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MODEL-BASED ASSESSMENT OF ASPEN RESPONSES
TO ELK HERBIVORY
IN ROCKY MOUNTAIN NATIONAL PARK

a report to Rocky Mountain National Park

prepared by

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ABSTRACT

In Rocky Mountain National Park (RMNP), aspen has been observed to be declining on elk winter range for many decades. While aspen appears to be regenerating successfully in portions of the winter range that are less heavily utilized, many aspen stands along the major river valleys and in the dry parks are deteriorating rapidly. The SAVANNA model was adapted to explore interactions between elk herbivory and aspen dynamics on elk winter range. Several scenarios were explored that considered: different levels of overall elk population; different levels of elk utilization of aspen, reflected by the length of time during which elk utilized the aspen stand; and, different fencing treatments where fences were removed following a specified number of years. Simulated outputs were obtained for aspen sucker production, aspen canopy cover, and the probability of aspen regeneration success, calculated as the number of instances where aspen stands satisfied a specific set of regeneration criteria, over 20 - 30 simulations where weather was varied randomly over a 60 year period.

Aspen regeneration success was much greater when elk use was less prolonged over the course of the year. Under the Heavy Use scenario (8 months of elk use), there was a threshold between 4 - 5 elk km⁻² where regeneration success became dramatically less. Under the Light Use scenario (3 months of elk use), aspen regeneration success was high at elk densities up to 10 elk km⁻², moderate at 11 elk km⁻², and essentially zero at 12 elk km⁻². Aspen regeneration success was significantly improved by fencing aspen stands, even without stimulating additional aspen suckering through burning or mechanical disturbance. However, the effects of fencing on allowing aspen establishment and growth beyond the reach height of elk were highly variable, depending on weather conditions during the time the fence was up.

At the landscape scale, aspen regeneration success under the Heavy Use scenario was little affected by elk population level, when this level was above 600 elk (50 - 60% current population). This was because elk distribution was highly aggregated, so that a high density of elk occupied Horseshoe Park, Beaver Meadows, and Moraine Park, even at low population levels overall. Aspen regeneration success increased markedly when elk population levels were less than 600, although at even 400 elk, more than 25% of winter range aspen stands failed to regenerate. Maintenance of declining aspen stands in heavily used areas will require management intervention at a local scale. Reductions of the elk herd at the scale of the whole winter range may have little effect on aspen regeneration success, when elk utilization of aspen is heavy and sustained over much of the winter. When elk use of aspen stands was limited to three winter months, aspen regeneration success increased steadily as elk population level decreased. Nearly 90% of aspen stands regenerated at the 700 elk level, under the Light Use Scenario.

With intensive management of elk distribution and elk access to aspen regeneration, it is likely that aspen could be maintained in its Estes Valley winter range locations without an overall reduction of the RMNP elk herd. The results of this modeling exercise suggest that managing the overall elk population level for the winter range may not be as effective for stimulating successful aspen establishment as managing local elk distributions and access to aspen stands. However, simulation results suggest that reducing elk population levels while simultaneously managing elk distribution and access to aspen stands may be particularly effective for stimulating aspen regeneration. It is recommended that RMNP management take action to control the overall elk herd size, while simultaneously conducting intensive, site-level management activities to propagate aspen within the Estes Valley portion of the winter range.

INTRODUCTION

The Aspen Problem

Ungulate species, both wild and domestic, can exert profound effects on the vegetation for which they depend as food base (Milchunas et al. 1989, Hobbs 1996). Intensive herbivory may alter the composition and structure of vegetation, or reduce the long-term productivity of a site. Ungulate browsing may shift the competitive balance in favor of herbaceous plant species, and cause woody species to decline or disappear.

The emergence of ecosystem management as a central focus of land managers (Christensen et al. 1996) has increased the importance of efforts to manage ungulates in reasonable balance with the vegetation that supports them. The difficulty lies in determining what constitutes a "reasonable balance." Since both ungulate populations and vegetation structure have fluctuated greatly over past millennia, perhaps it is best to think of a reasonable balance as being defined by a historic range of variability (Swanson et al. 1994). When ungulate populations exceed historic levels, as may occur when release from predation is not accompanied by culling or other means of population control, then their effects on vegetation may be especially pronounced, resulting in vegetation responses that are also outside the range of historic variability. For example, excessive white-tailed deer (*Odocoileus virginianus*) populations in many deciduous forests of the northeastern United States have resulted in regeneration failure for sugar maple (*Acer saccharum*), a dominant tree species. This effect, combined with increased mortality of American beech (*Fagus grandifolia*) due to introduced beech bark disease, may well result in a forest of much different structure and species composition.

Elk (*Cervus elaphus*) have been observed to exert pronounced effects on woody

vegetation throughout the western United States. Intensive herbivory by elk has been observed to suppress willow height and leaf biomass in Yellowstone National Park (Singer et al. 1994, Kay 1997), Rocky Mountain National Park (Singer et al. 1998) and interior Alaska (Wolff 1978). Although elk are primarily grazers, they require substantial browse in the winter in order to maintain adequate levels of protein (Hobbs et al. 1981). In Rocky Mountain National Park (RMNP), as much as 44% of the winter diet has been observed to be browse (Hobbs et al. 1981).

A favored browse species of elk, quaking aspen (*Populus tremuloides* Michx.) may constitute greater than 7% of the winter diet in Rocky Mountain National Park (Hobbs et al. 1981). Elk browse aspen leaves and twigs, and strip aspen bark. The effect of bark-stripping on aspen mortality is unknown, although it may create inoculation sites for pathogens that eventually lead to aspen mortality (Hinds 1985). The effect of browsing young aspen suckers is more apparent. Suckers may eventually die after being browsed for multiple years, resulting in critical losses of root reserves for the parent tree. Suckers that are able to persist despite high levels of browsing may develop a "bush" growth form as a result of repeated loss of the apical meristem (Olmsted 1977, 1997). Aspen has been observed to be in decline for much of the elk winter range within RMNP, manifested as failure of new shoots to regenerate and grow to tree size, while overstory mortality continues at a rapid rate (Olmsted 1997).

Utility of the Ecosystem Modeling Approach

If there is an aspen regeneration problem in Rocky Mountain National Park, it is important that this problem be understood at the process level, if managers are to make intelligent decisions. Much information has been collected on aspen, but information by itself is

not sufficient to foster intelligent management. Ecosystem simulation models are valuable tools for synthesizing information about various ecological components in a holistic manner that makes explicit the interactions between components. The interaction that matters most for this study is the interaction between elk herbivory and aspen population dynamics. A model well-suited for capturing that interaction as it unfolds over long time periods, as well as climatic influences on aspen responses to elk herbivory, would allow us to: (1) better understand causal mechanisms for observed effects of elk on aspen growth and regeneration; (2) predict what would happen to aspen regeneration given different levels of elk herbivory, and different assumptions about the effects of elk herbivory on aspen dynamics; and (3) identify gaps in our data and understanding that are critical for explaining and predicting elk effects on aspen dynamics.

The SAVANNA model was adapted to pursue these general objectives. This model is designed to represent the long-term dynamics of grazing system processes in a spatially explicit manner, and has been applied to grassland, shrubland, savanna, and forested ecosystems on three continents (Coughenour 1992, Buckley et al. 1993, Ellis et al. 1993, Coughenour and Singer 1996, Ellis and Coughenour 1998). The model is composed of interacting submodels for weather, soils, carbon, nitrogen, water, light, fire, predators, vegetation production and population dynamics, and ungulate production and population dynamics (Fig. 1). The model simulates: (1) vegetation dynamics in terms of changes in plant functional group composition, (2) plant production in response to climatic variables, including seasonal patterns, (3) plant responses to herbivory and fire, and (4) animal distributional, production, and population responses to climatic variables and changing patterns of plant production and vegetation

composition. For a more detailed description of SAVANNA, see Coughenour (1994 - available upon request).

The primary objective of this research was to determine levels of elk numbers that would be compatible with long-term, significant aspen regeneration. In addition to reduction of the elk herd, protection of aspen stands with fences represents a management option whose viability is attested to by the success of existing exclosures in allowing aspen establishment. I also considered the effects of fencing aspen stands for varying time periods, and at different elk population levels following removal of fences.

The SAVANNA model provides a suitable framework for exploring these objectives. Aspen growth in six size/age classes is modeled mechanistically, and elk herbivory interacts with aspen population dynamics by: (1) killing aspen suckers directly; (2) reducing biomass of leaves, woody stems, and current annual growth; and (3) reducing height of suckers so they cannot grow out of elk browsing reach. Lower levels of elk herbivory allow a number of seedlings to grow beyond elk reach height and form a viable regeneration cohort. Precise levels of biomass reduction or seedling mortality resulting from elk herbivory are calculated from various input parameters for growth, reproduction, and mortality, most of which come from the available literature, but many of which had to be estimated.

ASPEN DECLINE IN THE WEST, AND A CONCEPTUAL FRAMEWORK

The problem of aspen decline is not unique to Rocky Mountain National Park, but has been observed throughout the American West. Mueggler (1989) estimated that of 713 aspen-dominated stands sampled throughout Utah, southeastern Idaho, and western Wyoming,

approximately one-third were likely to experience regeneration problems, and one-sixth were likely to deteriorate within a few decades. He presented a general decision model for maintaining aspen stands, but did not explicitly address causes for aspen decline. Kay (1997) and White and others (1998) used historical photographs, archival information, and existing studies to conclude that aspen is in dramatic decline over much of the American West, due to a combination of fire suppression and elk herbivory. Fire suppression allows relatively long-lived, fast-growing conifers to overtop, and eventually replace, aspen in seral stands. Kay (1997) suggested that aboriginal burning and effects of aboriginal hunters on reducing ungulate populations were responsible for the establishment of many aspen stands. Bartos and Campbell (1998) estimated the decline in areal extent of aspen on six national forests in Utah to have been about 60% over the past 125 years. They attributed the decline primarily to fire suppression, and secondarily to overuse by ungulates.

The combination of fire suppression and elk browsing is also believed to have caused substantial decline of aspen, as evidenced by failure to establish successfully on elk winter ranges, in the Jackson Hole area (Gruell and Loope 1974). Except for some recent establishment of aspen in areas burned by the 1988 fires (Romme et al. 1997), this pattern of aspen decline has been observed throughout Yellowstone National Park, and attributed to a complex interaction between elk abundance, climatic variation, fire, and mammalian predators, such that conditions for successful aspen regeneration may have historically been infrequent and episodic (Romme et al. 1995). Schier (1975) points out that ungulate herbivory is not always to blame for aspen regeneration failure, and presents a hypothesis for aspen deterioration based on the genetic propensity of some aspen clones to maintain apical dominance even while the overstory is slowly

deteriorating. Clearly, aspen suckering densities are greatly increased when the overstory is abruptly eliminated through fire or mechanical means (Schier and Campbell 1978, Brown and DeByle 1989).

In Rocky Mountain National Park, aspen has been observed to be declining, in the low-elevation valleys and dry parks constituting core elk winter range, for many decades (Dixon 1939 from Gysel 1960, Stevens 1979, Hess 1993, Olmsted 1977, Baker et al. 1997). Elk effects upon aspen in RMNP have been a contentious issue, and have been repeatedly studied (Olmsted 1977, Baker et al. 1997, Olmsted 1997, Suzuki 1997). Aspen regeneration on core elk winter range has been episodic, and associated with periods of low elk population (Baker et al. 1997). Elk populations have fluctuated markedly over the past 150 years. Intensive hunting virtually extirpated elk from the park from about 1875 to 1913, when 49 elk were transplanted (Hess 1993). After elk population levels increased rapidly to over 1000 elk by the late 1930's, elk populations in RMNP were controlled by shooting from 1943 through 1962 (Olmsted 1979), and relocation and trapping through 1967 (Hess 1993). Elk population levels had stabilized at an average of 587 elk from 1953 - 1967 (Hess 1993). In 1968, the current natural regulation policy of elk management was implemented, after which elk numbers again increased to 800 - 1200 animals, and successful aspen regeneration on core winter range became very infrequent (Baker et al. 1997, Olmsted 1997).

Other causes for aspen decline in the Park have been postulated. Aspen is often successional to conifers, and its decline may be associated with the absence of disturbance, usually the result of fire suppression (Hess 1993, Olmsted 1997). Beaver harvesting of mature aspen may also have contributed to aspen regeneration prior to the reduction of beaver numbers

(Hess 1993). However, this effect was likely localized near riparian areas. Also, moist climatic episodes, that may occur infrequently, may be necessary for successful aspen regeneration following disturbance events, as observed for Yellowstone National Park (Romme et al. 1995).

It seems reasonable that multiple factors should interact to cause aspen decline. However, presence of abundant aspen regeneration within exclosures provides strong evidence for ungulate herbivory being a key factor for aspen decline in RMNP (Baker et al. 1997). Apparently, climatic and other factors have been suitable for aspen regeneration during the time period when aspen has failed to regenerate outside of exclosures. Also, Suzuki (1997) and Baker and others (1997) observed that the timing of such regeneration as has occurred has not been temporally synchronous, even within a site, suggesting that climatic constraints may not be especially limiting for aspen sucker establishment in RMNP.

Aspen decline has by no means been the rule everywhere in the western U.S. Near Crested Butte, Colorado, a comparison of aspen stand structures 30 years apart suggests that aspen communities there are persistent (Crawford et al. 1998). Diameter distribution, basal area, and understory species composition have changed remarkably little, except for expected changes due to tree growth and stand self-thinning. While succession to spruce and fir is slowly occurring on more mesic slopes, this process may take centuries. An earlier study of aspen in the Crested Butte area had also found slow rates of conifer establishment in aspen stands, and speculated that seed source availability for spruce and fir might be limiting in areas that had burned extensively over the past century (Morgan 1969). Recent expansion of aspen into parkland in western Canada has been widespread, and may be related to the extirpation of bison, which formerly may have been important for limiting aspen expansion (Campbell et al. 1994). It

is interesting to consider that bison were once present in RMNP as well, and may have exerted different impacts upon aspen than elk do today.

