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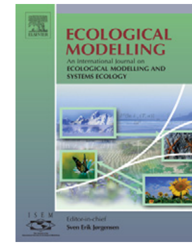


# A spatially explicit model to predict future landscape composition of aspen woodlands under various management scenarios

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ABSTRACT

Quaking aspen (*Populus tremuloides*) is declining across the western United States. Aspen habitats are among the most diverse plant communities in this region and loss of these habitats can result in shifts in biodiversity, productivity, and hydrology across a range of 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. Over the past century, fire intervals, extents, and intensities have been insufficient to regenerate aspen stands at historic rates; however the effects of various fire regimes and management scenarios on aspen vegetation dynamics at broad spatial and temporal scales are unexplored. Here 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 across two mountain ranges in the Owyhee Plateau, Idaho. Model outputs depict the future structural makeup and species composition of the landscape at selected time steps under simulated management scenarios. We found that under current fire regimes and in the absence of management activities, loss of seral aspen stands will continue to occur over the next two centuries. However, a return to historic fire regimes (burning 12–14% of the modeled landscape per decade) would maintain 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, underscoring the fact that fire is currently lacking in the system. 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.



## 1. Introduction

Widespread population decline of quaking aspen (*Populus tremuloides*) across the western United States has caused concerns that human alteration of vegetation successional and disturbance dynamics in this region jeopardize the long-term persistence of these woodlands (Kay, 1997; Bartos, 2001; Shepperd et al., 2001; Smith and Smith, 2005). Aspen is a critical component of ecosystem diversity in the conifer dominated western mountains and provides a disproportionately diverse array of habitats for flora and fauna for its relatively small area of occurrence on the landscape (Winternitz, 1980;

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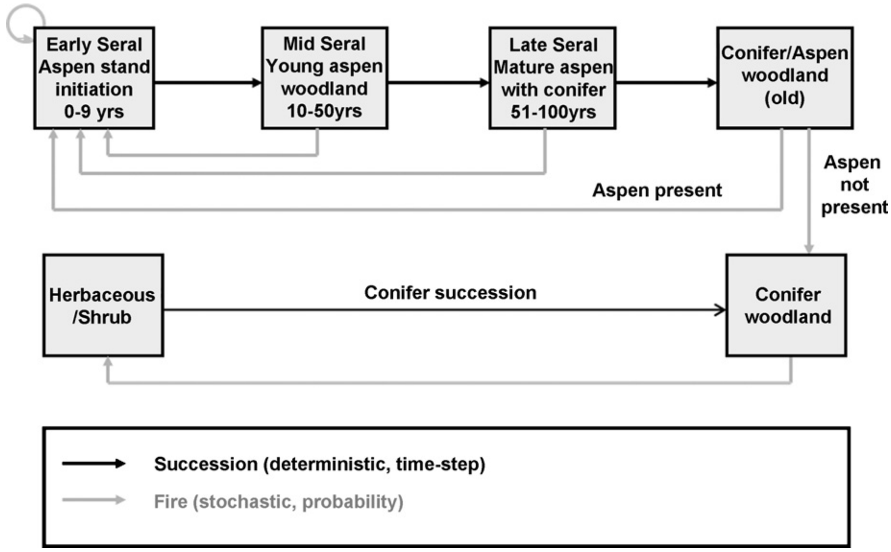


**Fig. 1 – Simplified pathway diagram for upland aspen/conifer communities that served as the conceptual model for vegetation dynamics in the Owyhee Mountains.**

Jones, 1993; Kay, 1997; Bartos, 2001; Chong et al., 2001; Rumble et al., 2001). 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 established that in mixed aspen/conifer stands, periodic fires are necessary to prevent conifer dominance and possible loss of the aspen stand (Baker, 1925; Bartos and Mueggler, 1981; DeByle et al., 1987). Although quaking 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 an aspen clone lost in this region is not likely to re-establish via seed. An example of recent successful establishment of aspen seedlings has occurred in response to severe Yellowstone National Park fires of 1988 (Romme et al., 2005). It is important to note that not all aspen stands are 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 rapid decline even in the absence of fire (Mueggler, 1989; Romme et al., 2001; Strand, 2007).

Although successional rates within pure and mixed aspen stands and interactions with fire and herbivory have been studied at the stand level, little work has examined these dynamics at the landscape scale, and over decadal time periods. Computer simulation models may be a means to better understand these dynamics in aspen landscapes. Early vegetation dynamics models were limited to applications at the stand level, for example the forest 'gap' models of the JABOWA family (Botkin et al., 1972), the individual tree model FOREST (Ek and Monserud, 1974) and later, spatially explicit stand level tree models such as SORTIE (Pacala et al., 1993). Due to the limited simulation extent (<0.1–10 ha) these models necessarily focused on succession rather than disturbance. Models capable of simulating landscape change incorporating both succession and disturbance processes have evolved over the last 15 years (McGarigal and Romme, 2003; Mladenoff, 2004). Continued evolvement of such models has been enabled by recent developments in landscape ecology, the availability of remotely sensed imagery, development of image processing techniques, and the improved computer power within geographic information systems (GISs). Landscape scale succession/disturbance models are important tools 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 (Keane et al., 1997; Franklin et al., 2001; Bunting et al., 2007).

