6.3 Forest Overstory

Prescribed fire and ungulate foraging, often in combination with landscape position, have altered the forest overstory. The impact of herbivory on stand structure has been greater than that of fire alone. Generally, forest succession appears to be an unimpeded and stable process outside the Park while inside, succession is taking place without stand rejuvenation.

Higher tree densities on the controls could suggest that intensive browsing is decreasing tree densities inside the Park. This is particularly true for Amelanchier alnifolia, Prunus virginiana, Prunus pensylvanica, and Populus tremuloides, but not Populus balsamifera. The absence of mature forms of the first three species inside the Park could be caused by either their high palatability and the resulting preference for them among browsers (Bichlmaier 1985; Noste and Bushey 1987), or by an increased sensitivity to defoliation. Permanent range transects within the Park, which indicate that browse rates have not been unusually high for these species (Olson and Blyth 1986), suggest it may be the latter.

The indifferent response of Populus balsamifera to high herbivory is unusual given that this species is similar in crude protein, fibre and lignin content to Populus tremuloides (Bishoff 1981). Although no data were found comparing the presence of taste averting secondary compounds, aversion should not have been a factor given that Populus balsamifera had the highest relative contribution to the number of twigs browsed on range transects sampled from 1974 to 1981 (Olson and Blyth 1986), exceeding that of even Populus tremuloides. Therefore, possible explanations for the neutrality of this species are that the lower numbers of Populus balsamifera, found mostly on toe slopes, may have been insufficient to detect a significant change, that browsing pressures on these toe slopes were lower, that Populus balsamifera is more tolerant of intense browsing, or that less damage from insect pests may have enabled more of this species to survive.

The insect Malacosoma disstria (forest tent caterpillar) is an important forest pest in central Alberta. It prefers and generally has the greatest impact on, Populus tremuloides. Forests in the EINP area have experienced moderate to severe infestations during the late

80's and early 90's (Cerezke and Gates 1991). Although complete defoliation often occurs, Populus tremuloides is generally well adapted to this insect and causes little lasting damage (Peterson and Peterson 1992). It is not known however, what effect continuous annual defoliation by the tent caterpillar, compounded by other additional stresses such as drought, burning, or herbivory, may have on long term tree vigour and survival. It is therefore possible, that the additive stress of another defoliating agent on Populus tremuloides may have caused it to decline compared to Populus balsamifera.

The largest differences in tree density between the inside and outside of the Park were found in the small diameter classes. The abundance of small stemmed trees outside the Park and their uniform distribution among size classes indicated that overstory replacement and stand rejuvenation were actively taking place. Thus, in the absence of major disturbances, stable forest succession appears to become the dominant ecological process. It is important to recognize that although the area outside the Park is called the control, it does receive some foraging by native ungulates. Therefore, forest succession is occurring despite this inherent level of use.

Young Populus tremuloides stands normally contain high stem densities, with some exceeding 100,000 stems per hectare (Bella and De Franceschi 1980; Bartos et al. 1991). In part, this is due to the increase in soil temperature associated with forest removal at the time of disturbance (Maini and Horton 1966). As stands get older, disease, insects, browsing, snow breakage and the shading of suckers under intense competition results in self thinning (Debyle 1985). In addition, increased shading of the forest floor by this time results in cooler soil temperatures which reduces suckering. Removal or opening up of the overstory due to fire or herbivory, normally reverses this process.

Inside the Park, however, few young stems were becoming established. The lack of regeneration was particularly unusual, because many of these areas were unforested and should be prime sites for active encroachment from adjacent clones. Neither Populus tremuloides expansion nor stand rejuvenation appeared to be taking place, because of the intensive browsing of emerging suckers which evidently results in their death. Several examples of this have been documented including those of Milner (1977) and Gruell and Loope (1974) for wapiti, and Fitzgerald and Bailey (1984) for cattle. A possible reason for this in EINP, where browsing is consistently heavy year round, is that sucker removal is more detrimental late in the growing season when stems are unable to replenish their carbohydrate reserves before the onset of winter dormancy (Fitzgerald and Hoddinnott 1983). Therefore, without a rest period from browsing, little survival of suckers is likely. The heavy use of Populus tremuloides in EINP extends beyond the sucker stage as well, with stems beyond the normal reach of ungulates often killed. Large numbers of trees in the 3 to 6 meter height range were observed to be broken off after the spring of 1992. Under deep snow conditions when most shrubs are inaccessible, moose will break Populus tremuloides stems up to 10 cm in diameter in order to obtain forage (Telfer and Cairns 1978). The resulting lack of regeneration inside the Park produces forest stands which are skewed in favour of the larger and older trees. It is possible that if forest succession continues and stocking rates are not reduced, these older treed stands will age and eventually die, thereby thinning out the overstory. Continued lack of recruitment may eventually result in the formation of semi-open shrublands or grasslands. This process will be aided by Populus tremuloides stand breakup which occurs when openings appear in the canopy, and the additional stress imposed on the trees by the new environment accelerates their susceptibility to insects and diseases (Peterson and Peterson 1992).

Prescribed burning also failed to increase the density of small diameter trees, despite being adapted to the effects of fire (Peterson and Peterson 1992). One explanation is that the lower burn intensities at the north and toe positions did insufficient damage to the parent trees to induce regeneration. Poor suckering has been observed under low intensity fires where few Populus tremuloides were killed (Brown and Debyle 1989). This same argument, however, cannot be made for the crest position where suckering was also low. Both field observations and recorded burn scorch heights indicate that fire intensities at this position were quite severe, with major tree kill occurring. Thus, abundant suckering should have taken place. The general lack of recruitment is probably due to continuous intensive ungulate browsing rather than poor quality prescribed fires. Basile (1979) found that wapiti utilized as much as 44% of the current annual growth in Populus tremuloides stands three years after burning.

Poor stand rejuvenation may also be caused by the overall reduction in the proportion of forested land within the burned area. This, combined with the attractiveness of browsing shrubby regrowth, would result in increased foraging within the remaining stands by the same ungulate populations. Thus, while burning may encourage suckering in general, it will also accentuate aspen control by reducing the effective area of forest cover and concentrating ungulate activity. Debyle (1979) noted that fire can only be used to regenerate Populus tremuloides stands if the area can be protected from browsing wapiti. Debyle (1985) also suggested that if several species of large ungulates are simultaneously using these forests as winter range, the impact will be even more severe and longer lasting. This is a close approximation to the situation in EINP.

The vegetative history of the Park contributes to the formation of the current forest stands within the study area. Paleoecological evidence suggests that the amount of tree cover occurring in the EINP area over the last century has been the highest levels experienced in the last 12 000 years (Vance 1979). Wildfire has long been a major factor in forming and maintaining the vegetation in the Beaver Hills. A large fire in 1895 removed much of the extensive forest cover present at that time (Kjorlien 1977). Therefore, what ratio of grassland to forest is modal for this region of the parkland is difficult to determine and remains speculative. It is worth noting that the recent historical evidence documenting an abundance of forest was supported in this study by the consistent finding of Luvisolic soils instead of Chernozems. Their dominance indicates that in the past, the Park's uplands must have been inhabited by deciduous forested vegetation for extended periods. The Luvisolic soils found on the grassy south facing slopes inside the Park, many of which have remained unforested since the Park's establishment, indicate that these areas also must have been forested, albeit well in advance of settlement of the area and creation of the Park. The exact time period over which this occurred, however, remains unknown, particularly because the specific rates of conversion from Chernozems to Luvisols are unknown in the region.

Aerial photographs taken shortly after 1922 reveal that many of the south facing slopes and crests were open grasslands or semi-open shrublands. Other areas such as the north and toe slopes had localized tree cover, presumably because of the reduced impact of the 1895 fire and favourable tree regrowth at these moister positions. Creation of the

Park marked the beginning of a period when wildfires were largely suppressed allowing forest succession to accelerate throughout the Beaver Hills. The result was that nearly all of the areas outside the Park became forested. As a consequence, the south aspects and crest positions in this area had intermediate or mid-successional stand structures while north and toe slopes were late successional stands. North slopes, which had the most advanced tree cover when fire suppression began, appeared to be the most mature.

Inside the Park, however, sustained intensive browsing on many south facing slopes after 1922 prevented trees from becoming established. Many of these sites have remained as open shrublands and grasslands. South facing aspects such as these are also the least favourable for Populus tremuloides growth making establishment additionally difficult (Scheffler 1976). Those areas which had larger trees present in 1922, particularly the north slopes, continued to develop and mature because they were well beyond the stage of being directly damaged by herbivores. Some forest development and stand expansion would have occurred in the Park's early years on the toe and crest positions where young trees were either already present or were encroaching from the adjacent forested areas (ie. the north). Those areas which did not have trees extending out of the reach of ungulates when moderate and high stocking rates were reached in the late 20's and early 30's, probably remained largely unforested. Blyth and Hudson (1987) documented an excerpt and accompanying photo from a statement by the park superintendent in 1937 where he noted that browsing was so great that whole areas of 160 acres to one square mile were relatively denuded of foliage. Stocking levels in the mid 30's were several times higher than at any other time (Blyth and Hudson 1987) and would have minimized the recruitment of Populus spp. during this period.

Additional events which may have helped release trees on the toe and crest positions took place in 1928-29, 1935-36, and again in 1959-60, when sizable reductions in bison populations were undertaken through slaughters. The brief time periods needed for populations to resurge may have enabled some of the young trees at these positions to reach heights beyond being susceptible to browsing. This may explain why the toe and crest positions inside the Park are now mid-successional forests, compared to the north slopes which remain late successional.

North slopes in general were dominated by larger stemmed trees indicative of older, relatively mature overstories. These mature forests probably account for the well developed Luvisolic soils found under them, as well as their lower organic matter content in the Ahe horizon. These stands, including those on the controls outside the Park, have fewer of the younger stems due to the size and vigour of the older trees. It is likely that these forests are more similar to the deciduous forest types documented by Corns and Annas (1986) in the boreal mixedwood ecoregion. This is further supported by the work of Nicholson (1993), who concluded that many of the depressional wetlands scattered throughout the Park are essentially outliers of the boreal mixedwood forest, with edaphic factors such as elevation, topographic position, and hydrology being more important causal factors than climate itself. This indicates that the north slopes, which are often contiguous to these depressions, probably represent microclimate conditions in between those of the riparian wetlands and those found on the dryer, more exposed, crest and south facing slopes. Another important consideration is that if forest succession on the south facing and crest positions outside the Park continues in the absence of a disturbance, these sites may approach a successional stage more similar to that of the north facing stands, depending on the degree of microclimate alteration in the understory by the Populus tremuloides canopy.

In comparison to herbivory, the resumption of burning inside the Park in the late 1970's resulted in several relatively minor changes in the forest canopy. Only Populus tremuloides densities decreased on the burned area. This species is distributed throughout the landscape making it more susceptible to an effective prescribed burn. Populus balsamifera was more abundant on the toe slopes where more moist conditions predominate. The moderate burn intensities found there, coupled with the thicker bark which this species possesses, may also have limited damage.

