.01
	Open young woodland	0.0008	0.001
	Young multistory woodland	0.0005	0.002
	Old multistory woodland	0.0004	0.006
Juniper woodlands/Mtn. big sagebrush steppe	Grassland	0.001	0.005
	Mtn. Big sagebrush steppe	0.001	0.02
	Stand initiation juniper	0.001	0.02
	Open young woodland	0.0007	0.01
	Young multistory woodland	0.0002	0.002
	Old multistory woodland	0.00009	0.001
Aspen woodlands/conifer	Young woodlands	0.0002	0.0002
	Mature woodlands	0.0002	0.005
	Woodlands with conifer	0.0002	0.01
	Conifer/aspen woodland	0.0002	0.0

Scenario 5: Prescribed fire in aspen/conifer woodlands and young juniper woodlands according to historic fire probabilities.

Although succession in TELSA is treated as a deterministic variable with a pre-determined time period between transitions, fire starts and fire size are stochastic components in the model. Because of this stochastic element, the model results will vary between runs even though the input variables and landscape maps are identical. Simulations were therefore run 10 times for each management scenario to quantify the variability between runs. Means and variances were calculated and displayed as error bars in the resulting graphs.

Results

Fire Occurrence, Size, and Probabilities

Fire perimeter data from the Bureau of Land Management (BLM) 1957–2002 show that only 94 ha of the combined

Table 5—This table provides a comparison of the current cover type distribution and the 100-year simulated current cover type distribution for South Mountain

Cover type	Current area ha	Simulated current ha
Aspen	2611	2610
Ceanothus / Mesic shrub	477	362
Curlleaf mountain-mahogany	223	117
Douglas-fir	298	284
Grasslands/Meadow	70	402
Juniper woodland	10193	11831
Sagebrush steppe	3053	1136

37 000 ha study region has burned in wildfires within this time period. Overlay analysis in GIS reveals that none of these fires occurred on soils that support aspen woodlands. Fire records prior to 1957 are not available. Prescribed fire in aspen stands has occurred on the Owyhee Plateau, but to this date not in modeled areas.

The current wildfire size distribution was estimated from the Interior Columbia Basin Ecosystem Management Project database (ICBEMP 1995, table 3), which indicates that most wildfires within the region become less than 1 hectare in size. Information about the historical wildfire size distribution is not available for the study area and we therefore simulated two historical wildfire scenarios with two different fire size distributions (scenarios 2 and 3, table 3) to test the sensitivity of fire size within the model. In scenario 2 we used the same fire size distribution as scenario 1 (90 percent of fires become < 1 ha in size) while in scenario 3 the proportion of fires larger than 1 ha was increased (see table 3 for more detail). Commonly, prescribed fires are in the size class 10-1000 ha (scenarios 4 and 5, table 3). Current wildfire probabilities were estimated via overlay analysis between current cover types (Roth, 2004) and the digital fire atlas obtained from the BLM for the time period 1957–2002. Historical wildfire probabilities were based on literature references (DeByle et al. 1987, Bunting et al. 2007; see table 4).

Management Scenarios

To evaluate the input model parameters, we tested the model by subtracting 100 years from the age of each landscape unit followed by a simulation 100 years into the future using assigned successional rates, fire probabilities, and size distributions. We compare the resultant modeled landscape composition to the actual current landscape composition in table 5. The model accurately simulated the current area of aspen using the inputs from 100 years back in time. The simulated area of juniper woodlands was larger, and the area in sagebrush steppe and grasslands was smaller than observed. These results suggest that the simulated successional rates within the juniper PVTs are slightly overestimated in the model. We attribute this to the fact that the juniper successional models were developed in a different study area on Juniper Mountain south of South Mountain.

Future landscape composition of aspen seral stages was predicted under varying management scenarios for South Mountain and the Silver City Range (figs. 3 and 4). Under current wildfire regimes the early, mid, and late seral woodlands are predicted to decrease within the next 100 years while the old woodlands are predicted to increase. Continuation of current fire management is predicted to result in loss of aspen woodlands within the next 100 years, with additional losses in the following century.

Modeled historical fire regimes predicted an increase in early and mid seral woodlands while the area in late seral woodlands decreased and old woodlands remained at current levels. Scenarios 2 and 3, historic fire probabilities with smaller and larger fire size distributions, yielded similar results with an increase in the mean area of the early and mid seral aspen classes for the scenario with larger fire size compared to the smaller fire size. This difference, however, falls within the variability of the 10 runs (figs. 3 and 4).