Modeling change in structural landscape composition through time is challenging because of many interacting factors such as successional rates, disturbance regimes, disturbance agents and management activities. It can be helpful to begin the modeling effort by developing a conceptual model of the ecosystem. Strand (2007) developed such a conceptual state-and-transition model for upland western aspen in mixed aspen/conifer stands. The state-and-transition model describes vegetation states of aspen along the aspen-conifer successional gradient, e.g. stand initiation, young and mature woodlands, and conifer dominated woodlands (Fig. 1). These states are connected by transitional pathways, where natural disturbance or management action enables transitions among states. This conceptual model has been parameterized using field data collected along a successional gradient in the Owyhee Mountains (Strand, 2007) and implemented in the vegetation dynamics computer simulation model VDDT (Kurz et al., 2000; Essa Technology, 2003b; Merzenich and Frid, 2005). Although VDDT is a landscape scale computer simulation model with the capability of estimating landscape proportion within vegetation types and structural stages at user defined disturbance probabilities and pathways, the model is not spatially explicit and does not incorporate disturbance (fire) spread between land cover types adjacent to each other nor the effect of disturbance size on landscape composition. To compensate for these shortcomings, VDDT models can be transferred to the spatially explicit simulation tool Tool for Exploratory Landscape Scenario Analyses (TELSA, Essa Technology, 2003a), which directly interface with both GIS and VDDT.

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 in TELSA. We utilized empirical 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. In addition, 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 (Brown and DeByle, 1989; Shepperd, 2001; Bates et al., 2004; Miller et al., 2005), little is known about how such management affects the vegetation composition and structure spatially at a landscape scale through time. We therefore also incorporated prescribed burning scenarios into our modeling runs. In particular, we address the following research questions:

- **Q I.** Can we simulate the historical fire regime that maintained aspen stands prior to Euro-American settlement?
- **Q II.** What extent and frequency of fire (burned area per decade) is required to stabilize the current land cover composition within aspen woodlands?
- **Q III.** What is the structural composition of aspen woodlands under historic and current fire occurrence probabilities, and under prescribed burning scenarios?
- **Q IV.** What is the effect of fire size on the long-term maintenance of aspen woodlands?

This study is a part of a larger body of research working towards a more holistic understanding of the historic, current, and future vegetation dynamics in the semi-arid mountains of southwestern Idaho (Yanish, 2002; Roth, 2004; Strand et al., 2006; Bunting et al., 2007; Strand, 2007).

## 2. Methods

### 2.1. Site description

The South Mountain and Silver City mountain ranges of the Owyhee Plateau in SW Idaho (116°W, 43°N) contain vegetation communities representative of many mountain ranges of the western U.S.A. The South Mountain study area encompasses 17,000 ha, while the Silver City Range covers 20,000 ha. Western juniper woodlands (*Juniperus occidentalis* ssp. *occidentalis*) and sagebrush (*Artemisia* spp) steppe, interspersed with pockets of aspen, mountain shrub species, and wet meadows, comprise the landscape at altitudes above 1700 m. Western juniper is the dominant conifer species in the area but is gradually replaced by Douglas-fir (*Pseudotsuga menziesii* ssp. *glauca*) at elevations greater than 1850 m elevation in both mountain ranges. Subalpine fir (*Abies lasiocarpa*) is the dominant conifer above 2400 m in the Silver City Range. Aspen stands are commonly located on cool northeast facing hill slopes, in concave snow and moisture accumulation areas. Soils in these areas are deep fine-loamy and loamy-skeletal mixed pachic or typic cryoborols, which are rich in organic material and have high water-holding capacity (USDA, 1998). 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, 2007). The 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 months. The summer and early fall in the Owyhee Mountains are warm and dry with an average high temperature in July of 26.7 °C (WRCC, 2003).

### 2.2. Field data collection

A total of 82 aspen clones along elevational and successional gradients were sampled across the study areas on South Mountain and in the Silver City Range. Within each clone we collected site characteristic information: 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% of the stand height, and trees taller than 75% of the stand height) and a list of the six major vegetative species based on canopy coverage. The increment cores were mounted and sanded and the annual growth rings were counted in a stereo-microscope for the age estimate. Faint annual rings in aspen were stained with phloroglucinol solution before ring counting (Patterson, 1959). A strong relationship was found between conifer cover and the time since onset of conifer encroachment into the stand. For a more detailed description of the field data collection and computation of successional rates, refer to Strand (2007).

### 2.3. Model requirements and assumptions

The Tool for Exploratory Landscape Scenario Analyses, TELSA (Essa Technology, 2003a), 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 (i.e. management-related) 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 (2007, Appendix I). Disturbance is 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 and treated in statistically meaningful ways. TELSA interfaces with a GIS for input and output of data.

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. Aspen woodlands were potentially present in three PVTs (Strand, 2007): 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 to come. Pure aspen stands have been observed on the Owyhee Mountains on south facing aspects above 1900 m in elevation (Strand, 2007). 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, 2007). This process of aspen decline has been described in the successional model developed by Strand (2007). Aspen/conifer stands that burn before they are permanently converted 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. Within the successional sequence (Fig. 1), transition from one successional stage to the next occurs within a pre-determined time period. The length of time that aspen stays in each successional stage on this study site, is described by Strand (2007). Each PVT is composed of a similar sequence of cover and structural classes. For the sagebrush/juniper PVTs we used successional models developed by Bunting et al. (2007).

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 and has also been reported by other researchers (Manier and Laven, 2001). To accurately estimate the rate of aspen expansion into adjacent cover types, we recorded 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. 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. 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. 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 nurtured 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, 2007). 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.

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 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 to 2002 and a recently developed land cover 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 to 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 and Rose, 1999; Bunting et al., 2007; Miller et al., 2005). For mid- and late seral juniper woodlands, we employed fire occurrence probabilities used by Bunting et al. (2007).