On a landscape scale, the most prominent effect of burning was the decrease in live canopy cover at the crest position. Intense burning, as evidenced by the extreme burn scorch heights, killed many of the trees at this location. Drier conditions, an abundance of fine and medium fuels, and increased wind speeds could all have contributed to the more severe fire intensities. Total tree densities were not reduced significantly at the crest position, only because of the variation in the responses among catenas. Two of the three crests which were burned were totally denuded of live tree cover. In contrast, the third was burned less severely with the result that few of the trees were killed. These differences reflect how the repetition of prescribed burning and variable nature of fire in the landscape can impose very different treatments on each catena and transect. The low and moderate burn intensities observed on the north and toe slopes, respectively, were not severe enough to kill the larger stemmed trees found at these positions in the landscape (Quintilio et al. 1991). It appears that unless burning is done under highly favourable conditions, little of the tree canopy may be damaged at these topographic positions. Therefore, prescribed burning of even large areas, may ultimately affect only a portion of the landscape and total tree cover.

6.4 Understory Response

6.4.1 Species Diversity

Wilson and Keddy (1988) found that although disturbances may cause a variety of changes in species abundances, these changes may not be appropriately reflected by variation among general plant community characters. This appears to be the case in EINP, where species richness and total diversity reacted indifferently to the various disturbances. Despite the neutral response in these factors, changes in species composition did occur, as was evident by the higher proportion of total diversity consisting of non-native invader species inside the Park. The rich variety and uniformly distributed populations of native species found on the lightly foraged controls, have been replaced to varying degrees by invaders within the Park. Intense ungulate foraging has contributed to this change because many introduced species are adapted to withstand heavy grazing (Looman 1983; O'Connor 1991). Non native invader species are often low in growth form, highly rhizomatous, and therefore tolerant of heavy grazing. This process of species replacement is based on competitive exclusion whereby changes in environmental stress (ie. grazing) cause the removal of some species, thereby allowing those species which are tolerant of the new environmental conditions, to invade (Grime 1973a).

The similarity in total diversity between the heavily foraged Park and lightly utilized control is unusual considering that year long heavy grazing normally reduces diversity (Waser and Price 1981). A possible explanation is that because maximum species diversity is associated with intermediate levels of an environmental factor (Grime 1973b; Connell 1978), these two treatments may represent opposite sides of the bell shaped diversity curve along the foraging gradient. Therefore, increased foraging outside the Park could possibly increase its diversity by decreasing the ability of community dominants (ie. shrubs) to competitively exclude other species (Quinn and Robinson 1987). In turn, reduced foraging inside the Park may increase diversity by removing the competitive edge the non-native invaders currently hold, particularly in those parts of the landscape where they dominate (ie. south slopes). It should also be noted that not all south facing slopes inside the Park are dominated by invaders to this degree. Many other south aspects exist which are smaller, have less relief, and have a greater portion of forest cover. These areas are only moderately affected by intensive grazing.

The increase in invader species inside the Park is particularly evident on the south facing slopes. These 'grazing islands' have unique vegetation and were the result of heavy grazing during the snow free period of the year. Ungulates use these areas to a greater extent because of their snow loss during the winter months and early green up in the spring. Grazing herbivores are attracted to these sites and congregate on them because of the ease with which they can obtain forage. Their palatable regrowth in late spring and early summer is then periodically regrazed, keeping the vegetation short and in poor vigour for extended periods. The general lack of upland grasslands inside the Park causes the two most abundant herbivores, wapiti and bison. to both utilize these select sites. This grazing pattern has continued in an intensive seasonal and yearly pattern creating significant changes in species composition on many of the south aspects inside the Park.

Positions other than the south facing slope were less likely to experience these heavy levels of use and have fewer invaders. Other positions were largely forested and able to trap considerably more snowfall. Partial shading of the understory limits premature snow loss and green up. Herbaceous species in these areas are unlikely to be grazed until early to mid summer after the main vegetation flush has begun. By that time, the growth of herbs and supply of forage would be large enough that utilization rates would remain relatively light until senescence begins in the fall. Given the above factors, the north slope, with the most well developed forest and shrub canopy, the greatest snow accumulation and least snow loss through the winter, and the least growth of herbs, had the smallest invader index. Little intensive grazing occurred there.

A further increase in invader species was found on the unburned south facing slope compared to the same position on the burned area. This could indicate that burning suppresses invaders. Although Stickney (1986) found exotics to be the most characteristic species which disappeared following a wildfire in Northern Idaho, the relatively small amount of fuel on many of the south aspects in EINP and their early green up makes this explanation somewhat unlikely. Opportunities for burning under heavily grazed Populus tremuloides stands are reduced and even negated, because of the poor fuel complex available (Brown and Simmerman 1986).

Another, more likely explanation for the above difference in diversity, is that variation exists within ungulate foraging patterns throughout the Park. Cairnes (1976) found that wapiti used only one fifth of the Park during the winter months. Thus, if the unburned south slopes are part of their preferred wintering area, they will receive heavy use by wapiti at this time. Large wapiti herds have been observed on the unburned south facing slopes in March and may be a major reason that the vegetation found there is short and consists predominantly of invader species. The burned south facing slopes also receive heavy summer use, but may be subject to less early spring grazing, enabling a more even mixture of native and invader forbs and grasses to occur.

Although some evidence exists which indicates that burning decreases overall species diversity after a single burn (Collins and Barber 1985; Wilson and Shay 1990), other work suggests that herb richness is actually increased by annual burning (Anderson and Bailey 1980). No detectable response, however, was evident in this study. A possible explanation is that because burning took place at least two growing seasons previous to sampling, retrogression towards the original vegetation may already be taking place. In addition, because wildfire was quite common in the parkland, many of the species found there are probably adapted to fire indicating that drastic shifts in diversity are less unlikely. An alternative explanation, however, is that the effect of burning may have been masked by high herbivory within the Park. That is, while burning may have increased the number of species, intensive grazing may have simultaneously removed many others. It may therefore be, that if only one disturbance (ie. fire) had been investigated in the EINP study, the effect of burning on diversity may have been different.

Other minor changes in species richness and diversity were evident among the landscape positions as a result of burning. A decrease in species richness on the burned crest and burned toe positions within the Park suggested that some species may have been reduced or eliminated as a result of burning. Those species affected would be intolerant of fire because of their growth habit. Generally, plants having concealed growing points below the mineral surface are less likely to experience long term damage or death (Brown and Debyle 1989). Those fires with high enough intensities, however, were more likely to penetrate deeper into the LFH layer and damage the resident plant crowns. The crest and toe positions experienced the two highest fire intensities, respectively, as indicated by the burn scorch heights. Species remaining on these sites were either adapted to withstand intense fires or were able to recolonize the area immediately following the disturbance (Stickney 1986; Bradley et al. 1992). Stickney (1986) found that despite an overall increase in the number of species from 103 to 120 ten years after a burn, the net increase of 17 was actually made up of the loss of 19 and a gain of 36 species. Thus, the identity of those species which changed, rather than the number of species (ie. species richness), may provide more insight into the true ecological response of burned areas.

Of all the topographic positions, only the toe slope affected total diversity and species richness. The increase in these attributes was probably caused by the favourable moisture conditions present. These sites remain very moist without extensive flooding. This enables wetland adapted species to extend up from the depressional meadows or sloughs and dryland species to extend down from the south aspect. The result is a richer mosaic of species inhabiting the toe slopes. Maximum species diversity was once again associated with intermediate levels of an environmental factor, in this case moisture and drainage.

6.4.2 Herb Layer

Most herbaceous species found during the inventory were uniformly distributed across the disturbances and topographic positions. This reflects both the wide tolerance of these species to variation in their environment and the homogeneity of most environmental factors among sample sites. Although there were several species documented in this study that were abundant, these were not always important from an ecological perspective. For example, Aralia nudicaulis was found throughout most of the study sites, but similar to the findings of Hardy and Associates (1986), its abundance meant no strong ecological interpretations could be made concerning its presence. Instead, several noteworthy indicator species and species groupings were documented by the ordination biplots (Figures 23 and 24) and TWINSPAN dendrogram (Figure 22).

A group of non native invader species was closely associated with the south facing slopes inside the Park. Of these, Poa pratensis was predominant. This highly competitive, early growing, cool season species is grazing tolerant (Vallentine 1980). Although many invader species are unpalatable and maintain prolific seed production even under heavy grazing (O'Connor 1991), this species is palatable and nutritious when kept in a vegetative state, and increases under this regime because of its abundant creeping rhizomes (Looman 1983). The increases of this species on the south slopes inside the Park may also be due to intermediate nitrogen enrichment (Wilson and Tilman 1991), associated with increased mineralization as a result of intensive, localized grazing (Crawley 1983; Brisk and Heitschmidt 1991). Another plant which occurs concurrently with Poa pratensis, is Taraxacum officinale. This species is also an early growing, highly competitive, non-native invader (Looman 1983). It should be noted that the dominant native grass once found in the northern portion of the parkland, Festuca scabrella (Coupland 1950), was not present in any community, including the sole grassland type. This trend towards 'local extinction' of dominant native species is characteristic of changes in the temporal and spatial patterns of grazing in human influenced systems (O'Connor 1991). Increases in the intensity and duration of grazing in EINP have probably lead to the disappearance of Festuca scabrella.

The second group of species includes those low growing herbs which favour more moist, partly shaded growing conditions. Included in this group were Oryzopsis asperifolia, Rubus pubescens (dewberry), Cornus canadensis, Mitella nuda, Pyrola asarifolia, and the cover of moss. These species were closely associated with the north aspects where heavier forest canopies and poorer solar reception occur. Many of these species are widespread and common throughout the boreal forest of northern and western Alberta under mature deciduous, mixedwood, and coniferous forests (Corns and Annas 1986; Willoughby 1993a). This further supports the theory that the north facing slopes in EINP were more representative of boreal forest conditions. The other positions investigated were probably too warm, too dry, and too exposed for any of these species to dominate. In addition, the north facing slopes experience lower fire intensities. Bradley et al. (1992) list Galium triflorum, Oryzopsis spp., and Pyrola spp. among those that are susceptible to fire-kill. All three of these appeared as indicators for community types found on north facing slopes suggesting they may also be more abundant there as a refuge from exposure to severe fire.

The lack of tall forbs in each of the above two groups, indicates that tall forbs were favoured by either lower foraging intensities or younger successional forests. Willoughby (1993a) suggested that an absence of tall forbs meant grazing by cattle was replacing tall forbs with grazing tolerant low ones, or that forest succession was advancing to a point where tall forbs could no longer compete in the understory. Both of these theories appear to have validity in EINP.

Tall forbs no longer dominate on the heavily grazed south facing slopes inside the Park. The continued presence of tall forbs across the remaining positions inside the Park might suggest that herbivory limits the development of tall forbs only when it occurs at a high intensity. In addition, the contrary may also be true, with moderate browsing of the shrub layer stimulating tall forb development, by removing part of the competitive shrub canopy. The uninhibited shrub growth outside the Park, particularly on the north aspects suppresses tall forb species. Although not as prominent, forest succession also appeared to be a factor, particularly when stands become very mature as was evident on the north facing slopes.