In Rocky Mountain National Park, much successful aspen regeneration has been observed when the portion of the winter range under investigation has been expanded to include the Kawuneeche Valley, Meeker Park, Wild Basin, Black Canyon, the McGraw Ranch, and nearby sites on the Roosevelt National Forest (Suzuki 1997). Aspen decline may be localized within the Estes Valley, where elk winter density is greatest, while aspen regeneration successfully occurs elsewhere in RMNP (Suzuki 1997).

Given the spatial variability in the pattern of aspen decline in RMNP, it would be helpful to consider that there are really two general categories of aspen stands present on the winter range. The aspen stands for which regeneration failure and stand deterioration have been most frequently observed are located in the core of elk winter range, in dry parks and valley bottoms, where elk congregate most densely. These stands have little or no coniferous regeneration in the understory (Olmstead 1979, Baker et al. 1997), and will likely be replaced by grassland if they disintegrate completely. Aspen stands with coniferous regeneration in the understory, which are likely seral to coniferous forest given the continued absence of disturbance, tend to be located at the periphery of elk winter range, where elk densities are lower. It is in these types of stands that Suzuki (1997) observed significant aspen regeneration. Analysis of observed trends in aspen dynamics, and consideration of appropriate management action for aspen in RMNP, may be facilitated if this distinction between aspen stand types is considered explicitly. The two types of stands also exhibit different structures in terms of both overstory and understory composition and productivity, and likely represent different environments and habitats for plant and animal

species.

For aspen stands that are seral to conifers, fire is probably very important for maintaining aspen at both site and landscape levels (Fig. 2). In the absence of fire or other stand-replacing disturbances, one would expect many aspen stands to be replaced eventually by a forest of lodgepole pine. Aspen rootstocks are not likely to persist more than a generation beyond death of the aboveground aspen component, and so absence of fire for more than a few centuries will make it unlikely that aspen stands return to these areas any time soon, barring subsequent crown fires followed by successful establishment from seed blown in from adjacent aspen stands. The role of ungulate herbivory for such stands is secondary to that of stand-replacing disturbance events. However, sufficiently high ungulate population levels could destroy enough post-fire aspen regeneration to maintain the stand as coniferous forest.

However, such aspen stands that are seral to conifers are not the focus of this study, since these are not the stands which are experiencing imminent problems of deterioration and decline due to elk herbivory. Instead, I will focus on aspen stands that are seral to grassland (Fig. 3). Such stands have the potential to be multi-aged and self-replacing even in the absence of fire, since there are insufficient conifers present to overtop and shade out the aspen canopy. Therefore, fire is not needed to eliminate competition from conifers, and all that is required for aspen persistence is that successful aspen establishment in the understory occurs before stands are so overmature that insufficient suckers are produced. For these stands, elk herbivory may be the critical driving variable for aspen regeneration success, although climatic influences on aspen growth and population dynamics are certainly important, and fire does help to stimulate abundant suckering.

METHODS

SAVANNA Model Adaptation

SAVANNA implementation followed four general steps: model parameterization using available literature and existing data, model calibration using long-term data from Olmsted (1997) for a single site; model validation using eight additional sites from Olmsted (1997), and application to the research objectives using a set of experimental simulations. A single, one-hectare aspen stand was modeled over a range of elk densities (from 0 - 13 elk km⁻², depending on the treatment), and results were extrapolated to the winter range using GIS coverages for aspen stand locations and elk distribution for the 1994-1998 period.

I used SAVANNA to model three functional groups of plants (aspen, bunchgrasses, and forbs) and one animal species (elk). The focal organism was aspen, and other model elements were parameterized to be ecologically “sensitive” only insofar as they might influence aspen dynamics. For example, elk production, population dynamics, energetics and distribution were not explicitly simulated. To explore the effects of different levels of elk herbivory on aspen, a fixed number of elk were maintained for a fixed time period in aspen stands. Since aspen represents only a small proportion (7%, Hobbs et al. 1981) of the winter elk diet, it may not be unrealistic to exclude negative feedbacks of aspen browse availability on elk condition or population dynamics.

Elk consumption of aspen was permitted to reach a maximum of 0.005 kg aspen per kg elk, per day. This value was obtained by calibrating the model to achieve levels of elk offtake observed by Olmsted (1997), a procedure discussed in more detail below. Since maximum elk

intake rates are approximately 0.026 kg aspen/kg elk/day¹, maximum elk consumption of aspen in the model could reach as high as 19% of elk maximum intake, a greater value than the 7% proportion of diet estimated by Hobbs and others (1981). However, the Hobbs' estimate included only aspen leaves, while it is known that elk diets include some aspen browse. Also, elk intake rates generally did not reach the maximum value. Intake rate was calculated as:

$$\text{rintk} = \text{crm}x * \min(\text{efresp}, \text{effs}, \text{efq}) * \text{effsat} \quad (1)$$

where:

rintk = intake rate (for a particular plant species at a particular location and time)

crm_x = maximum intake rate (input parameter)

efresp = the user-specified functional response curve (feedback of forage availability upon forage intake rate, Spalinger and Hobbs 1992)

effs = the effect of snow (a function of snow depth, presence of a crust layer, and the proportion of forage buried)

efq = an input function specifying the effect of forage quality (percent of digestible dry matter) on intake rate, and

effsat = the effect of satiation on intake rate

¹The 0.026 estimate was calculated for a 240 kg cow, from an estimate of 12.6 g/min for maximum elk intake rate (Wickstrom et al. 1984), and the observation that Rocky Mountain elk on winter range spend 32% of the time feeding (Green and Bear 1990).

Elk were assumed to have a reach height of 2 m (above snow level, if present), and intake rate as a function of snow depth was represented as a linear function from no effect at 5 cm to complete suppression of forage intake at 40 cm (based on Sweeney and Sweeney 1984). To simplify the model, elk were not permitted to consume herbaceous forage in aspen stands (it was assumed that they would obtain such forage elsewhere), and neither shrub species nor coniferous trees were included.

Aspen was modeled using 6 age/size classes in 25-year increments, allowing aspen to attain a maximum age of 150 years. Individual aspen trees can live for longer than 200 years (Jones and Schier 1985), but most aspen stands in the region are likely to succumb to senescence and disease, and deteriorate by 150 years. Simulated aspen population stages are hybrids of age and size classes because trees are only promoted from one age class to the next if they have attained the minimum size for the next larger class. Individual trees within classes are not modeled explicitly, although each class may be represented by a "mean tree." The maximum size for each class, with regard to stem diameter, canopy diameter, root diameter, upper canopy height, lower canopy height, stem biomass, total root biomass, fine root biomass, and fine twig biomass, was estimated using allometric equations and other information from a variety of sources. First, the maximum diameter for each of the six 25-year classes was calculated as the 90th percentile of sampled diameters at breast height (dbh) from a pooled data set of RMNP winter range aspen trees (Olmsted 1977; K. Suzuki, unpublished data) (Fig. 4). Resulting maximum dbh values were 71, 130, 192, 246, 262, and 301 mm for the six classes. The same methodology was then applied to tree height, from the same sources (Fig. 5), giving maximum height values of 8, 9.5, 11, 13, 14, and 15 meters. Height to the bottom of the canopy was not

known from the literature, and would be expected to be highly variable depending if trees are in open or closed stands. Quaking aspen is very shade intolerant and develops a long clear bole with a small rounded crown when in dense stands (Harlow et al. 1979). However, most aspen stands on RMNP winter range are fairly open, so aspen was modeled as having moderate to high live crown ratios (0.57 to 0.88, decreasing with age).

Crown diameters for different stem diameters have been reported for aspen in Wyoming by Beetle (1974), and these values were used to interpolate crown diameters for the six age/size classes. Reliable data for root zone diameters were not found in the literature, so root zone diameters were set equal to crown diameters for trees less than 50 years old, and from 15% to 20% greater than crown diameters for older trees. Starting with estimated values for dbh and tree height for each age/size class, I used allometric equations from Bartos and Johnson (1978) to calculate aboveground wood biomass, equations from Wang and others (1995) to calculate leaf biomass, and equations from Ruark (1985) to calculate root biomass. Maximum growth rates were set so that trees under reasonable growing conditions could grow from one age class to the next in 25 years.

Actual tree growth is determined in SAVANNA by a mechanistic plant production module that simulates photosynthesis as the set of equations:

$$P(n, nsp) = (1/4) \sum_{l=1}^4 \frac{\alpha * parx(l)}{1 + ((\alpha * parx(l)) / pnetmx(nsp))^2 * effmult} \quad (2)$$

where:

$P(n, nsp)$ = Photosynthesis for size class n , species nsp

α = initial slope of the light response curve, or quantum efficiency (umol CO₂/mmol quanta)

$parx(l)$ = quantity of photosynthetic radiation reaching canopy layer l (shading is taken into account)

$pnetmx$ = maximum photosynthetic rate for species nsp

l = one of four canopy layers the canopy is divided into, and

$$effmult = \min(efwp, efsrp, eftp, efco2, efnp) \quad (3)$$

where:

$effmult$ = net environmental effect on photosynthesis, expressed as Liebig's Law of the Minimum

$efwp$ = the effect of soil water on photosynthesis,

$efsrp$ = the effect of shoot:root ratio on photosynthesis,

$eftp$ = the effect of temperature on photosynthesis,

$efco2$ = the effect of atmospheric carbon dioxide concentration on photosynthesis, and

$efnp$ = the effect of available nitrogen on photosynthesis.

Equation 2 scales an optimal photosynthetic rate for each canopy layer by limitations on photosynthesis reduced to the single most limiting factor. The photosynthetic rate is optimal for the amount of incident PAR on each canopy layer, according to the efficiency with which each species converts sunlight to photosynthate (quantum efficiency). Aspen, a shade-intolerant

species, has a low quantum efficiency and so will photosynthesize well only in abundant sunlight. Quantum efficiency for aspen was set as 30 $\mu\text{mol CO}_2/\text{mmol quanta}$, estimated from a figure in Bonan (1993). The maximum photosynthetic rate for aspen was set at 22 $\mu\text{mol}/\text{m}^2/\text{s}$, from experimental work presented by Kubiske and others (1997).

Equation 3 determines the most limiting factor on photosynthesis. For this study, the effect of carbon dioxide was set to null, and the shoot:root ratio effect was minimal. Optimal temperature for aspen photosynthesis was 18°C, and photosynthesis was permitted to occur from -2°C to 36°C (Jones et al. 1985, Bonan 1993). The effect of soil moisture on aspen photosynthesis was calibrated to be significant, and was tuned such that aboveground net primary production was correlated with precipitation (Fig. 6).

Photosynthesis for each species at each location is then calculated as the weighted average of photosynthesis for each age/size class present at that location, where the weight given each age/size class is determined by the proportion of leaf area in that size class:

$$P(nsp) = \sum_{n=1}^6 P(n, nsp) * frlai(n, nsp) \quad (4)$$

Without getting into further details of model mechanics, net primary productivity is calculated by subtracting growth respiration and maintenance respiration from gross primary productivity. Photosynthate is then allocated to various plant tissues (shoots, roots, flowers and seeds) according to their demand. Where insufficient photosynthate is available for maintenance, tissue death occurs. Tissue death also occurs for roots, stems, and leaves according to user input

functions for the effects of soil water availability and temperature. For this study, aspen tissue mortality was made especially sensitive to soil moisture deficits.

Aspen regeneration was modeled as occurring under two different mechanisms, both considered to represent suckering in the context of this study. Regeneration by seed was not considered a possibility, as it has very seldom been observed in the western United States, with the exception of following rare events such as extensive and severe wildfires (Kay 1990, Romme et al. 1997). The first mechanism for suckering requires setting, for each age/size class, the maximum number of suckers per month, per each living tree. The second mechanism requires setting suckering rates associated with tree mortality, such that a specified number of suckers attempt to establish following mortality of a tree in a given age/size class. In both cases, rates of establishment were set to be greatest for trees between 50-100 years of age. Older trees were assumed to have lost some of their potential for suckering, due to depletion of root reserves for tree maintenance, while younger trees do not command as much area, or resources in the form of root reserves. For both mechanisms of suckering regeneration, simulated rates of establishment are further influenced by a variety of factors:

$$eff = ewatr * etemp * \min(eherb, ewlai, ewcv) \quad (5)$$

where:

eff = the effect of environmental factors on tree regeneration,

ewatr = the effect of available soil moisture,

etemp = the effect of temperature,

eherb = the effect of herbaceous root biomass,

ewlai = the effect of leaf area index, and

ewcv = the effect of woody canopy cover

The precise relationships between each of these factors and tree regeneration are defined by user input functions in the parameter files.

Once established, aspen trees of all size/age classes may be killed as a function of water deficiency and browsing effects. Seedling mortality may also be modeled as a function of temperature. For this study, the main mortality influence was simulated as the effect of elk herbivory on seedling (Age/Size Class 1) mortality. As part of the calibration process, this parameter was adjusted until simulated results for aspen production and elk intake matched observed values as closely as possible (see section below on Calibration and Validation).

Simulated effects of elk herbivory on aspen thus included, as in the real world, biomass effects and population effects. Biomass effects occurred when elk herbivory maintained aspen seedlings at low heights and low levels of shoot biomass. Population effects occurred when elk herbivory killed aspen suckers according to a specified relationship between the proportion of the seedling browsed and the probability of seedling mortality. Seedling mortality probability was simulated as 1.0 when 8.2% of the seedling was browsed. This value differs from the “breakeven level” of 30% removal proposed by Olmsted (1977, 1997), because the Olmsted value includes only current annual growth of twigs, while the seedling mortality parameter considers all aboveground seedling biomass available for browsing. The 8.2% value was arrived at through the model calibration process described below, by allowing the parameter value to vary until

simulated results most closely matched observed results. In addition, a small amount of elk-induced mortality was simulated for older trees (age/size classes 2 - 6), to represent the effects of barking and antler-rubbing. These activities may hasten aspen mortality by enhancing the opportunity for fungal infection (Hinds 1985).