During a TELSA run, fires start in random locations according to the assigned probability. A fire that starts in a landscape unit may 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.
(2) Aspen is not allowed to spread laterally into other potential vegetation types in the absence of a disturbance.
(3) Adjacency between vegetation types does not affect succession.
(4) Fire will convert a conifer dominated aspen stand to an aspen dominated stand initiation structural stage regard-

less 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 on aspen and conifers are excluded.

The potential effects of these assumptions and simplifications on model outcome and interpretation are discussed in Section 4.2.

### 2.4. *Classification of potential vegetation types (PVTs)*

The digital Owyhee County soil survey (USDA, 1998) provides a description of the potential vegetation for each mapped soil unit. In many instances several potential vegetation types occur within the same soil unit. For example, aspen woodlands occur on north facing slopes and sagebrush steppe occurs on south facing slopes within the same soil unit. In such cases a digital elevation model (USGS, 1999) and spatial overlay analysis in a GIS was used to separate the soil polygon into two PVTs. Decision rules developed by Strand (2007) were then applied as follows:

- Aspen occurring on south facing slopes at elevations >1900 m were classified as aspen woodland PVT in which aspen will remain in self-regenerating uneven aged stands without encroachment from conifers.
- Aspen above 1850 m were classified into an aspen/Douglas-fir PVT where the potential vegetation is Douglas-fir in the absence of a disturbance.
- Aspen below 1850 m were classified into an aspen/western juniper PVT where the potential vegetation is western juniper in the absence of a disturbance.

### 2.5. *Classification of current cover type*

Broad land cover classes were classified via a maximum likelihood supervised classification procedure of a Landsat 7 Enhanced Thematic Mapper Plus (ETM+) image acquired on August 2002, using the ERDAS Imagine image processing software (Leica Geosystems, 1991–2003). Image preprocessing included conversion of the band digital numbers to spectral reflectance values using the biases, gains, and solar irradiance values specific to this image, followed by an atmospheric correction according to the dark body subtraction method. Training data for the classification were obtained from previous studies in the Owyhee Mountains (Bunting et al., 1999; Yanish, 2002; Roth, 2004; Strand, 2007). Altogether over 1000 ground reference plots were included, of which 120 were pure and mixed aspen stands. The ground reference locations were recorded using Garmin Map 76 and Trimble GeoXT GPS units. Polygons were drawn around these training areas and pixels within the polygons were randomly selected for the map validation process. Seventy-five percent of the ground reference plots were used for the classification and the remaining plots were used for an independent accuracy assessment. An error matrix, where mapped pixels are compared to ground verified areas for each mapped vegetation type, was created for both the PVT and the cover type classifications (Congalton, 1991). Overall accuracy, omission and commission errors and user's and producer's accuracy were computed according to methods outlined by Jensen (1996).

### 2.6. *Classification of mixed aspen-conifer stands*

We applied a linear spectral unmixing technique to map aspen along a seral gradient where the mid- and late seral stages and old woodlands (Fig. 1) are composed of a mixture of aspen and conifer trees along with understory grasses and forbs. The linear spectral unmixing was selectively applied within the aspen/conifer PVTs. Traditional image classification results in thematic maps where each image pixel is allocated to a single cover type. Linear mixture modeling (Settle and Drake, 1993) is a well-established remote sensing technique designed to quantify the proportions of cover types occurring *within* a single pixel. This method has been successfully applied to create fraction and coverage maps from Landsat TM and other imagery in a variety of ecosystems (Adams et al., 1995; Drake et al., 1998; Roberts et al., 1998; Sabol et al., 2002; Chen et al., 2004).

We implemented a principal component analysis (PCA) method to select endmembers along the aspen-conifer sere and confirmed the selection of spectrally pure endmember pixels using known locations of pure pixels from fine scale aerial photography and ground reference data (Smith et al., 1985; Theseira et al., 2002). We performed the image processing and linear mixture analysis in the ENVI image processing software (RSI, 2005) with three endmembers: aspen, Douglas-fir and western juniper. The accuracy of the resulting fraction maps was assessed using field data collected in 82 aspen stands in the Owyhee Mountains (Strand, 2007). Based on the sub-pixel proportion of aspen, each pixel within the aspen/conifer PVTs was classified into young aspen, aspen/conifer, conifer/aspen and conifer, the input classes for the TELSA model. The final raster map was smoothed using the *majorityfilter* function in ArcInfo Grid. We then converted the raster to a polygon coverage, the input format necessary for initializing TELSA. Polygons smaller than 0.2 ha were eliminated using the *eliminate* command in ArcInfo. Using pre-processing steps available in TELSA, we tessellated the landscape into landscape units approximately 1 ha in size. Tessellation allows disturbances to affect a portion of initial landscape units while the other portion is unaffected, allowing for a change in landscape structural composition within the original landscape units.

### 2.7. *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, disturbance probabilities, and disturbance size distributions. The actual current landscape composition was then compared to the modeled composition. Future landscape compositions for the South Mountain and the Silver City areas were evaluated at 25, 50, 100 and 200 years from current time, i.e. 200 years

**Table 1 – Areas of mapped cover types within the South Mountain and Silver City Range study sites.**

| 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 |

into the future. Fire management regimes assessed for each mountain range 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.
Scenario 5: Prescribed fire in aspen/conifer woodlands and young juniper woodlands according to historic fire probabilities.

Although succession in the TELSA model is treated as a deterministic variable with a pre-determined time period between successional transitions, fire start location and final fire size are stochastic components in the model. Because of this stochastic element, the model results will vary slightly between runs even though the input variables and landscape maps are identical. Simulations were therefore run 10 times for each management regime in the South Mountain and Silver City study areas to quantify the variability between runs. Means and variances were calculated from these results and displayed as error bars in the resulting graphs.

