MODEL-BASED ASSESSMENT OF ASPEN

RESPONSES TO ELK HERBIVORY

IN ROCKY MOUNTAIN NATIONAL PARK, U.S.A.

PETER J. WEISBERG[1*]

MICHAEL B. COUGHENOUR[2]

1. Mountain Forest Ecology Group, Department of Forest Sciences, Swiss Federal Institute of Technology, ETH-Zentrum HG F21.5, CH-8092, Zurich, Switzerland. Phone: +41 1 632 0901, Fax: +41 1 632 1146, Email: weisberg@fowi.ethz.ch

2. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499 USA.

* Author to whom correspondence should be addressed

Running Title: Aspen Responses to Elk Herbivory

1 ABSTRACT

2   In Rocky Mountain National Park (RMNP), aspen (*Populus tremuloides* Michx.) has

3 been observed to be declining on elk (*Cervus elaphus nelsoni*) winter range for many

4 decades. To support elk management decisions, the SAVANNA ecosystem model was

5 adapted to explore interactions between elk herbivory and aspen dynamics. The simulated

6 probability of successful vegetative regeneration for senescent aspen stands declines sharply

7 when elk densities reach levels from 3 - 5 elk km^{-2}, depending on model assumptions for the

8 seasonal duration of elk foraging activities. For aspen stands with a substantial component of

9 younger trees, the simulated regeneration probability declines more continuously with

10 increasing elk density, dropping below 50% at densities from 8 - 14 elk km^{-2}.

11   At the landscape scale, simulated aspen regeneration probability under a scenario of

12 extensive seasonal use was little affected by elk population level, when this level was above

13 300 – 600 elk (25 – 50% current population) over the ca. 107 km^2 winter range. This was

14 because elk distribution was highly aggregated, so that a high density of elk occupied certain

15 areas, even at low population levels overall. At approximately current elk population levels

16 (1000 - 1200 elk), only 35% – 45% of senescent aspen stands are simulated as having at least

17 a 90% probability of regeneration, nearly all of them located on the periphery of the winter

18 range. Successful management for aspen persistence on core winter range will likely require

19 some combination of elk population reduction, management of elk distribution, and fencing

20 to protect aspen suckers from elk browsing.

21

22 KEYWORDS: herbivory, national park management, simulation models, ungulate population

23 management, *Populus tremuloides*, *Cervus elaphus*, plant-animal interactions

24

25 INTRODUCTION

26 Ungulate species, both wild and domestic, can profoundly influence the vegetation for which

27 they depend as a food base (Milchunas and others 1989, Hobbs 1996). Elk (*Cervus elaphus*

28 *nelsoni*) have been observed to exert pronounced effects on woody vegetation throughout the

29 western United States. For example, intensive herbivory by elk has suppressed willow (*Salix*

30 spp.) height and leaf biomass in Yellowstone National Park (Singer and others 1994, Kay

31 1997b), Rocky Mountain National Park (Singer and others 1998) and interior Alaska (Wolff

32 1978). Although elk are primarily grazers, they require substantial browse (i.e. leaf and twig

33 growth of woody plants) in the winter to maintain adequate levels of protein (Hobbs and

34 others 1981). In Rocky Mountain National Park (RMNP), as much as 44% of the winter diet

35 has been observed to be browse (Hobbs and others 1981).

36   A favored browse species of elk, quaking aspen (*Populus tremuloides* Michx.) may

37 constitute greater than 7% of the winter diet in Rocky Mountain National Park (Hobbs and

38 others 1981). Elk browse aspen leaves and twigs, and strip aspen bark. The effect of bark-

39 stripping on aspen mortality is unknown, although it may create inoculation sites for

40 pathogens that eventually lead to aspen mortality (Hinds 1985, Hart and Hart 2001). The

41 effect of browsing young aspen suckers is more apparent. Suckers may eventually die after

42 being browsed for multiple years, resulting in critical losses of root reserves for the parent

43 tree (Schier 1975). Suckers that are able to persist despite high levels of browsing may

44 develop a shrubby growth form as a result of repeated loss of the apical meristem (Olmsted

45 1977, 1997).

46   In Rocky Mountain National Park, aspen has been observed to be declining, in the

47 low-elevation valleys and dry parks constituting core elk winter range, for many decades

48 (Dixon 1939 from Gysel 1960, Olmsted 1977, Stevens 1979, Hess 1993, Baker and others

49   1997). Elk effects upon aspen in RMNP have been a contentious issue, and have been

50   repeatedly studied (Olmsted 1977, Baker and others 1997, Olmsted 1997, Suzuki and others

51   1999). Aspen regeneration on core elk winter range has been episodic, and associated with

52   periods of low elk population (Baker and others 1997). Elk populations have fluctuated

53   markedly over the past 150 years. Intensive hunting virtually extirpated elk from the park

54   from about 1875 to 1913, when 49 elk were transplanted to the ca. 107 km^2 winter range

55   (Hess 1993). After population levels increased rapidly to over 1000 elk by the late 1930's, elk

56   populations in RMNP were controlled by shooting from 1943 through 1962 (Olmsted 1977),

57   and relocation and trapping through 1967 (Hess 1993). Elk population levels were stabilized

58   by hunting and culling to an average of 587 elk from 1953 - 1967 (Hess 1993). In 1968, the

59   current natural regulation policy of elk management (i.e., no direct population management)

60   was implemented, after which elk numbers again increased to 800 - 1200 animals, and

61   successful aspen regeneration on core winter range became very infrequent (Baker and others

62   1997, Olmsted 1997). Since then, aspen has been observed to be in decline for much of the

63   RMNP elk winter range. Decline is manifested as failure of new shoots to regenerate and

64   grow to tree size, while overstory mortality continues at a rapid rate (Olmsted 1997).

65   The problem of aspen decline is not unique to Rocky Mountain National Park, but has

66   been observed throughout the American West (Gruell and Loope 1974, Mueggler 1989,

67   Romme and others 1995, Kay 1997a, White and others 1998). However, recent extensive

68   surveys employing unbiased sampling techniques suggest that earlier studies may have

69   underestimated the extent of aspen regeneration at the landscape level, for both Rocky

70   Mountain National Park and the southern portion of the Greater Yellowstone Ecosystem

71   (Suzuki and others 1999, Barnett and Stohlgren 2001). Aspen decline is commonly

72   attributed to a combination of fire suppression and elk herbivory (Gruell and Loope 1974,

73   Kay 1997a, Bartos and Campbell 1998). Fire suppression allows relatively long-lived, fast-

74   growing conifers to overtop, and eventually replace, aspen in seral stands. Kay (1997a)

75   suggested that aboriginal burning and effects of aboriginal hunters on reducing ungulate

76   populations were responsible for the establishment of many aspen stands.

77   If there is an aspen regeneration problem in Rocky Mountain National Park, it is

78   important that this problem be understood at the process level, to assist managers in making

79   intelligent decisions. Ecosystem simulation models are valuable tools for synthesizing

80   information about various ecological components in a holistic manner that makes explicit the

81   interactions between components. The interaction that matters most for this study is the

82   interaction between elk herbivory and aspen population dynamics. A model well-suited for

83   capturing that interaction as it unfolds over long time periods would allow us to: (1) better

84   understand causal mechanisms for observed effects of elk on aspen growth and regeneration;

85   (2) forecast what would happen to aspen regeneration given different levels of elk herbivory,

86   and different assumptions about the effects of elk herbivory on aspen dynamics; and (3)

87   identify gaps in our data and understanding that are critical for explaining and predicting elk

88   effects on aspen dynamics.

89   The primary objective of this research was to use an existing ecosystem model

90   (SAVANNA) to estimate levels of elk numbers that would be compatible with long-term,

91   significant aspen regeneration. We also considered the effects of fencing aspen stands for

92   varying time periods, and at different elk population levels following removal of fences.

93

94   MATERIALS AND METHODS

95   *SAVANNA Model Adaptation*

96   The SAVANNA model is composed of interacting submodels for weather, soils,

97   carbon, nitrogen, water, light, vegetation production and population dynamics, and ungulate

98   production and population dynamics, and has been applied to grassland, shrubland, savanna,

99   and forested ecosystems (Coughenour 1992, Ellis and others 1993, Ellis and Coughenour

100   1998, Peinetti 2000, Weisberg and others 2002). The model represents, at a weekly time step:

101   (1) vegetation dynamics as changes in plant functional group composition, (2) plant

102   production in response to climatic variables, including seasonal patterns, (3) plant responses

103   to herbivory, and (4) animal distribution, production, and population responses to climatic

104   variables and changing patterns of plant production and vegetation composition. We used

105   SAVANNA to model a single, one-hectare aspen stand over a range of elk densities (from 0 -

106   16 elk km^{-2}). Results were extrapolated to the whole winter range using Arc/Info GIS

107   software, and GIS coverages for aspen stand locations and historical elk distribution.

108   We modeled three functional groups of plants (aspen, bunchgrasses, and forbs) and

109   one animal species (elk). The focal organism was aspen (Fig. 1), and other model elements

110   were parameterized to be ecologically "sensitive″ only insofar as they might influence aspen

111   dynamics. For example, elk production, population dynamics and energetics were not

112   explicitly simulated. To explore the effects of different levels of elk herbivory on aspen, a

113   fixed number of elk were maintained for a fixed time period in aspen stands. Since aspen

114   represents only a small proportion (7%, Hobbs and others 1981) of the winter elk diet, it is

115   realistic to exclude negative feedbacks of aspen browse availability on elk condition or

116   population dynamics.

117   Key model parameters are presented in Table 1. It is beyond the scope of the paper to

118   present the mathematical formulation of SAVANNA; for a detailed model description, see

119   Coughenour (2001; available upon request from Rocky Mt. National Park, Estes Park, CO).

120   Elk density was treated as a model input variable (Fig. 1), derived from either aerial

121   survey or simulated elk distribution data. Elk consumption of aspen was permitted to reach a

122   maximum of 0.012 kg aspen per kg elk, per day (Table 1). This value was obtained by

123   calibrating the model to achieve levels of aspen production and elk offtake observed by

124   Olmsted (1997). However, elk intake rates generally did not reach the maximum value, and

125   were calculated as:

126          $I = I_{max} * MIN(F_{fresp}, F_{snow}) * F_{sat}$ (1)

127

128   where: I = intake rate (kg forage / kg animal / day); I_{max} = maximum intake rate (kg forage /

129   kg animal / day); F_{fresp} = effect of functional response (feedback of forage availability (g m^{-2})

130   upon forage intake rate, Spalinger and Hobbs 1992) (0 – 1 scalar); F_{snow} = effect of snow

131   depth (cm) on forage intake rate multiplier (0 – 1 scalar); and, F_{sat} = effect of satiation on

132   forage intake rate (0 – 1 scalar).

133   Aspen population dynamics were modeled using 6 age classes in 10-year increments.

134   Using this approach, it was feasible to consider the youngest age class as aspen suckers.

135   Mortality rate parameters for the oldest age class were chosen to allow aspen to attain a

136   maximum age of 150 years. Individual aspen trees can live for longer than 200 years (Jones

137   and Schier 1985), but most aspen stands in the region are likely to succumb to senescence

138   and disease, and deteriorate by 150 years. Individual trees within classes are not modeled

139   explicitly, although each class may be represented by a "mean tree." The maximum size for

140   each class, with regard to stem diameter, canopy diameter, root diameter, upper canopy

141   height, lower canopy height, stem biomass, total root biomass, fine root biomass, and fine

142   twig biomass, was estimated using allometric equations and other information from a variety

143   of sources (Table 1; Beetle 1974, Olmsted 1977, Bartos and Johnson 1978, Ruark 1985,

144   Wang and others 1995). Potential growth rates were set so that trees under reasonable

145   growing conditions could grow from one age class to the next in 10 years. Actual growth

146   rates are calculated according to a semi-mechanistic photosynthesis submodel, where net

147   primary production (NPP) is influenced by light, water, temperature, nitrogen, and

148   temperature. The NPP submodel is explicitly linked to a water budget submodel through

149   transpiration and plant water use (Ball and others 1987). Allocation of NPP among plant

150   tissues utilizes an allometric approach, where allometry varies with aspen age class (Table 1).

151   Aspen regeneration was modeled as occurring under two different mechanisms, both

152   considered to represent suckering. Regeneration by seed was not considered a possibility, as

153   it has very seldom been observed in the western United States, except following rare events

154   such as extensive and severe wildfires (Kay 1993, Romme and others 1997). The first

155   mechanism allows suckering to occur in the presence of an overstory. The maximum number

156   of suckers per month, per living tree, is specified for each age/size class (Table 1).