Calibration of the Savanna Model

The model was first calibrated in a general sense, by adjusting parameters so that biomass and population variables for aspen, grasses, and forbs exhibited reasonable dynamics over time (e.g., aspen does not die out rapidly for no apparent reason, or aspen does not expand rapidly, shading out all understory vegetation within a decade). These simulation exercises were conducted both in the presence and absence of elk herbivory, under varying levels of elk population, under variable climatic conditions, and starting with different densities and size class distributions for aspen stands, to ensure that the calibration was robust to a variety of conditions for the driving variables.

Also, as part of the general calibration, aspen aboveground net primary production was calibrated to between 350 and 700 g/m², reasonable values according to Waring and Schlesinger (1985), and was calibrated to be sensitive to annual precipitation (Fig. 6). Mean daily photosynthesis was calibrated to be 8 - 12 $\mu\text{mol}/\text{m}^2/\text{s}$, and peak stomatal conductance to be 150-250 $\text{mmol}/\text{m}^2/\text{s}$, which are representative values for aspen (Iacobelli and McCaughey 1993). Herbaceous production was calibrated to stay within reasonable limits (50 - 150 g/m²), with greater herbaceous production occurring under conditions of reduced aspen canopy cover, or in wetter years.

An aspen stem density model, where stem density as a function of stand age was plotted for 234 stands in the Rocky Mountains² (Shepperd 1990, Shepperd 1993) (Fig. 7), was used to calibrate aspen recruitment and mortality in a general way. I was not able to tightly calibrate aspen stem density dynamics using this model because of limitations imposed by modeling aspen in six broad age/size classes. For example, it was impossible to simulate seedling densities of 16546 stems ha⁻¹ at age 1 year, as predicted by the stem density model, because the mean size of age/size class 1 in the SAVANNA model was too large. However, the stem density model was used to guide calibration of aspen recruitment and mortality wherever possible, and to provide a broad guide for a negative exponential relationship between aspen density and stand age.

The model was then calibrated specifically to the Beaver Meadows-Deer Ridge (BMDR) site of Olmsted (1977, 1997). This site was selected from the nine Olmsted (1977) sites for which age data were available and re-sampling occurred in 1985-6 and 1995-6 (Olmsted 1997), on the basis of its having an older age structure representative of decadent lower-elevation aspen stands in the Park, having a moderate level of crown cover, having a moderate to high winter elk density, and lacking successful establishment of a regenerating aspen cohort. Specific information for the BMDR site used in the calibration were its elevation (2652 m), slope (12 degrees), aspect (east, modeled as 90 degrees), winter elk density in 1995-6 (from Francis Singer aerial survey data), canopy cover in 1975-6 (65 %), and age class structure (31% from 50-75 years, 62% from 75-100 years, 7% from 100-125 years). Except for elk density, this information comes from Olmsted (1977), Olmsted (1997), and unpublished data from Olmsted's work. To

²This model, and the raw data, were provided by Wayne D. Shepperd, Rocky Mountain Forest and Range Experiment Station, US Forest Service, Fort Collins, CO. Data were pooled from the two cited studies.

estimate canopy cover for the site, I averaged the canopy cover estimates of Olmsted (1977), obtained using vertical projection photos every 4 m along the transect. I did not count estimates of 0 on either side of the transect that were not bounded on the outside by points of positive canopy cover. Since estimates of tree density were not available, I varied overall tree density values, given the reported age/size distribution for 1975-6, until the reported value for canopy cover in 1975-6 was obtained.

Winter elk densities from 1994 to 1998 were obtained from aerial survey data, and interpolated across all 1 ha pixels, in the portion of elk winter range within Park boundaries, using standard GIS operations³ (Fig. 8). A map of mean interpolated elk density from 1994 to 1998 was used to calculate a map of relative elk distribution, that was then used to predict elk density for the BMDR site over the 1915 - 1998 period for which elk population estimates were available for RMNP. Elk density was predicted as the relative elk density for BMDR, multiplied by the elk population estimate for the Park winter range as a whole. The implicit assumption behind this approach is that elk distribution for the 1994-1998 period is representative for the 1915-1998 period.

I then simulated aspen dynamics at BMDR from 1970 to 1998, using historical weather data. Observed data for aspen production and elk offtake were available for the winters of 1975-6, 1985-6, and 1995-6 (Olmsted 1997). For these three years, I compared observed shoot production of current years' growth on all twigs up to 2 m in height with simulated current

³Elk density and population data were provided by Michael Rock, Natural Resource Ecology Lab., Colorado State University, Fort Collins, CO, 80523, on behalf of Francis Singer, at the same address. Michael Rock also performed the GIS interpolation and provided the GIS coverages.

annual growth of aspen in size/age class 1. Observed shoot production, measured in October, was provided in units of twig volume. I converted twig volume (cubic cm) to twig wet weight (g) using the empirical relationship from Olmsted (1977):

$$\text{Weight} = (0.671 * \text{Volume}) + 0.236 \quad (6)$$

After calibrating several parameters so that simulated and observed aspen production were in good agreement, I calibrated elk intake rate for aspen until there was reasonable agreement between observed and simulated elk offtake. Observed elk offtake was calculated as the difference between twig volume measured in May and twig volume measured in October, converted to units of weight. It is important to note that observed elk offtake includes only current annual growth, while simulated elk offtake includes both current annual growth and browse from previous years' growth. This bias may be offset somewhat because loss of twig volume between October and May may be due to factors other than elk browsing (e.g., mechanical breakage, other browsers). I attempted to calibrate elk offtake such that simulated values were slightly greater than observed values.

Simulation Experiments

The 1970 - 1999 calibration run for the BMDR site was used to initialize a set of experimental runs for the 2000- 2059 period. Experimental runs used randomized weather patterns with a mean and variance for temperature and precipitation similar to that of the 1910 -

1998 period. The following experiments were conducted:

Treatment	Levels of Elk Density	Replicates
Elk Density (per km ²) x Heavy Use	0, 1, 2, 3, 4, 5, 6, 7	30
Elk Density (per km ²) x Light Use	5, 6, 7, 10, 11, 12, 13	20
Elk Density (per km ²) x Heavy Use x 10-Year Fence	5, 6, 7, 10	20
Elk Density (per km ²) x Heavy Use x 20-Year Fence	5, 6, 7, 8, 9, 10	20
Elk Density (per km ²) x Heavy Use x 30-Year Fence	5, 6, 8, 10, 12	20

The Heavy Use and Light Use treatments refer to the duration of elk access to the aspen stand over the course of the year. For Heavy Use, elk densities in the simulated aspen stand are at their maximum level for November, December, January, February, March, and April; at 80% of their maximum level for October; at 50% of their maximum level for May and September; and at 10% of their maximum level for June, July, and August. Note that this scenario provides for some use of aspen stands by elk in the summer. This general pattern of elk distribution is consistent with a recent, detailed study of elk movements (Larkins 1997), but may not be representative of aspen stands that are utilized for shorter periods during winter, and not at all during summer. Therefore, I also simulated a Light Use scenario, where elk densities are at their maximum level for December and January; at 50% of their maximum level for November and February; and are at 0 for the rest of the year. A field survey of winter elk movement and habitat use in the Park found elk use of aspen stands to be substantial (as much as 35 % of total habitat use) from October through December, but virtually zero from January through April, when elk increased their use of grassland habitats (Clarke et al. 1994). These results suggest the Light Use scenario

may more accurately describe elk use of aspen stands.

At elk densities below 5 elk km⁻² for the Light Use scenario, aspen regeneration was always successful (aspen regeneration success is defined below), and so results for these density levels were not reported. At elk densities above 7 and 13 elk km⁻² for the Heavy Use and Light Use scenarios, respectively, aspen stands would never have successfully regenerated, and so these simulations were not conducted.

Fence scenarios were simulated by setting elk population density to zero for the duration of the fencing treatment (10, 20, or 30 years), and then setting elk population density to the specified level upon completion of the treatment.

Data Analysis

To explore how various treatments affected the simulated aspen stand's ability to persist on the landscape, I considered three variables for analysis: (1) density of suckers and saplings (age/size class 1 individuals); (2) aspen canopy cover; and (3) the proportion of random weather runs where the aspen stand successfully regenerated, or maintained the potential to do so. Regeneration success or potential was considered to have occurred if one of the following conditions was met by the end of the 60-year run:

- (1) at least 2500 suckers per ha
- (2) at least 1000 stems in size/age class 2 that established over the course of the simulation
- (3) at least 500 stems in size/age class 3 that established over the course of the simulation

These criteria are based on the work of Mueggler (1989), who suggested that the number of suckers in an aging aspen stand provides a useful index of that stand's ability to persist. He

considered stands with 1000 suckers per acre to be likely to successfully replace themselves.

Stand-level results were extrapolated to the landscape scale, over the extent of elk winter range, within Park boundaries, in the Estes Valley area. The official RMNP GIS coverage for vegetation was overlaid on the coverage of mean relative elk density (Fig. 8) for the 1994-1998 period. Note that aspen stands are under-represented by this vegetation coverage, since aspen stands are often quite small (Stohlgren et al. 1997). The effects of a given elk population level on the probability of regeneration success, as estimated using the simulation results for the BMDR stand, were then extrapolated to actual aspen stands, using estimates of elk numbers for each stand. First, the value for elk population on the winter range was multiplied by the gridded GIS layer for mean relative elk density to obtain a map of expected elk population level. Then, the expected probability of aspen regeneration success was calculated for each 1-ha grid cell in each aspen stand, based solely on estimated elk population levels in that grid cell. One hectare aspen cells with a regeneration success probability of 90% or greater were then separated from other aspen cells, and the spatial pattern of aspen regeneration success, under different assumptions concerning elk population level and intensity of elk use, was shown in map form.

The proportion of regenerating aspen stands on the winter range was described graphically, for Heavy Use and Light Use scenarios, and for the following elk population levels: 200, 400, 500, 600, 700, 800, 900, 1000, 1200, 1400, 1600, 1800, 2000, 2200, 2400, 2600, 2800, 3000. The 200 elk level would represent a density of about 1.5 elk km⁻², while the 3000 elk level would represent a density of about 22.6 elk km⁻², if elk density were homogeneous over the winter range. The 1999 elk population level in the Park's eastern winter range was estimated to be 1036 elk, based on aerial surveys (Lubow et al., unpublished manuscript). However, an

additional 2431 elk were estimated to occur in the town of Estes Park, adjacent to the winter range and not separated by any physical boundaries. Temporary migration between Park and Town has been shown to occur regularly, although the two herds appear distinct with regard to their population dynamics (Lubow et al., unpublished manuscript).

RESULTS

Model Validation

I performed an independent validation of the model on the remaining eight sites from Olmsted (1997), excluding the BMDR site, which was used for calibration, and the Beaver Meadows - South Side site, for which no data on age class structure were available. I used environmental and stand structural data specific to each site, and compared aspen sucker production and winter elk offtake from aspen suckers between observed and simulated data, as described in the Model Calibration section, with the exception that parameters used to tune the model during calibration were not altered during validation. Results of the validation exercise are shown in Table 1. Mean aspen production does not differ significantly between observed and simulated values. Simulated elk offtake is greater than observed elk intake. However, this may be acceptable since simulated elk offtake includes previous year's growth while observed offtake includes only current annual growth.

Although validation results appear acceptable when only the means are considered, the model did not do a very good job of predicting aspen sucker production at a given site for a given year (Fig. 9). There is a very wide scatter around the line of perfect fit. I attribute the poor performance of the model at this level to uncertainty associated with elk density and browsing

pressure for a given site and year. The assumption that the distribution of elk on the winter range over the 1970-1999 period precisely mirrors that of 1994-1999 for any particular year is clearly an oversimplification. Unfortunately, elk densities on the nine Olmsted (1997) sites are unknown for 1975-76 and 1985-86. Since elk browsing pressure is the primary driving variable controlling aspen sucker production in the model, it is no surprise that aspen sucker production is poorly predicted. Another important driving variable that is relatively unknown is the effect of a given intensity of elk browsing on aspen sucker mortality, and on root reserves of parent trees.

Despite there not being a tight clustering around the line of perfect fit (Fig. 9), the graph reiterates the results of the t-test comparisons of means (Table 1), that there does not appear to be significant bias in predicting aspen production between sites or years. Points are about equally as likely to appear below the line of perfect fit as above. Errors associated with incorrect estimates of elk density may average out between multiple observations. The graph suggests a tendency for 1995-96 simulated estimates to be too high relative to observed estimates, but the difference in means is not statistically significant (Table 1).

Stand-level Results

Aspen regeneration success is clearly much greater when elk use is less prolonged over the course of the year (Fig. 10). Under the Heavy Use scenario, there is a threshold between 4 and 5 elk km⁻² where regeneration success is dramatically less. Under the Light Use scenario, aspen regeneration success is high through 10 elk km⁻², moderate at 11 elk km⁻², and zero at 12 elk km⁻². Aspen regeneration success is significantly improved by fencing aspen stands, even without stimulating additional aspen suckering through burning or mechanical disturbance (Fig.

11). As might be expected, fencing aspen stands for longer time periods improves the probability of aspen persistence. However, aspen regeneration probability does not appear to be ensured even at relatively low elk densities with the 30-year fence scenario. This is because the success of aspen regeneration with fencing depends greatly on climate conditions during the period the fence is up. If climate is not conducive over that period, regeneration may not occur fast enough, and growth may not be fast enough, for suckers to have escaped the reach of elk upon removal of the fences.