Other individual species which had notable responses included Solidago canadensis, Calamagrostis canadensis, and Lathyrus ochroleucus. Solidago canadensis was abundant on all areas except the heavily forested north slopes. This suggests that this species will not tolerate extensive shading. Although Calamagrostis canadensis was found on nearly all sites, it was particularly abundant inside the Park on aspects other than the north. Work by Leiffers and Stadt (1993) indicates that an overstory canopy transmitting only 20-30% of light should provide sufficient shade to suppress this grass. They further found that mature Populus tremuloides stands transmit as little as 20% of total light. Thus, suppression of this grass may be occurring on north facing slopes. In contrast, the higher Calamagrostis canadensis levels on all other positions inside the Park may be due to its release from the mature canopy, brought on by the reduction in overstory tree density and canopy cover associated with burning and increased herbivory. Lathyrus ochroleucus was the only herb to display a large detectable positive response to fire. This is similar to the large increase in canopy cover, from 0 to 30.8%, documented by Quintilio et al. (1991) following repeated spring fires in central Alberta. Anderson and Bailey (1979) also documented a favourable response to fire among various legume species and suggested it may be due to fire's ability to break their seed dormancy in the soil. Lathyrus ochroleucus is important because it is abundant, productive, and nutritious in deciduous forests, although remaining susceptible to overutilization (Beckingham 1991). The poor response of other species to fire is somewhat surprising because there are numerous species, including Epilobium angustifolium, which are known to respond very positively to fire (Looman 1983; Stickney 1986; Bradley et al. 1992). The impact of high herbivory immediately following burning, may have limited the growth of these fire adapted forbs. It is also possible that increases may have taken place immediately following each fire, but that they were relatively short lived (ie. one season). The composition of the understory normally reverts back to pre-burn conditions, at a rate which is dependent on the intensity of the fire itself (Bartos and Mueggler 1981). Understanding these rates of reversion are important when managing any area using fire.

6.4.3 Shrub Layer

Extensive browsing has maintained shrubs in a shorter growth form throughout the Park. Bishoff (1981) found browse consumption in the forests of EINP to be approximately twice that of current annual production, indicating that much of the browse consumed was two and three year old wood. This intensity of use has resulted in short, thick stemmed shrubs, with numerous leaders at the top which are regularly removed by ungulates producing a distinct browse line. In complete contrast, and despite light browsing, shrubs outside the Park possess a tall and bushy growth form.

The tallest shrubs were consistently on the north facing slopes. These aspects are often the site of deep snow accumulations during the winter months. Deep snow affects the selection of forage by ungulates (Telfer 1978) by reducing the accessibility and subsequent browsing in the area.

Further reductions in shrub heights at the burned crest position were caused by the higher fire intensities as suggested by burn scorch heights. Fire intensity is a direct result of the net heat of combustion, the amount of fuel consumed, and the fire's rate of advance (Alexander 1982). Intense fires at the crest position would arise as a result of the site's reduced duff moisture, brought about by increased exposure, an abundance of both fine and medium fuels, and a greater accessibility of wind to accelerate fire spread. Fires at the crest were therefore more likely to top kill shrubs. Most of the shrubs found at this position were the result of regrowth from the forest floor. Many of the shrubs present at the other landscape positions were better able to withstand the lower fire intensities, and remain within the community. For example, north slopes had the lowest fire intensities, probably because of the sparse amount of fine fuels and the high duff moisture which would occur as a result of poor solar reception.

Stem densities had the opposite response of shrub heights, being higher inside the Park. The moderate increase in shrub density may be caused by several factors, acting either independently, or in combination. Many shrub species respond physiologically to defoliation by increasing the number of stems produced (Stoddart et al. 1975; Crawley 1983). Abundant basal resprouting and/or growth from rhizomes often accounts for part of this increase. It is important to recognize that much of the browsing in EINP occurs during the winter months when alternate forages are unavailable. Certain shrubs can withstand heavy utilization year after year, providing the majority of use is during this dormant period (Stoddart et al. 1975). In comparison to the results in EINP, work by Bailey et al. (1990) showed that heavy grazing by cattle during the growing season actually decreased the density of all woody species. This indicates that the current level of use inside the Park, particularly during the critical summer period, may not be as heavy as the prominent browse line suggests. Instead, the larger proportion of browsing probably occurs during the winter.

Further examination of the response of stem density among topographic positions indicates that no increase occurred on the north facing slope. Therefore, another factor which may be responsible is the more open forest and shrub canopies found inside the Park. Increased light reception and higher soil temperatures at the forest floor may directly stimulate sprouting, as occurs with Populus tremuloides (Schier 1976). The north slopes inside the Park have retained prominent overstories and are logistically less likely to experience these increases in soil temperature, thereby minimizing the potential for resprouting.

The most dramatic increases in stem density inside the Park were apparent on the burned area. Increased densities across all topographic positions indicate that fires of all intensities were able to induce sprouting among shrubs. This response was far greater than the moderate increase observed on the unburned areas inside the Park. The favourable response to fire was not unexpected because numerous shrubs have been documented to respond favourably to fire (Bradley et al. 1992). The similar response of shrub stem densities among positions was explained by Johnston (1981). The latter simulated various burning intensities using fuel loadings and found that burn intensity affected the rate of recovery of Corylus cornuta and Rubus idaeus sprouts, rather that the actual number of stems produced. While fire reduces the cover and therefore, vigour, of shrubs, increases in stem density may still occur (Anderson and Bailey 1980).

It is important to note that the increased densities caused by burning were not consistent among species. Although both Rubus idaeus and Corylus cornuta were correlated with an increase, only the former produced a significant response in the regression model. This may be because while both species increase as a result of basal resprouting, Rubus idaeus also regenerates in large part from seed (Johnston 1981). The positive correlations observed here were similar to the results of other studies involving Rubus idaeus (Foote 1976; Anderson and Bailey 1979) and Corylus cornuta (Buckman 1964; Perala 1974; Ohmann and Grigal 1979). The more significant response of Rubus idaeus was somewhat unexpected, however, because Johnston (1981) concluded that this species was actually more susceptible to damage from fire than Corylus cornuta, primarily because of the relatively shallow depth of the Rubus idaeus root crowns. It is possible, however, that Corylus cornuta is less fire resistant when exposed to repeated fires over relatively short intervals, as was done here. Another explanation could be that at the specific postburn time period when the data were collected, this species may still have been increasing while Rubus idaeus was peaking in density. Ohmann and Grigal (1979) found that the latter increases rapidly and then declines after fire, while Corylus cornuta takes longer periods to increase.

Whereas most shrubs showed no correlation to burning, other species displayed a negative relationship including Amelanchier alnifolia and Symphoricarpos occidentalis. Despite the tolerance of Amelanchier alnifolia to fire (Noste and Bushey 1987; Bradley et al. 1992) and the positive response documented by Anderson and Bailey (1980), this species decreased in stem density. The reduction observed here may be caused by preferential selective browsing of the regrowth of this palatable species. Although Symphoricarpos occidentalis has been found to rapidly increase following a single fire (Anderson and Bailey 1979), Anderson and Bailey (1980) documented a decline under a multiple burning regime. A decrease was also found by Bartos and Mueggler (1981). The unpalatable nature of Symphoricarpos occidentalis compared to other major browse species (Fitzgerald et al. 1986), indicates that heavy browsing was probably not the major reason for its decline. Instead, repeated exposure to burning, particularly while these shrubs were weakened and still recovering, may have caused irreparable damage. Determining the specific response of vegetation to fire is generally difficult because many factors influence post-burn vegetation including the pre-fire vegetation, species adaptations, environmental conditions, and chance (Brown and Debyle 1989).

Although individual species responses varied little, Viburnum edule did display a strong preference for the heavier forest canopies found on north aspects, regardless of disturbance. This species was closely associated with the group of low lying herbs, and is abundant throughout the boreal mixedwood forest types (Corns and Annas 1986), where it was found in both seral (aspen) and climax (spruce) communities. Despite adding little in total cover or production, this species remains potentially important because resource managers can identify sites high in Viburnum edule as mature, late successional, Populus tremuloides stands.

6.5 Forage Production

Current annual growth of the various vegetative components was influenced by both the disturbances and topographic positions. The higher production of grasses, forbs, and total biomass on most positions inside the Park compared to the lightly foraged controls, was probably caused by the reduction in shrub heights and tree canopy caused by years of intensive browsing. Reduced yields in the undergrowth of Populus tremuloides stands has been attributed to intense root competition which reduced soil moisture (Ellison and Houston 1958). Shrubs also compete with forbs and grasses for space, nutrients, moisture, and light (Spurr and Barnes 1980). A reduction in shrub competition would allow forb and grass production to increase. North aspects inside the Park did not experience as large a decrease in shrub and tree cover, and as a result, no herb production increase was evident. A major reason for the changes in production may have been from the shifts among dominant species. For example, increased levels of Poa pratensis and Calamagrostis canadensis inside the Park probably accounted for the higher grass production, while an increased abundance of tall forbs increased forb production. Maximum grass production was evident on the south facing slopes inside the Park where altogether few trees and shrubs were found.

The additional increase in herb production within the burned area inside the Park is unlike the decrease found by Anderson and Bailey (1980) after annual burning, but is similar to that found by other investigators after occasional fire (Harniss and Murray 1973; Bartos and Mueggler 1981; Brown and Debyle 1989). The former discrepancy may be caused by differences in fire intensities, the postburn growing conditions, or most likely, the frequency of fire. Frequent fire is more likely to damage plants and decrease their annual growth. The observed increase could be attributed to several factors including a further decrease in competition from the shrub and forest overstories. An indirect response is also possible through increased soil temperatures and the release of nutrients (Ahlgren and Ahlgren 1960; Daubenmire 1968a; Wright and Bailey 1982).

Browse production responded in a manner opposite to the herbaceous components. Twig and leaf production were lower inside the Park than on the controls, despite displaying higher stem densities. The decrease probably results from the reduced size and vigour of the shrub strata, with the relative amount of twig and leaf growth per live stem being lower. Proportionately larger decreases on both the crest and toe positions on both the burned and unburned areas, suggest that heavier browsing may be occurring at these locations within the landscape. This may relate to their reduced snow cover and closer proximity to the preferred south facing slopes during the winter months. Further decreases were evident on the burned crest where intense burning would have slowed the rate of regrowth (Johnston 1981). Both Bartos and Mueggler (1981) and Brown and Debyle (1989) found that fires with higher intensities resulted in proportionately larger and more prolonged reductions in available browse.

Variability in twig production was substantially less than that in the leaf pool, particularly between topographic positions. This may be attributed to changes in the abundances of shrub species producing the browse. Greater differences in the size, density, and shape of leaves create more variability in leaf production. For example, Symphoricarpos occidentalis leaves are small and thin, and will contribute much less to production than the large, thick, compound leaves of Rubus idaeus.

The lack of significance among differences in total annual production suggests that vegetation pools act in a compensatory manner. A decrease in one vegetative component is likely countered by an increase in one or more of the others as alternate plant species increase in number or size.

6.6 Summary and Management Implications

6.6.1 Summary

This study has effectively utilized multivariate techniques to determine that topographic position, herbivory, and fire were the dominant factors influencing the composition and structure of plant communities in EINP. Furthermore, six distinct community types were documented and could be interpreted with respect to the previous environmental factors.