157   Unfortunately, there are no useful data on suckering rates of aspen in the absence of

158   overstory mortality. Therefore, these age-class-specific values were calculated using data for

159   stem density as a function of stand age (Shepperd 1990, 1993), on the assumption that 2000

160   suckers per ha per year is a representative suckering rate under optimal conditions. The

161   second mechanism requires setting suckering rates associated with overstory tree mortality,

162   such that a specified number of suckers attempt to establish following mortality of a tree in a

163   given age/size class (Table 1). These values were based on a maximum suckering

164   establishment rate, following complete overstory removal, of 40,000 suckers per ha per year,

165   as has been observed following fire (Bartos and Mueggler 1980). Simulated rates of

166   establishment are further influenced by water availability, temperature, and competition with

167   herbaceous plant species (Table 1):

168         $Eff = F_{watr} * F_{temp} * MIN(F_{herb}, F_{wcv})$ (2)

169   where: Eff = the effect of environmental factors on tree regeneration; F_{watr} = the effect of

170   available soil moisture; F_{temp} = the effect of temperature; F_{herb} = the effect of herbaceous root

171   biomass; and, F_{wcv} = the effect of woody canopy cover.

172   For this study, the main mortality influence on aspen suckers was modeled as the

173   effect of elk herbivory. Simulated effects of elk herbivory on aspen included biomass effects

174   and population effects. Biomass effects occurred when elk herbivory maintained aspen

175   suckers at low heights and low levels of shoot biomass. Lower levels of elk herbivory

176   allowed a number of suckers to grow beyond elk reach height and form a viable regeneration

177   cohort. Population effects occurred when elk herbivory killed aspen suckers according to a

178   specified relationship between the proportion of the sucker browsed and the probability of

179   sucker mortality (Table 1). Sucker mortality probability was simulated as 1.0 when 20% of

180   the sucker woody biomass was browsed. This value is similar to the "breakeven level" of

181   30% twig volume reduction proposed by Olmsted (1977, 1997), where aspen stands in the

182   study area with greater reduction were more likely to have experienced declining stand

183   density over the 20-year period of study. The 20% value was arrived at through the model

184   calibration process described below, by starting with the 30% Olmsted value, and then

185   allowing the parameter to vary until simulated results for aspen production most closely

186   matched observed results. Elk-induced mortality of older trees (e.g. from bark-stripping) was

187   not represented, suggesting that our results for elk effects on aspen may be conservative.

188

189   *Model Calibration and Testing*

190   The model was calibrated and tested using data for nine aspen stands on elk winter

191   range in RMNP, for which long-term data were available for aspen production, elk offtake of

192   aspen, and aspen sucker density. These sites were originally sampled in 1975-6 (Olmsted

193   1977), and re-sampling occurred in 1985-6 and 1995-6 (Olmsted 1997). Specific information

194   for each site used in model calibration were its elevation, slope steepness, slope aspect,

195   winter elk density (see below), canopy cover in 1975-6, and age class structure in 1975-6.

196   Except for elk density, this information comes from Olmsted (1977), Olmsted (1997), and

197   unpublished data from Olmsted's work.

198   Winter elk densities for model calibration were obtained from spatially explicit

199   SAVANNA runs of elk distribution, utilizing habitat suitability algorithms that include

200   forage availability (total forage biomass, herbaceous green biomass), slope steepness,

201   modeled climatic variables (snow depth, mean daily temperature), and the existing density of

202   elk on a particular patch. Outputs from spatially explicit SAVANNA runs were at a 25 ha

203   resolution, coarser than the 1 ha resolution of the GIS coverage used for delineating aspen

204   stands. Average annual winter elk density for each aspen stand was calculated as the mean

205   simulated elk density at that location, from January – April, for each year from 1970 – 1998.

206   We simulated aspen dynamics at the nine sites from 1970 - 1998, using historical

207   weather data. Observed data for aspen production and elk offtake were available for the

208   winters of 1975 - 1976, 1985 - 1986, and 1995 - 1996 (Olmsted 1997). For these three

209   seasons, we compared observed and simulated shoot production of current year's growth on

210   all twigs up to 2 m in height. Observed shoot production, measured in October, was provided

211   in units of twig volume. We converted twig volume (cubic cm) to twig wet weight (g) using

212   the empirical relationship from Olmsted (1977):

213         $Weight = (0.671 * Volume) + 0.236$ (3)

214   Elk intake rate for aspen was calibrated until there was reasonable agreement between

215   observed and simulated elk offtake. Observed elk offtake for the winter months was

216   calculated as the difference between twig volume measured in October and twig volume

217   measured in May of the following year, converted to units of weight.

218   We conducted statistical testing of model outputs, using all nine sites. This does not

219   represent an independent validation, since all sites were used in model calibration, but does

220   provide some indication as to the predictive ability of the model, for this particular

221   application. A statistical validation of SAVANNA for a nearby area in northern Colorado is

222   reported in Weisberg and others (2002), where simulated herbaceous biomass and offtake by

223   elk closely matched observed data from a controlled grazing field experiment. The basic

224   model operation has been validated elsewhere, in various studies (e.g. Ellis and others 1993,

225   Coughenour 2001, Boone and others 2002). For the RMNP application, we used

226   environmental and stand structural data specific to each site, and compared aspen sucker

227   production, sucker density, and winter elk offtake from aspen suckers between observed and

228   simulated data. Aspen sucker density and offtake data were sufficiently skewed to require

229   square root and logarithmic transformations, respectively, prior to statistical validation.

230   We also analyzed the sensitivity of aspen canopy cover, aspen sucker production, and

231   aspen sucker density, to variation in several of the key input parameters. Following Friend

232   and others (1993), each parameter was increased (P_1) and decreased (P_0) by 10%, and a

233   sensitivity index calculated as:

234     $$\beta = \frac{R_1 - R_0}{R_0} \bigg/ \frac{P_1 - P_0}{P_0},$$ (4)

235   where R = response variable, R_0 = R when parameter is P_0, and R_1 = R when parameter is P_1.

236

237   *Simulation Experiments*

238   The 1970 - 1998 calibration runs for the Beaver Meadows-Deer Ridge (BMDR) and

239   Lower Beaver Meadows (LBM) sites were used to initialize a set of experimental runs for the

240   2000-2059 period. These two sites were chosen to represent different aspen stand structures

241   now present on the winter range. The BMDR site (*i.e.*, senescent stand) has an older age

242   structure representative of decadent lower-elevation aspen stands in the Park, having a

243   moderate level of crown cover, a moderate to high winter elk density, and lacking successful

244   establishment of a regenerating aspen cohort. The LBM site (*i.e.,* young stand) represents

245   aspen stands including a younger age cohort of aspen, due to successful aspen regeneration

246   during the herbivore population control period of the 1950s and 1960s (Olmsted 1977). The

247   great majority of aspen stands on core winter range more closely resemble the BMDR site

248   (Baker and others 1997).

249   The seasonal duration of elk habitat use of RMNP winter range aspen is surprisingly

250   little known, so we simulated multiple scenarios reflecting different assumptions. For the

251   Heavy Use scenario, elk densities in the simulated aspen stand are at their maximum level for

252   November, December, January, February, March, and April; at 80% of their maximum level

253   for October; at 50% of their maximum level for May and September; and at 10% of their

254   maximum level for June, July, and August. This general pattern of elk distribution is

255   consistent with a recent, detailed study of elk movements (Larkins 1997), but may be not be

256   representative where aspen stands are utilized for shorter periods during winter, and not at all

257   during summer. Therefore, we also simulated a Light Use scenario, where elk densities are at

258   their maximum level for December and January; at 50% of their maximum level for

259   November and February; and are at 0 for the rest of the year. A field survey of winter elk

260   movement and habitat use in the Park found elk use of aspen stands to be substantial (as

261   much as 35% of total habitat use) from October through December, but virtually zero from

262   January through April, when elk increased their use of grassland habitats (Clarke and others

263   1994). These results suggest the Light Use scenario may more accurately describe elk use of

264   aspen stands. We also simulated a Moderate Use scenario, where elk densities are maximal

265   from January through April; at 50% of their maximum level for May, November and

266   December; and are at 0 from July through October.

267   Fence scenarios were simulated by setting elk population density to zero for the

268   duration of the fencing treatment (10, 20, or 30 years), and then setting elk population density

269   to the specified level upon completion of the treatment. All fence experiments used the

270   Moderate Use scenario for elk use, and simulated senescent stands.

271   Experimental runs used randomized weather patterns with a mean and variance for

272   temperature and precipitation similar to that of the 1910 - 1998 period. Elk density was

273   systematically varied between $0 – 16$ elk km^{-2} for nine simulation experiments (Table 2).

274

275   *Data Analysis*

276   To explore how various treatments affected the probability of aspen persistence, we

277   calculated the proportion of 60-year, random weather runs where the simulated aspen stand

278   successfully regenerated. An aspen canopy cover of at least 40% was considered a necessary

279   condition for regeneration success, while a canopy cover of at least 60% was considered a

280   sufficient condition. Note that the initial (1976) aspen canopy cover values for the BMDR

281   and LBM stands were 50% and 58%, respectively. Where aspen canopy cover was between

282   40% and 60%, regeneration success was considered to have occurred if one of the following

283   conditions were true: (1) Sucker density ≥ 1000 per ha; (2) Age class 2 ($11 – 20$ years)

284   density ≥ 500 per ha; (3) Density ≥ 1000 stems per ha in age classes 3 ($21 – 30$ years), 4 (31

285    $– 40$ years), and 5 ($41 – 50$ years) combined; (4) Density ≥ 300 stems per ha each for ≥ 3 age

286   classes from age class 3 to age class 6 ($51 – 150$ years). While these criteria are somewhat

287   arbitrary, they guarantee that only those stands are considered to have successfully

288   regenerated which have either increased in cover after 60 years, or have maintained most of

289   their original cover while younger cohorts have established.

290   Stand-level results were extrapolated to the landscape scale, over the extent of elk

291   winter range within Park boundaries, in the Estes Valley area. The official RMNP GIS

292   coverage for vegetation, based on 1987 aerial photography and estimated to be 80-85%

293   accurate, was used to represent the distribution of aspen stands at a 1-ha resolution. Aspen

294   stands are likely under-represented by this vegetation coverage, since they are often quite

295   small (Stohlgren and others 1997). The aspen data layer was overlaid on two coverages of

296   mean relative elk density, each obtained using 2 data sources: (1) aerial surveys of winter elk

297   distribution from 1994 – 1998; and, (2) simulated elk density from spatially explicit

298   SAVANNA runs of elk distribution from 1960 - 1998, as described in the Model Calibration

299   and Testing section. Results from each method are interpreted and reported separately, to

300   provide an indication of the sensitivity of our interpretations to the estimated spatial

301   distribution of elk, a highly uncertain parameter.

302   Winter elk densities derived from 1994 - 1998 aerial survey (i.e., empirical) data were

303   interpolated for each winter across all 1-ha pixels, in the portion of elk winter range within

304   Park boundaries, using standard GIS operations (Fig. 2a). Interpolated elk density averaged

305   over the 5 years was used to calculate a map of relative elk distribution, that was then used to

306   predict elk population for each pixel, based on an overall elk population level for the RMNP

307   winter range. Elk population level for each pixel was predicted as:

308     $n_i = \left(\rho_i / \sum \rho \right) * N_y$ (5)

309   where: n_i = the number of elk occupying pixel i; ρ_i = interpolated mean 1994 to 1998 elk

310   density for pixel i; $\sum \rho$ = the sum of interpolated 1994 to 1998 elk densities over all pixels on

311   the Park winter range; and N_y = the elk population level for the Park winter range as a whole,

312   which was varied systematically from 100 – 3000.

313   Elk population levels for each pixel using the simulated elk distribution data were

314   also calculated using Equation 5, except that, in this case, ρ_i = the simulated mean elk density

315   for one of three historical time periods, representing different elk population levels for the

316   RMNP winter range as a whole: 1960 – 1975 (400 – 600 elk), 1975 – 1982 (600 – 1000 elk),

317   1982 – 1998 (1000 – 1400 elk). This approach permits the relative distribution of elk to

318   change as total elk population changes.

319   Then, the expected probability of aspen regeneration success was estimated for each

320   stand given its estimated elk population level, according to threshold values derived from

321   simulation results. One hectare aspen stands with a regeneration success probability of $\geq$

322   90%, or $\leq$ 10%, were separated from other aspen stands, and the spatial pattern of aspen

323   regeneration success was shown in map form, under different assumptions concerning elk

324   population level, elk distribution patterns, seasonal intensity of elk use, and developmental

325   stage of aspen stands.