## 3. Results

### 3.1. *Classification of PVT, cover, and structure*

The area distribution of cover types and potential vegetation types within the two mountain ranges differed considerably (Tables 1 and 2). Independent validation data were used to assess the accuracy of the cover type and PVT maps and the overall accuracy for the five main PVTs was 80.2% (Table 3). Aspen PVTs (pure aspen, aspen/Douglas-fir, and aspen/western juniper) were then combined into one class. The largest portion of the error was caused by confusion between the two juniper woodland PVTs; western juniper/low sagebrush and western juniper/mountain big sagebrush. Producer's accuracy for the aspen PVTs was 98% and the user's accuracy was 86%. The overall accuracy for the cover type map was 72.3%, with most of the confusion occurring between the two juniper PVT types, the two sagebrush types and confusion of pure aspen with the mountain shrub class.

Linear spectral unmixing was performed in areas classified as aspen or aspen/conifer mix to yield information about the proportions of aspen and conifers within pixels. A scatter plot of the principal component bands 1 and 2 resulted in a plot with three apices, where the pixels at each apex represent the three endmembers pure aspen, Douglas-fir and western juniper. The pixels at the apices were assigned endmember status and fraction maps of the three endmember components were derived. A statistically significant relationship ($p = 0.05$, $n = 83$, $r^2 = 0.52$) was found between the fraction map of aspen cover and ground reference data (Fig. 2). Potential vegetation type maps were produced for both study areas according to above described methods (Fig. 3).

### 3.2. *Aspen expansion*

Data from four transects on the aspen/sagebrush steppe ecotone indicate the rate at which aspen expands into sagebrush steppe (Fig. 4). The four transects show similar expansion rates of approximately 0.5 m per year (20 m expansion in 40 years). Although we realize that, at a regional scale, the expansion rate likely varies with annual rainfall, site productivity, and other environmental conditions, the average expansion

**Table 2 – Areas of mapped potential vegetation types within the study area.**

| PVT | South Mountain area (ha) | Silver City Range area (ha) |
|---|---|---|
| Aspen woodland | 496 | 236 |
| Aspen/Douglas-fir woodland | 1669 | 2925 |
| Aspen/western juniper woodland | 745 | 527 |
| Bare/Rock | 2 | 72 |
| 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 |

**Table 3 – Confusion matrix for PVT classification.**

| Mapped PVT | Ground reference PVT Curlleaf mountain-mahogany | Juniper/low sagebrush | Juniper/mtn. big sagebrush | Meadow | Aspen | Total | Error | Commission error % | User's accuracy (%) |
|---|---|---|---|---|---|---|---|---|---|
| Curlleaf mountain-mahogany | 9 | 0 | 4 | 0 | 1 | 14 | 5 | 35.7 | 64.3 |
| Juniper/low sagebrush | 0 | 19 | 4 | 0 | 0 | 23 | 4 | 17.4 | 82.6 |
| Juniper/mountain big sagebrush | 4 | 13 | 65 | 0 | 0 | 82 | 17 | 20.7 | 79.3 |
| Meadow | 0 | 0 | 2 | 2 | 0 | 4 | 2 | 50.0 | 50.0 |
| Aspen | 1 | 1 | 7 | 1 | 59 | 69 | 10 | 14.5 | 85.5 |
| Total | 14 | 33 | 82 | 3 | 60 | 192 | | | |
| Omission error | 5 | 14 | 17 | 1 | 1 | Correct: 154 | | | |
| Omission error (%) | 37.5 | 42.4 | 20.7 | 33.3 | 1.7 | Total: 192 | | | |
| Producer's accuracy (%) | 64.3 | 57.6 | 79.3 | 66.7 | 98.3 | Total accuracy: 80.2 | | | |

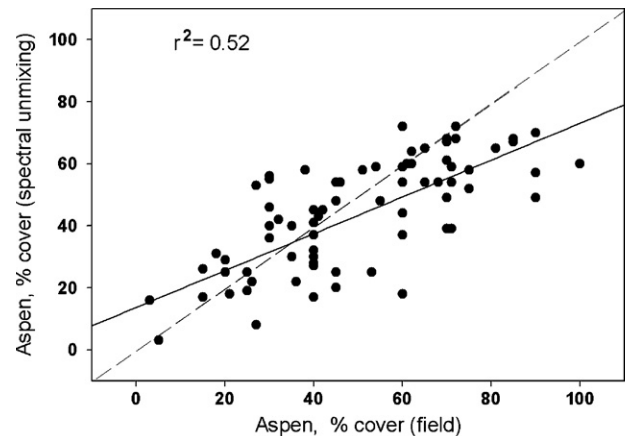


**Fig. 2 – Aspen fraction predicted by linear spectral unmixing vs. field measurements. The dotted line represents the identity line.**

rate estimated here provides a guideline for assumptions made regarding the importance of aspen expansion within this landscape model. The length of the aspen/sagebrush steppe boundary within the South Mountain study area was computed to be 68 km. In the unlikely event that aspen expanded along all available edge, the maximum area gained by aspen clones in 100 years would be 340 ha, corresponding to 13% 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.

### 3.3. *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 37,000 ha study region has burned in wildfires within this time period. Overlay analysis in GIS revealed that none of these fires occurred on soils that support aspen woodlands. Fire records prior to 1957 are not available; however, Strand (2007) recorded fire scars on aspen stems in several aspen stands, particularly in aspen stands that are becoming dominated by western juniper at lower elevations. Prescribed fire in aspen stands has occurred in other areas on the Owyhee Plateau, but however not to this date in areas that are included in this modeling effort.