Position was consistently the most important factor, and was shown to significantly interact with each of the disturbances. In general, north facing slopes were dominated by larger and more mature *Populus tremuloides*. As a result, herbaceous current annual production was lower, but was partially offset by the higher production of browse from the taller shrub layer. Two community types were documented which were primarily associated with these north facing slopes. They differed from one another only in their location, with one found outside the Park, and the other inside. Although the manipulation of topographic position is unrealistic in resource management, it is important to recognize that other vegetation and ungulate management strategies will depend heavily on position, and in many cases, may be constrained by it.

Herbivory was the second most important environmental factor affecting plant communities, with its impact reflected in their composition, structure, and productivity. Increased herbivory since the Park's establishment appears to be the factor preventing the rejuvenation and spread of *Populus tremuloides* inside the Park. In addition, grazing has resulted in an increased abundance of non-native invader species such as *Poa pratensis*, particularly on many of the south facing slopes. This change in species composition likely contributed to the higher current annual production of grass on these sites, and the formation of a unique grassland community type.

Higher browsing pressure inside the Park has reduced shrub heights and current annual browse production inside the Park. The resulting lower shrub stratum is accompanied by a more uniform distribution, and increased current annual production of, tall herbs such as Calamagrostis canadensis, forming yet another community type. In a somewhat similar community type found outside the Park, a taller, more vigorous shrub stratum underneath a dense, middle aged Populus tremuloides canopy, limits the abundance of many tall herbs. In some locations, shade tolerant, low growing herbs form the major herbaceous component.

Between the disturbances, fire currently appears to be less important from a community perspective, although still affecting the shrub and tree strata, particularly at the crest position. Both tree cover and shrub heights were reduced, while shrub density and the abundance of fire adapted species such as Lathyrus ochroleucus, were higher. Herb current annual production was also highest within the burned area. Fire appeared to be an important factor in the determination of a single community type.

6.6.2 Management Implications

The management of any land area, including that of a national park, depends heavily on the underlying body of knowledge about the natural resources in the area. Information obtained in this study could have several implications for resource managers at EINP. The exact nature of the implications, however, may be limited in reality due to the restrictions imposed by the current policy and objectives of the National Parks Act.

Objectives of the National Parks Act are to preserve and manage both the features and the natural processes representative of the ecosystem found in the moraine of the Beaver Hills (Blyth and Hudson 1987). Tradeoffs will undoubtedly occur whether managing from a vegetative, wildlife, or landscape perspective, because not all individual objectives will be mutually attainable. Ultimately, any management actions will have to consider all of these aspects collectively.

6.6.2.1 Landscape Considerations

Although the data collected in this study was gathered at a local landscape, or ecosite, level, this information can be used to help interpret, with the aid of assumptions, the ecology of EINP on a broader scale, such as at the ecodistrict and ecoregion level. The main assumption made is that the information collected in this study is generally representative of the Beaver Hills, and therefore, can be compared to other geographical areas. Management of the vegetation in EINP depends in large part on what type of landscape setting is deemed acceptable and desirable to both society and park managers. Several years ago, the Beaver Hills were classed as grassland transition by the Ecoregions Working Group (1989) of Canada. Although Strong (1992) recognized the Beaver Hills as lying in the center of the aspen parkland, he classified the area as an outlier of the low boreal mixedwood ecoregion.

Ecoregions, or ecoclimatic regions, are broad landscape areas characterized by distinctive ecological responses to climate, as expressed by vegetation and reflected in the area's soils, wildlife, and water (Ecoregions Working Group 1989). Climate, in turn, is reflective of characters such as average long term precipitation, temperature, and frost free period, which are determined by factors such as elevation and distance from oceanic waterbodies. Although the Beaver Hills vary in elevation from the surrounding plains, the extent to which this may alter climate remains uncertain, particularly because the concept of a vegetative climax hinges on an accurate understanding of what constitutes 'modal' conditions on that portion of the earth's surface (Daubenmire 1968b). Thus, it could be argued, that if EINP were a prime example of 'transitional grassland', or the parkland ecoregion, the communities found there should differ significantly from that of the boreal mixedwood ecoregion. Furthermore, the climate and growing conditions should differ sufficiently to prevent forest development on at least part of the area. In other words, the prairie influence should be reflected within the Park's natural communities across the landscape, thereby representing topographically driven climaxes, particularly in the absence of disturbance (Daubenmire 1968b). Presumably, changes in microclimate throughout the highly variable topography would be the major cause, such as the presence of hotter, drier conditions on sharp, south facing slopes. The data collected in this study and the work of others (Nicholson 1993), however, tends to support the concept that EINP grades much closer toward the low boreal mixedwood ecoregion. This is further supported by the major difference in dominant soil types found inside the Park (eg.

Luvisols) compared to those found on the surrounding plains (eg. Chernozems). The evidence implies that, climatically, EINP has the same potential to develop into deciduous, and perhaps even coniferous forested vegetation at climax, as do areas north of the Beaver Hills.

Why then, did the vegetation in Elk Island resemble that of an intermittent aspen groveland at the time of park establishment? One of the main reasons was wildfire. Instead of climate, repeated, sporadic disturbance via burning kept the area in a semi-forested, sub-climax 'parkland-like' state, with those areas that were drier burning more often and more intensely resulting in patchy control of the tree cover. The occurrence of Luvisols throughout the Park indicates that burning was probably infrequent enough to allow succession to regularly cover much of the area with forest. With the absence of fire in the twentieth century, forest succession clearly became dominant as was evident outside the Park. This also supports the inclination of Strong (1992) to classify the Beaver Hills as an outlier of the boreal mixedwood. It is also possible that part of the surrounding plains which he classified as parkland, particularly the northern portion, could indeed be subject to forest expansion in the absence of fire, if these lands were not cultivated intensively today.

Another question concerns the actual classification and extent of coverage of the aspen parkland ecoregion. If climate, and not disturbance, is the factor determining the boundaries of an ecoregion, it is possible that the transitional grassland may be more appropriately classified as subunits of the prairie and boreal ecoregions. Only improved climate data at a greater spatial resolution could establish this for certain. These classification subunits, known as ecodistricts, are based in part upon physiographic and geologic patterns (Ecoregions Working Group 1989). The findings of this study support the opinion of Strong (1992), who points out that a much broader and important perspective of ecodistricts is required to deal with macro-topographic features at the provincial level, to which the Beaver Hills belong.

The current landscape inside the Park consists of a mosaic of grassland, shrubland, and forest, which have formed as a result of prescribed fire and decades of intensive ungulate foraging. It appears that many of the grasslands now found in the Park remain in this state because of the intensity of foraging which inhibits forest encroachment. The effectiveness of prescribed burning in altering the forest cover has also been substantial, but somewhat limited to that part of the landscape where the effects of fire were more pronounced. The complicated relationship of using fire as a tool in landscape and habitat management, indicates that specific, strategic objectives must be set before implementing a burning program.

Managers of EINP are faced with the decision of what type of landscape constitutes a 'natural' feature, as dictated by the Park's objectives. The use of historical evidence to decide this is clearly unreliable, particularly because the time frame for which this information is available is relatively recent, and that arguments for maintaining either a semi-open parkland or a boreal forest are possible. As a result, and given the dynamic history of the vegetation of EINP, it may be more realistic to preserve natural processes rather than natural features.

The two processes that were historically important in altering the landscape were wildfire and variable grazing intensities created by ungulate migrations and wildfire. These are currently most closely represented by the prescribed burning and ungulate trapping programs. Although ungulate harvests are often not perceived as natural per se, this process should be acceptable given that the migrating bison herds which depended on the Beaver Hills during the winter months (Morgan 1980) were harvested by indigenous people. The major difficulty today stems from the lack of animal movement on a regional scale. To achieve true migration and seasonal variation in stocking rates, the Park would have to expand to include a portion of the adjacent plains.

In contrast, prescribed fire is easier to carry out. In the process, a more heterogenous landscape is established, by maintaining a mosaic of forest and grassland cover. The increased variety of community types associated with this condition represents a further increase in biodiversity within the Park. Both community and landscape diversity are important considerations in rangeland conservation management (West 1993).

There is evidence for a natural progression of forested communities towards more open landscapes without the use of fire. This, however, appears to depend on continued high stocking rates which have other, undesirable impacts on the vegetation. Changes in the abundance and relative composition of shrubs and herbs make this option unrealistic.

A decision not to burn would allow forest succession to take over, provided sufficient recruitment of trees takes place. A reduction in stocking rates would likely be needed to ensure this (Polster and Watson 1979). Forest expansion, however, may produce a forested 'monoculture' over most of the Park's uplands and would result in less diversity on a landscape scale. This in turn would produce less variation among habitat types for wildlife species.

Ultimately, it is important to establish specific target objectives before undergoing any major management changes. The preservation of natural processes and features, should play a major role in deciding future management. It may also be reasonable given the complexity of the landscape ecology in EINP, for managers to give habitat availability, species diversity, and forage productivity, priority over landscape concerns.

6.6.2.2 Vegetation Management Considerations

The composition of plant communities at these sites in EINP were only moderately affected by the disturbances. In particular, most species were found consistently across all disturbances and on at least several topographic positions. One exception which should be noted was in the forest overstories, where mature forms of Amelanchier alnifolia, Prunus pensylvanica, and Prunus virginiana were absent inside the Park. For these species to reach maturity, a reduction in browsing pressure is necessary.

It appears that prescribed burning at present does not remove specific species and, obecause of its variable impact throughout the landscape, may actually increase community diversity. This is because areas such as the north slopes, where burns are less intense, continue to be dominated by the low forb community type while other positions are represented by tall forb communities. Burning therefore appears to be compatible with maintaining diversity among community types and species within the Park.

Although species richness and total diversity were essentially unaffected by the disturbances, invader diversity was much higher inside the Park, particularly on the south aspects. If the objective of Park policy is to maintain maximum species diversity regardless of the origin of the species, then current management is acceptable. However, if the intent is to minimize the number of invader species within the Park, current management would have to be rated as only partly successful. Past stocking levels of ungulates have been heavy enough to shift many sites in favour of introduced species. Some, such as Poa pratensis, Taraxacum officinale, and Trifolium repens are very competitive and can exclude other, less competitive, native species. In large part, these species can be attributed to human influence. This pattern, evident in EINP, is explained by O'Connor (1991), who suggests that human activity on and around rangelands interrupts migration patterns thereby changing grazing pressure from a seasonal pulse to a regular, systematic cropping. This in turn, favours the establishment of grazing tolerant, invasive species.