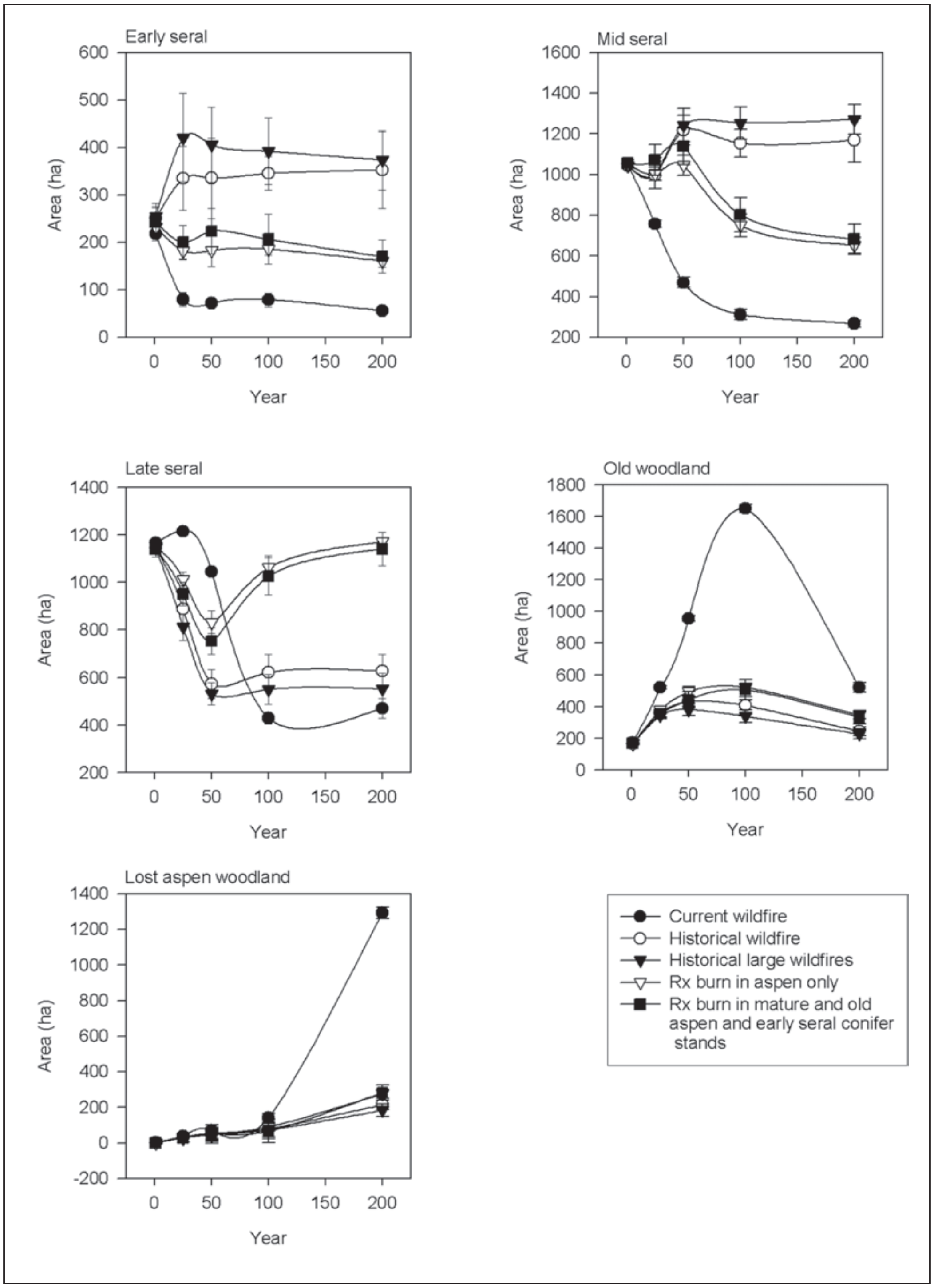

Figure 3—Area of aspen woodland in different seral stages under five simulated management scenarios on South Mountain. The total area in aspen vegetation is currently 2610 ha.