These results are mirrored in results for aspen sucker density and canopy cover for the various experimental scenarios, shown in Tables 2 - 6. For the Heavy Use treatment, mean sucker density and canopy cover decline dramatically at elk densities between 4 and 5 elk km⁻² (Table 2). While there is a gradual decrease in both variables from 0 to 4 elk km⁻², there appears to be a clear threshold between 4 and 5 elk km⁻² where aspen suckers can no longer grow tall enough to escape from elk browsing pressure. As a result, aspen stands decline sufficiently after 60 years to yield quite low values for canopy cover. These stands appear well on their way to becoming grassland sites.

For the Light Use treatment, sucker density does not significantly decline until elk densities of greater than 10 elk km⁻² have been achieved (Table 3). There is less of a threshold effect than for the Heavy Use treatment, since stands with elk densities of 11 elk km⁻² have a high enough mean sucker density that regeneration success is not unlikely.

For the fencing treatments, it is interesting to observe that the variability of sucker density and canopy cover, as measured by the standard deviation in Tables 4 - 6, is much greater than for the non-fence treatment. Also, standard deviations decrease with increasing time the fence is up.

This is because of the importance of climate conditions during the period the fence is up, discussed earlier. If climate conditions are good, establishment and growth are sufficiently rapid for regenerating stems to have grown beyond the reach of aspen by the time the fence is removed. If climate conditions are not conducive to aspen establishment and growth, and the fence is removed at the specified time in spite of this, elk will decimate the aspen regeneration that has taken hold.

Landscape-level Results

At the landscape level, the Heavy Use scenario yields the interesting result that aspen regeneration probability is little affected by elk population level (Figs. 12 - 14), except at levels below 600 elk (Fig. 14). Even at 400 elk, more than 25% of winter range aspen stands fail to regenerate. This is because elk distribution in the winter range is highly aggregated (Fig. 8), so that a high density of elk occupy Horseshoe Park, Beaver Meadows, and Moraine Park, even at low population levels overall. Furthermore, aspen stands on the periphery of elk winter range maintain low levels of elk density, and so have high aspen regeneration probabilities even at high elk population levels overall, provided they are not overtopped by conifers, a process I did not simulate. This result is in accord with the field observations of Suzuki (1997), who observed ample aspen regeneration on peripheral elk winter range in RMNP, including the Black Canyon Creek area.

There is a greater difference between elk population extremes given the Light Use Scenario (Figs. 14 - 16). Under the 600 elk scenario, less than 10% of aspen stands are sufficiently affected by elk browsing so as to be suspect to regeneration failure, on the basis of

elk effects alone. At approximately current elk population levels (1000 elk), nearly 30% of aspen stands are simulated as experiencing regeneration failure (Fig. 14). However, most of the difference between the 600 and 1000 elk population levels occurs for aspen in the vicinity of Horseshoe Park (Fig. 15). At 3000 elk, the map of aspen re-establishment potential resembles that for 3000 elk given the Heavy Use scenario (Fig. 16).

This analysis suggests that aspen will be present on the winter range regardless of overall elk population levels, as elk population levels in peripheral aspen stands may seldom achieve high local elk population levels. However, this analysis further suggests that aspen stands at lower elevations in the winter range, that are not successional to conifers and occur as islands in a sea of grassland habitats, may be in jeopardy regardless of overall elk population level. For example, model results suggest the Moraine Park aspen stand would not re-establish successfully even at 200 elk under the Heavy Use scenario, and would require elk population levels of less than 400 elk for successful establishment under the Light Use scenario. If elk distribution in winter is actually as aggregated as Figure 8 suggests, and if this is so regardless of elk population level, then maintenance of declining aspen stands will require management intervention at a local scale. Reductions of the elk herd at the scale of the whole winter range may have little effect on aspen regeneration success in core winter range areas.

DISCUSSION

Validity of the Modeling Exercise

Caution must be exercised in utilizing the results from this study. As demonstrated by the validation exercise (Fig. 9), results are likely to be imprecise, due to uncertainty concerning key

driving variables for the elk-aspen interaction. These driving variables include:

(1) Elk distribution for varying population levels and climatic conditions. This could be modeled using SAVANNA, as is currently being done by M. Coughenour.

(2) Effect of elk herbivory on aspen sucker mortality. Surprisingly, I could not find useful information on this effect, which is perhaps the most important parameter in this modeling application. This effect could be studied by conducting a long-term (5-10 years) clipping study in one of the exclosures with abundant suckering.

(3) Effect of barking on aspen tree mortality. There is no consensus in the literature as to whether elk stripping of bark from larger aspen trees represents a significant source of mortality. If it does, it could significantly hasten the rate of overstory disintegration relative to my simulation results.

Therefore, the results of this study should be interpreted only in a general sense, and have value for suggesting hypotheses worthy of future study, that should be tested through field observations and experimental work. Estimates for elk densities at which aspen stands are likely to experience regeneration success or failure are likely to have significant and unknown errors associated with them. That being said, I believe I have demonstrated the value of this modeling approach for integrating diverse pieces of information into a coherent package that can be used to explore ecological relationships, and the potential impacts (given certain assumptions) of management activities.

Implications for Elk and Aspen Management

Implications of these results for elk and aspen management in the Park depend very much

on the specific nature of management goals. Management goals addressing the Park's mandate to "...try to maintain all the components and processes of naturally evolving park ecosystems, including the natural abundance, diversity, and ecological integrity of plants and animals (National Park Service 1988)," may be expressed along a gradient of complexity and spatial resolution. The specific goal might be to: (1) maintain aspen as a species in RMNP winter range; (2) maintain a component of valley bottom/dry park aspen, represented as islands in a matrix of grassland and woodland vegetation types, present on core elk winter range; or (3) try to maintain the existing aspen stands in the dry parks and valley bottoms on core elk winter range. The second goal permits aspen stands to fluctuate across the landscape, while the third goal takes a more static approach.

If the goal is simply to maintain some aspen in winter range, then the current natural regulation policy for elk management would be satisfactory. It is unlikely that elk population levels would ever get high enough for aspen stands along the periphery of the winter range to experience high enough levels of elk herbivory to prevent successful aspen regeneration. At some point in the future, fires or silvicultural treatments might be required for these areas to maintain aspen (Fig. 2).

Continuation of the current natural regulation policy would not satisfy goals 2 and 3 without intensive management of aspen regeneration. Natural regulation is not effective for allowing aspen regeneration on core winter range because aspen may be thought of as a "secondary prey" species, unable to exert a negative feedback on elk population levels because it constitutes only a small portion of the elk diet, but susceptible to the impacts of high elk population levels supported by the availability of other winter forage sources. The only way to

maintain sufficient levels of aspen regeneration to ensure persistence of aspen in Horseshoe Park, Beaver Meadows, and Moraine Park, while continuing the policy of natural regulation, would be to intensively manage for aspen regeneration by fencing aspen stands for long time periods (at least a 30-year period is suggested, Fig. 11). In addition to fences, prescribed fire and mechanical disturbances (ripping, bulldozing) might be useful for stimulating abundant suckering. Ripping roots around the periphery of a deteriorating aspen stand might stimulate abundant suckering at the edge of the stand, while avoiding the risk of destroying the existing stand for naught if regeneration is unsuccessful⁴. However, it is unlikely such methods would generate enough suckers to maintain aspen stands in these areas without using fences to protect the stands from subsequent elk herbivory.

Discontinuing the policy of natural regulation, in favor of a policy that reduces the size of the elk herd, may not be sufficient to create aspen persistence in the core of Estes Valley winter range. Even at a population level of 600 elk in the Park, one-half of the current level, and the threshold level identified by Baker et al. (1997) as having been associated with aspen regeneration in the past, the probability of aspen stand persistence is quite low for many stands under the Heavy Use scenario (Fig. 14). The results of this modeling exercise suggest that managing the overall winter range elk population level may not be as effective as managing local elk distribution for stimulating successful aspen establishment. If elk use of aspen stands were limited to only a few months of the year, then aspen stand persistence may become much more likely (Figs. 10, 14-16). Furthermore, protecting aspen regeneration using fences may not be as effective as reducing elk density at the stand level, or decreasing the level of elk use (Figs. 10-

⁴Wayne Shepperd, USFS, personal communication.

11).

If aspen stands on core winter range were younger and more vigorous, greater sucker production would likely occur, for a given elk density, than estimated here. Also, the establishment of dense patches of young aspen would likely present a physical barrier to elk herbivory, allowing additional aspen suckers to establish. It is therefore possible that, while elk densities required for establishment of vigorous, multi-aged aspen stands might be initially low, such aspen stands once established would be able to withstand greater elk densities.

Successful management for aspen persistence in the Estes Valley will likely require some combination of: overall population reduction; management of elk distribution; fencing to protect aspen suckers from elk browsing; mechanical disturbance and limited prescribed fire to stimulate suckering for stands with inherently low reproductive potential; and even chemical repellents to deter elk browsing at specific locations (Baker et al. 1999). Since abundant aspen suckering has occurred in most of the existing exclosures, demonstrating the reproductive potential of these stands while an aspen overstory is still present, protection from elk browsing should play a far greater role in management plans than prescribed fire or mechanical disturbance.

With intensive management of elk distribution and elk access to aspen regeneration, it is likely that aspen could be maintained on Estes Valley winter range locations without an overall reduction of the RMNP elk herd. However, simulation results suggest that reducing elk population levels while simultaneously managing elk distribution and access to aspen stands may be particularly effective for stimulating aspen regeneration. It is recommended that RMNP management take some action to control the overall elk herd size, while simultaneously conducting intensive, site-level management activities to propagate aspen within the Estes Valley

portion of the winter range.

Future Research

Large gaps in our understanding of the relationship between elk browsing and aspen regeneration surfaced from this modeling exercise. We have only a qualitative understanding of elk effects on aspen, while quantitative measurements are necessary for modeling the elk-aspen relationship in a more rigorous, realistic, and predictive manner. In particular, it would be useful to know more about:

- (1) effects of elk herbivory on the survival of aspen suckers, and carbohydrate root reserves of parent trees;
- (2) effects of elk barking on the long-term survival of aspen trees of different ages;
- (3) effects of climate variability on aspen establishment and mortality of aspen suckers;
- (4) historic landscape patterns - - - how has the cover and distribution of aspen fluctuated with disturbance, climate, elk and successional processes in the past?
- (5) historic patterns of elk population density - - how has elk density fluctuated over space and time, and how have these patterns been associated with historic aspen dynamics?

Hopefully, the modeling effort will continue to evolve in synchrony with fieldwork designed to reduce our uncertainty about critical processes and causal relationships.

Management can only benefit from an increased understanding of ecological relationships, and hopefully can help add to our understanding through the use of adaptive management techniques, where multiple management treatments are tested in a quasi-experimental manner.

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REFERENCES

- Baker, D.L., Andelt, W.F., Burnham, K.P., and W.D. Shepperd. 1999. Effectiveness of Hot Sauce and Deer Away repellents for deterring elk browsing of aspen sprouts. *Journal of Wildlife Management* 63(4): 1327-1336.
- Baker, W.L., Munroe, J.A., and A.E. Hessel. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. *Ecography* 20: 155-165.
- Bartos, D.L. and R.B. Campbell, Jr. 1998. Decline of quaking aspen in the Interior West - Examples from Utah. *Rangelands* 20(1): 17-24.
- Bartos, D.L. and R.S. Johnson. 1978. Biomass and nutrient content of quaking aspen at two sites in the western United States. *Forest Science* 24(2): 273-280.
- Beetle, A.A. 1974. Range survey in Teton County, Wyoming. Part 4 - quaking aspen. Agricultural Experiment Station, Research Journal 31, 124 p. Laramie, WY.
- Bonan, G.B. Physiological controls of the carbon balance of boreal forest ecosystems. *Canadian Journal of Forest Research* 23: 1453-1471.
- Brown, J.K. and N.V. DeByle. 1989. Effects of prescribed fire on biomass and plant succession in western aspen. USDA Forest Service Research Paper INT-412. Intermountain Research Station, Ogden, Utah.
- Buckley, D.J., Coughenour, M. B., Blyth, C.B., O'Leary, D.J., and Bentz, J. A. 1993. Ecosystem management model - Elk Island National Park: A case study of integrating environmental models

with GIS. Proceedings of the Second International Conference on Integrating GIS and Environmental Modeling. Breckenridge, Colorado. National Center for Geographic Information and Analysis, University of California, Santa Barbara.

Campbell, C., Campbell, I.D., Blyth, C.B., and J.H. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. *Ecography* 17(4): 360-362.

Clarke, J.A., Olmsted, C.E., and K. Larkins. 1994. Patterns of habitat use, movement, and distribution of elk adjacent to the eastern boundary of Rocky Mountain National Park. Summary Report to RMNP.

Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., and D.J. Parsons. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6(3): 665-691.

Coughenour, M.B. 1992. Spatial modeling and landscape characterization of an African pastoral ecosystem: a prototype model and its potential use for monitoring droughts. In: D.H. McKenzie, D.E. Hyatt, and V.J. McDonald, eds. *Ecological Indicators*, Vol. I. Elsevier Applied Science, London and New York, pp. 787-810.

Coughenour, M.B. 1994. *The SAVANNA Landscape Model - Documentation and Users Guide*. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.

Coughenour, M. B. and Singer, F. J. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecological Applications* 6:573-593.

Crawford, J.L, McNulty, S.P., and J.B. Sowell. 1998. Changes in aspen communities over 30 years in Gunnison County, Colorado. *American Midland Naturalist* 140: 197-205.

Ellis, J. E., Coughenour, M. B, and D.M. Swift. 1993. Climate variability, ecosystem stability and the implications for range and livestock development. pp. 31-41 In: Behnke, R., Scoones, I. and Kerven, C. (eds.) *Range ecology at disequilibrium*. Overseas Development Institute, London.

Ellis, J. E. and M. B.. Coughenour. 1998. The SAVANNA integrated modelling system: an integrated remote sensing, GIS and spatial simulation modelling approach. pp. 97-106 In: Squires, V. R. and Sidahmed, A.E. (eds.), *Drylands: Sustainable Use of Rangelands into the Twenty-First Century*. Chapter 7. IFAD Series: Technical Reports.