326   The proportion of regenerating aspen stands on the winter range was described

327   graphically, for Heavy Use and Light Use scenarios, and for elk population levels from 100 –

328   3000 elk km^{-2}. Given a study area of ca. 107 km^2, the 100 elk level would represent a density

329   of about 1 elk km^{-2}, while the 3000 elk level would represent a density of about 28 elk km^{-2},

330   if elk density were homogeneous over the winter range. However, elk density over the winter

331   range is far from homogeneous (Fig. 2). For example, using the empirical data, an overall

332   population level of 1219 elk in 1998 corresponded to a density of about 7 elk km^{-2} at the

333   BMDR site, but to a density of about 56 elk km^{-2} at the heavily utilized Moraine Park site.

334

335   RESULTS

336   *Model Testing*

337 A sensitivity analysis found that model outputs for aspen canopy cover, aspen sucker

338 production, and aspen sucker density, were especially sensitive to the user-defined function

339 specifying the relationship between browsing intensity and aspen sucker mortality (Table 3).

340 Sucker production and density were also quite sensitive to the other parameters tested,

341 representing different aspects of aspen population dynamics. Aspen canopy cover was the

342 least sensitive of the three response variables tested, supporting its use as the primary

343 criterion for specifying simulated aspen regeneration success.

344 Based on the statistical testing of model predictions for the nine sites, mean aspen

345 production does not differ significantly between observed and simulated values for any of the

346 years considered (Table 4). Coefficients of determination for the regression fit between

347 observed and simulated production values range from 0.62 to 0.91. The simultaneous F-Test

348 for regression bias indicates that the hypothesis of a biased model cannot be rejected for the

349 1995-6 season, and confidence intervals for regression slope do not include 1.0 for all years

350 except 1975-6. These results suggest that, with regard to aspen production, the model

351 generates quite reasonable results with a minor but significant bias, where the model under-

352 predicts for low values, but over-predicts for high values, of aspen production (Fig. 3a).

353 Mean elk offtake of aspen does not differ significantly from observed offtake,

354 although simulated offtake is lower for all years (Table 5). While validation results appear

355 acceptable when only mean values are considered, the model poorly predicted offtake at a

356 given site for a given year (Table 5, Fig. 3b). The model underpredicts offtake at low values,

357 there is a wide scatter around the line of perfect fit, and linear regression relationships

358 between observed and predicted offtake are not significant for individual years. We attribute

359 the poor performance of the model at this level to uncertainty associated with elk density for

360 a given site and year. Simulated elk distributions may be accurate as generalizations, but lack

361   sufficient precision to predict the number of elk at a fine temporal and spatial resolution. This

362   is demonstrated by the occurrence of high observed offtake values in the Olmsted (1997) data

363   set, for particular sites and winters for which no or few elk were predicted. For example, elk

364   offtake of aspen at the Little Horseshoe Park (LHRS) site was observed by Olmsted (1997) to

365   be 15.49 g/m^2 in 1975-76, while estimates of mean elk density for that winter at that site were

366   only 2.88 and 5.01 elk km^{-2} using the empirical and simulation elk distribution methods,

367   respectively. Even though 1975 aspen sucker production was predicted fairly accurately for

368   this site (19.53 g/m^2 observed vs. 17.13 g/m^2 predicted), there would be no chance for the

369   model to predict offtake accurately given available estimates for mean elk density. However,

370   errors associated with incorrect estimates of elk density may average out, over the 60 year

371   period of the experimental runs, and at the scale of the entire winter range.

372   Model output for aspen sucker density is not directly comparable with observed aspen

373   density, since observed aspen density includes suckers of very small size, while simulated

374   aspen suckers have minimum heights and crown diameters of 0.5 m and 0.15 m, respectively.

375   However, observed and simulated sucker density are positively associated according to the

376   following linear regression relationship ($R^2 = 0.45$; $F_{(1,25)} = 20.73$; $p < 0.01$):

377          $y = 2.61x + 48.09$ (6)

378   where y = square-root transformed observed aspen sucker density, and x = square-

379   root transformed simulated aspen sucker density.

380

381   *Stand-level Results*

382   Aspen regeneration success is clearly much greater when elk use is less prolonged

383   over the course of the year (Fig. 4a). Under the Heavy Use scenario, aspen regeneration

384   success for the senescent stand is high at 1 elk km^{-2}, moderate at 2 elk km^{-2}, and decreases

385 sharply between 2 and 3 elk km^{-2}. For this same stand under the Moderate Use scenario,

386 aspen regeneration success is still moderate at 3 elk km^{-2}, is low at 4 elk km^{-2}, and is 0 at elk

387 densities of 5 km^{-2} or greater. Under the Light Use scenario, simulated aspen at the senescent

388 stand has a greater than 50% chance of regeneration at elk densities of up to 5 km^{-2}, but

389 declines gradually to 0 by 8 elk km^{-2}.

390   An alternative means of estimating elk density levels beyond which senescent aspen

391 stands may decline is through the analysis of simulated aspen canopy cover (Fig. 5a). By the

392 end of the 60-year simulations, mean aspen canopy cover has dropped sharply below the

393 initial level of 50.5% at densities of 3 elk km^{-2}, 4 elk km^{-2}, and 6 elk km^{-2}, for heavy use,

394 moderate use, and light use scenarios, respectively.

395   The probability of aspen regeneration success despite moderate or high levels of elk

396 browsing increases greatly if a younger aspen age cohort is present (Fig. 4b). For such stands,

397 aspen regeneration success under the Heavy Use scenario is ≥0.90 for up to 3 elk km^{-2}, ≥0.50

398 for up to 7 elk km^{-2}, and 0 by 9 elk km^{-2}. Simulated aspen canopy cover drops significantly

399 below its initial value of 57.5% by 8 elk km^{-2} (Fig. 5b). Under the Moderate Use scenario,

400 aspen regeneration success is ≥0.90 for up to 4 elk km^{-2}, ≥0.75 for up to 7 elk km^{-2}, then

401 drops off sharply, reaching 0 by 12 elk km^{-2}. Simulated aspen canopy cover drops to 40% by

402 8 elk km^{-2}, and drops sharply lower to about 20% by 10 elk km^{-2}. Aspen regeneration success

403 for the Light Use scenario does not drop below 0.40 by the maximum elk density tested, of

404 16 elk km^{-2} (Fig. 4b). At least 90% of simulation stands regenerated at density levels of up to

405 7 elk km^{-2}. Simulated canopy cover drops slightly below its initial level at a density of 14 elk

406 km^{-2} (Fig. 5b).

407   Aspen regeneration success is also significantly improved by fencing senescent aspen

408 stands (Fig. 4c). As might be expected, fencing aspen stands for longer time periods improves

409   the probability of aspen persistence. Fencing for 10 years, followed by a 50-year period

410   without fences, does not improve the probability of aspen persistence much relative to a

411   control scenario of no fencing at all. However, aspen regeneration probability does not

412   appear to be ensured even at moderate elk densities with the 30-year fence scenario. This is

413   because the aspen stands again begin to deteriorate, once the fences come down.

414

415   *Landscape-level Results*

416   The landscape-level results for the proportion of regenerating aspen stands (*i.e.*,

417   PRegen = at least a 90% probability of regenerating) as a function of winter range elk

418   population level show similar patterns, regardless of whether elk distributions are derived

419   from empirical or simulated data (Figs 6 & 7). However, PRegen using the simulated

420   distributions shows more of a steady rise with decreasing elk population, for elk population

421   levels below about 600 elk (heavy use – senescent stands), 900 elk (light use – senescent

422   stands), and 1300 elk (light use – younger stands). Also, PRegen is generally lower using the

423   simulated elk distribution data (Fig. 6). This is because simulated elk distribution is less

424   concentrated than that derived directly from empirical data (Fig. 2), but is also more focused

425   on aspen stand locations. Also, simulated elk distributions are output at a coarser resolution

426   (25 ha) than that produced by the empirical GIS interpolation (1 ha), resulting in the steplike

427   response curves shown in Fig. 6b.

428   The Heavy Use scenario yields the interesting result that PRegen for senescent stands

429   is little affected by elk population level (Figs 6 & 7), except at levels below about 300 elk

430   where empirical data are used to specify elk distributions (Fig. 6a), or below about 600 elk

431   where simulated elk distributions are used (Fig. 6b). Using the empirical distributions, fewer

432   than 60% of senescent aspen stands have a $\geq$ 90% probability of regenerating even at 200

433   elk, although most of the remaining stands (85%) have at least a 10% probability of

434   regenerating (Fig. 7). Using the simulated elk distributions, PRegen at 200 elk is even lower.

435   The landscape-level results for the Moderate Use scenario are only slightly different

436   from those of the Heavy Use scenario, and are not shown in Figures 6 and 7. There is a

437   greater difference between elk population extremes for senescent stands, given the Light Use

438   Scenario (Figs 6 & 7). Given the empirical elk distributions, there is little effect of elk

439   population level on PRegen until population levels of below about 500 elk have been reached

440   (Fig. 6a). Given the simulated elk distributions, there is a 10% increase in PRegen as elk

441   population level is reduced from 1000 to 900, and then little effect of elk population on

442   PRegen until about 400 elk, below which PRegen increases markedly (Fig. 6b).

443   Younger stands (dashed lines on Fig. 6) are better able to perpetuate themselves under

444   elk browsing pressure than senescent stands. Since the threshold value of 90% aspen

445   regeneration probability is 3 elk km^{-2} for both Heavy Use-Senescent Stands and Light Use-

446   Younger Stands scenarios (Figs. 4a, b), these two scenarios produce identical results for

447   landscape-level PRegen. The Light Use-Younger Stands scenario shows PRegen increasing

448   significantly with decreasing elk population levels below population levels of about 1000 elk

449   (empirical elk distributions) or 800 elk (simulated elk distributions) (Fig. 6).

450   At approximately current elk population levels (1000 - 1200 elk), only 35% – 45% of

451   senescent aspen stands are simulated as having a 90% probability of regeneration success

452   (Fig. 6). Nearly all of these are located on the periphery of the winter range (Fig. 7). Given

453   the Heavy Use scenario, most of the difference between the 200 and 1000 elk population

454   levels occurs for aspen in the vicinity of Horseshoe Park and Beaver Meadows, although

455   some stands in these areas still fail to regenerate even at the lower elk levels (Fig. 7). Given

456   the Light Use scenario, the only stands that fail to regenerate at 200 elk are in Moraine and

457   Horseshoe Parks.

458

459   DISCUSSION

460   *Elk Distribution Patterns and Aspen*

461   The landscape-level analysis suggests that senescent aspen stands at lower elevations

462   on the core winter range, that are not successional to conifers and occur as isolated forest

463   patches within a grassland matrix, may be in jeopardy except at extremely low elk population

464   levels (Figs 6 & 7). This is because elk distribution in the winter range is highly aggregated

465   (Fig. 2), so that a high density of elk occupy Horseshoe Park, Beaver Meadows, and Moraine

466   Park, even at low population levels overall. For example, model results suggest the heavily

467   utilized, Moraine Park aspen stand would have less than a 10% probability of successful

468   regeneration even at 200 elk, under either the Heavy or Moderate Use scenarios. If elk

469   distribution in winter is actually as aggregated as Figure 2 suggests, then maintenance of

470   declining aspen stands may require management intervention at a local scale. Reductions of

471   the elk herd at the scale of the whole winter range may have little effect on aspen

472   regeneration success in core winter range areas. The only scenarios where reductions of

473   overall elk population level below current levels (approximately 1000) were simulated as

474   having a relatively continuous effect on the probability of aspen regeneration, were those

475   involving aspen stands which included a younger (< 30 years old) cohort. Such stands are

476   now exceedingly rare on core winter range (Baker and others 1997).

477   Furthermore, aspen stands on the periphery of elk winter range maintain low levels of

478   elk density, and so have high aspen regeneration probabilities even at high elk population

479   levels overall, provided they are not overtopped by conifers, a process we did not simulate

480   (Fig. 7). This result agrees with field observations of Suzuki and others (1999), who observed

481   ample aspen regeneration on peripheral elk winter range in RMNP.

482

483   *Data Gaps and Model Uncertainty*

484   This model application has helped to identify critical gaps in our understanding of

485   elk-aspen interactions in RMNP. The effect of elk herbivory on aspen sucker mortality has

486   been insufficiently quantified, but is a parameter to which the model is extremely sensitive

487   (Table 3). Also relatively unknown is the effect of bark removal by elk on long-term survival

488   of mature aspen trees, of different sizes and ages. It would also be useful to know much more

489   about aspen suckering rates, both under a closed aspen canopy, as well as in disturbed stands.

490   Ideally, this should be studied in exclosures, to allow quantification of maximum potential

491   rates of aspen sucker establishment, under different climatic conditions.

492   Our results clearly show that the seasonal extent of elk use of aspen stands is a very

493   important driving variable, if we are to understand the impacts of elk on long-term aspen

494   dynamics. We need to learn more about elk use of aspen for forage and cover in RMNP, over

495   time scales from hours to years.

496   While more empirical research needs to be done on certain key model parameters

497   before we can confidently forecast the results of a given management scenario, our modeling

498   results represent an integration of a vast amount of available data, and our best assessment at

499   this time. Ideally, the modeling effort should evolve in synchrony with field research

500   designed to reduce our uncertainty about critical processes and causal relationships.