Prescribed fire applied in aspen only (scenario 4) and in aspen and young juniper (scenario 5) resulted in a decrease in early and mid seral aspen woodlands. The area in late seral aspen woodlands initially decreased but reached a stable level, similar to the current area, approximately 100 years into the future. The area in old aspen and the loss

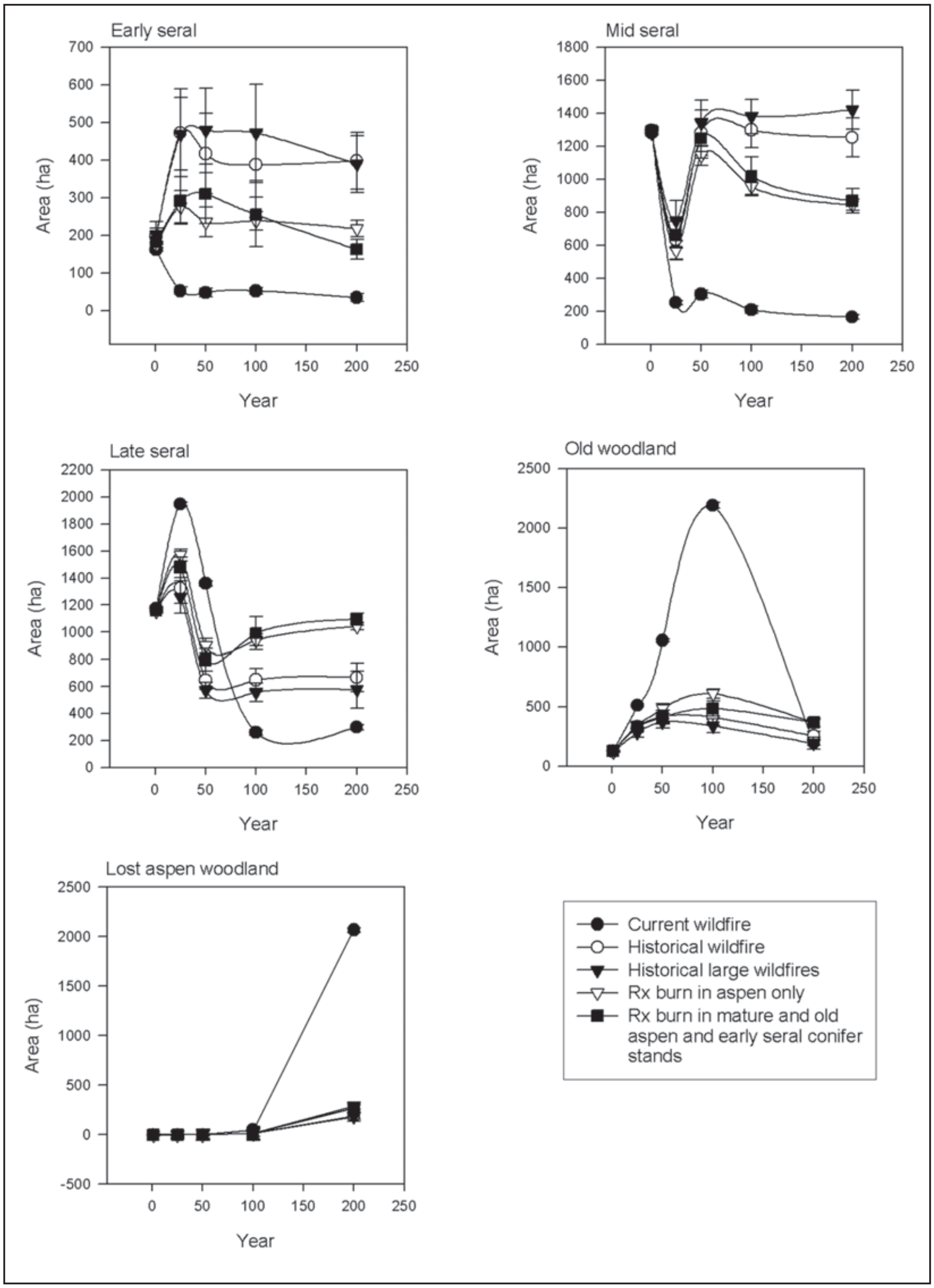

Figure 4—Area of aspen woodland in different seral stages under five simulated management scenarios in the Silver City Range. The total area in aspen vegetation is currently 2765 ha.

of aspen is similar for the prescribed fire and historical fire management scenarios. Under historical fire regimes a larger portion of the landscape was stable in mid seral woodlands, while for the prescribed fire simulations a larger portion of the area stabilized in late seral woodlands. These predictions indicate that the aspen loss can largely be