Green, R. A., and Bear, G. D. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. *Journal of Wildlife Management* 54(2): 272-279.

Gysel, L.W. 1960. An ecological study of the winter range of elk and mule deer in the Rocky

Mountain National Park. *Journal of Forestry* 58: 696-703.

Harlow, W.M., Harrar, E.S., and F.M. White. 1979. *Textbook of Dendrology*. Sixth Edition. McGraw-Hill Publishing Company.

Hess, K. 1993. *Rocky times in Rocky Mountain National Park: an unnatural history*. Univ. Press of Colorado.

Hinds, T.E. 1985. Diseases. in: DeByle, N.V. and R.P. Winokur (eds.), *Aspen: Ecology and Management in the western United States*. USDA Forest Service General Technical Report RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Hobbs, N.T., Baker, D.L., Ellis, J.E., and D.M. Swift. 1991. Composition and quality of elk winter diets in Colorado. *Journal of Wildlife Management* 45(1): 156-171.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60(4): 695-713.

Iacobelli, A. and J.H. McCaughey. 1993. Stomatal conductance in a northern temperate forest: temporal and spatial patterns. *Canadian Journal of Forest Research* 23: 245-252.

Jones, J.R., Kaufmann, M.R., and E.A. Richardson. 1985. Effects of water and temperature. pp. 71-76 in: DeByle, N.V. and R.P. Winokur (eds.), *Aspen: Ecology and Management in the western United States*. USDA Forest Service General Technical Report RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Jones, J.R. and G.A. Schier. 1985. Growth. in: DeByle, N.V. and R.P. Winokur (eds.), *Aspen: Ecology and Management in the western United States*. USDA Forest Service General Technical Report RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Kay, C.E. 1993. Aspen seedlings in recently burned areas of Grand Teton and Yellowstone National Parks. *Northwest Science* 67: 94-104.

Kay, C. E. 1997. Is aspen doomed? *Journal of Forestry* ? : 4-11.

Kay, C.E. 1997. Viewpoint: Ungulate herbivory, willows, and political ecology in Yellowstone. *Journal of Range Management* 50: 139-145

Kubiske, M.E., Pregitzer, K.S., Mikan, C.J., Zak, D.R., Maziasz, J.L., and J.A. Teeri. 1997. *Populus tremuloides* photosynthesis and crown architecture in response to elevated CO₂ and soil N availability. *Oecologia* 110: 328-336.

Larkins, K.F. 1997. Patterns of elk movement and distribution in and adjacent to the eastern

boundary of Rocky Mountain National Park. M.S. Thesis, University of Northern Colorado, Greeley, Colorado.

Lubow, B.C., Singer, F.J., Johnson, T., and D. Bowden. Unpublished manuscript. Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park: density, migration, and environmental influences. *Journal of Wildlife Management*, In Review.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L., and M.K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80: 11-23.

Morgan, M.D. 1969. Ecology of aspen in Gunnison County, Colorado. *The American Midland Naturalist* 82(1): 204-227.

Mueggler, W.F. 1989. Age distribution and reproduction of intermountain aspen stands. *Western Journal of Applied Forestry* 4: 41-45.

National Park Service. 1988. Management Policies. U.S. Department of the Interior, Washington, D.C., 242 pp.

Olmsted, C.E. 1977. The effect of large herbivores on aspen in Rocky Mountain National Park. Ph.D. Dissertation. University of Colorado, Boulder.

Olmsted, C.E. 1997. Twenty years of change in Rocky Mountain National Park elk winter range aspen. Unpublished report to Rocky Mountain National Park.

Romme, W.H., Turner, M.G., Wallace, L.L., and J.S. Walker. 1995. Aspen, elk, and fire in Northern Yellowstone National Park. *Ecology* 76: 2097-2106.

Romme, W.H., Turner, M.G., Gardner, R.H., Hargrove, W.W., Tuskan, G.A., Despain, D.G., and R.A. Renkin. 1997. A rare episode of sexual reproduction in aspen (*Populus tremuloides* Michx.) following the 1988 Yellowstone fires. *Natural Areas Journal* 17: 17-25.

Ruark, G. A. 1985. Biomass, net primary production, and nutrient distribution in successional *Populus tremuloides* Michx. stands on an entic haplorthod in north-central Wisconsin. Ph.D., University of Wisconsin, Madison, WI.

Schier, G.A. 1975. Deterioration of aspen clones in the Middle Rocky Mountains. USDA Forest Service, Research Paper INT-170, Intermountain Forest and Range Experiment Station, Ogden, Utah.

Schier, G.A. and R.B. Campbell. 1978. Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. *Forest Science* 24(2): 303-308.

Shepperd, W.D. 1990. A classification of quaking aspen in the Central Rocky Mountains based on growth and stand characteristics. *Western Journal of Applied Forestry* 5(3): 69-75.

Shepperd, W.D. 1993. Initial growth, development, and clonal dynamics of regenerated aspen in the Rocky Mountains. USDA Forest Service Research Paper RM-312, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Singer, F.J., Mark, L.C., and R.C. Cate. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. *Journal of Range Management* 47: 435-443.

Singer, F., Elliott, T., Coughenour, M., Welker, J., Valentine, D., Williams, S., Zeigenfuss, L., Alstad, K., Menezes, R., Peinetti, R., Barnett, D., Cates, R., and J. Zou. 1998. Large mammalian herbivores, plant interactions, and ecosystem processes in five national parks. Third Annual (unpublished) Report on Cooperative Agreement 1445-0009-94-1074, Subagreement 2, to Midcontinent Ecological Science Center, Biological Resources Division of U.S. Geological Survey, Ft. Collins, CO.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* 140: 325-348.

Stevens, D.R. 1979. Effect of elk on vegetation in Rocky Mountain National Park. Unpublished report to Rocky Mountain National Park.

Stohlgren, T.J., Chong, G.W., Kalkhan, M.A., and L.D. Schell. 1997. Multiscale sampling of plant diversity: effects on minimum mapping unit size. *Ecological Applications* 7(3): 1064-1074

Suzuki, K. 1997. Aspen regeneration in elk winter range of Rocky Mountain National Park and Roosevelt National Forest, Colorado. M.S. Thesis, Colorado State University, Fort Collins.

Swanson, F.J., Jones, J.A., Wallin, D.O., and J.H. Cissel. 1994. Natural variability – implications for ecosystem management. Pages 89-106 in M.E. Jensen and P.S. Bourgeron (tech. eds.). *Eastside forest ecosystem health assessment - - Volume II: ecosystem management: principles and applications*. USDA Forest Service General Technical Report PNW-GTR-318. Pacific Northwest Research Station, Portland, Oregon, USA.

Sweeney, J.M. and J.R. Sweeney. 1984. Snow depths influencing winter movements of elk. *Journal of Mammalogy* 65(3): 524-526.

Wang, J.R., Zhong, A.L, Comeau, P., Tsze, M., and J.P. Kimmins. 1995. Aboveground biomass and nutrient accumulation in an age sequence of aspen (*Populus tremuloides*) stands in the Boreal White and Black Spruce Zone, British Columbia. *Forest Ecology and Management* 78: 127-138.

Waring, R.H. and W.H. Schlesinger. 1985. *Forest Ecosystems: Concepts and Management*. Academic Press, Inc., San Diego.

White, C.A., Olmsted, C.E., and C.E. Kay. 1998. Aspen, elk and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin* 26(3): 449-462.

Wickstrom, M. L., Robbins, C. T., Hanley, T. A., Spalinger, D. E., and Parish, S. M. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management*, 48(4), 1285-1301.

Wolff, J.O. 1978. Burning and browsing effects on willow growth in interior Alaska. *Journal of Wildlife Management* 42(1): 135-140.

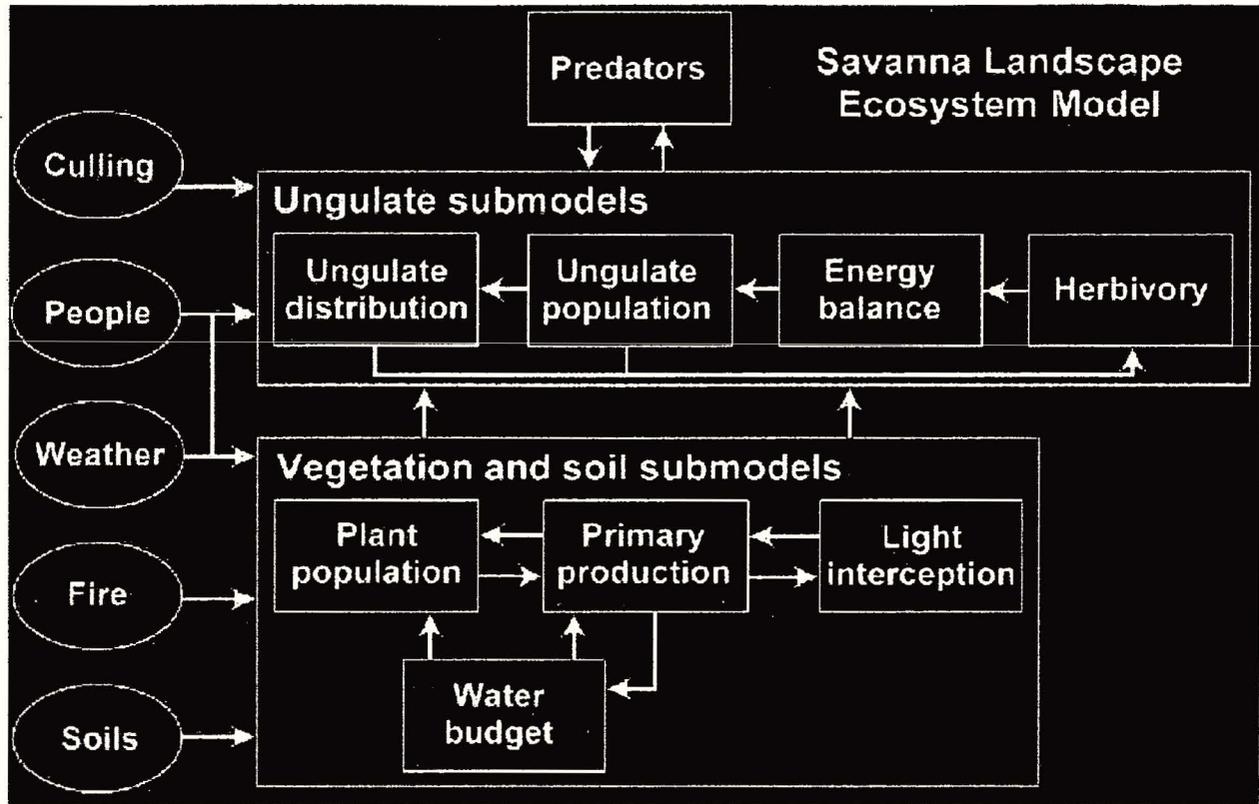


Fig. 1. The general structure of the SAVANNA model.

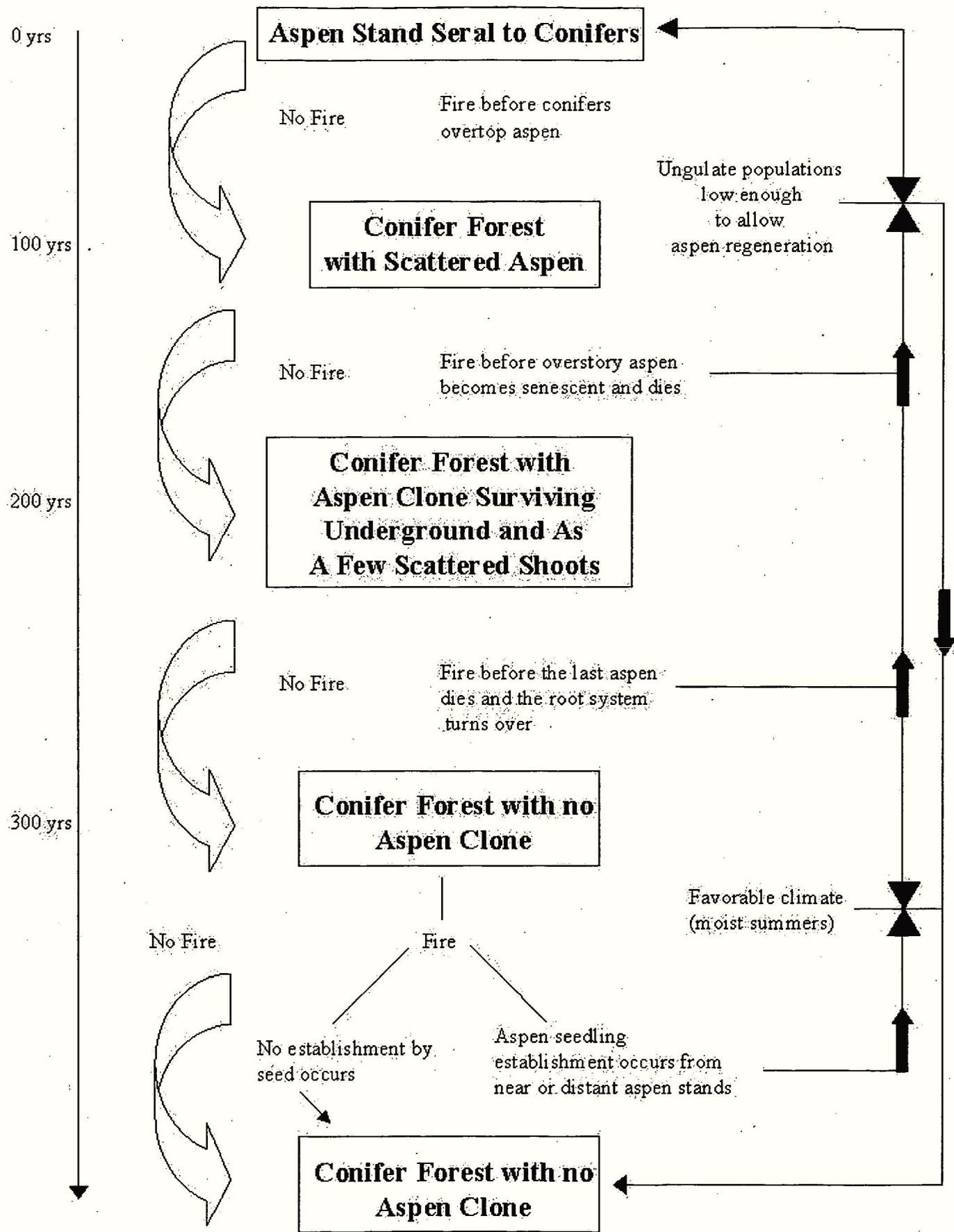


Fig. 2. Conceptual model of aspen dynamics for stands successional to conifers.