501   Unfortunately, certain key model parameters and inputs (e.g., elk distribution at fine spatial

502   scales) may never be known for the historical period over which the model can be verified

503   using time series or repeat sampling data.

504

505   *Implications for Elk and Aspen Management*

506   Implications of these results for elk and aspen management in RMNP depend very

507   much on the specific nature of management goals. Management goals addressing RMNP's

508   mandate to "...try to maintain all the components and processes of naturally evolving park

509   ecosystems, including the natural abundance, diversity, and ecological integrity of plants and

510   animals" (National Park Service 1988), may be expressed along a gradient of complexity and

511   spatial resolution. The specific goal might be to: (1) maintain aspen as a species on RMNP

512   winter range; (2) maintain a component of valley bottom and dry park aspen on core elk

513   winter range; or (3) try to maintain the existing aspen stands in the dry parks and valley

514   bottoms on core elk winter range. The second goal permits aspen stands to fluctuate across

515   the landscape, while the third goal takes a more static approach.

516   If the goal is simply to maintain some aspen in winter range, then the current natural

517   regulation policy for elk management would be satisfactory. It is unlikely that elk population

518   levels would become high enough for aspen stands along the periphery of the winter range to

519   experience high enough levels of elk herbivory to prevent successful aspen regeneration. At

520   some point in the future, fires or silvicultural treatments might be required for these areas to

521   maintain aspen. Aspen stands at the periphery of elk winter range are higher in elevation and

522   tend to be successional to conifers.

523   Continuation of the current natural regulation policy is not likely to satisfy goals 2

524   and 3 without intensive management of aspen regeneration. Our simulation results suggest

525   that aspen decline on core winter range areas in RMNP would be expected solely on the basis

526   of elk population densities over the past several decades. These results are corroborated by

527   empirical observations of successful aspen establishment and multi-cohort stands within

528   exclosures, and widespread failure of aspen to regenerate outside exclosures (Olmsted 1977,

529   Baker and others 1997). Natural regulation is not effective for allowing aspen regeneration on

530   core winter range because aspen may be thought of as a "secondary prey" species, unable to

531   exert a negative feedback on elk population levels because it constitutes only a small portion

532   of the elk diet, but susceptible to impacts of high elk population levels supported by the

533   availability of other winter forage sources.

534   To maintain sufficient levels of aspen regeneration to ensure persistence of aspen in

535   heavily utilized areas (e.g., Horseshoe Park, Beaver Meadows, and Moraine Park), while

536   continuing the policy of natural regulation, it may be necessary to intensively manage for

537   aspen regeneration by fencing aspen stands for long time periods (at least a 30-year period is

538   suggested, Fig. 4c). However, aspen stands are likely to decline should fencing be followed

539   by a long (e.g., 30-year) period without fences (Fig. 4c). In addition to fences, prescribed fire

540   and mechanical disturbances (ripping, bulldozing) might be useful for stimulating abundant

541   suckering (Shepperd 1996).

542   Discontinuing the policy of natural regulation, in favor of a policy that reduces the

543   size of the elk herd, may not be sufficient to create aspen persistence in the core of Estes

544   Valley winter range. In a study of aspen population dynamics at RMNP, Baker and others

545   (1997) found that aspen cohorts in the past have regenerated only when there were fewer than

546   600 elk on the winter range, or approximately one-half of the current level. This is consistent

547   with our simulation results for the Heavy Use scenario where simulated elk distributions are

548   used, and for the Light Use scenario where empirical elk distributions are used (Fig. 6). For

549   these scenarios of elk habitat use and distribution, aspen regeneration probability begins to

550   increase with decreasing elk population level at levels below 500-600. However, even at the

551   600 elk level, the probability of aspen regeneration may be quite low for many senescent

552   stands under all scenarios of elk use (Figs 6 & 7). Apparently, the 600-elk threshold

553 identified in Baker and others (1997) represents a population level where aspen cohorts can

554 initiate in certain places, but not in others where local elk densities reach higher levels.

555   Our results suggest that a population reduction to 100 – 300 elk may be necessary to

556 allow regeneration of 90% of the Park's senescent aspen stands. Less extreme reductions of

557 the overall winter range elk population level may not be effective unless they are combined

558 with management of local elk distribution for stimulating successful aspen establishment.

559   If aspen stands on core winter range were younger and more vigorous, formation of

560 new age cohorts would be more likely to occur, for a given elk density (Fig 4b). Also, the

561 establishment of dense patches of young aspen might present a physical barrier to elk

562 herbivory, allowing additional aspen suckers to establish. Our results suggest that, while elk

563 densities required for establishment of vigorous, multi-aged aspen stands might be initially

564 low, such aspen stands once established would be able to withstand greater elk densities.

565   Wolf reintroduction in RMNP might also facilitate aspen regeneration over much of

566 the winter range. In Yellowstone National Park, where wolf reintroduction began in 1995,

567 aspen suckers appear to be significantly taller in riparian areas heavily utilized by wolves

568 than in areas of low wolf use (Ripple et al. 2001). Prior to their extirpation, wolves may have

569 limited the RMNP herd to fluctuations within a range of 300 – 800 elk (Coughenour 2001).

570 However, several recent studies from Yellowstone National Park and the Canadian Rockies

571 suggest that wolves may influence herbivore-plant interactions more through their behavioral

572 effects, by altering elk spatial distributions, than through their numerical effects of reducing

573 elk numbers (Ripple and Larsen 2000, Ripple and others 2001, White and others 2003). One

574 might reasonably hypothesize that, if wolves were present, aspen on core winter range might

575 be sustained at higher elk population levels than otherwise. This also implies that results from

576 this modeling study for RMNP should not be directly extrapolated to other nature reserves

577   where predators are present.

578   Successful management for aspen regeneration in the Estes Valley will likely require

579   some combination of: overall elk population reduction; management of elk distribution;

580   fencing to protect aspen suckers from elk browsing; mechanical disturbance or limited

581   prescribed fire to stimulate suckering for stands with inherently low reproductive potential;

582   and even chemical repellents to deter elk browsing at specific locations (Baker and others

583   1999). Since abundant aspen suckering has occurred in most existing exclosures,

584   demonstrating the reproductive potential of these stands while an aspen overstory is still

585   present, protection from elk browsing should play a far greater role in management plans

586   than prescribed fire or mechanical disturbance.

587   Even with intensive management of elk distribution and elk access to aspen

588   regeneration, it is unlikely that aspen could be maintained on Estes Valley core winter range

589   locations without an overall reduction of the RMNP elk herd. This study suggests that, if

590   preserving aspen stands on core winter range is a goal, RMNP management will need to

591   reduce the overall elk herd size, while simultaneously conducting intensive, site-level

592   activities to propagate aspen within the Estes Valley portion of the winter range.

593   While the recommended level of intervention (i.e., culling and fencing) may be

594   controversial for a natural area such as RMNP, such measures may be necessary for

595   maintaining aspen stands on core elk winter range. Whether these measures are consistent

596   with RMNP`s overall mandate to manage for a "natural system" is a complex, philosophical

597   question that cannot be resolved using the methods of this study. It is arguable that, in the

598   absence of large predators, human intervention may sometimes be necessary to maintain

599   natural vegetation patterns and processes where large ungulate herds are present.

600

REFERENCES

Baker, D.L., W.F. Andelt, K.P. Burnham, and W.D. Shepperd. 1999. Effectiveness of Hot
Sauce and Deer Away repellents for deterring elk browsing of aspen sprouts. *Journal of Wildlife Management* 63:1327-1336.

Baker, W.L., J.A. Munroe, and A.E. Hessl. 1997. The effects of elk on aspen in the winter
range in Rocky Mountain National Park. *Ecography* 20:155-165.

Ball, J.T., I.E. Woodrow, and J.A. Berry. 1987. A model predicting stomatal conductance and
its contribution to the control of photosynthesis under different environmental
conditions. Pages 221-224 in *I. Biggins (ed.)* Progress in photosynthesis research.
Martinees Nijhof, Dordrecht.

Barnett, D.T., and T.J. Stohlgren. 2001. Aspen persistence near the National Elk Refuge and
Gros Ventre Valley elk feedgrounds of Wyoming, USA. *Landscape Ecology* 16:569-580.

Bartos, D.L., and R.B. Campbell, Jr. 1998. Decline of quaking aspen in the Interior West -
Examples from Utah. *Rangelands* 20:17-24.

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* 24:273-280.

Bartos, D.L., and W.F. Mueggler. 1980. Influence of fire on vegetation production in the aspen ecosystem in western Wyoming. Pages 75-78 in *M.S. Boyce and L.D. Hayden-Wing (eds.)* North American elk: Ecology, behavior, and management. University of Wyoming Press, Laramie.

Beetle, A.A. 1974. Range survey in Teton County, Wyoming. Part 4 - quaking aspen. Agricultural Experiment Station, Research Journal 31, Laramie, WY.

Boone, R.B., M.B. Coughenour, K.A. Galvin, and J.E. Ellis. 2002. Addressing management questions for Ngorongoro Conservation Area, Tanzania, using the Savanna Modeling System. *African Journal of Ecology* 40:138-150.

Clarke, J.A., C.E. Olmsted, 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 Rocky Mountain National Park. Estes Park, Colorado.

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

Coughenour, M.B. 2001. Elk in the Rocky Mountain Park ecosystem – a model-based assessment. Final Report to U.S. Geological Survey Biological Resources Division and U.S. National Park Service,132 pp.

Ellis, J. E., M.B. Coughenour, and D.M. Swift. 1993. Climate variability, ecosystem stability and the implications for range and livestock development. Pages 31-41 in *R. Behnke, I. Scoones, and C. Kerven (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. Pages 97-106 in *V.R. Squires and A.E. Sidahmed (eds.)* Drylands: Sustainable use of rangelands into the Twenty-First Century. IFAD Series: Technical Reports.

Friend, A.D., H.H. Shugart, and S.W. Running. 1993. A physiology-based gap model of forest dynamics. *Ecology* 74:792-797.

Gruell, G.E., and L.L. Loope. 1974. Relationships among aspen, fire, and ungulate browsing in Jackson Hole, Wyoming, U.S. Department of Agriculture, Forest Service, Intermountain Region.

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.

Hart, J.H., and D.L. Hart. 2001. Interaction among cervids, fungi, and aspen in northwest Wyoming. Pages 197-205 in *W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew (eds.)* Sustaining aspen in western landscapes: symposium proceedings. USDA Forest Service Proceedings RMRS-P-18, Rocky Mountain Research Station, Fort Collins.

Hess, K. 1993. Rocky times in Rocky Mountain National Park: An unnatural history. Univesity Press of Colorado, Boulder.

Hinds, T.E. 1985. Diseases. Pages 87-106 in *N.V. DeByle 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.

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

Hobbs, N.T., D.L. Baker, J.E. Ellis, and D.M. Swift. 1981. Composition and quality of elk

winter diets in Colorado. *Journal of Wildlife Management* 45:156-171.

Jones, J.R., and G.A. Schier. 1985. Growth. Pages 19-24 in *N.V. DeByle 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.

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. 1997a. Is aspen doomed? *Journal of Forestry* 95:4-11.

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

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.

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

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.

Olmsted, C.E. 1977. The effect of large herbivores on aspen in Rocky Mountain National Park. Ph.D. thesis. 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. Estes Park,

Colorado.

Peinetti, R. 2000. Riparian willow dynamics and their interaction with environmental and
    biological factors in the elk winter range of Rocky Mountain National Park
    (Colorado) - A multi-scale analysis. Ph.D. thesis. Colorado State University, Ft.
    Collins.

Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern
    Yellowstone National Park, USA. *Biological Conservation* 95:361-370.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among
    wolves, elk and aspen on Yellowstone National Park's northern range. *Biological
    Conservation* 102:227-234.

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

Romme, W.H., M.G. Turner, R.H. Gardner, W.W. Hargrove, G.A. Tuskan, D.G. Despain,
    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
    successionary Populus tremuloides Michx. stands on an entic haplorthod in north-
    central Wisconsin. Ph.D. thesis, University of Wisconsin, Madison.

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.

Shepperd, W.D. 1990. A classification of quaking aspen (ASPENCLS) in the Central Rocky
    Mountains based on growth and stand characteristics. *Western Journal of Applied*

Forestry 5:69-75.

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.

Shepperd, W.D. 1996. Response of aspen root suckers to regeneration methods and post-harvest protection. USDA Forest Service, Research Paper RM-RP-324, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

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

Singer, F., T. Elliott, M. Coughenour, J. Welker, D. Valentine, S. Williams, L. Zeigenfuss, K. Alstad, R. Menezes, R. Peinetti, D. Barnett, R. Cates, and J. Zou. 1998. Large mammalian herbivores, plant interactions, and ecosystem processes in five national parks. Third Annual 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., G.W. Chong, M.A. Kalkhan, and L.D. Schell. 1997. Multiscale sampling of plant diversity: effects on minimum mapping unit size. Ecological Applications 7:1064-1074.