Table 6—Fire rotation and decadal proportion of the landscape burned under modeled fire regimes

Study area	Scenario	Fire rotation (years)	Fire area per decade (percent)
South Mountain	Current wildfire (1)	340	2.9
South Mountain	Historic fire probabilities (2)	82	12.2
South Mountain	Historic prob. large fires (3)	72	13.9
South Mountain	Prescribed fire in aspen (4)	466	2.1
South Mountain	Prescribed fire in aspen+young juniper (5)	192	5.2
Silver City	Current wildfire (1)	449	2.2
Silver City	Historic fire probabilities (2)	79	12.7
Silver City	Historic prob. large fires (3)	66	15.1
Silver City	Prescribed fire in aspen (4)	448	2.2
Silver City	Prescribed fire in aspen+young juniper (5)	178	5.6

mitigated by implementing appropriate prescribed burning programs.

Fire rotation is a measure of how many years it would take to burn an area equal to the study area under a given fire regime. Under historical fire probabilities, our simulations indicate that the fire rotation for the two study areas was 70–80 years, while at current fire management the estimated fire rotation was 340 years on South Mountain and 449 years in the Silver City area (table 6). Fire rotations were also computed for the prescribed fire scenarios, although these numbers may not be meaningful for aspen management because the simulated prescribed fire programs here target aspen stands. According to this model, the historical fire regimes—which are able to maintain the majority of aspen stands in early and mid seral woodlands—required that approximately 12–14 percent of the area burns per decade. Currently, only 2–3 percent of the landscape burns per decade, of which the majority of the burned area is sagebrush steppe rather than juniper or aspen woodlands.

Aspen Expansion

Given the aspen expansion rate into sagebrush of approximately 0.5 m per year (20 m expansion in 40 years) and the length of the aspen/sagebrush steppe boundary within the South Mountain study area, the maximum area gained by aspen clones in 100 years would be 340 ha, corresponding to 13 percent of the current aspen cover. These results indicate how much assumption 2, "Aspen is not allowed to spread laterally in the model", affects the interpretation of the model results. Although we realize that the expansion rate likely varies with annual precipitation, site productivity, and other environmental conditions, the average expansion rate estimated here provides a guideline for assumptions made regarding the importance of aspen expansion for landscape composition.

Discussion

Fire Disturbance and Landscape Dynamics

Modeling results suggest that under a continuation of current fire regimes, aspen will continue to decline on both South Mountain and in the Silver City Range. Current mid- and late seral aspen/conifer stands will continue to age over the next 50–100 years and eventually become permanently converted to conifer woodlands in the absence of disturbance (figs. 3 and 4). Through simulations of succession-disturbance dynamics in TELSA under current and historic fire regimes and prescribed fire scenarios, we are able to address the four questions posted in the introduction.

1) Can we simulate the historical fire regime that maintained aspen stands prior to Euro-American settlement?

Results produced under the historical fire conditions yield a landscape where over half of the aspen area is in early or mid seral successional classes and the loss of aspen is low. The distribution between successional stages is:

14 percent in the early seral stage, 45 percent in mid seral and 35 percent in late seral (late seral and old combined, see figs. 3 and 4). We predict an ~ 6 percent loss of aspen (compared to the current area occupied by aspen) over the 200 year simulated time period even under historic fire regimes, which is likely due to caveats in the model assumptions. Within the model there is no avenue for aspen recruitment via seed or expansion of aspen into previously aspen free habitats. Under stochastic and randomly distributed application of fire, by necessity, some aspen stands will by chance escape fire for a long enough time period to convert to conifer woodlands. Sexual reproduction of aspen is not likely to occur in the West, although such infrequent severe fire events enabling seedling establishment may be important for aspen regeneration long term. This model also did not include expansion of aspen into shrub and grasslands. We here estimate that the maximum estimated expansion rate for aspen on South Mountain (340 ha in 100 years or 13 percent of the current aspen area) would more than counteract the predicted loss of 6 percent in our model.