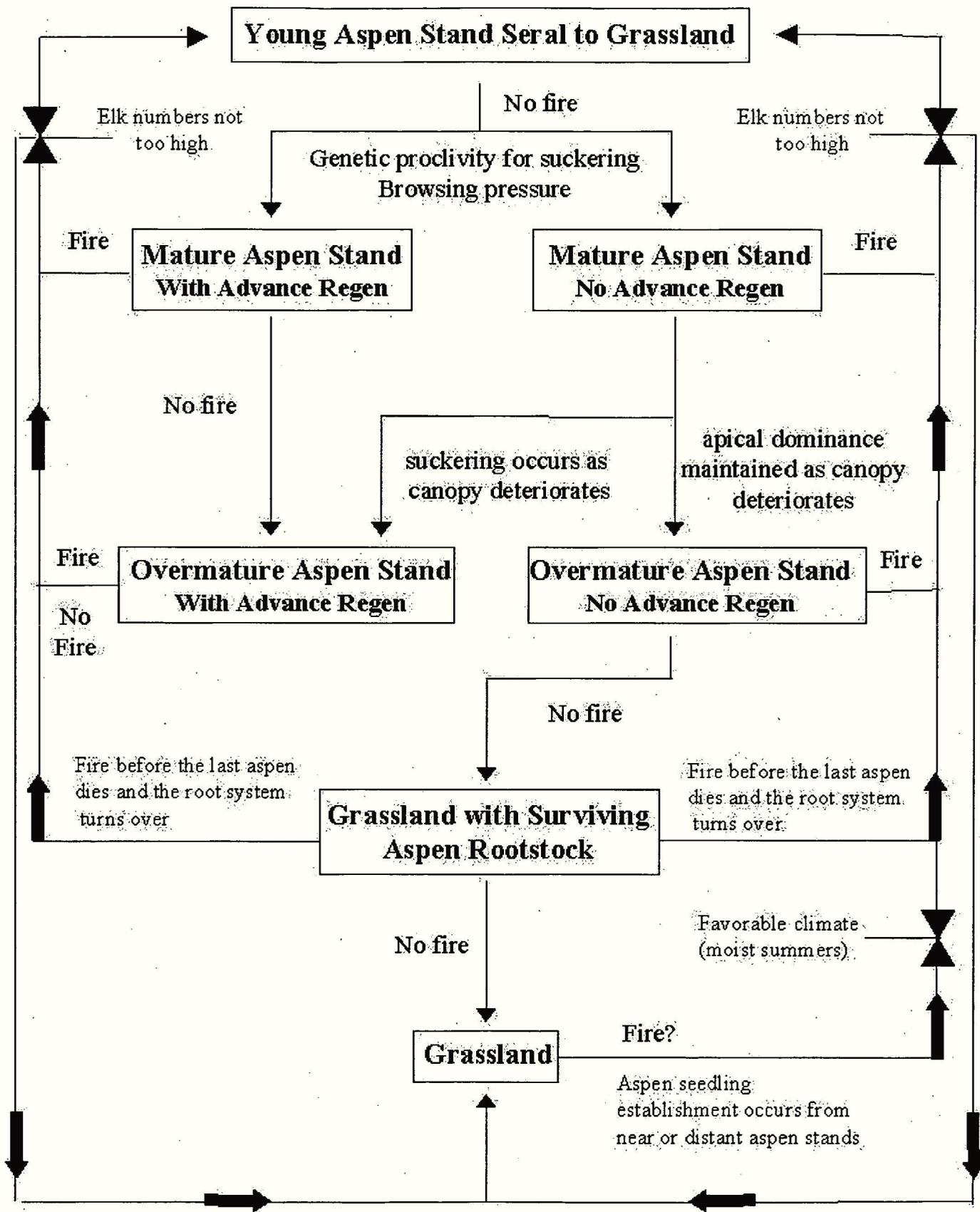


Fig. 3. Conceptual model of aspen dynamics for stands successional to grassland.

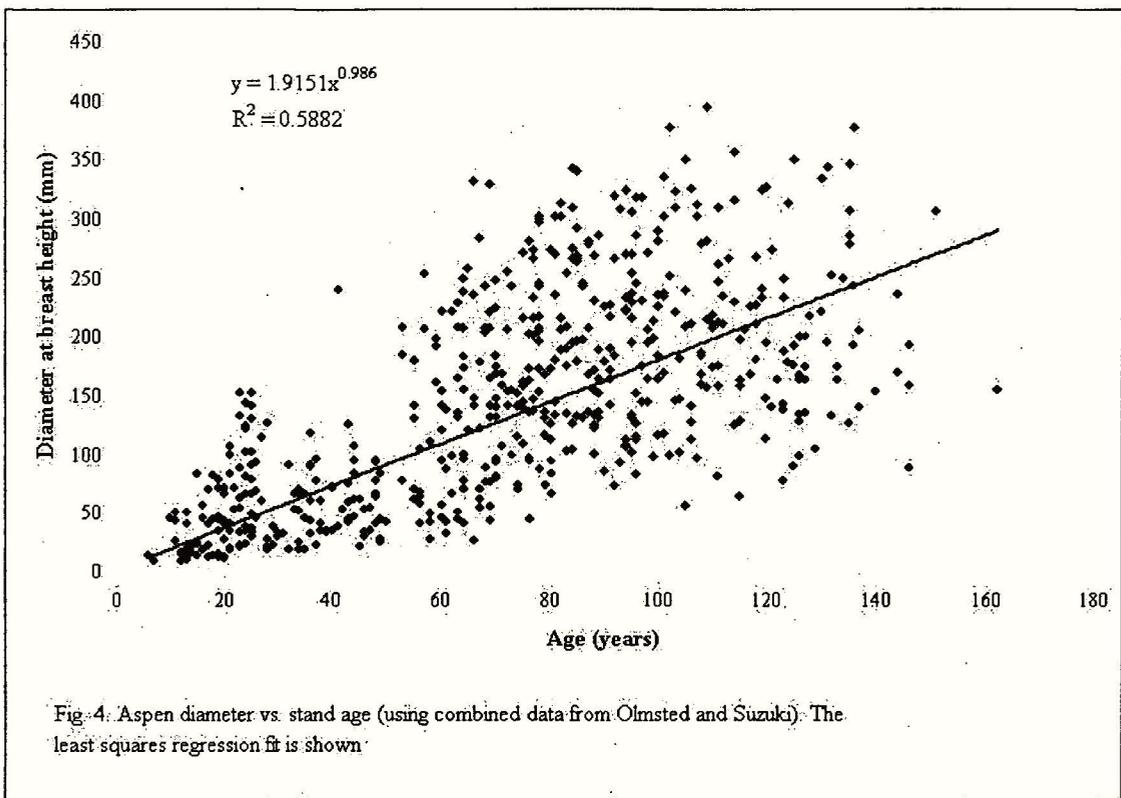


Fig. 4. Aspen diameter vs. stand age (using combined data from Olmsted and Suzuki). The least squares regression fit is shown.

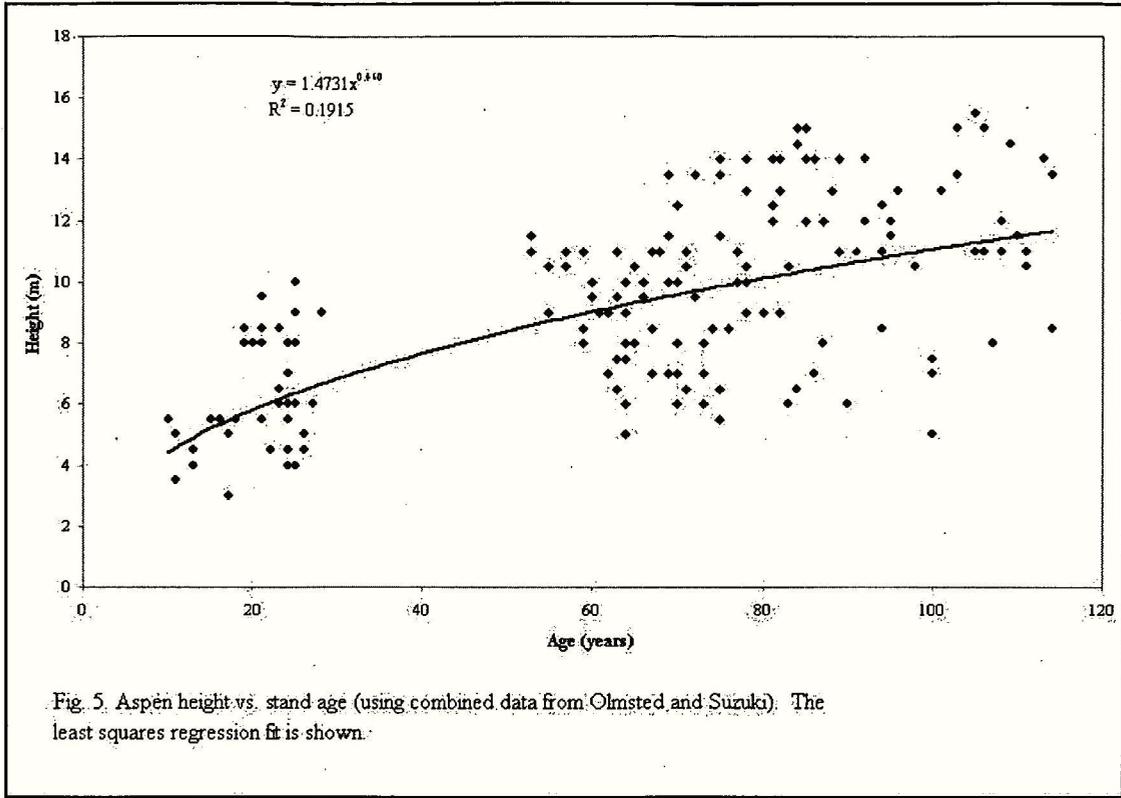


Fig. 5. Aspen height vs. stand age (using combined data from Olmsted and Suzuki). The least squares regression fit is shown.