The change in vegetation evident on the grassy south facing slopes inside the Park probably represents a fundamental change, wherein the original community crossed an ecological threshold (Figure 25), moving from one successional pathway, or domain, to another (Westoby et al. 1989; Bosch and Kellner 1991). Not only do invader species suppress native vegetation (Wilson 1989), but heavy grazing increases the germination of weedy species (Johnston et al. 1969). Although a reduction in overall stocking rates may decrease the rate at which the remaining native communities are invaded by these species, it is unlikely that those areas already converted would be fully recolonized back to native herbs. Any attempts to re-establish the dominant native grass once found in the area, Festuca scabrella, would be unlikely to succeed given the inability of this species to withstand intensive grazing and competition from established invaders. Further support of this can be found in the permanent monitoring exclosures in the Alberta foothills where Poa pratensis continued to dominate overgrazed rangelands after 40 years of rest from cattle grazing (Willoughby 1993b). Simply decreasing stocking rates is unlikely to offer any solution. Instead, the use of intensive inputs (ie. breaking and reseeding) is probably required to cross back over the threshold (dashed arrow in Figure 25), which was passed when herbivory shifted these sites from one stable domain to another (Friedel 1991; Laycock 1991). These specific practices of range improvement though, are not likely to occur on a widespread scale in an area such as EINP. Nevertheless, burning also represents a commonly used input (Westoby et al. 1989; George et al. 1992) and can be used to control invader species such as Poa pratensis (Curtis and Partch 1948; Anderson et al. 1970; Hadley 1970). For effective, high intensity fires to be achieved, however, simultaneous reductions in stocking rates would have to be undertaken to accumulate sufficient fuel, particularly on the heavily grazed south facing slopes. The continued use of prescribed fire would also be beneficial by opening up larger areas of grassland and increasing the production of herbaceous forage, thereby alleviating the isolated intensive grazing and limiting the spread of introduced species.

An altogether different management approach would be to redefine invader species as naturalized, thereby recognizing them as an acceptable part of the Park's vegetation and actively incorporating them into the Park's management plans. These species require special management consideration because of their early season of growth, competitive nature, and low forage value in winter. An important part of the Park's overall management plan is an evaluation of range condition (Blyth and Hudson 1987). The traditional method classifies individual species as decreasers, increasers, and invaders, the latter which are absent in the climax vegetation and therefore unacceptable (Stoddart et al. 1975). Unless invader species are included, using this condition classification will find virtually all the south facing slopes investigated in this study to be in poor condition, despite being productive and critical for wildlife use. Only a change in management philosophy including alterations in the overriding policy and mandate of the National Parks Act, would end this trend. These alterations would no doubt create debate because not all invader species would be accepted as naturalized (ie. weedy species), thus requiring decisions as to which species constitute 'weeds'.

Managing for individual species within communities can only be done successfully if their specific responses to disturbances are understood. The variable nature of the EINP landscape and the disturbances found within it, indicates that a more consistent and accurate method of monitoring vegetative change should be adopted. Regular monitoring over prolonged periods within permanently delineated plots distributed throughout the landscape, under both burned and unburned and foraged and unforaged (exclosure) conditions, are required to evaluate the specific response of various plant species to each disturbance. This information would provide valuable baseline data imperative for making proper management decisions. Several models for establishing benchmark programs already exist including those of the United States Department of Agriculture, the Alberta Forest Service, and Alberta Public Lands.

6.6.2.3 Ungulate Management Considerations

Managing the large herbivores in EINP centers around their dependence of various habitat types. Both prescribed burning and years of intensive foraging have altered the relative amount and distribution of community types as well as their production of browse and herbaceous material.

The early seal vegetation resulting from burning provides better habitat for large ungulates by expanding the food resource and improving the quality of forage (Reynolds 1969). This is particularly true for species which prefer semi-open areas such as wapiti and bison. Forests on the north slopes have a natural resistance to fire which ensures that pockets of cover remain to provide protective and thermal cover. Given that grazing species make up the largest populations in the Park, large scale burning would seem advisable to convert much of the Park to this state, particularly because there is a large increase in forb and grass production associated with this action. Although no net change occurs in the production of browse due to fire, shifts between the dominant types of species may be changing the quality of production. For example, Bisoff (1981) and Renecker and Hudson (1988) found Corylus cornuta to be lower in crude protein compared to many other primary browse species such as Rubus idaeus, Rosa spp., Populus tremuloides, and even Symphoricarpos occidentalis. These depressed levels also appear to be consistent among seasons (Renecker and Hudson 1988), including the important winter period. Bishoff (1981) also concluded that Corylus cornuta is unable to provide ungulates with sufficient phosphorus, even during the summer months. Maintaining a balance among the various forage species available is more likely to meet the dietary requirements of herbivores (Oldemeyer et al. 1977).

In addition to changes in the types of forage species available to wildlife, prescribed burning can directly improve forage quality. Increases in crude protein and phosphorus have been found in both the shrub and tree regrowth following fire (Debyle et al. 1989).

Burning does have other important implications for wildlife, in addition to those involving forage quality and quantity. For example, an estimated 97% of reproductive female Dermacentor albipictus (winter tick) were killed by prescribed burning in the aspen parkland (Drew et al. 1985). This parasite is a serious pest of moose, making burning a practical option for it's control in a confined area such as EINP.

Widespread burning, however, is not without drawbacks. Reducing the overall area of forest will reduce the amount of leaf fall which is an important source of winter forage for wapiti (Nietfield 1983). Although burned areas are often beneficial for moose, no moose were seen on any of the burned catenas during the lengthy data collection process, suggesting that the area may now be too open for this species. This may be explained by the lack of Populus tremuloides regrowth and high fire frequency because the optimal successional stage for moose is from 11 to 30 years after burning (Bradley et al. 1992). Other ungulate species also require larger forested tracts for cover during critical times such as during severe winter storms and calving. To maintain areas more favourable for these species, some regions would have to be either not burned at all, or burned at lower frequencies, making it critical to have a comprehensive long term burn management plan in place.

Ungulate populations are currently controlled through trapping and removal programs. This is important because foraging has clearly been a major factor in altering the Park's vegetation by limiting stand rejuvenation, altering the growth form of the shrub understory, and reducing browse production.

This latter factor is a key alteration, because while the largest proportion of total production is provided by herbaceous material, most of this is no longer available during the winter months. Early senescence and deterioration in the autumn along with the accumulation of snow can render much of this material inaccessible. Therefore, all ungulates, including bison and wapiti, increase their use and dependence on browse material. Holsworth (1960) found that these two grazing species will increase the amount of browse in their diet up to 30% and 10%, respectively. A further difficulty is that much of the shrub leaf material is below the snow line. Thus, although twigs make up the smallest part of total production, this component provides the most critical portion of all the forage produced. Twigs are more accessible during the winter and remain higher in nutritive value until late in the dormant season (Stoddart et al. 1975, Bishoff 1981). The result is that an increasing ungulate population may be supported by an excess of herbaceous growth during the summer and fall, while a diminishing browse pool may sustain these same herbivores during the critical winter months. This type of foraging supply and demand pattern is more susceptible to fluctuations which could lead to severe forage shortages. Surges in ungulate populations, heavy snowfalls, poor summer precipitation, or other anomalies, may make this forage production scheme undesirable.

Any manipulation of the shrub layer through burning or other means will have important ramifications on the supply of browse for ungulates. For example, a reduced twig supply would force ungulates to turn to alternate sources of lower quality forage. The implications for management are that larger population reductions may be required to reduce the risk of encountering problems in forage availability. It is currently unknown whether the trend in browse production is increasing or decreasing. This information is clearly necessary in order to monitor forage availability patterns more closely and predict any surpluses and/or shortages.

Another related factor to consider is the role of the south facing slopes inside the Park. The early green up and nutritious herbaceous forage produced may actually be critical in diverting some of the early spring browsing pressure from forested areas. Without the south slopes, even heavier browsing pressures are probable, which would further alter the shrub strata within the Park, particularly because these grasslands are very productive. The main disadvantage of these sites is that the introduced species found here are early curing, and therefore provide poor quality winter forage compared to native species. It would thus seem preferable to limit those areas on which these species dominate because most of the forage use in EINP occurs during the dormant season.

6.7 Additional Research

One of the priorities of national parks, enabling them to resolve the dilemma of how to perpetuate natural forest ecosystems that include fire as a factor of their environment, is to obtain information on fire ecology (Van Wagner 1990). This is required to make affective management decisions. While a large body of information exists for all of North America, little is applicable to EINP because of the area's unique vegetation and climate. The limited amount of information collected on fire ecology in Western Canada to date, particularly with respect to the autecology of specific understory species, leaves much of the baseline data lacking. This information could be collected through the use of long term monitoring programs and tools such as grazing exclosures.

Other gaps which appear in our understanding of the aspen parkland, include establishing a detailed classification of Populus tremuloides forests based on ecological parameters. In addition, information on the rates of conversion of Chernozemic grassland soils to Luvisolic forested soils would be beneficial for determining more accurately the historical ratio between these vegetation types in the EINP landscape. Although this study provides important baseline data, a larger number of stands should be sampled from a wider range of environmental variables to create a more comprehensive and inclusive classification. Additional research could then be directed towards establishing a clearer identity for the parkland, including its position in a broader classification scheme.

Finally, for EINP, a greater understanding must be reached concerning the impact of herbivory and fire throughout the Park. The significant but variable response of plant communities to disturbances within the landscape requires that managers be able to predict how large scale burning or changes in ungulate populations will affect the habitat and forage resources available to ungulates, before they are actually undertaken. In addition, because a goal of herbivore management is to maintain a sustainable system, it is critical to identify the various environmental thresholds within the Park, and manage landscapes so that they are not exceeded (Archer and Smeins 1991). Modelling may prove effective in monitoring the dynamics and responses of both vegetation and ungulates to management strategies in EINP.

7. LITERATURE CITED

Aayad M.A.G. and R.L. Dix. 1964. An analysis of a vegetation micro environmental complex on prairie slopes in Saskatchewan. Ecological Monographs 34: 421-442.

Acton D.F. 1965. The relationships of pattern and gradient of slopes to soil type. Canadian Journal of Soil Science 45: 96-101.

Agriculture Canada Expert Committee on Soil Survey. 1987. The Canadian system of soil classification. 2nd ed. Agriculture Canada Publication 1646, 164 pp.

Ahlgren I.F. and C.E. Ahlgren. 1960. Ecological effects of forest fires. Botanical Review 26: 483-535.

Alexander M.E. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60: 349-357.

Anderson K.L., E.F. Smith and C. Owensby. 1970. Burning bluestem range. Journal of Range Management 23(2): 81-92.

Anderson M.L. and A.W. Bailey. 1979. Effect of fire on a Symphoricarpos occidentalis shrub community in central Alberta. Canadian Journal of Botany 57: 2819-2823.

Anderson H.G. and A.W. Bailey. 1980. Effects of annual burning on grassland in the aspen parkland of east-central Alberta. Canadian Journal of Botany 58: 985-996.

Archer S. and F.E. Smeins. 1991. Ecosystem-level processes. chapter 5 from: Grazing Management: An Ecological Perspective. edited by R.K. Heidtschmidt and J.W. Stuth. Timber Press, Portland, Oregon, pp 109-139.

Bailey A.W., B.D. Irving, and R.D. Fitzgerald. 1990. Regeneration of woody species following burning and grazing in Aspen Parkland. Journal of Range Management 43: 212-215.

Bailey A.W. and M.L. Anderson. 1978. Prescribed burning of a festuca-stipa grassland. Journal of Range Management 31: 446-449.

Bailey A.W. and R.A. Wroe. 1974. Aspen invasion in a portion of the Alberta parklands. Journal of Range Management 27: 263-266.

Bartos D.L. and W.F. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. Journal of Range Management 34: 315-318.