Suzuki, K., H. Suzuki, D. Binkley, and T.J. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: differences at local and landscape scales. *Landscape Ecology*

14:231-237.

Wang, J.R., A.L. Zhong, P. Comeau, M. Tsze, 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.

Weisberg, P.J., N.T. Hobbs, J.E. Ellis, and M.B. Coughenour. 2002. An ecosystem approach
to population management of ungulates. *Journal of Environmental Management*
65:181-197.

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

White, C.A., M.C. Feller, and S. Bayley. 2003. Predation risk and the functional response of
elk-aspen herbivory. *Forest Ecology and Management*, In Press.

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

Table 1. Selected input parameters for the SAVANNA model as applied to this study. Where (X, Y) pairs are given, these refer to user-input "table functions" where the modelled functional relationship is a linear interpolation between coordinate pairs (i.e., for a given X value, a Y value is interpolated). Where six values are listed continuously on a line, these refer to each of six age classes in 10-year increments.

Parameter	Value	Units	Source
		FORAGING SUBMODEL	
I_{max}	0.012	kg forage / kg animal / day	fit (see text)
F_{fresp}	(0., 0.), (4.6, 0.7), (15., 1.)	(gm^{-2} forage; unitless)	fit (see text)
F_{snow}	(5.,1.), (40., 0.)	(cm snow depth; unitless)	Sweeney and Sweeney (1984)
R	2.0	meters	Murie 1951
		ASPEN ALLOMETRY	
H	2.00, 5.81, 6.83, 7.67, 8.38, 13.0	m	Olmsted (1977), Suzuki data
D_C	0.60, 1.10, 1.30, 1.50, 1.95, 3.60	m	Beetle (1974)
D_s	3.60, 11.4, 13.5, 15.2, 16.6, 26.1	cm	Olmsted (1977), Suzuki data
M_L	0.08, 0.29, 0.48, 0.70, 1.20, 5.10	kg	Wang *et al.* (1995)
M_W	1.59, 26.6, 40.6, 56.6, 73.7, 212.	kg	Wang *et al.* (1995)
M_{FB}	0.08, 0.14, 0.30, 0.44, 0.76, 3.21	kg	Bartos and Johnson (1978)
M_R	0.64, 6.40, 8.43, 10.7, 13.6, 21.6	kg	Ruark (1985)
M_{FR}	0.08, 0.29, 0.48, 0.70, 1.20, 5.10	kg	guess
		ASPEN ESTABLISHMENT AND MORTALITY	
E	0.00, 0.01, 0.08, 0.12, 0.16, 0.17	suckers mo^{-1}	see text
S	0.00, 0.02, 1.62, 2.45, 3.33, 3.39	suckers mo^{-1}	see text
F_{watr}	(0.9, 0.), (1., 1.)	(relative water content; unitless)	Jones *et al.* (1985)
F_{temp}	(5., 0.), (11., 1.)	(^{o}Celsius; unitless)	Jones *et al.* (1985)
F_{herb}	(0., 1.), (410., 0.)	(gm^{-2} biomass; unitless)	fit
F_{wcv}	(0., 1.), (0.4, 0.2), (0.9, 0.0)	(proportional cover; unitless)	fit
B	(0., 0.), (0.2, 1.0)	(proportion browsed; unitless)	fit (see text)
N_m	0.28, 0.02, 0.02, 0.02, 0.02, 0.02	proportion stems per year	fit

Table 1. Continued.

<u>Abbreviations</u>

I_{max} = maximum intake rate; F_{fresp} = effect of functional response (feedback of forage availability upon forage intake rate, Spalinger & Hobbs 1992); F_{snow} = effect of snow depth on forage intake rate multiplier; R = elk reach height (above snow level, if present); H = tree height; D_C = crown diameter; D_s = stem diameter (dbh) ; M_L = leaf biomass; M_w = wood biomass (stem + branch); M_{FB} = fine branch biomass; M_R = total root biomass; M_{FR} = fine root biomass; E = maximum suckering rate per living tree per month; S = maximum suckering rate per dying stem per month; F_{watr}= effect of water (relative water content of soil) on establishment; F_{temp} = effect of temperature on establishment; F_{herb} = effect of herbaceous root biomass on establishment; F_{wcv} = effect of woody canopy cover on establishment; B = fraction of current annual growth browsed vs. fraction suckers killed; N_m = nominal (background) mortality rate

Table 2. Simulation experiments conducted using the SAVANNA model. All experiments ran for 60 years, using 20 stochastic weather replicates. BMDR refers to the senescent Beaver Meadow-Deer Ridge stand, while LBM refers to the Lower Beaver Meadows stand, which includes a younger aspen cohort. See text for explanation of elk use levels.

Elk Density (per km^2)	Level of Elk Use	Duration of Fence Period (yrs)	Simulated Aspen Stand
0 - 16	Heavy	0	BMDR
0 - 16	Moderate	0	BMDR
0 - 16	Light	0	BMDR
0 - 16	Heavy	0	LBM
0 - 16	Moderate	0	LBM
0 - 16	Light	0	LBM
0 - 16	Moderate	10	BMDR
0 - 16	Moderate	20	BMDR
0 - 16	Moderate	30	BMDR

Table 3. Sensitivity of aspen canopy cover, aspen sucker production, and aspen sucker density to selected model input parameters. For parameter abbreviations and values used in the model, see Table 1.

Parameter	Aspen Canopy Cover	Aspen Sucker Production	Aspen Sucker Density
E	0.32	4.84	4.47
S	0.18	4.26	4.11
I_{max}	-3.53	-4.17	-4.09
B	15.18	33.20	29.78
N_m	-3.78	-4.02	-3.92

Table 4. Statistical comparison of simulated and observed data for aspen production (g/m^2).
The paired t-test tests the hypothesis that the mean difference between simulated and
observed values is 0. All regression relationships between observed and predicted values are
signficant at $\alpha = 0.01$. The simultaneous F-statistic for model bias tests the hypothesis that
slope = 1 and intercept = 0.

Winter Season	1975-76	1985-86	1995-96	Overall
Number of observations	9	9	9	27
Mean (simulated)	6.88	4.41	2.20	4.50
Mean (observed)	7.33	3.63	2.49	4.48
Paired t-test statistic	0.54	-0.61	0.33	-0.03
(2-sided p-value)	0.60	0.56	0.75	0.98
Regression R^2	0.91	0.62	0.83	0.76
Regression slope	1.11	0.50	0.51	0.80
(95% CI)	0.77 to 1.45	0.15 to 0.85	0.30 to 0.71	0.61 to 0.98
Regression Bias F	0.78	2.83	7.94	1.29
(p-value)	0.50	0.15	0.02	0.29

Table 5. Statistical comparison of simulated and observed data for elk offtake of aspen (g/m^2). Original units are reported for mean values, although all statistical analyses use logarithmically transformed values. The paired t-test tests the hypothesis that the mean difference between simulated and observed values is 0. Only regression relationships between observed and predicted values signficant at $\alpha = 0.05$ are shown. The simultaneous F-statistic for model bias tests the hypothesis that slope = 1 and intercept = 0.

Winter Season	1975-76	1985-86	1995-96	Overall
Number of observations	9	9	9	27
Mean (simulated)	2.36	0.86	0.61	1.27
Mean (observed)	3.43	1.48	0.98	1.96
Paired t-test statistic	0.56	0.47	1.11	1.11
(2-sided p-value)	0.59	0.65	0.30	0.28
Regression R^2	ns	ns	ns	0.15
Regression slope	ns	ns	ns	0.39
(95% CI)	ns	ns	ns	0.01 to 0.77
Regression Bias F	ns	ns	ns	0.37
(p-value)	ns	ns	ns	0.69

Figure Headings.

1. The conceptual framework for our adaptation of the SAVANNA model to the problem of elk herbivory on aspen in Rocky Mountain National Park.

2. Maps of elk distribution (elk density, scaled to standard deviation units). (a) based on mean February elk density for the 1994 - 1998 period, estimated from aerial surveys (Singer *et al.* 1998). (b) based on SAVANNA simulations of winter (January – April) elk distribution, 1960 – 1998.

3. Model verification, using data derived from field observations of aspen sucker volume production, for 3 winters at decadal intervals, over 9 sites (Olmsted 1997). (a) Comparison of observed vs. simulated aspen sucker production (current annual growth up to 2 m in height). (b) Comparison of observed vs. simulated elk offtake of aspen. The data have been transformed using the natural logarithm.

4. Aspen regeneration success for different levels of elk density. The Heavy, Moderate, and Light Use treatments refer to the duration of elk access to the aspen stand over the course of the year (see text for detailed explanation). The proportion of regenerating stands (y-axis) refers to the propotion of stochastic simulation runs where the simulated aspen stand successfully regenerated by the end of the 60-year simulation runs (see text for detailed explanation). (a) reported for Heavy, Moderate, and Light Use treatments, for senescent aspen stands without fences. (b) as for (a), but for stands with a younger cohort present. (c) for fencing scenarios of varying duration, followed by a moderate level of seasonal elk use. Elk densities are those following removal of fences.

Figure Headings. Continued.

5. Aspen canopy cover (mean of 20 random simulation runs, after 60 years), reported for Heavy, Moderate, and Light Use treatments, and for different levels of elk density. (a) for senescent aspen stands. (b) for aspen stands with a younger cohort. The solid horizontal lines indicate the initial canopy cover of each treatment.

6. The proportion of aspen-dominated area on elk winter range with successful aspen regeneration for at least 90% of random simulation runs, for different elk population levels (x-axis), seasonal use intensities, and for senescent (solid curves) vs. younger (dashed curves) aspen stands. (a) using elk distribution map based on interpolated aerial survey data (1994 – 1998). (b) using SAVANNA simulations of winter (January – April) elk distribution (1960 – 1998).

7. Predicted effects of three different elk population levels aspen regeneration success of senescent aspen stands, for heavy use (columns 1 – 2) and light use (column 3) scenarios. Results for the heavy use scenario are compared between GIS extrapolations using either simulated elk distribution maps (column 1) or empirical elk distribution maps (column 2) as inputs. The aspen regeneration probability, defined in the text, is calculated over 20 random weather scenarios where elk population is held constant.

a.