The current wildfire size distribution was calculated from the Interior Columbia Basin Ecosystem Management Project database (Table 4). 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 4) to test the sensitivity of fire size within the model. Commonly, prescribed fires are in the size class 10–1000 ha (Scenarios 4 and 5, Table 4).

Current wildfire probabilities were estimated via overlay analysis between current cover types (Roth, 2004) and a digital fire atlas in GIS. Historical wildfire probabilities were based on literature references (see Table 5).

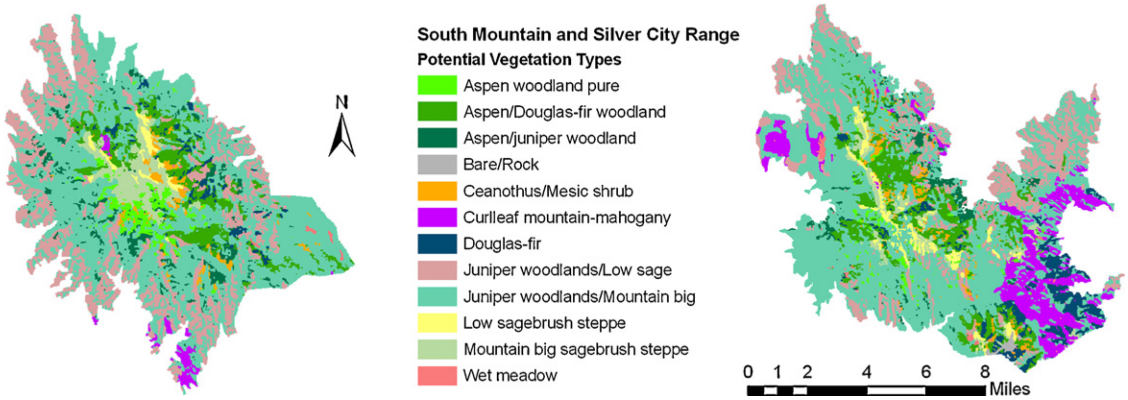


**Fig. 3 – Potential vegetation maps of the South Mountain (left) and the Silver City (right) areas.**

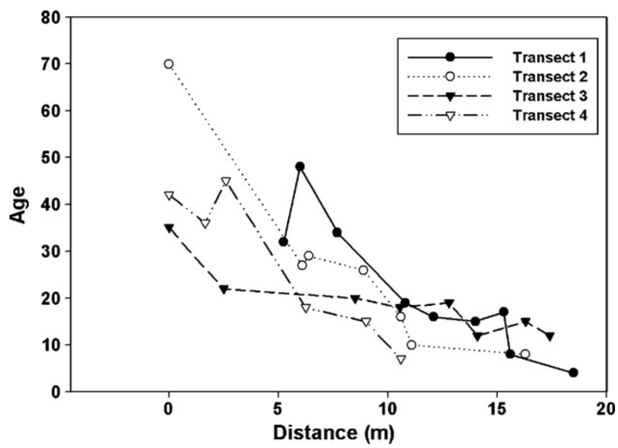


**Fig. 4 – Gradient of aspen age at the aspen woodland/sagebrush steppe boundary. The *x*-axis represents the distance from the mature aspen stems along the stand edge.**

### 3.4. *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, disturbance probabilities, and disturbance size distributions. We compare the resultant modeled landscape composition to the actual current landscape composition in Table 6. The model accurately simulated the current area of aspen using the inputs from 100 years back in time, which is an important finding because this simulation focuses on dynamics in aspen woodlands. The simulated area of juniper woodlands was larger, and the area in sagebrush steppe and grasslands was smaller than the mapped current area for these cover types. This result suggests 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. However, this deviation in juniper successional rates will have minor (if any) effects on this model focusing on aspen succession.

Future landscape composition of aspen seral stages was predicted under varying management scenarios for South Mountain and the Silver City Range (Figs. 5 and 6). 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.

By incorporating historical fire regimes into the model, we 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. 5 and 6).

Prescribed fire programs applied in aspen only (Scenario 4) and in aspen and young juniper (Scenario 5) resulted in a

**Table 4 – Distribution of the percent of fires in each size for the simulation scenarios.**

| 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 5 – 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 | 0.02 |

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 stands and the loss 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. According to these predictions, the aspen loss can largely be mitigated by implementing appropriate prescribed fire 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 indicated that the fire rotation for the two study areas was 70–80 years, while at current fire management conditions the fire rotation was estimated to 340 years on South Mountain and 449 years in the Silver City area (Table 7). Fire rotations were also computed for the prescribed fire scenarios, although these numbers may not be meaningful in the context of 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% of the area burned per decade. Currently, only 2–3% of the landscape burns per decade, of which the majority of the burned area is sagebrush steppe rather than juniper or aspen woodlands.