Whether this model scenario is indeed a fair representation of fire regimes prior to European settlement is difficult to assess, but comparisons can be made to independent estimates from other researchers. Our simulated historical fire regime resulted in a fire rotation of 70–80 years, which is somewhat longer than the mean fire frequency of 50 years suggested by Jones and DeByle (1985a). We also compared the area in successional classes to predictions presented as part of the LANDFIRE Rapid Assessment Reference Condition Models. For the aspen biophysical setting in mapping zone 18, which includes southern Idaho, the suggested distribution among successional stages is 14 percent in early seral, 40 percent in mid seral and 45 percent in the late seral class, which is very similar to our modeled results. Loss of aspen is avoided in the LANDFIRE reference models by including an insect/disease outbreak every 200 years, which reverts aging aspen stands to earlier successional stages.

2) What extent and frequency of fire (burned area per decade) is required to stabilize the current land cover composition within aspen woodlands?

Under historical conditions we predict that 12–14 percent of the landscape burned per decade and that this amount of fire largely maintained the aspen stands in early and mid seral stages. Current fire regimes, resulting in approximately 2 percent of the landscape burned per decade, is (according to model predictions) clearly not enough to avoid aspen loss or to maintain aspen in early and mid seral stages. Prescribed fire applied in aspen and young juniper woodland results in 5–6 percent of the landscape burned per decade while application of fire in aspen stands only results in 2 percent of the landscape burned per decade. By targeting only aspen/conifer stands, aspen could theoretically be kept on the landscape with minimal burning efforts. In reality this may not be a feasible management scenario considering that all surrounding conifer woodlands would be allowed to mature to late successional stages providing an increasing source of conifer seeds and probability for conifer establishment. Application of prescribed fire in both aspen and young juniper according to historic fire occurrence probabilities would both maintain aspen in a younger stage and minimize the source of conifer seeds. Prescribed fire applied also in mature juniper woodlands was not considered due to the practical difficulty of burning such areas. In both prescribed fire scenarios, all conifer woodlands that currently exist in mature successional stages would therefore continue to mature and remain on the landscape.

3) What is the structural composition within aspen woodlands under historical and current fire probabilities? What is the structural composition under prescribed burning scenarios?

Landscape composition at user selected times is reported by TELSA at defined disturbance regimes and initial landscape composition. The initial landscape composition is only important to gain understanding about a certain study area over a relatively short period. As the model is allowed to run for a sufficiently long time period the landscape composition at the equilibrium state is independent of the initial landscape composition. Under historic fire regimes approximately 60 percent of the aspen woodlands exist in an early or mid successional stage, while this proportion is ~10 percent for current fire regimes and ~30 percent for the prescribed burning scenarios. Under prescribed burning scenarios ~45 percent of the aspen develop into late 406 seral woodlands, of which the majority is the self-regenerating pure aspen stands where 407 prescribed fire was not applied. The amount of aspen in the old successional class and lost aspen woodlands is similar in the historic and prescribed burning scenarios (figs. 3 and 4).

4) What is the effect of fire size on the long-term maintenance of aspen woodlands?

Historical fire regimes (scenarios 2 and 3) were simulated with two fire size distributions (table 3). Although the scenario with larger fires (scenario 3) results in a larger area in early and mid seral woodlands, the difference is within the error bar generated for multiple runs. Based on these results we conclude that there is marginal effect of fire size on the structural composition of aspen woodlands and the long-term maintenance of aspen woodlands. It is important to note that these results in the "model world" do not necessarily apply to the "real world". A closer evaluation of the model assumptions leads us to believe that this model is not well suited to answer question 4. One could speculate that larger fires would benefit the fire dependent aspen woodlands in several ways. Larger fires would reduce the conifer seed source and probability of conifer establishment within newly established aspen stands. Modeling of this phenomenon would require the spatial model to account for seed dispersal to adjacent stands such that aspen stands that are closer to conifer woodlands would be more likely to experience conifer establishment and eventually dominance. Larger fires would also clear larger areas, into which aspen could expand. Aspen clones surrounded by closed conifer woodlands have no means of extending their area. The ability for aspen to expand into adjacent grass and shrub lands was not incorporated in this model. An improved model where the distance to seed source and expansion of existing aspen stands were included would likely show different results with regards to the importance of fire size.

Model Assumptions and Their Potential Effects on Model Outcomes

The full complexity of ecosystem interactions is neither feasible nor necessary to capture in a model to improve the understanding for how the system functions. The model presented here is a form of deductive reasoning where the model results are a product of the input data and model assumptions. In the following section, we discuss the major assumptions and their potential effect on model outcomes.