Bartos D.L., W.F. Mueggler and R.B. Campbell Jr. 1991. Regeneration of aspen by suckering on burning sites in western Wyoming. USDA Forest Service, Intermountain Research Station, Research Paper INT-448. 10 pp.

Basile J.V. 1979. Elk-aspen relationships on a prescribed burn. Forest Service, USDA Forest Service, Intermountain Research Station, Research Note INT-271. 7 pp.

Beckingham J. 1991. The influence of microclimate and grazing on the growth of Lathyrus ochroleucus (Hood) in central Alberta. M.Sc. Thesis, University of Alberta, 171pp.

Bella I.E. and J.P. De Franceschi. 1980. Biomass productivity of young aspen stands in western Canada. Forestry Canada, Information Report NOR-X-219. 23 pp.

Bichlmaier M. 1985. Response of understory vegetation of some boreal mixedwood forest communities to native ungulate foraging. M.Sc. Thesis. University of Alberta, Edmonton, Alberta. 123 pp.

Bird C.D. 1961. Ecology of the aspen parkland of western Canada. Canadian Department of Agriculture Publication 1066. 153 pp.

Bishoff K.W. 1981. Forage in Elk Island National Park, Alberta. M.Sc. Thesis, University of Alberta, Edmonton, Alberta, 141 pp.

Blyth C.B. and R.J. Hudson 1987. A plan for the management of vegetation and ungulates - Elk Island National Park. 343 pp.

Bosch O.J.H. 1989. Degradation of the semi-arid grasslands of southern Africa. Journal of Arid Environments. 16:143-147.

Bosch O.J.H. and K. Kellner. 1991. The use of a degradation gradient for the ecological interpretation of condition assessments in the western grassland biome of southern Africa. Journal of Arid Environments 21:21-29.

Bowser W.E., A.A. Kjearsgaard, T.W. Peters, and R.E. Wells. 1962. Soil Survey of Edmonton Sheet 83-H. Canadian Dept. of Agriculture, Research Council of Alberta and University of Alberta Soil Survey Report No.21. 66 pp + maps.

Bradley A.F., N.V. Noste and W.C. Fischer. 1992. Fire ecology of forests and woodlands in Utah. USDA Forest Service, Intermountain Research Station. INT-287. 128 pp.

Brisk D.D. and R.K. Heidtschmidt. 1991. An ecological perspective. chapter 1 from: Grazing Management: An Ecological Perspective. edited by R.K. Heidtschmidt and J.W. Stuth. Timber Press, Portland, Oregon, pp 1-26.

Brown J.K. and N.V. Debyle. 1989. Effects of prescribed fire on biomass and plant succession in western aspen. USDA Forest Service, Intermountain Research Station. Research Paper INT-412. 16 pp.

Brown J.K. and D.G. Simmerman. 1986. Appraising fuels and flammability in western aspen: a prescribed fire guide. USDA Forest Service, Intermountain Research Station. INT-205. 48 pp.

Buckman R.E. 1964. Effects of prescribed burning on hazel in Minnesota. Ecology 45: 626-629.

Caimes A.L. 1976. Distribution and food habits of moose, wapiti, deer, bison, and hare in Elk Island National Park, Alberta. M.Sc. Thesis, University of Calgary, Calgary, Alberta, 171 pp.

Campbell B.M. 1986. Montane plant communities of the fynbos biome. Vegetatio 66: 3-16.

Cerezke H.F. and H.S. Gates. 1992. Forest insect and disease conditions in Alberta, Saskatchewan, Manitoba, and the Northwest Territories in 1991. Forestry Canada, Info. Report NOR-X-325. 24 pp.

Collins S.L. and S.C. Barber 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64: 87-94.

Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Cook C.W. and J. Stubbendieck. 1986. Range Research: Basic Problems and Techniques. Society for Range Management, Denver Colorado, 317 pp.

Corns I.G.W. and R.M. Annas. 1986. Field guide to forest ecosystems of west-central Alberta. Northern Forestry Center, Edmonton, Alberta, 250 pp.

Coupland R.T. 1950. Ecology of mixed prairie in Canada. Ecological Monographs 20: 271-315.

Crawley M.J. 1983. Herbivory. The Dynamics of Animal-Plant Interactions. Studies in Ecology. Volume 10. Blackwell Scientific Publications, London. 437 pp.

Crown P.H. 1977. Soil survey of Elk Island National Park, Alberta. Alberta Institute of Pedology. Report S-77-38, 128 pp.

Curtis J.T. and M.L. Partch. 1948. Effect of fire on competition between bluegrass and certain prairie plants. American Midland Naturalist 39: 437-443.

Daubenmire R.F. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33: 43-64.

Daubenmire R. 1968a. Ecology of fire in grasslands, from Advances in Ecological Research. vol.5., Academic Press, pp 209-266.

Daubenmire R. 1968b. Plant Communities: A Textbook of Plant Synecology. Harper and Row Publishers, New York, 300 pp.

Daubenmire R. 1976. The use of vegetation in assessing the productivity of forest lands. Botanical Review 42(2): 115-143.

Debyle N.V. 1979. Potential effects of stable versus fluctuating elk populations in the aspen ecosystem. p 13-19. In North American Elk, Ecology, Behavior, and Management. ed. by M.S. Boyce and L.D. Hayden-Wing, University of Wyoming, Laramie, Wyoming, pp 13-19.

Debyle N.V. 1985. Animal impacts. chapter in: Aspen: ecology and management in the Western United States. edited by N.V. Debyle and R.P. Winokur. USDA Forest Service, General Technical Report RM-119, Fort Collins, Colorado, pp 115-123.

Debyle N.V., P.J. Urness, and D.L. Blank. 1989. Forage quality in burned and unburned aspen communities. USDA Forest Service, Intermountain Research Station, Research Paper INT-404. 8 pp.

Deering P. 1987. Fire management plan (interim). Elk Island National Park Resource Conservation Report. 111 pp.

Dix R.L. and F.E. Smeins. 1967. The prairie, meadow, and marsh vegetation of Nelson County, North Dakota. Canadian Journal of Botany 45: 21-58.

Dormaar J.F. and L.E. Lutwick. 1966. A biosequence of soils of the rough fescue prairie-poplar transition in southwestern Alberta. Canadian Journal of Earth Sciences 3:457-471.

Downing D. and E. Karpuk. 1992. Aspen vegetation types of the low boreal mixedwood ecoregion, East Central Alberta. Unpub. Report, Alberta Forestry, Land, and Wildlife, Land Information Services, 164 pp.

Drew M.L., M.W. Samuel, G.M. Lukiwski and J.N. Willman. 1985. An evaluation of burning for control of winter ticks, Dermacentor albipictus, in central Alberta. Journal of Wildlife Diseases, 21(3): 313-315.

Ecoregions Working Group. 1989. Ecoclimatic region of Canada. Canada Committee on Ecological Land Classification, Environment Canada, Ecological Land Classification No. 23.

Ellison L. and W.R. Houston. 1958. Production of herbaceous vegetation in openings and under canopies of western aspen. Ecology 39(2): 337-345.

Environmental Management Associates Ltd. 1993. Deciduous forest types of the lower boreal cordilleran ecoregion, west central Alberta. First Approximation. Resource Information Branch, Alberta Forestry, Lands, and Wildlife, Edmonton, Alberta. 159 pp.

Fitzgerald R.D. and A.W. Bailey. 1984. Control of aspen regrowth by grazing with cattle. Journal of Range Management 37(2): 156-158.

Fitzgerald R.D. and J. Hoddinott. 1983. The utilization of carbohydrates in aspen roots following partial or complete top removal. Canadian Journal of Forest Research 13: 685-689.

Fitzgerald R.D., R.J. Hudson and A.W. Bailey. 1986. Grazing preferences of cattle in regenerating aspen forest. Journal of Range Management 39(1): 13-18.

Foote J. 1976. Classification, description, and dynamics of plant communities following fire in the taiga of interior Alaska. Final report, BLM contract 53500-CT2-224, Fire Effects Study. 211 pp.

Friedel M.H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. Journal of Range Management 44(5): 422-426.

Gauch H.G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge, 298 pp.

George M.R., J.R. Brown and W.J. Clawson. 1992. Application of nonequilibrium ecology to management of Mediterranean grasslands. Journal of Range Management 45(5): 436-440.

Grigal D.F. and H.F. Arneman. 1970. Quantitative relationships among vegetation and soil classifications from northeastern Minnesota. Canadian Journal of Botany 48: 555-566.

Grime J.P. 1973a. Competitive exclusion in herbaceous vegetation. Nature 242: 344-347.

Grime J.P. 1973b. Control of species diversity in herbaceous vegetation. Journal of Environmental Management 1: 151-167.

Gruell G.E. and L.L. Loope. 1974. Relationships among aspen, fire, and ungulate browsing in Jackson Hole, Wyoming. USDA Forest Service, General Technical Report.

Hadley E.B. 1970. Net productivity and burning responses of native eastern North Dakota prairie communities. American Midland Naturalist 84: 121-135.

Hardy and Associates. 1986. Ecological land classification of Elk Island National Park. Parks Canada. Hardy Associates (1978) Ltd., Calgary, Alberta.

Harniss R.O. and R.B. Murray. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. Journal of Range Management 26: 322-325.

Hausenbuiller R.L. 1985. Soil Science Principles and Practices. 3rd ed., William C. Brown Publishers, Dubuque, Iowa. 610 pp.

Hill M.O. 1973. Reciprocal averaging: An eigenvector method of ordination. Journal of Ecology 61: 237-249.

Hill M.O. 1979. TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca, New York, 90 pp.

Hill M.O., R.G.H. Bunce and M.W. Shaw. 1975. Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. Journal of Ecology 63: 597-613.

Hill M.O. and H.G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47-58.

Holling C.S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systems 4: 1-23.

Holsworth W.N. 1960. Interactions between moose, elk, and bison in Elk Island National Park. M.Sc. Thesis, University of British Columbia, Vancouver, British Columbia. 92 pp.

Johnston A., S. Smoliak and P.W. Stringer. 1969. Viable seed populations in Alberta prairie topsoils. Canadian Journal of Plant Science 49: 75-82.

Johnston M. 1981. The effect of fire disturbance level on plant re-establishment in Elk Island National Park, Alberta. M.Sc. Thesis. University of Alberta, Edmonton, Alberta. 138 pp.

Jones J.R. and N.V. Debyle. 1985. Fire. chapter in: Aspen: ecology and management in the Western United States. edited by N.V. Debyle and R.P. Winokur. USDA Forest Service, General Technical Report RM-119, Fort Collins, Colorado, pp 77-81.

Jones R.K., G. Peirpoint, G.M. Wickware, and J.K. Jeglum. 1982. A classification and ordination of forest ecosystems in the great clay-belt of northeastern Ontario. In Proceedings from the: Resources and Dynamics of the Boreal Zone Conference, ed. by Wein et al., pp 83-96.

Jongman R.H.G., C.J.F. ter Braak and O.F.R. van Tongeren. 1987. Data Analysis in Community and Landscape Ecology. Center for Agricultural Publishing and Documentation, Pudoc, Wageningen, 299 pp.

Kabzems A., A.L. Kosowan and W.C. Harris. 1986. Mixedwood section in an ecological perspective. Saskatchewan Parks and Renewable Resources, Forestry Canada.