Black Canyon Creek

Horseshoe
Park

Beaver
Meadows
Moraine
Park

Mill Creek
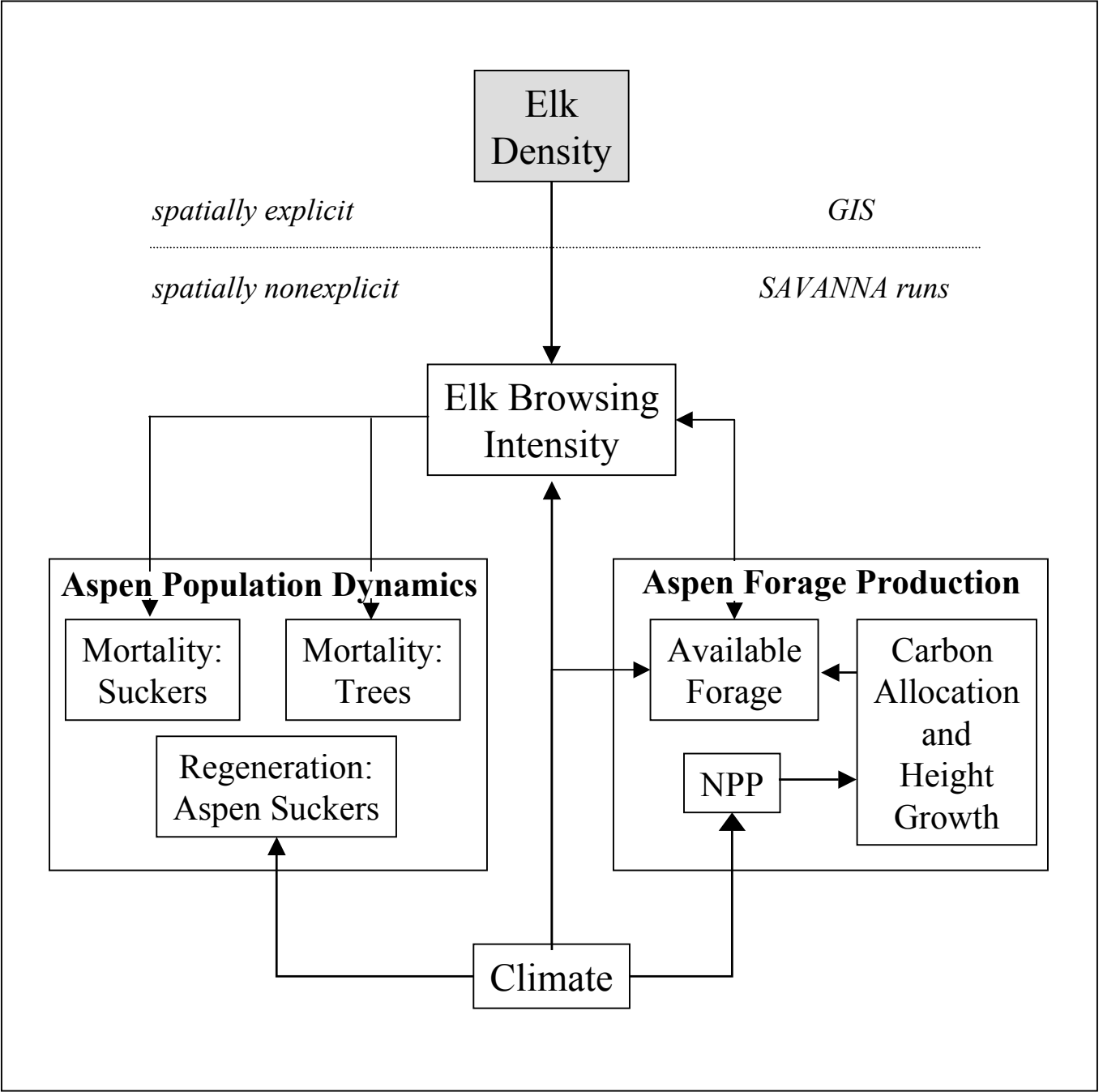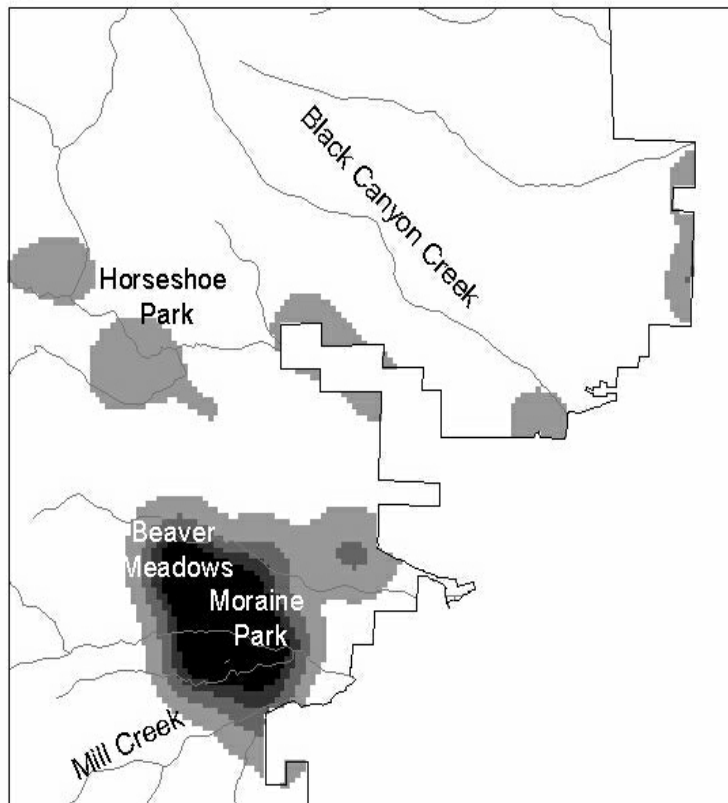
Aerial Survey,
1994 - 1998

Relative Elk Density
(standard deviation units)

-1 - 0
0 - 1
1 - 2
2 - 3
> 3

N

b.

Black Canyon Creek

Horseshoe
Park

Beaver
Meadows
Moraine
Park

Mill Creek
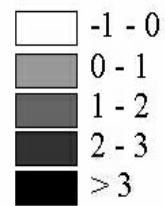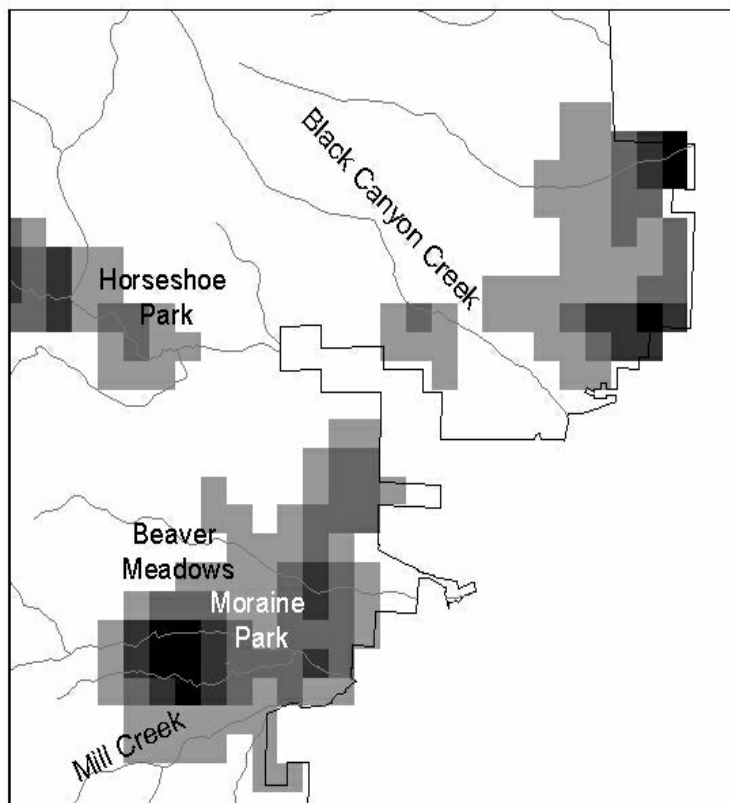
Simulated Distribution
1960 - 1998

2   0   2   4

Kilometers

a. Aspen Sucker Production
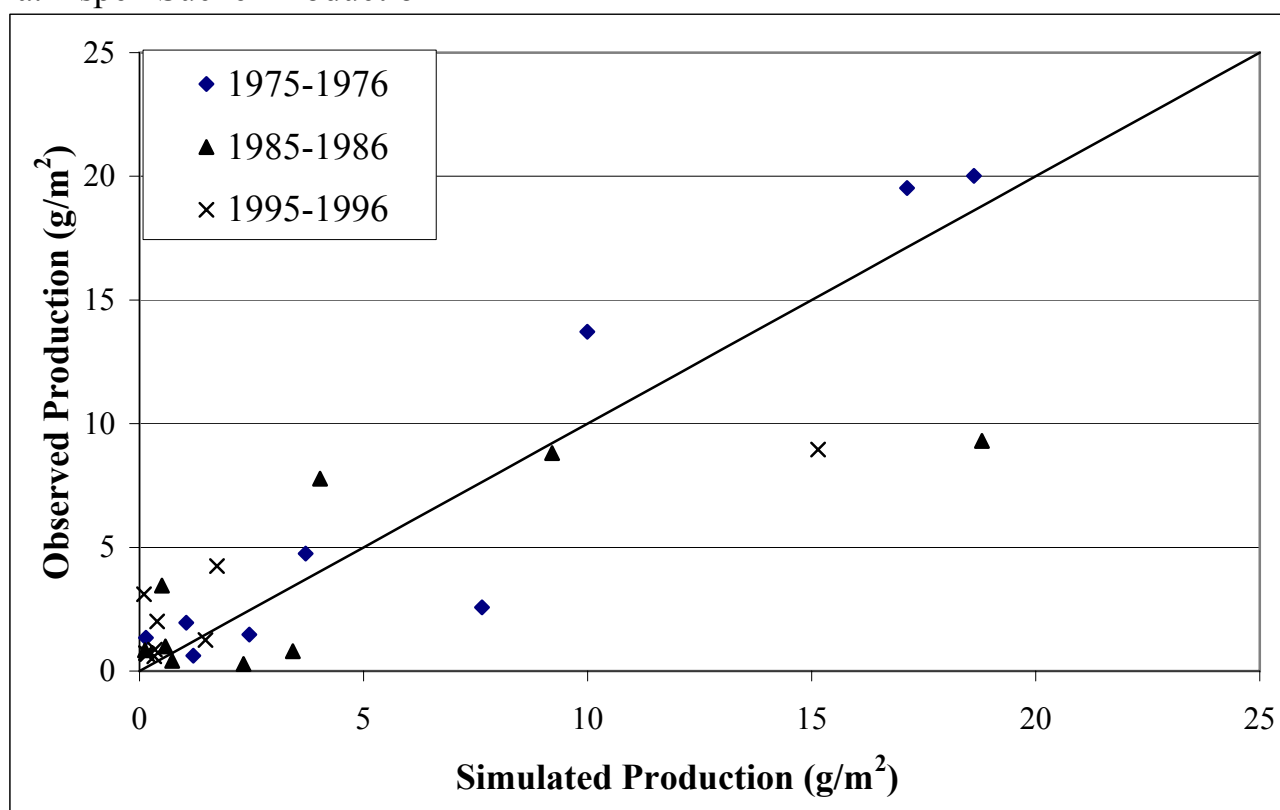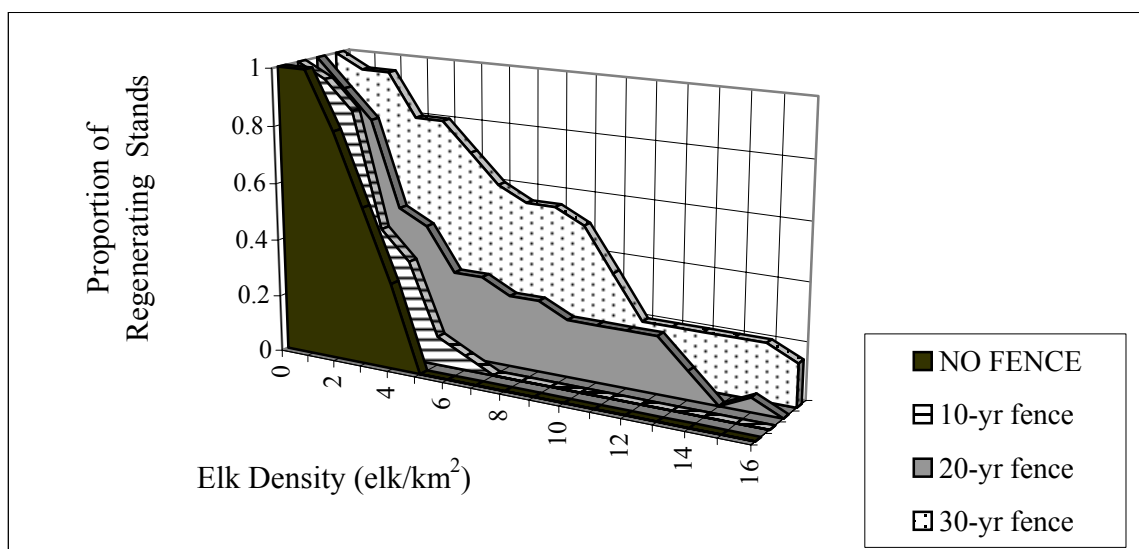