1) *Aspen reproduction from seed is not included.* Although aspen in the western mountains reproduce primarily via vegetative suckering (Baker 1925, Barnes 1975, Mitton and Grant 1996, Romme et al. 2005), recruitment via sexual reproduction has occurred after severe fires such as the 1988 fires in Yellowstone National Park (Romme et al. 2005). We did not include the occurrence of such infrequent and severe fires because the occurrence probability and the probability of aspen establishment are unknown. Also, such a fire is unlikely to occur within the modeled time period due to the stochastic nature of these events combined with fire suppression. Such large infrequent fire events represent non-equilibrium conditions (Turner and Romme 1994) over the spatial and temporal extents addressed in this model. Including infrequent severe fires leading to aspen regeneration by seed would require modeling over a much longer time period and extent.

2) *Aspen cannot spread into other potential vegetation types.* Expansion of aspen into adjacent shrub- or grasslands has been observed (Manier and Laven 2001). We calculated that aspen on South Mountain could expand as much as 340 ha in 100 years (13 percent of the current aspen cover) in the absence of fire if all aspen along aspen/sagebrush boundaries were expanding. This expansion would to some extent counteract the small aspen loss predicted under historical fire regime scenarios.

3) *Adjacency between vegetation types does not affect succession.* In our model, the presence of a conifer seed source near an aspen stand does not affect the rate of succession. Incorporation of such effects would result in variability in successional rates between stands far away and close to conifers. Considering adjacent conifer seed sources would increase successional rates in scenarios where only

aspen stands are burned while conifer stands are left to mature and become a neighboring seed source.

4) *Fire will convert a conifer dominated aspen stand to a young aspen stand regardless of the pre-disturbance conifer cover in the stand, i.e. no legacy effects are considered.* It can be expected that an aspen stand with high cover of seed producing conifers is more likely to experience more rapid succession after a fire than a stand with only a few conifer seedlings pre-fire. Western juniper seeds, for example, are persistent in the seed bank (Chambers et al., 1999) and may survive a low severity fire and hence become an immediate source of juniper seedlings after a fire.

5) *Aspen stands are permanently converted to conifer stands 120 years after aspen suckering has ceased due to conifer dominance, i.e. ~230 years after conifer initiation into the stand.* Reduced vegetative reproduction in aspen stands that are becoming dominated by conifers has been observed by several researchers (Bartos and Campbell 1998, Kaye et al. 2005, Strand et al. 2009). It is however not known how long an aspen clone can remain dormant in a non-reproductive state and still return to an aspen woodland after a fire, hereafter referred to as the persistence time. The actual time an aspen clone can remain under conifer dominance could be significantly different from 120 years. The 120-year time period was selected because this can be considered the life expectancy of existing mature aspen ramets in the conifer-dominated stand. When all mature ramets are gone and the stand is no longer regenerating, permanent loss of the stand is assumed to occur resulting in a change from an aspen/conifer PVT to a conifer PVT. Strand et al. (2009) show that the length of the persistence time only affects the starting point of rapid aspen decline (see figs. 3 and 4). The length of the persistence time is also extremely important when considering the possibility that one avenue for aspen rejuvenation is infrequent intense wildfires creating a substrate suitable for aspen seedling establishment. In a scenario of effective fire suppression where large intense fires (ones not possible to suppress) occur at an interval longer than the persistence time for all aspen clones in the area, local extinction of aspen will occur in aspen/confer PVTs.

6) *Effects of insects, disease, and animal use on aspen and conifers are not included in this model.* Fire is the only disturbance included in this model, although previous work has demonstrated that insects, disease, animal browsing, and wind felling are examples of other disturbances affecting aspen and conifer succession (Jones and DeByle 1985b, Jones et al. 1985, Kay and Bartos 2000, Kaye et al. 2005). We deliberately omitted these disturbance agents in the model to gain a clearer understanding of the effects of fire disturbance alone on the ecosystem. The LANDFIRE rapid assessment program (http://www.Landfire.gov) has produced a series of reference condition (RC) models, which provide an estimate of the expected distribution of successional classes under pre-European settlement conditions. The LANDFIRE RC model for aspen in the northern Great Basin incorporates an insect/disease disturbance in aging aspen/conifer stands every 200 years which restores aspen to an earlier successional state and maintains aspen on the landscape. Regardless of whether the infrequent catastrophic event is a large severe fire promoting sexual reproduction of aspen, an infrequent disease outbreak, or a land- slide, it is questionable whether managers of aspen resources can rely on such infrequent stochastic events for ecosystem maintenance. Kulakowski et al. (2006, p. 1397) state that "*human perceptions of ecosystems are often on time scales that are shorter than the cycles of natural variation within ecosystems*". With the help of field observations, mapping, and modeling we can begin to comprehend aspen ecosystem succession and disturbance dynamics at multiple spatial and temporal scales. The question is, can we manage aspen and other resources at such broad temporal scales?