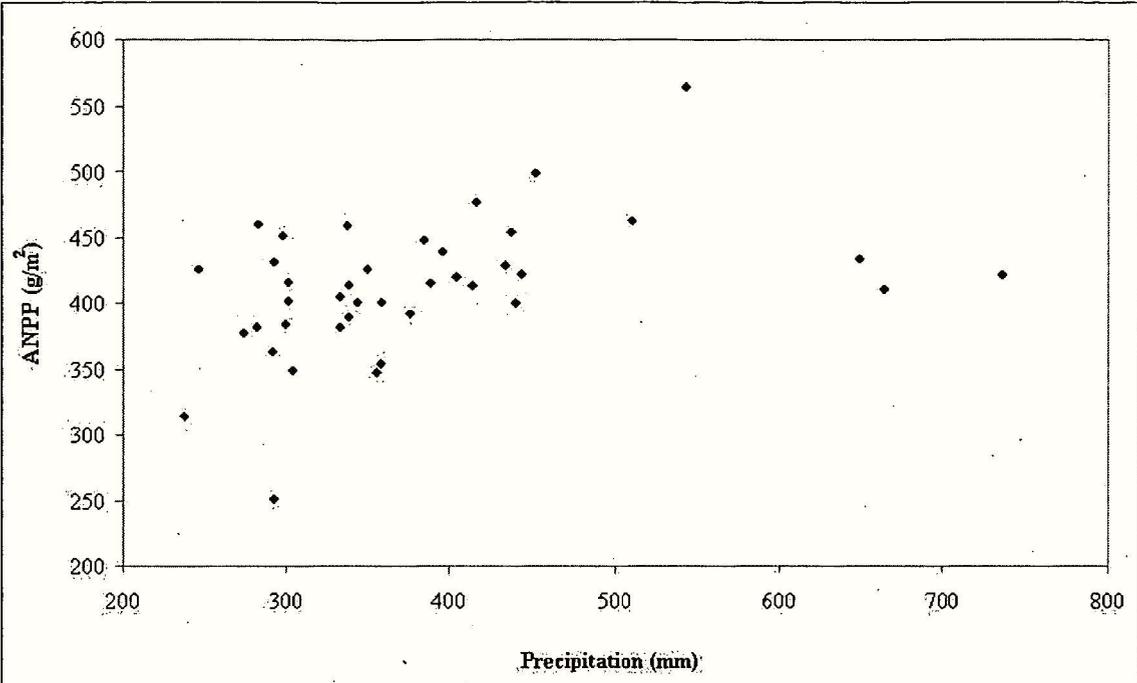
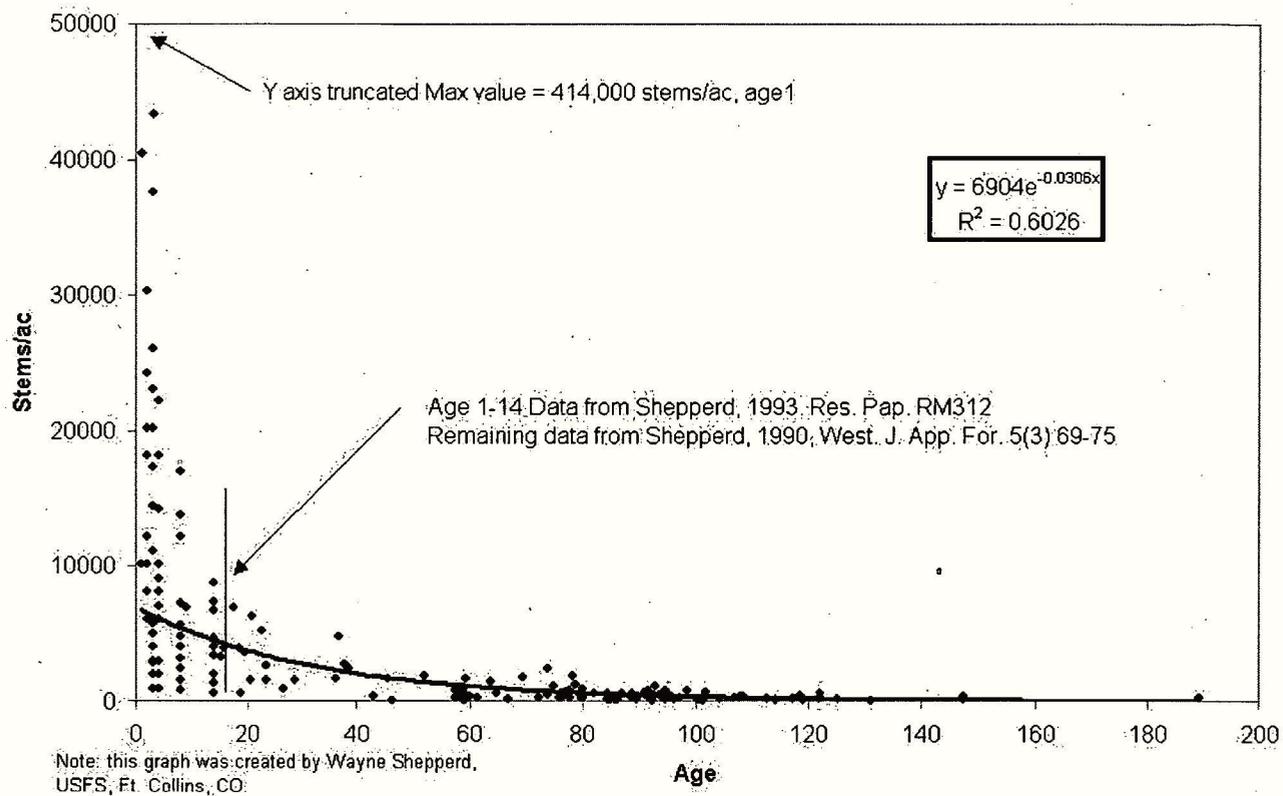
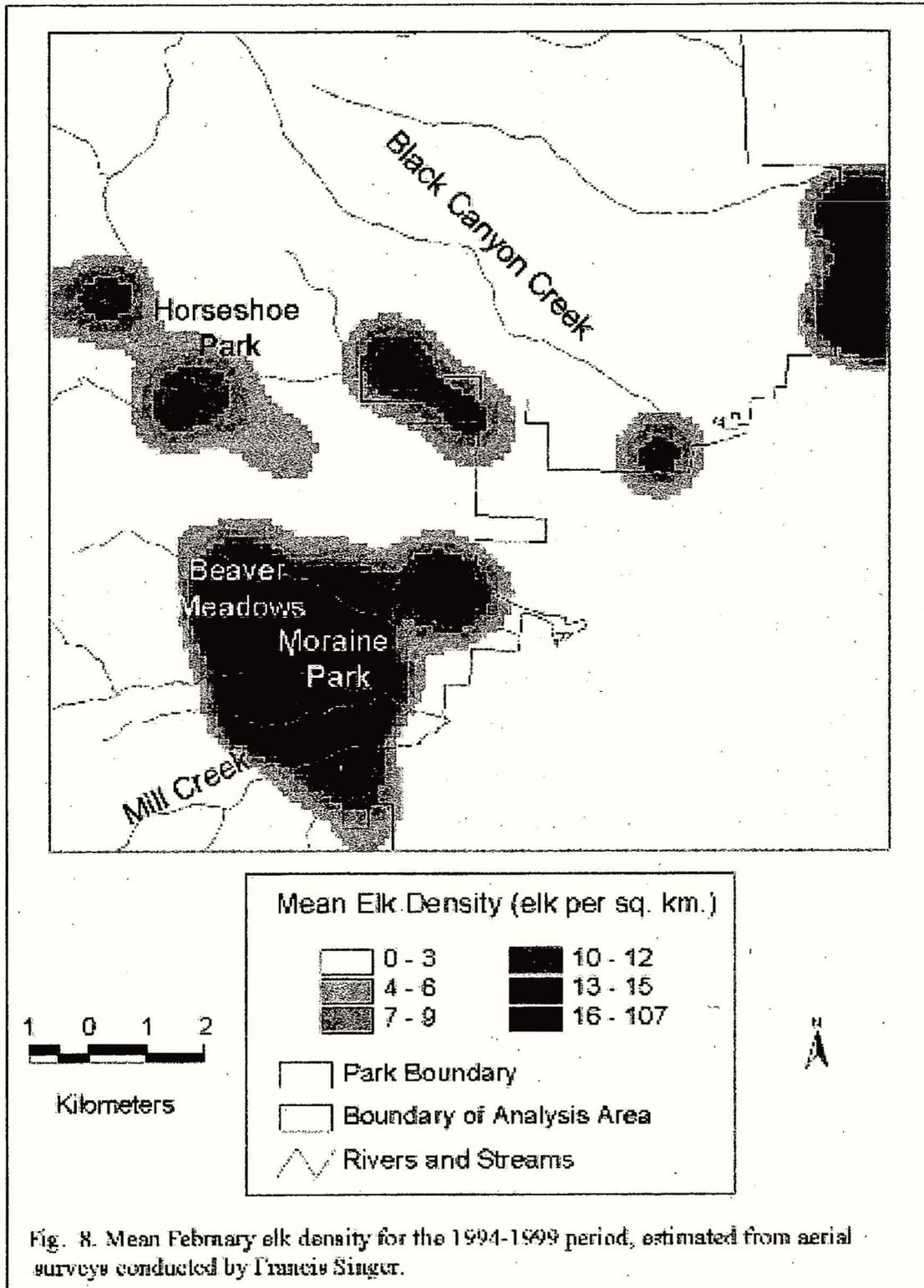


Fig. 6. Annual aboveground net primary production for aspen as a function of annual precipitation.

Fig. 7. Aspen Stem Density Model





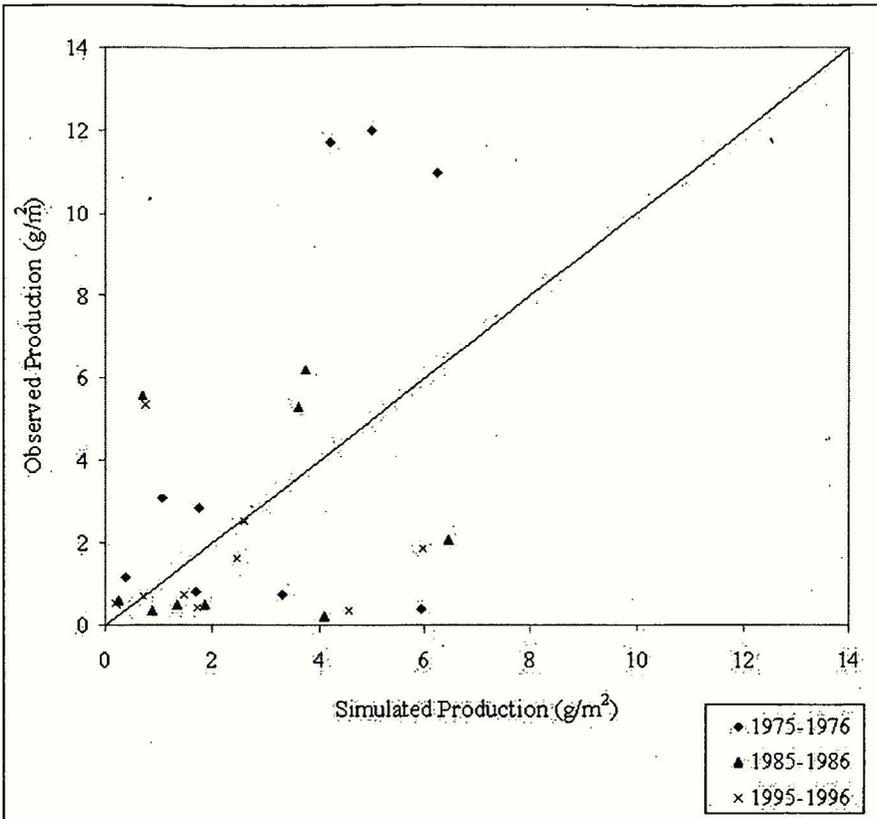
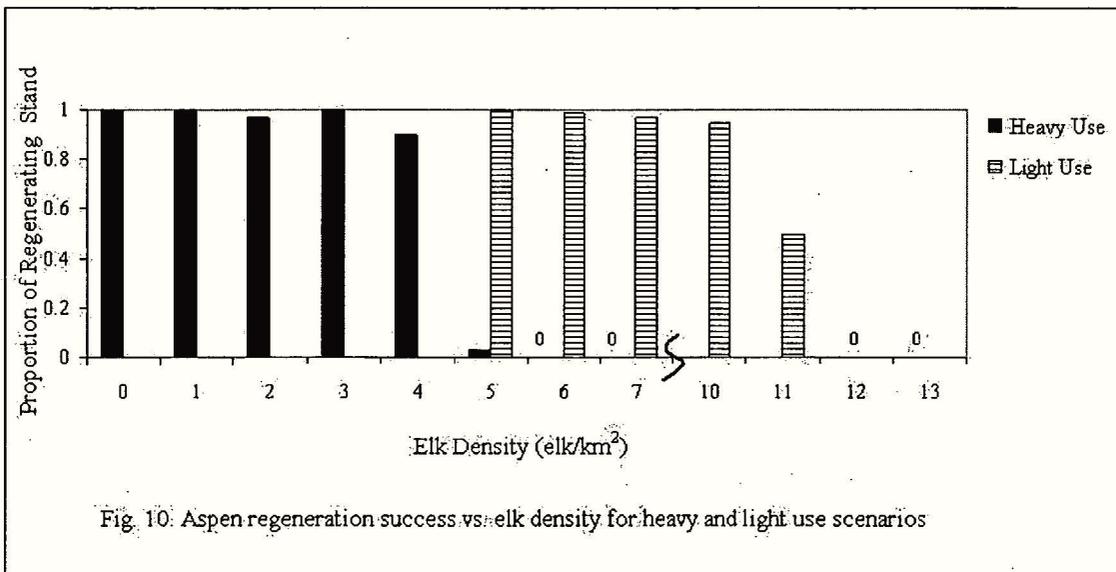
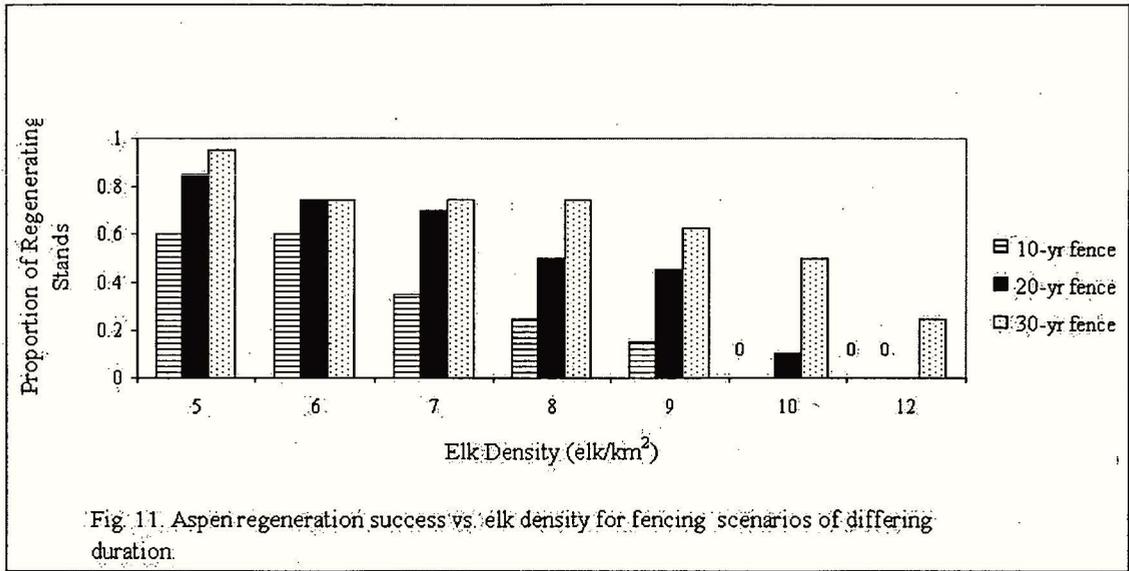
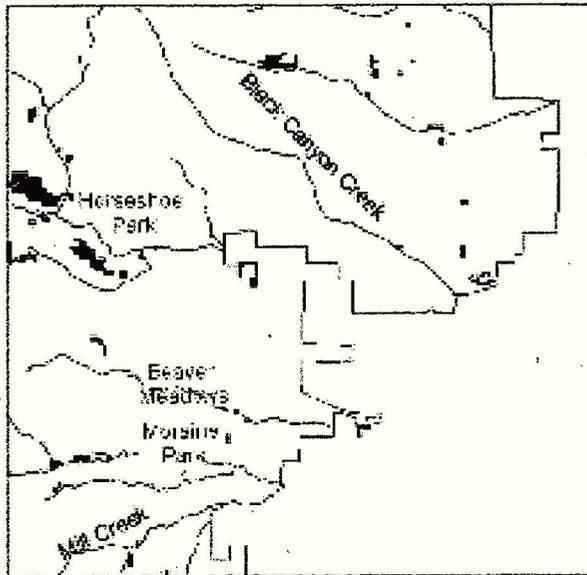