**Table 6 – 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 | 2,611 | 2,610 |
| Ceanothus/Mesic shrub | 477 | 362 |
| Curlleaf mountain-mahogany | 223 | 117 |
| Douglas-fir | 298 | 284 |
| Grasslands/Meadow | 70 | 402 |
| Juniper woodland | 10,193 | 11,831 |
| Sagebrush steppe | 3,053 | 1,136 |

## 4. Discussion

### 4.1. *Remote sensing of aspen for landscape modeling*

Natural resource management has for the last 70–80 years relied on aerial photographs for remote sensing of rangeland and forest resources. As satellite imagery from a number of sensors (e.g. Landsat, SPOT, IKONOS) has become increasingly available, scientists have begun to experiment with techniques for detecting aspen via automated and affordable image processing. Fine scale imagery (1–2 m pixel resolution) of forest canopies are difficult to classify using automated image classification methods because the picture elements are smaller than the objects to be classified, i.e. the aspen and conifer tree crowns. Within a crown the pixel spectral values can vary from dark shadow to bright sunlit leaves, and the variance within a vegetation class is too large for successful classification using unsupervised or supervised classification techniques. This problem can to some extent be overcome by smoothing the image using a $3 \times 3$ or $5 \times 5$ neighborhood filters prior to classification (Heyman et al., 2003). Supervised classification of aspen and aspen/conifer stands into classes of pure aspen and three levels of aspen/conifer mixtures using Landsat 7 ETM+ data was explored with moderate success by Heide (2002). Pure aspen and Douglas-fir were here successfully classified while the classification accuracy of the three aspen/Douglas-fir mixtures was rather low. Many factors

**Table 7 – Fire rotation and decadal proportion of the landscape burned under modeled fire regimes.**

| Study area | Scenario | Fire rotation (years) | Fire area per decade (%) |
|---|---|---|---|
| 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 |

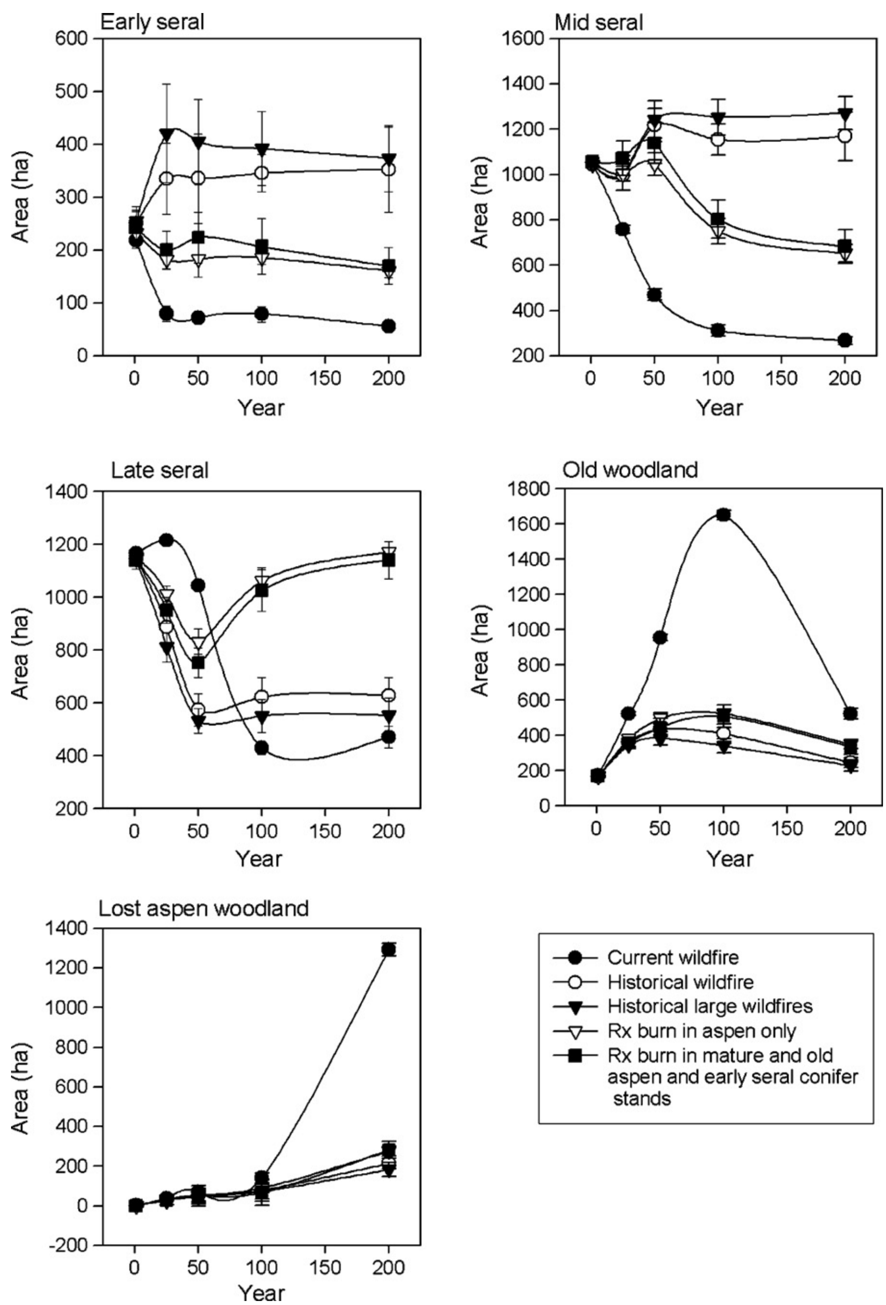


**Fig. 5 – Area of aspen woodland in different seral stages under five simulated management scenarios on South Mountain. The total area in aspen vegetation is currently 2610 ha.**