Management Implications

Over long time periods (i.e. centennial) aspen will most likely remain a part of the western landscape unless the climate changes drastically such that it is unfavorable for the species. Quaking aspen are apparently tolerant to a variety of fire frequencies and severities; vegetative reproduction occurs when fires are less severe and more frequent. Reproduction via seed can occur after extensive severe fire events if the soil moisture and weather conditions are within the 'window of opportunity' for aspen regeneration (Romme et al. 2005). Therefore, even if aspen that is seral to conifers are eliminated from the landscape due to fire suppression, eventually a large-scale disturbance event will likely occur and pure aspen stands, riparian aspen, and aspen occurring on microsites may provide seed for aspen recruitment and establishment. This optimistic outlook does not offer a solution to the immediate concern over the current aspen declines across the West. Human activity and needs, and current fire policy makes it unlikely that aspen woodlands within the West will return to historic fire regimes and active management has been proposed in locations where maintenance of aspen is a priority. Before engaging in management activities it is naturally important to make appropriate ecological field assessments to evaluate the current state of the aspen stands, their successional trajectories in a landscape context, and the presence of possible stressors.

In this analysis we show via modeling that the historical fire frequency suggested by Jones and DeByle (1985a) maintains aspen on the landscape. In many areas it is not feasible or desirable to return to historic fire regimes, and prescribed burning may be an alternative. Model predictions suggest that in theory prescribed burning programs can mitigate aspen loss and maintain aspen woodlands in younger seral stages. Restoration of aspen woodlands has been suggested (Bartos et al. 1991, Brown and DeByle 1989, Miller et al. 2005) and such restoration projects (e.g., Bates and Miller 2004, Bates et al. 2004, Brown and DeByle 1989) have been carried out by managers. Ecological factors that must be considered prior to burning are the fuels composition and structure, current understory composition, presence of weeds, and the successional stage of aspen woodland development (Miller et al. 2005). Other concerns are post-fire wildlife and animal use (Bartos and Campbell 1998, Kay and Bartos 2001, Kaye et al. 2005), which can jeopardize aspen suckers and prevent the aspen clone recovery. Post-treatment monitoring is recommended to better understanding the browsing pressure on the treated aspen clone.

Where fire is undesirable for restoration, Shepperd (2001) has suggested a series of alternative management activities including commercial harvest, mechanical root stimulation, removal of competing vegetation, protection of regeneration from herbivory and regeneration from seed. Cutting of conifers followed by prescribed fire has also been applied (Bates and Miller 2004). The felled conifers provide a fuel ladder that help carry the fire in aspen stands which are commonly difficult to burn.

Ecosystem management requires assessment of interactions among succession, natural disturbance regimes and management activities. Landscape dynamics models such as TELSA provide an avenue for managers, scientists, and stakeholders to evaluate the long-term effect of changing natural disturbance regimes and management activities on landscape vegetation composition. All models have limitations. It is important to clearly understand the model assumptions during interpretation of model results and during the decision making process. The ultimate test of a model is not how accurate or truthful it is, but only whether one is likely to make a better decision with it than without it (Starfield 1997).

The modeling results presented here indicate that active management is necessary in areas where aspen are seral to conifers and aspen maintenance is a management goal unless we rely on infrequent severe disturbance events to maintain these aspen resources. Reliance on severe disturbance will likely lead to continued decline of aspen in our study region and across the western U.S.

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English Equivalents

When you know:	Multiply by:	To find:
Millimeters (mm)	0.039	Inches
Centimeters (cm)	.394	Inches
Meters (m)	3.28	Feet
Kilometers (km)	.621	Miles
Hectares (ha)	2.47	Acres
Square meters (m^2)	10.76	Square feet (ft^3)
Square kilometers (km^2)	.386	Square miles
Cubic meters per second (m^3/sec)	35.3	Cubic feet per second (cfs)
Degrees Celsius	1.8 °C + 32	Degrees Fahrenheit

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