b. Elk Offtake of Aspen (logarithmic transformation)
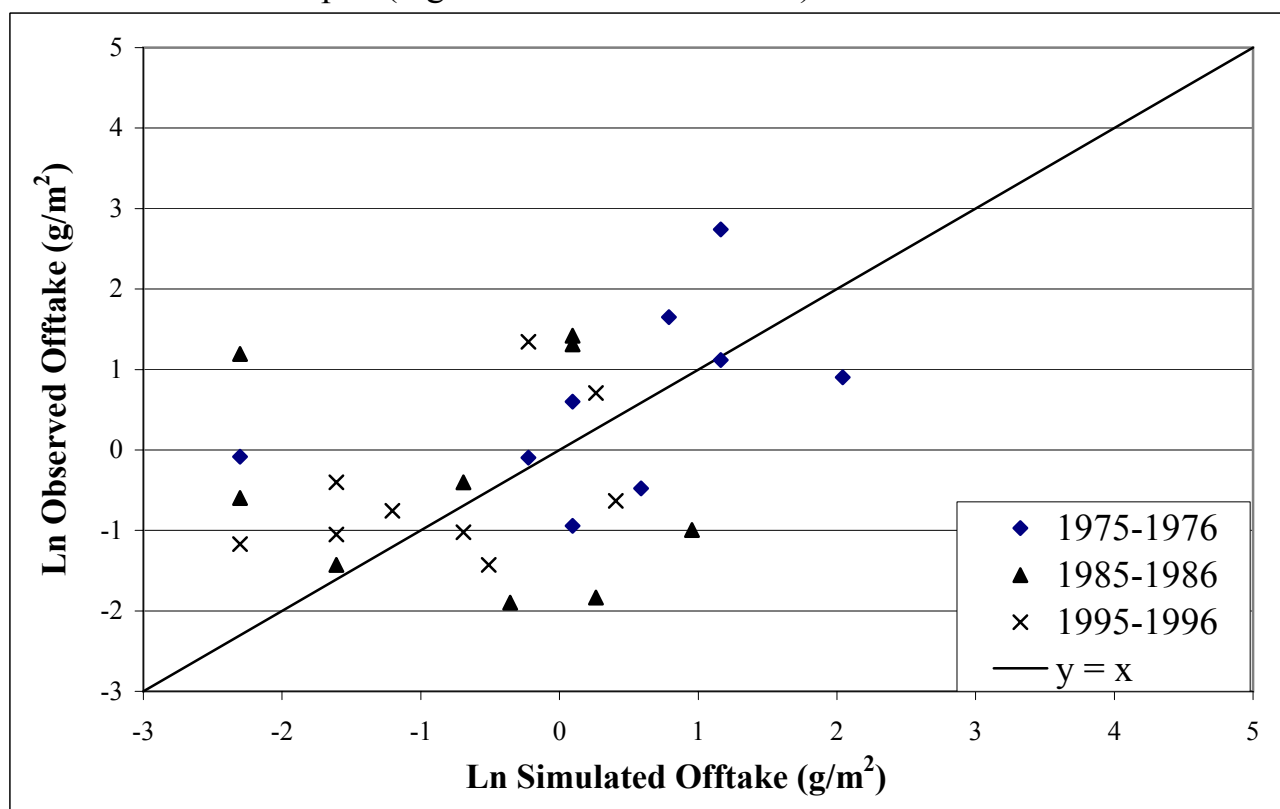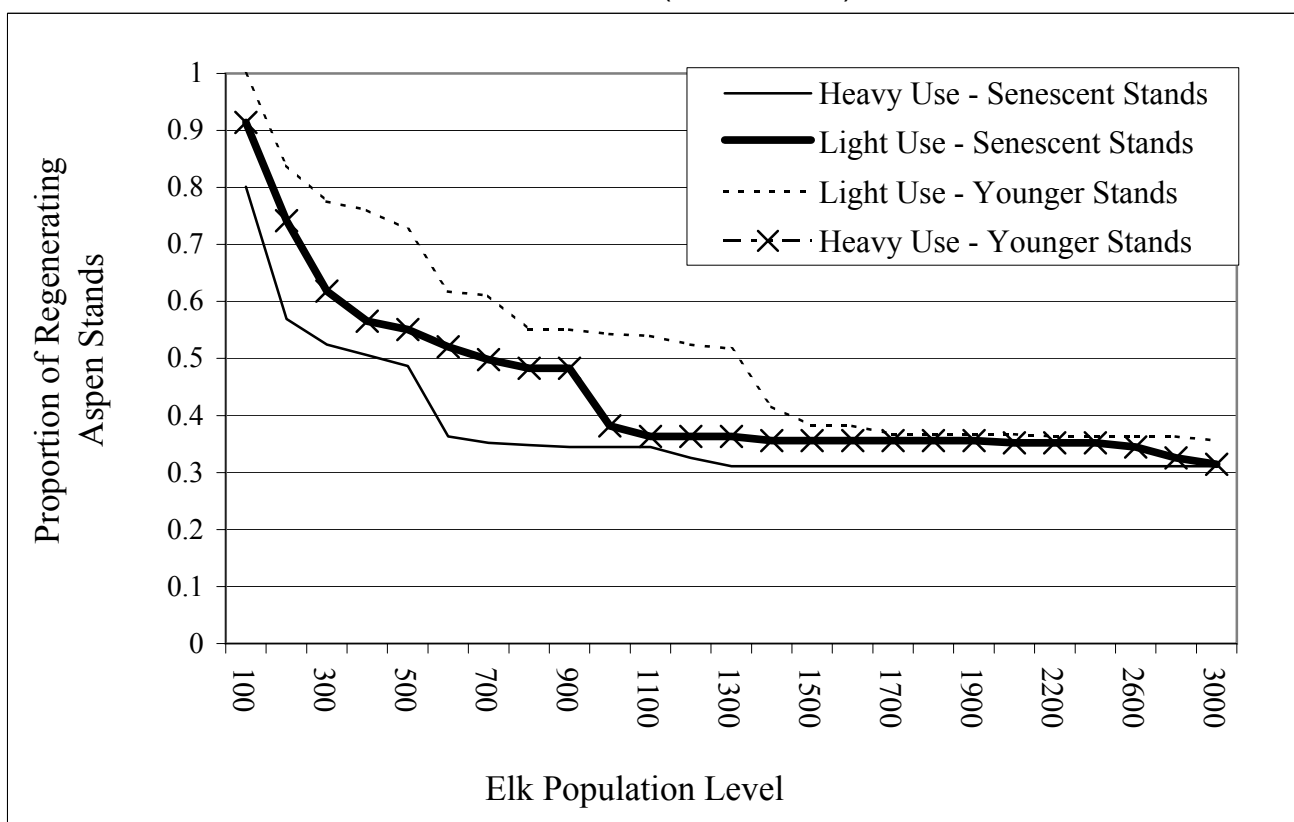
a. No Fences, Senescent Stand
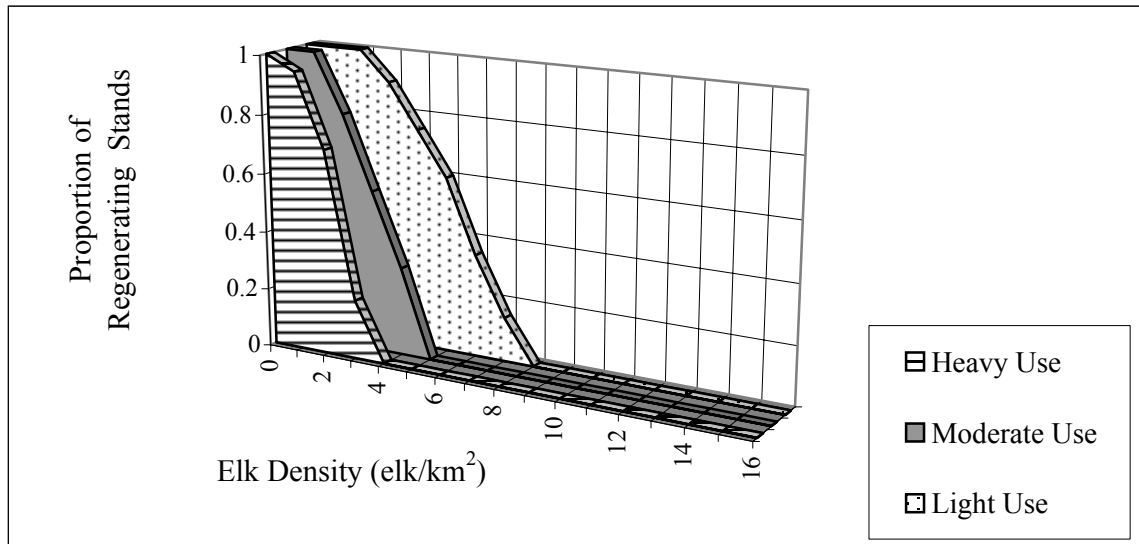
b. No Fences, Stand with a Younger Cohort
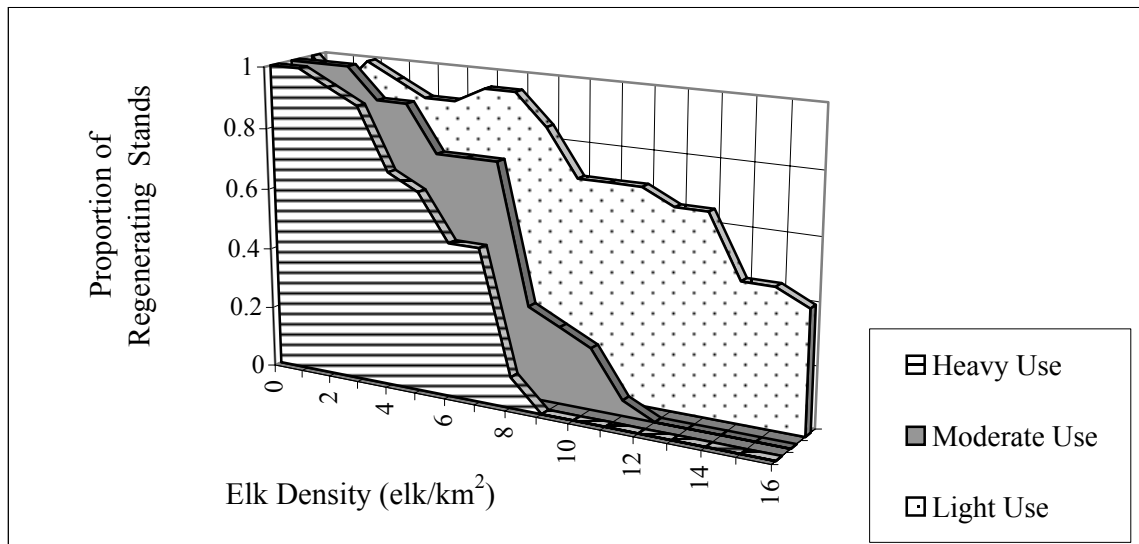
c. Moderate Use After Fences, Senescent Stand

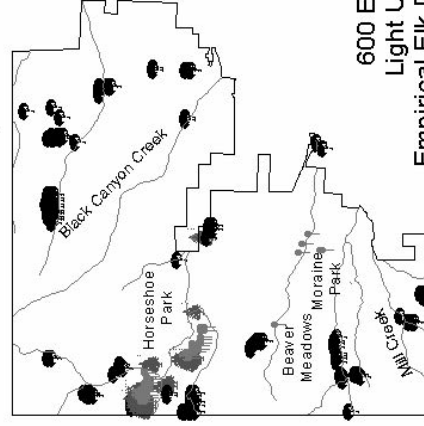## a. Senescent Stand
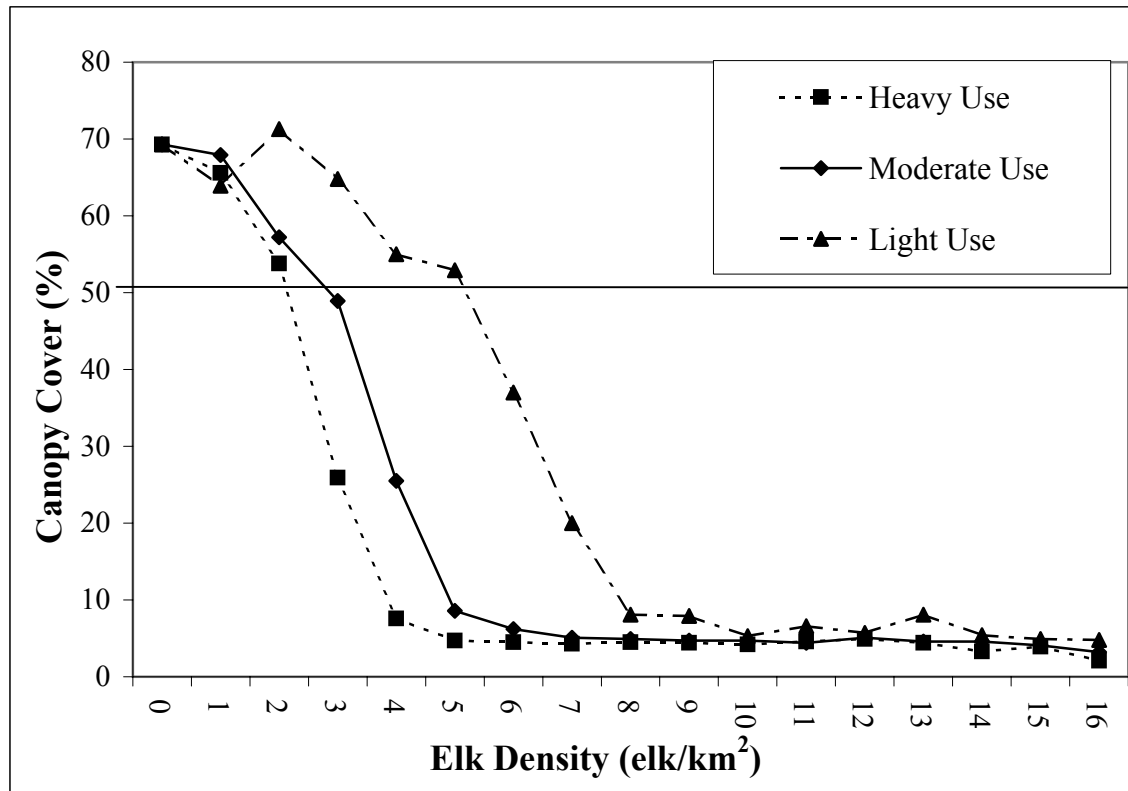
b. Stand with a Younger Cohort
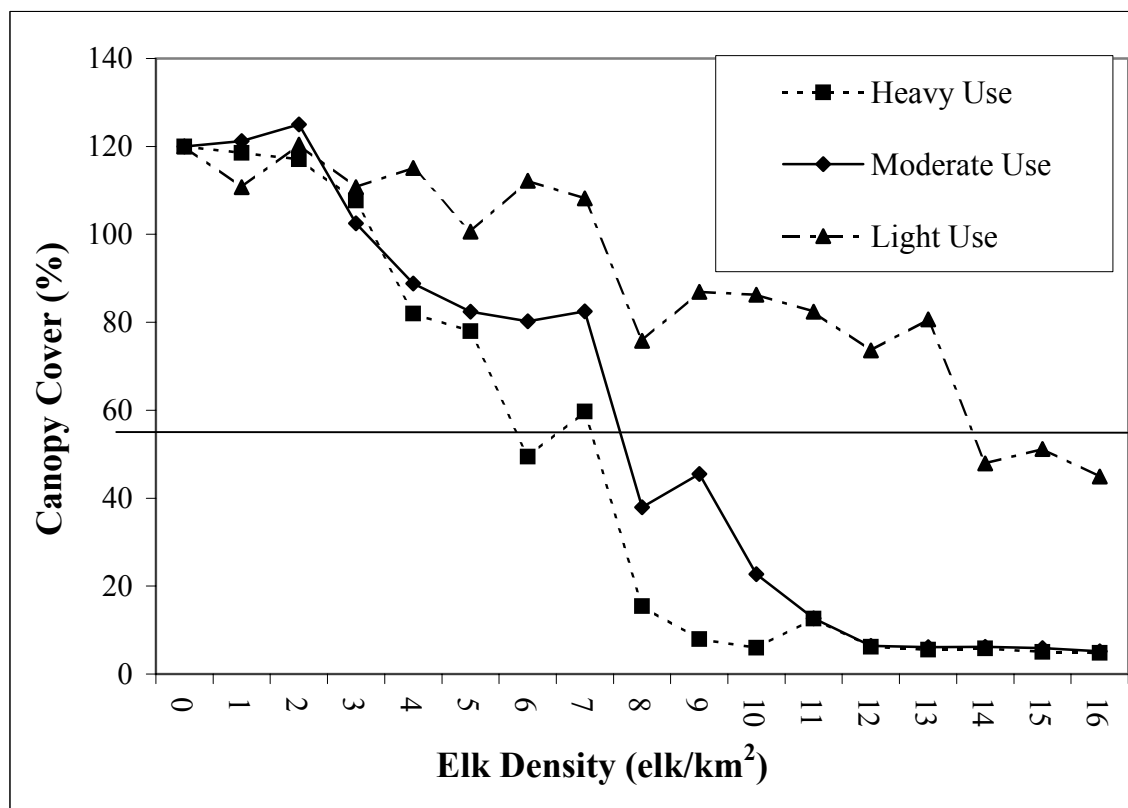
a. Elk Distribution from Aerial Surveys (1994 - 1998)