Krebs C.J. 1972. Ecology. Harper and Row, New York, 694 pp.

Kjorlien M. 1977. A review of historical information of fire history and vegetation description of Elk Island and the Beaver Hills. Resource Conservation, Elk Island National Park, Parks Canada, 30 pp.

Komarek E.V. 1962. Fire ecology. chapter in: Proceedings of First Annual Tall Timbers Fire Ecology Conference, Florida State University, Tall Timbers Research Station, Tallahassee, Florida, pp 95-107.

Laycock W.A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. Journal of Range Management 44(5): 427-433.

Leiffers V.J. and K. Stadt. 1993. Growth of understory Picea glauca, Calamagrostis canadensis, and Epilobium angustifolium in relation to overstory light transmission. Paper submitted to the Canadian Journal of Forest Research.

Looman J. 1983. 111 Range and Forage Plants of the Canadian Prairies. Research Branch, Canada Agriculture, Publication 1951. 255 pp.

Lotan J.E., M.E. Alexander, S.F. Arno, R.E. French, O.G. Langdon, R.M. Loomis, R.A. Norum, R.C. Rothermel, W.C. Schmidt, and J.W. van Wagtendonk. 1981. Effects of fire on flora. USDA Forest Service, Washington, DC. General Technical Report WO-16. 71 pp.

Lyon L.J. and P.F. Stickney. 1976. Early vegetal succession following large Northern Rocky Mountain wildfires. In: Proceedings of the Tall Timbers Fire Ecology Conference No.14, Missoula, Montana, Oct. 8-10, 1974, Missoula, Montana.

Macyk T.M., S. Pawluk and J.D. Lindsay. 1978. Relief and microclimate as related to soil properties. Canadian Journal of Soil Science 58: 421-438.

Maini J.S. and K.W. Horton. 1966. Vegetative propagation of Populus spp. I. Influence of temperature on formation and initial growth of aspen suckers. Canadian Journal of Botany 44: 1183-1189.

McIntosh R.P. 1978. Phytosociology. Dowden, Hutchinson, and Ross Inc., Stroudsberg, Pensylvania, 388 pp.

Milchunas D.G., W.K. Laurenroth, 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.

Milner B.J. 1977. Vegetation analysis of ungulate range exclosures, Elk Island National Park. Canadian Wildlife Service Report. 95 pp.

Minchin P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 67: 1167-1179.

Morgan R.G. 1980. Bison movement patterns on the Canadian plains: an ecological analysis. Plains Anthropologist 25: 143-159.

Moss E.H. 1932. The vegetation of Alberta. IV.The poplar association and related vegetation of central Alberta. Journal of Ecology 20: 380-415.

Moss E.H. 1983. Flora of Alberta. 2nd ed. Revised by J.G. Packer, University of Toronto Press, Toronto, Ontario. 687 pp.

Mueggler W.F. 1965. Cattle distribution on steep slopes. Journal of Range Management 18: 255-257.

Mueggler W.F. and R.B. Campbell. 1982. Aspen community types on the Caribou and Targhee National Forests in southeastern Idaho. USDA Forest Service, Research Paper INT-294. 32 pp.

Mueggler W.F. 1985. Forage. chapter in: Aspen: ecology and management in the Western United States. edited by N.V. Debyle and R.P. Winokur. USDA Forest Service, General Technical Report RM-119, Fort Collins, Colorado, pp 129-134.

Mueggler W.F. 1988. Aspen community types of the intermountain region. USDA Forest Service, Intermountain Research Station. INT-250. 135 pp.

Mueller-Dombois D. and H. Ellenburg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York, 547 pp.

Naeth M.A., D.J. Pluth, D.S. Chanasyk, A.W. Bailey, and A.W. Fedkenheuer. 1990. Soil compacting impacts of grazing in mixed prairie and fescue grassland ecosystems of Alberta. Canadian Journal of Soil Science 70: 157-167.

Naeth M.A., A.W. Bailey, D.S. Chanasyk, and D.J. Pluth. 1991a. Water holding capacity of litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. Journal of Range Management 44(1): 13-17.

Naeth M.A., A.W. Bailey, D.J. Pluth, D.S. Chanasyk, and R.T. Hardin. 1991b. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. Journal of Range Management 44(1): 7-12.

Nelson J.G. and R.E. England. 1971. Some comments on the causes and effects of fire in the northern grasslands area of Canada and the nearby United States, C.A. 1750- 1900. Canadian Geographical Journal 4: 295-306.

Nicholson B. 1993. The wetlands of Elk Island National Park. Ph.D. Thesis, University of Alberta, Edmonton, Alberta, 166 pp.

Nietfield M.T. 1983. Foraging behavior of wapiti in the boreal mixed-wood forest, central Alberta. M.Sc. thesis, University of Alberta , Edmonton, Alberta, 187 pp.

Noste N.V. and C.L. Bushey. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. USDA, Intermountain Research Station, INT-239, 22 pp.

Noy-Meir I. and B.H. Walker. 1986. Stability and resilience in rangelands. In: Proceedings of the Second Rangeland Congress Report, Dynamics of Range Ecosystems, pp 21-25.

O'Connor T.G. 1991. Local extinction in perennial grasslands: a life-history approach. The American Naturalist 137(6): 753-773.

Oldemeyer J.L., A.W. Franzmann, A.L. Brundage, P.D. Arneson, and A. Flynn. 1977. Browse quality and the Kenai moose population. Journal of Wildlife Management 41: 533-542.

Olson W. and C. Blyth. 1986. Browse survey - herd recommendations report. Elk Island National Park, Parks Canada, Resource Conservation. 131 pp.

Ohmann L.F. and D.F. Grigal. 1979. Early revegetation and nutrient dynamics following the 1971 Little Sioux forest fire in northeastern Minnesota. Forest Science Monograph No. 21. 80 pp.

Parks Canada. 1992. Elk Island National Park climate data analysis. Unpublished decade reports. Elk Island National Park, Alberta.

Perala D.A. 1974. Prescribed burning in an aspen-mixed hardwood forest. Canadian Journal of Forest Research 4: 222-228.

Peterson E.B. and N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada, Northwest Region, Special Report 1. 252 pp.

Pettapiece W.W. 1969. The forest-grassland transition. In: Pauluk S. (ed.). Pedology and Quaternary Research. Symposium May 14. Edmonton. pp 102-113.

Polster D.F. and L.E. Watson. 1979. Vegetation classification and evaluation - Elk Island National Park. Techman Ltd. for Parks Canada. 134 pp.

Pritchett W.L. 1979. Properties and Management of Forest Soils. John Wiley and Sons, Toronto, Ontario. 500 pp.

Quinn J.F. and G.R. Robinson 1987. The effects of experimental subdivision on flowering plant diversity in a California grassland. Journal of Ecology 75: 837-856.

Quintilio D., M.E. Alexander and R.L. Ponto. 1991. Spring fires in a semimature trembling aspen stand in central Alberta. Forestry Canada, Information Report NOR-X-323, 30 pp.

Renecker L.A. and R.J. Hudson. 1988. Seasonal quality of forages used by moose in the aspen dominated boreal forest, central Alberta. Holartic Ecology 11: 111-118.

Reynolds H.G. 1969. Aspen grove use by deer, elk, and cattle in southwestern conifer forests. USDA Forest Service, Research Note RM-138. 4 pp.

Rowe J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quaternary Research 3: 444-464.

Scheffler E.J. 1976. Aspen forest vegetation in a portion of the east central Alberta parklands. M.Sc. Thesis, University of Alberta, Edmonton, Alberta, 160 pp.

Schier G.A. 1976. Physiological and environmental factors controlling vegetative regeneration of aspen. in: Utilization and marketing as tools for aspen management in the Rocky Mountains. Proceedings of Symposium. USDA Forest Service, General Technical Report RM-29, pp 20-23.

Shaw J.H. 1985. Introduction to Wildlife Management. McGraw Hill Book Co., New York, 316 pp.

Stickney P.F. 1986. First decade plant succession following the Sundance Forest Fire, Northern Idaho. USDA Forest Service, Intermountain Research Station, General Technical Report INT-197. 26 pp.

Stoddart L.A., A.D. Smith and T.W. Box. 1975. Range Management. 3rd ed., McGraw Hill Book Co., New York, 532 pp.

Spurr S.H. and B.V. Barnes. 1980. Forest Ecology. 3rd ed., John Wiley and Sons, New York, 687 pp.

Steel R.G. and J.H. Torrie. 1980. Principles and Procedures of Statistics: A Biometrical Approach. 2nd ed., McGraw-Hill Publishing Co., Toronto, Ontario, 633 pp.

Strong W.L. 1992. Ecoregions and ecodistricts of Alberta. vol.1, Alberta Forestry, Lands, and Wildlife, Edmonton Alberta, 77 pp. + maps.

Strong W.L. and K.R. Leggat. 1981. Ecoregions of Alberta. Alberta Energy and Natural Resources, Edmonton Alberta, 64 pp. + maps.

Telfer E.S. 1978. Cervid distribution, browse, and snow cover in Alberta. Journal of Wildlife Management 42(2): 352-361.

Telfer, E.S. and A. Cairns. 1978. Stem breakage by moose. Journal of Wildlife Management 42: 639-642.

ter Braak, C.J.F. 1992. CANOCO - a FORTRAN program for canonical community ordination. Microcomputer Power, Ithaca, New York. 95 pp.

ter Braak C.J.F. and I.C. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research 18: 271-317.

Thomas G. 1977. Fire in the Beaver Hills. Research Bulletin No.45 National Historic Parks and Site Branch 12 pp.

Vallentine J.F. 1980. Range Development and Improvements. 2nd ed., Brigham Young University Press., Provo, Utah, 545 pp.

Van Wagner C.E. 1973. Height of crown scorch in forest fires. Canadian Journal of Forest Research 3: 373-378.

Van Wagner C.E. 1990. Six decades of forest fire science in Canada. Forestry Chronicles 66: 133-137.

Van Wagner C.E. and I.R. Methven. 1980. Fire in the management of Canada's national parks: philosophy and strategy. National Parks Occasional Paper No. 1. Ottawa, Ontario. 18 pp.

Vance R.E. 1979. Late Holocene paleoecology of the aspen parkland region of western Canada. M.Sc. Thesis. University of Alberta. Dept. of Anthropology, Edmonton, Alberta. 113 pp.

Waser N.M. and M.V. Price. 1981. Effects of grazing on diversity of annual plants in the Sonoran Desert. Oecologia 50: 407-411.

Weatherill R.G. and L.B. Keith. 1969. The effect of livestock grazing on an aspen forest community. Department of Lands and Forests, Fish and Wildlife Division, Ottawa, Technical Bulletin 1. 31 pp.

Wein R.W. and M.A. El-Bayoumi. 1982. Limitations to predictability of plant succession in northern ecosystems. In: Proceedings of Resources and Dynamics of the Boreal Zone. pp 214-225.

West N.E. 1993. Biodiversity of rangelands. Journal of Range Management 46(1): pp 2-13.

Westoby M., B. Walker and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42(4): 266-274.

Whittaker R.H. 1962. Classification of natural communities. Botanical Review 28: 1-239.