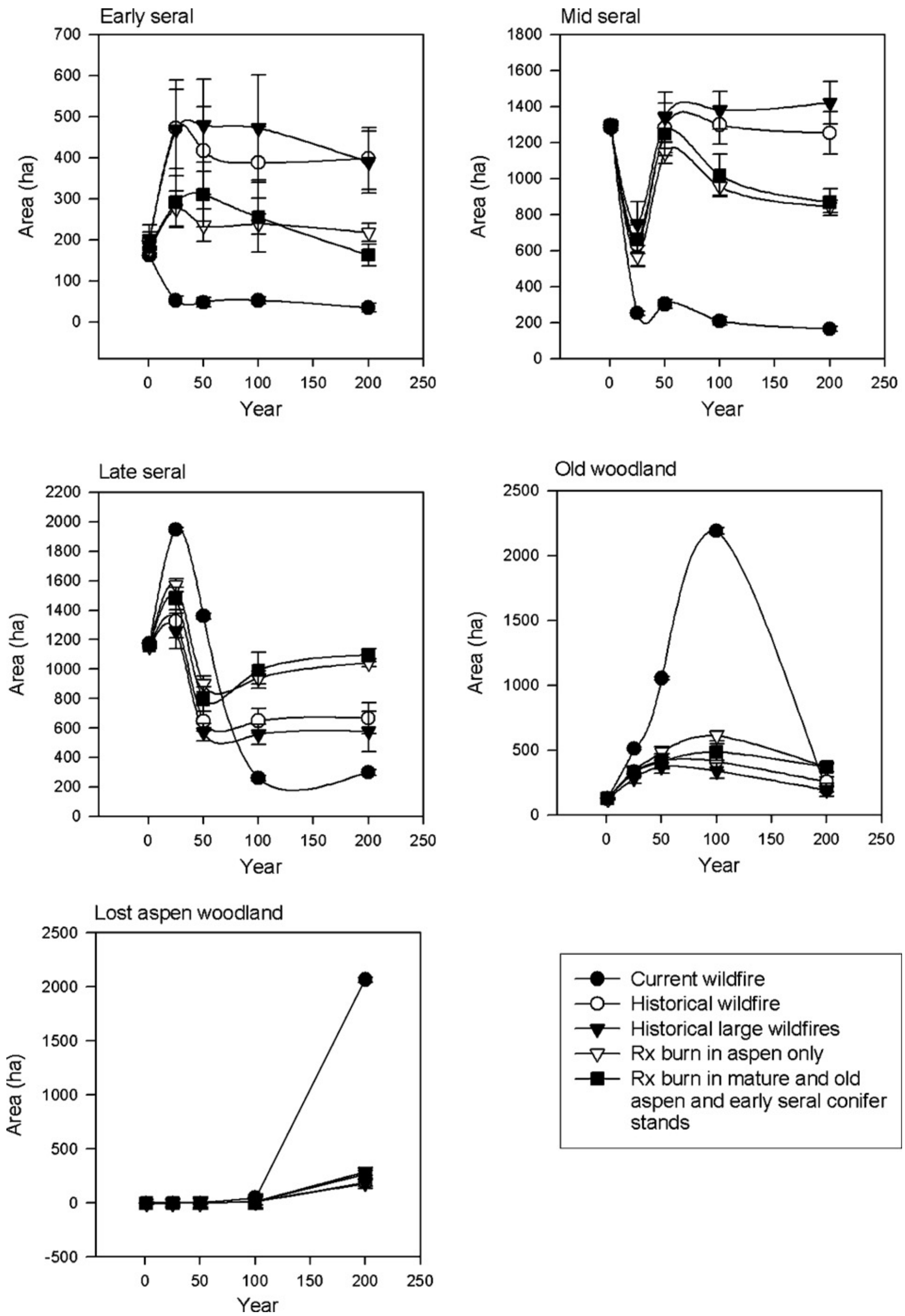


**Fig. 6 – Area of aspen woodland in different seral stages under five simulated management scenarios in the Silver City Range. The total area in aspen vegetation is currently 2765 ha.**

contribute to low accuracy in such a classification, including georegistration errors, difficulties in assessing aspen and conifer proportions in the field, and the fundamental fact that identifying sources of radiance present within a single pixel is a major challenge (Cracknell, 1998).

Linear spectral unmixing constrained by the potential vegetation type, as presented here, offers several advantages. First, by only performing the linear spectral unmixing within aspen/conifer PVTs, we minimize the possibility of including other vegetation types such as shrubs and meadows in the aspen/conifer classification. This is important because mesic broadleaf mountain shrub species cannot be successfully separated from aspen using multispectral data (Strand, 2007). Secondly, the resulting aspen fraction map produced during the unmixing procedure provides aspen cover along a continuum rather than in discrete pre-defined classes. Following such a classification, the user can combine the cover classes as desired, or use the fraction cover map as is.

The spatial resolution of Landsat 7 ETM+ data (30 m pixels) is suitable for development of input maps to simulate landscape dynamics. Although landscape simulation models are becoming increasingly powerful and can handle increasingly large landscapes and greater numbers of landscape units, maps at finer resolutions would result in software processing problems and unnecessarily long processing times. In applications where it is important to detect small aspen stands, finer resolution imagery than Landsat and different analysis techniques will yield higher accuracy maps (e.g. Heyman et al., 2003; Strand, 2007).

A problem that remains unsolved in using remote methods to characterize aspen succession is that the initial appearance of young conifer plants under the aspen canopy is difficult or impossible to detect during the growing season (because of aspen leaves obscuring the understory), and during the winter (due to snow and shadows in the understory). By the time the conifer crowns are visible within the aspen clone from an overhead perspective conifer dominance and reduced aspen regeneration is likely already occurring. Heide (2002) gained an improved classification accuracy in a supervised classification of aspen/conifer classes by stacking the bands from a summer and a fall Landsat scene. In the Owyhee study area this approach was investigated, however the mountainous terrain of the area results in variations in phenology and snowcover along the elevational gradient, which unfortunately leads to multi-modal training spectra and causes intractable inaccuracies in the classification.