Proportion of Regenerating Aspen Stands vs Elk Population Level

Legend:
- Heavy Use - Senescent Stands
- Light Use - Senescent Stands
- Light Use - Younger Stands
- Heavy Use - Younger Stands
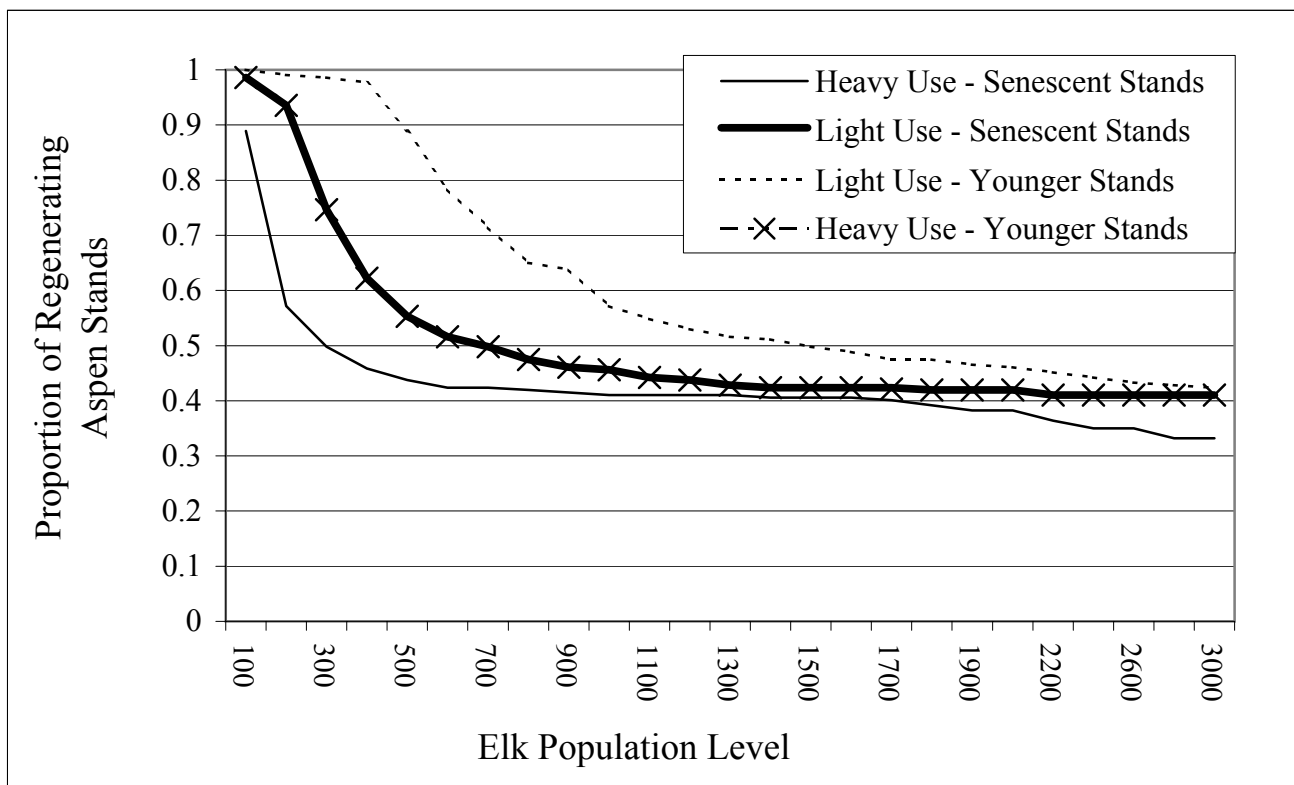
b. Elk Distribution from SAVANNA Simulations (1960 - 1998)

Proportion of Regenerating Aspen Stands vs Elk Population Level

Legend:
- Heavy Use - Senescent Stands
- Light Use - Senescent Stands
- Light Use - Younger Stands
- Heavy Use - Younger Stands
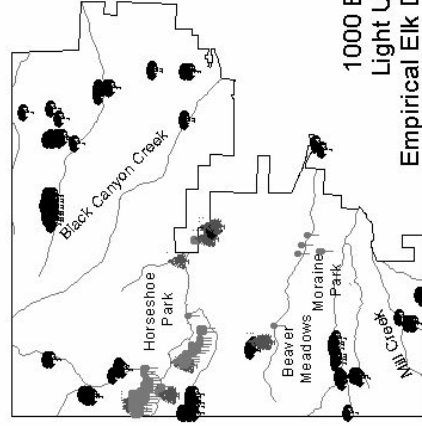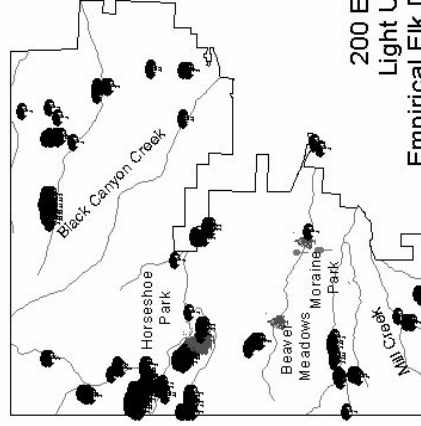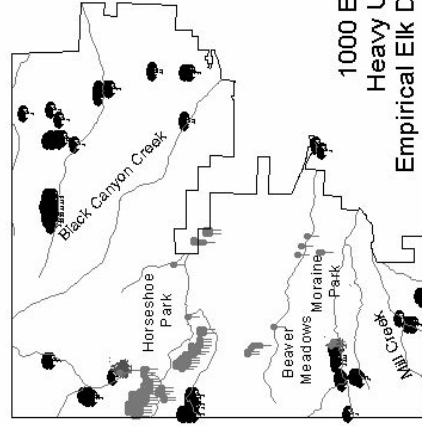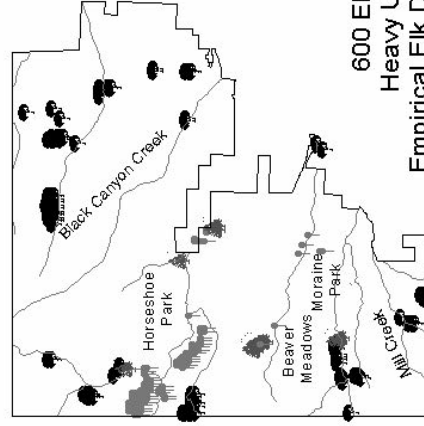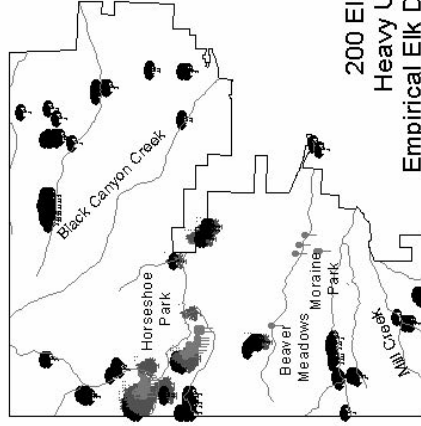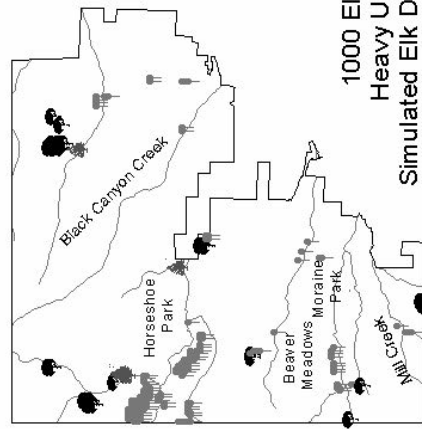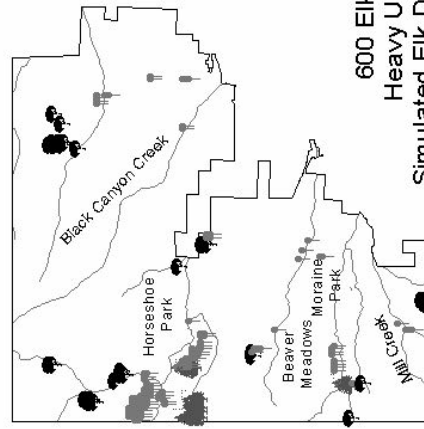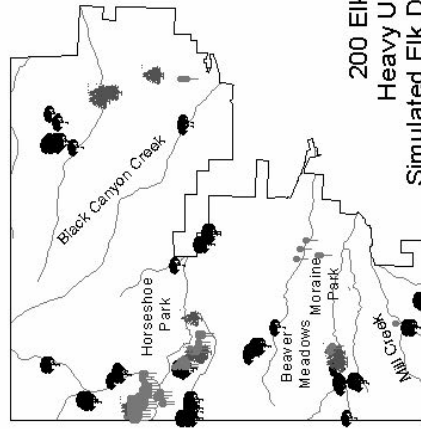
Aspen Regeneration Probability
> 90%
11 – 89%
< 10%

200 Elk
Heavy Use
Simulated Elk Distribution

200 Elk
Heavy Use
Empirical Elk Distribution

200 Elk
Light Use
Empirical Elk Distribution

600 Elk
Heavy Use
Simulated Elk Distribution

600 Elk
Heavy Use
Empirical Elk Distribution

600 Elk
Light Use
Empirical Elk Distribution

1000 Elk
Heavy Use
Simulated Elk Distribution

1000 Elk
Heavy Use
Empirical Elk Distribution

1000 Elk
Light Use
Empirical Elk Distribution

Black Canyon Creek

Horseshoe Park

Beaver Meadows Moraine Park

Mill Creek