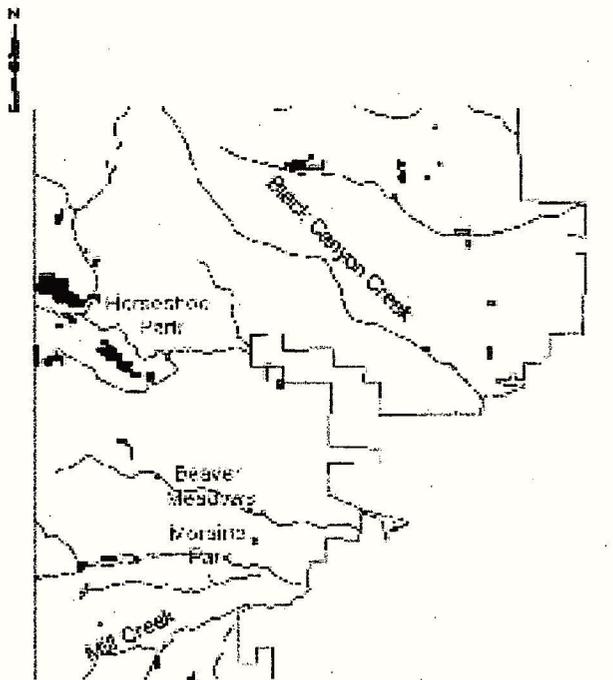
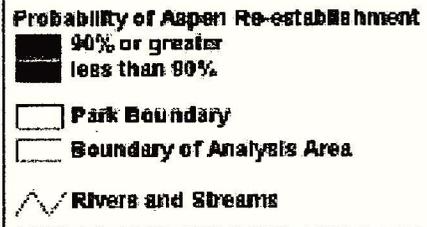
Fig. 9. Observed vs. simulated production of aspen suckers, based on unpublished data from C. Olmsted, for 3 winters at decadal intervals.







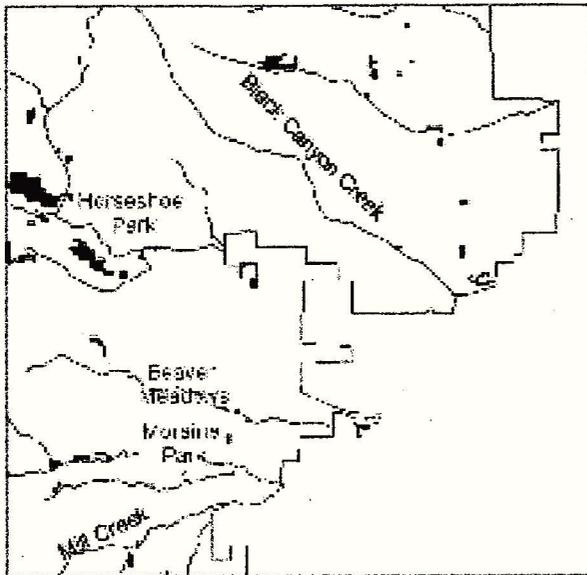
**600 Elk:
Heavy Use Scenario**



**1000 Elk:
Heavy Use Scenario**

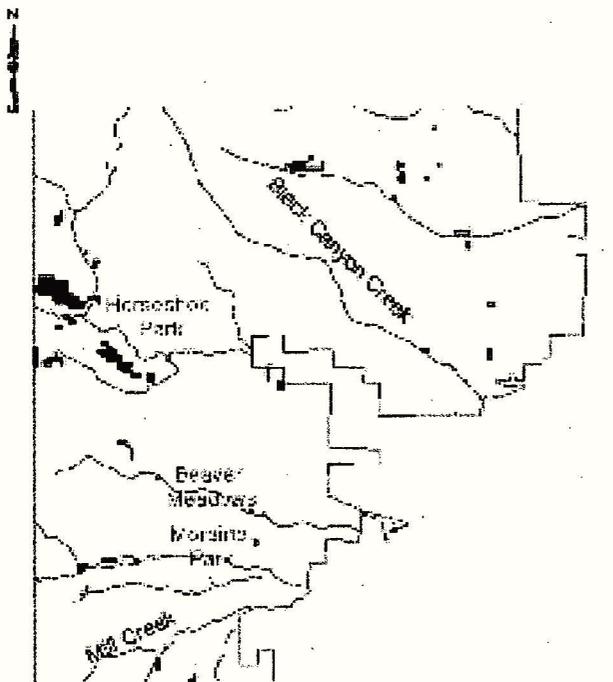


Fig. 12. Predicted effects of two different elk population levels on aspen regeneration success. The probability of regeneration success, defined in the text, is calculated over 30 random weather scenarios where elk population is held constant.



**2000 Elk:
Heavy Use Scenario**

Probability of Aspen Re-establishment
 ■ 90% or greater
 ▨ less than 90%
 □ Park Boundary
 □ Boundary of Analysis Area
 ~ Rivers and Streams

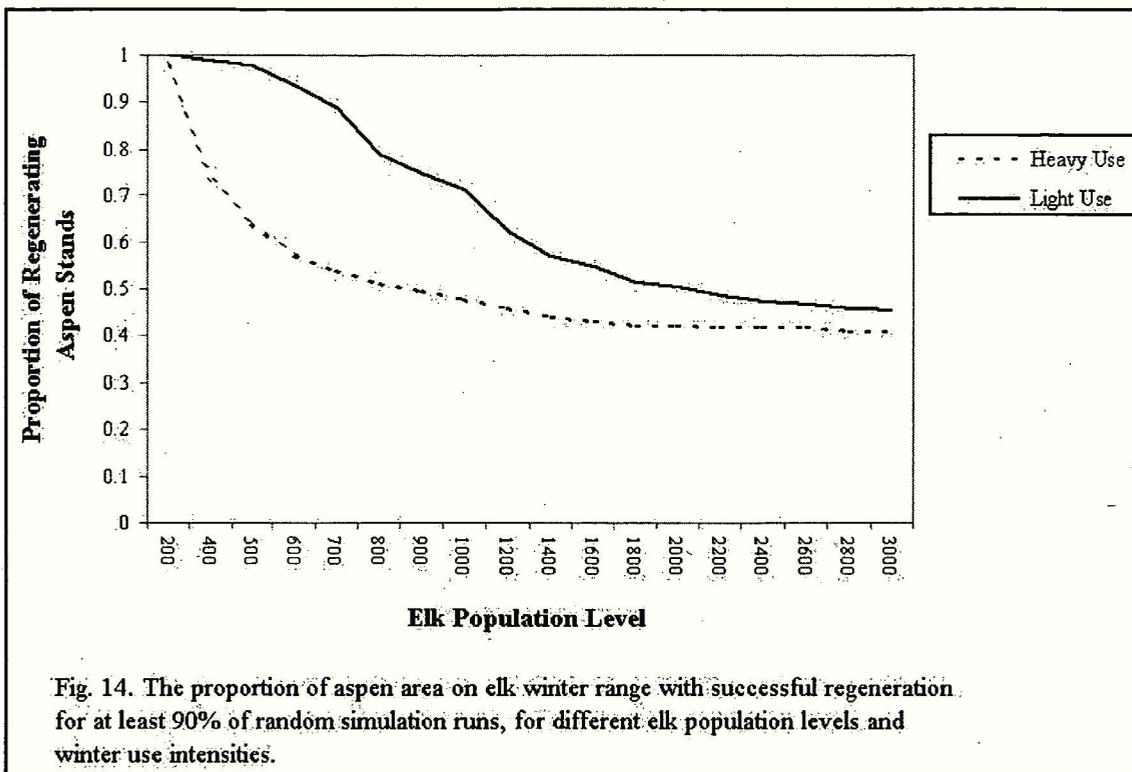


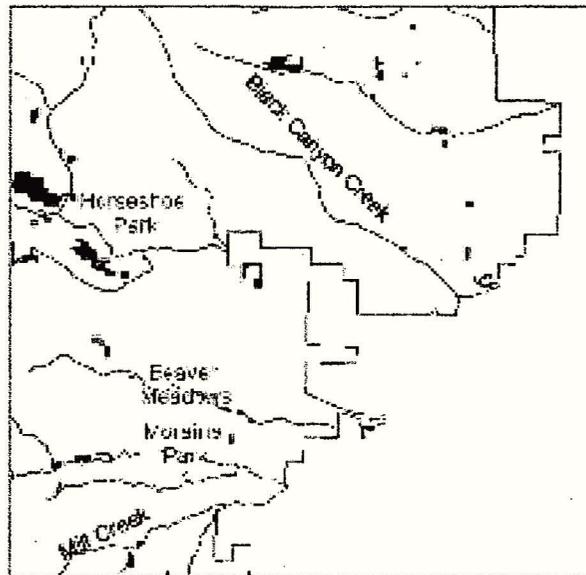
**3000 Elk:
Heavy Use Scenario**



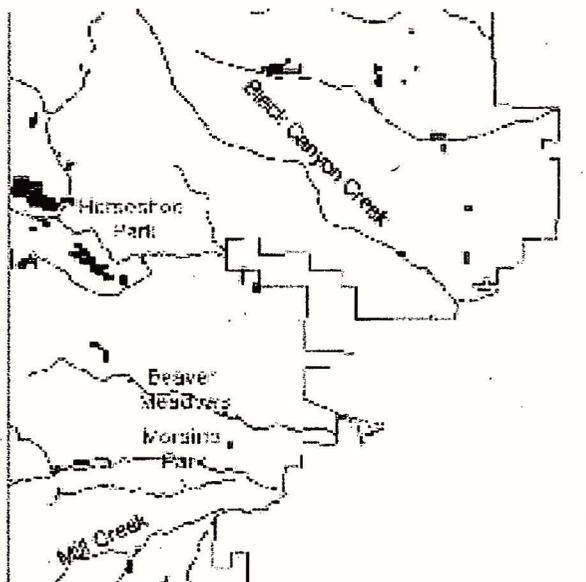
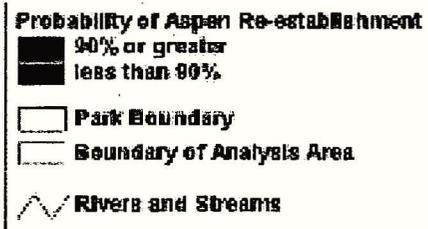
Kilometers

Fig. 13. Predicted effects of two different elk population levels on aspen regeneration success. The probability of regeneration success, defined in the text, is calculated over 30 random weather scenarios where elk population is held constant.





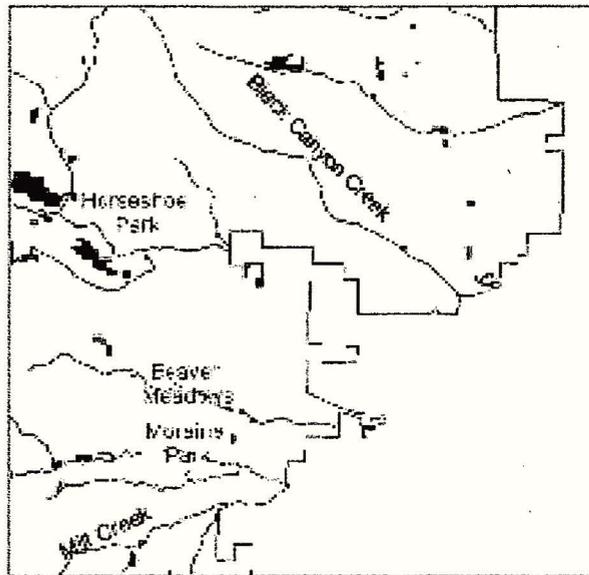
**600 Elk:
Light Use Scenario**



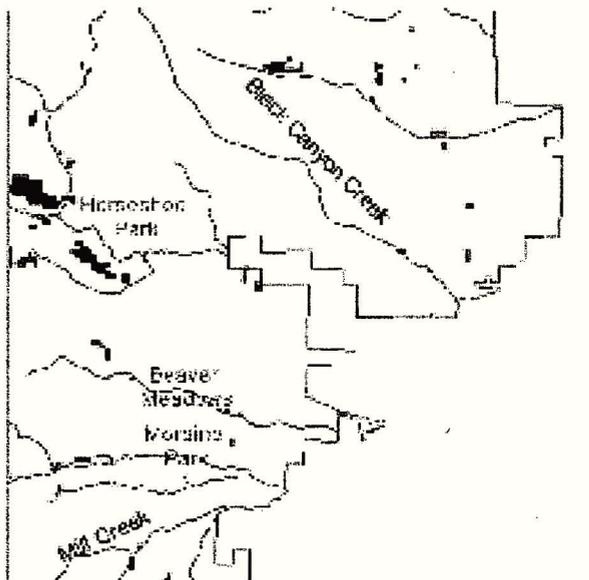
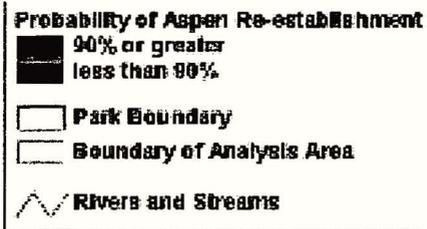
**1000 Elk:
Light Use Scenario**



Fig. 15. Predicted effects of two different elk population levels on aspen regeneration success. The probability of regeneration success, defined in the text, is calculated over 30 random weather scenarios where elk population is held constant.



**2000 Elk:
Light Use Scenario**



**3000 Elk:
Light Use Scenario**



Kilometers

Fig. 16. Predicted effects of two different elk population levels on aspen regeneration success. The probability of regeneration success, defined in the text, is calculated over 30 random weather scenarios where elk population is held constant.