### 4.2. *Model assumptions and their potential effects on model outcomes*

The full complexity of interactions within ecosystems is neither feasible nor necessary to capture in a model to gain a better 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. Here, 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 not known. 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. Indeed, 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 and would show a much larger range of variability in stand structure in the aspen ecosystem.

(2) *Aspen cannot spread into other potential vegetation types*. Expansion of aspen into adjacent shrub steppe 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% 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*. For example, in the current model the presence of a conifer seed source near an aspen stand does not affect the rate of succession. Incorporation of adjacency effects would result in variability in successional rates between stands far away and close to conifers. Adjacency effects would also increase successional rates in scenarios where only aspen stands are burned while conifer stands are left to mature and become a neighboring seed source to many aspen stands.

(4) *Fire will convert a conifer dominated aspen stand to an aspen dominated stand initiation structural stage 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 a high conifer cover, especially if the conifers are seed producing, is more likely to experience more rapid succession after a fire than a stand that housed only a few conifer seedlings prior to the 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. Further research addressing the fire effects along the aspen/conifer successional gradient is required to better understand legacy effects and other consequences of this assumption.

(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 in western mountains (Bartos and Campbell, 1998; Kaye et al., 2005; Strand, 2007). It is however not known how long an aspen clone can remain dormant in a non-reproductive state and still return to an aspen initiation 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 have occurred resulting in a change from an aspen/conifer PVT to a conifer PVT. Strand (2007) showed that the length of the persistence time only affects the starting point of rapid aspen decline (see also Figs. 5 and 6). The length of the persistence time is also extremely important when considering the possibility that one avenue for aspen rejuvenation is infrequent catastrophic wildfires creating a substrate suitable for aspen seedling establishment. In a scenario of effective fire suppression where large catastrophic 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/conifer 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 (Hinds, 1985; Jones and DeByle, 1985b; Jones et al., 1985; Kay and Bartos, 2000; Kaye et al., 2005). We deliberately did not include any of 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 are intended to 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 reverts 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?

### 4.3. *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. 5 and 6). 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.

**Q I.** *Can we simulate the historical fire regime that maintained aspen stands prior to Euro-American settlement?*

Results produced under the historical fire regime conditions show a landscape where over half of the aspen area is in early or mid seral successional classes and the loss of aspen is low. In particular, predictions show 14% in the early seral stage, 45% in mid seral and 35% in late seral (late seral and old combined, see Figs. 5 and 6). We predict a ~6% 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 such as sagebrush steppe or grasslands. 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% of the current aspen area) would more than counteract the predicted loss of 6% 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% in early seral, 40% in mid seral and 45% in the late seral class. This distribution is very similar to our modeled results. Loss of aspen woodlands is avoided in the Landfire reference condition models by including an insect/disease outbreak every 200 years, which reverts aging aspen stands to earlier successional stages.

**Q II.** *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% 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% 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% of the landscape burned per decade while application of fire in aspen stands only results in 2% 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 eliminate 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.

**Q III.** *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 time intervals is reported by TELSA under 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 composition of the landscape. Under historic fire regimes approximately 60% of the aspen woodlands exist in an early or mid successional stage, while this proportion is ~10% for current fire regimes and ~30% for the prescribed burning scenarios. Under the prescribed burning scenarios ~45% of the aspen develop into late seral woodlands, of which the majority are the self-regenerating pure aspen stands where prescribed fire was not applied. The amount of aspen in the old successional class and lost aspen woodlands is quite similar in the historic and the prescribed burning scenarios (Figs. 5 and 6).

**Q IV.** *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 4). 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 via multiple runs. Based on these results we conclude that there is no 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 Q IV. One could speculate that larger fires would benefit the fire dependent aspen woodlands in several ways. Larger fires would decrease conifer cover over a larger area and thereby 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 as the clones grow. 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.

### 4.4. *Management implications*

Over long term (i.e. centennial) time periods 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 is 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 occur and pure aspen stands, riparian aspen, and aspen occurring on microsites may initiate aspen establishment from seed. This optimistic outlook for aspen however 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 assessments in the field 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 management scenarios are presented as an alternative. Model predictions suggest that in theory prescribed burning programs can mitigate aspen loss and maintain aspen woodlands in younger seral stages. Such restoration of aspen woodlands has been suggested (Brown and DeByle, 1989; Bartos et al., 1991; Caprio and Graber, 2000; Miller et al., 2005) and carried out in aspen restoration projects (e.g. Brown and DeByle, 1989; Bates and Miller, 2004; Bates et al., 2004). 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, 2000; Hart and Hart, 2001; Kaye et al., 2005), which can jeopardize recently established aspen suckers and prevent the aspen clone recovery.

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 conifers on the ground here 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 that follows a modeling exercise. 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 is seral to conifers and aspen maintenance is a management goal unless we rely on infrequent catastrophic disturbance events to maintain these aspen resources. Such reliance is likely to lead to continued decline of aspen in our study region and across the western U.S.

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## Appendix A. Models for successional development in western aspen/conifer woodlands

The successional development in upland aspen/conifer woodlands on the Owyhee Plateau can be characterized using a positive exponential function where the proportion conifer in the stand is fit against time since conifers were introduced to the stand (Strand, 2007).

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

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

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

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 during model development. Notice that this model was estimated using only upland aspen/conifer stands, and does not apply to aspen in riparian areas nor anomalously wet 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. This exponential increase in conifer dominance marks the transition of mid seral aspen into late seral aspen (Fig. 1).

Fire disturbance is a critical component in this landscape model and the probabilities for fire occurrence in represented vegetation types were estimated via analysis of current land cover and fire atlas data complemented with literature information about historic fire return intervals (Table 5) as described in the methods section of this paper.

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