Whittaker R.H. 1973. Ordination and Classification of Communities. Dr. W. Junk b.v., the Hague. 737 pp.

Whittaker R.H. 1978. Classification of Plant Communities. Dr. W. Junk b.v., the Hague. 408 pp.

Willoughby M. 1986. The forage growth cycle and range communities of the Poplar Lake range unit, northcentral British Columbia. M.Sc. Thesis, Dept. of Plant Science, University of Alberta, 179 pp.

Willoughby M. 1992. Species diversity and how it is affected by livestock grazing in Alberta. Pub. T/207, No. 13, 3 pp.

Willoughby M. 1993a. Carrying capacity guide for deciduous forests in the green area. 2nd Approximation. Unpublished report. Alberta Forestry, Lands, and Wildlife, Forest Service, 63 pp.

Willoughby M. 1993b. Rangeland reference areas: plant communities, ecology, and response to grazing in division 2. First Approximation, Alberta Forestry, Lands, and Wildlife, Forest Service, Pub. T/268, 42 pp.

Wilson S.D. 1989. The suppression of native prairie by alien species introduced for revegetation. Landscape and Urban Planning 17: 113-119.

Wilson S.D. and P.A. Keddy. 1988. Species richness, survivorship, and biomass accumulation along an environmental gradient. Oikos 53: 375-380.

Wilson S.D. and J.M. Shay. 1990. Competition , fire, and nutrients in a mixed-grass prairie. Ecology 71(5): 1959-1967.

Wilson S.D. and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72(3): 1050-1065.

Wright H.A. 1974. Range burning. Journal of Range Management 27: 5-11.

Wright H.A. and A.W. Bailey. 1982. Fire Ecology: United States and Southern Canada. John Wiley and Sons, Toronto Ontario. 501 pp.

Wroe R.A. 1971. Synecology of a Festuca scabrella (Torr.) grasssland. M.Sc. Thesis, University of Alberta, 126 pp.

8. APPENDICES

Appendix I: Review of environmental and vegetative data collected.

Environmental Data:	Data Type:	Units:
Level of Herbivory	Nominal (classes)	High & Low
Burn Scorch Height	Continuous (cm/ tree)	Ave. / Transect
Topographic Position	Nominal (classes)	Toe, South, Crest, & North
Slope	Continuous	% / Transect (Ave. of 3)
Soil Type (Great Group)	Nominal (classes)	Orthic Gray Luvisol, Gleyed Gray Luvisol, & Orthic Humic Gleysol
Soil Organic Matter	Continuous	%
Soil pH	Continuous	pH
Soil Texture	Continuous	% Sand, Silt, & Clay
Thickness of Ah	Continuous	cm / Transect
Thickness of Ahe	Continuous	cm / Transect
Thickness of Ae	Continuous	cm / Transect

Vegetative Data :	Method of Data Collection:	Analysis Units:
Tree Density	Stem Counts / Macroplot	# Stems / Hectare
Basal Area (BA)	BA / Tree / Macroplot	Total BA (m^2) / Hectare
Overstory Canopy Cover	Line Intercept Transect (50 m)	% / Transect
Shrub Canopy Cover	Cover / Species / Mesoplots (1 x 1 m)	Ave. % / Transect
Herb Canopy Cover	Cover / Species / Microplots (40 x 50 cm)	Ave. % / Transect

Appendix I (continued): Review of environmental and vegetative data collected.

Vegetative Data :	Method of Data Collection:	Analysis Units:
Diversity Index	From Canopy Covers	Index / Transect
Species Richness	Total # of Species	Species / Transect
Shrub Density	Stem Counts / Microplot	# Stems / m^2
Shrub Height	Maximum Height / Microplot	Ave. Height (cm) / Transect
Current Annual Above Ground Production (Grass, Forb, Twig, & Leaf)	Production / 0.5 m^2 Clip Plot	Ave. Kg / Hectare (Dryweight)

Appendix II: Standard error of the mean's for EINP data.

Stand Factor:	Test Factor: Disturbance	Position	Disturbance x Position
Total Tree Density	149.2	172.3	298.4
Aspen Density	100.4	116.0	200.9
Balsam Density	48.1	55.5	96.1
Total Basal Area	3.10	3.56	6.17
Live Canopy Cover	4.77	5.51	9.54
Total Diversity Index	0.068	0.079	0.137
Invader Diversity Index	0.023	0.026	0.045
Species Richness	1.16	1.34	2.32
Total Shrub Density	0.830	0.959	1.661
Shrub Height Index	2.437	2.814	4.875
Grass Production	43.98	50.78	87.96
Forb Production	53.84	62.16	107.66
Leaf Production	96.24	111.14	192.50
Twig Production	25.94	29.96	51.88
Total Production	128.34	148.18	256.66

Appendix III: Two-way site by species table derived from the analysis of the Elk Island data using TWINSPAN.

```
                           Sample Site Number:

                223333  12122231332   1 11122   1121
Species:        840362486025671545313715379192690824

 6 LONI    INV  21-1-111-------------------11-------  000000
18 VIBU    EDU  41-131222122--1------------1--------  000000
52 LINN    BOR  11-------1--------------------------  000000
56 MITE    NUD  11-12311113--------------1-11-------  000000
 5 LONI    DIO  221121131111--11--1----211111-----1-  000001
12 RIBE    TRI  11111311311--1-1-------12-1-1-------  000001
35 CORN    CAN  331333332331--21--3--11-12122-----1-  000001
36 DISP    TRA  3111122222212211121---1--11---------  000001
60 PYRO    ASA  2232412112111-311-11-11111111--1----  000001
 2 CORN    STO  2-----12-1111-12--1-----11----------  000010
20 ACTA    RUB  --1-1-21112--1---2-1--111--1--------  000010
23 ALLI    CER  ---2------------1-------------------  000011
44 GALI    TRI  1111-1-----1-1---1------1---2-------  000011
54 MAIA    CAN  3121211112111-222221111121222-----1-  000011
61 PYRO    CHL  1-1211-----1--1----------1121-------  000011
86 ORYZ    ASP  -1121-----------231----11--1--------  000011
11 RIBE    LAC  11-2-221111---1--------123122--1----  00010
55 MERT    PAN  -11111-1-11--------1---112111--1----  00010
57 PETA    PAL  -3-11211-11-------------12-11--1----  00010
16 SHEP    CAN  -1-2-11212------211-----3-31------1-  00011
48 HERA    LAN  -122-11----1-1-----1-1-1--213--1--1-  00011
63 RUBU    PUB  4443443333332-32-2421224343321121-11  00011
 9 PRUN    PEN  3----------214------1---------------  00100
39 EQUI    ARV  -1-1-----1-3-----------1-1-23-------  00100
42 GALE    TET  --1---------11--------------3-------  00100
72 STEL    LON  --1--1-------11----------11-1-------  00100
 4 CRAT    ROT  ---------------33-------------------  001010
67 SMIL    STE  -----------1----1--1----------------  001010
31 CAST    MIN  --------------------------1---------  001011
46 HABE    HYP  -------------------------1----------  001011
58 PETA    SAG  ------------------------1-----------  001011
62 RANU    ACR  ------------------------1-----------  001011
65 SCUT    GAL  ----------------------------2-------  001011
66 SENE    TRI  ------------------------1-----------  001011
76 URTI    DIO  ----------------------------2-------  001011
53 LYSI    CIL  ---1------------13-312-4------1-----  0011
88 POA    PALU  -----11-------11----2---2---1----1--  0011
92 COV    MOSS  3332332312211111121----112114---13-2  0100
```

Appendix III (continued):

3	CORY	COR	55555555555523555553445132514332454-	010100
8	POPU	TRE	21333331111131211222131211113121112-	010100
27	ARAL	NUD	34434445343225443453554-44454141-25-	010100
37	EPIL	ANG	------222-211--1---2-13132----12----	010100
50	LATH	OCH	12323234234121412233333422222242122-	010100
7	POPU	BAL	---11---1--1----------1-11-11--1-1--	010101
13	ROSA	SPP	123434334344454455333444434233443222	010101
14	RUBU	IDA	255534434555555543454453334354443431	010101
17	SYMP	OCC	222222323323344443411224233423444421	010101
28	ASTE	CIL	13132233232222132334242432332324344-	010101
51	LATH	VEN	-122--3-42-1453433444-22-11133-44-21	010101
64	SANI	MAR	-1221111-11211112113122323231123--2-	010101
77	VICI	AME	1222222422321-3113233444222133342131	010101
84	CALA	CAN	12341432435122231345555455533555443-	010101
1	AMEL	ALN	212431212122342243211232112132223111	01011
10	PRUN	VIR	1113211111122431321111-2111-12123-11	01011
29	ASTE	CON	2----132224425222-322321--11-32--11-	01011
34	CERA	ARV	----------11---1-11-------------1---	01011
15	SALI	SPP	------1----1---12--1---11-111-11----	011
21	AGAS	FOE	-----------221--23-11112-1-2-2111-1-	011
26	APOC	AND	1---1-11-114432321-2133--121-11-1-11	011
71	STAC	PAL	-----2-----111--11-1211111--11111---	011
79	VIOL	CAN	1-1-1-11-11-1-1-2-11-111--111312-11-	1000
41	FRAG	VIR	-11112112212211122231-112122313221221	1001
43	GALI	BOR	-12212322211222322222233122222333212	1001
68	SOLI	CAN	--1--2----3323-41324343445343455424-	100110
82	BROM	CIL	----1----2-11---1-1------1121--131--	100110
74	THAL	VEN	-122--11--2---1-21-23133111222332-1-	100111
80	AGRO	TRA	-3-1--11---11--1-121--1-1221-21--22-	100111
90	SCHI	PUR	-1-11-1-11------1111-1-21-22-21--12-	100111
22	AGRI	STR	------1----1----1-11---212-33111-22-	10100
33	CIRS	FLO	---------------------------1------1-	10100
47	HALE	DEF	--------------------------1------1--	10100
38	EPIL	CIL	-----------------------1------1-----	10101
45	GEUM	ALL	---1------------1------111-1-1-1-1--	10101
70	SONC	ARV	--------------------1--------1------	10101
85	CARE	SPP	--32-11----121--1--221222-1221214214	1011
49	HEIR	UMB	---------1---------1-------1--1--1-1	110
73	TARA	OFF	1--1-11-11-1---131111-1-121212113441	110
89	POA	PRAT	-1-1-----21----3211213242143-5555555	110
91	BARE	SOI	--------------------2-111----2214134	111000
19	ACHI	MIL	----------------1--------111-21-1212	111001
40	ERIG	GLA	---------------------------------2-3	111001
69	SOLI	MIS	-----------------------------------1	111001
78	VIOL	ADU	---------------------------------1-1	111001
87	PHLE	PRA	----------------1-------3-------2123	111001

Appendix III (continued):

```
25 ANTE  PAR  ---------------------------------1--  11101
59 PLAN  MAJ  ------------------------1-----1--211  11101
75 TRIF  REP  -1----------------1--1--1-12--1-2542  11101
81 AGRO  SCA  ---------------------------------1--  11101
24 ANEM  CAN  --------------1-----------1-112-2-1-  1111
30 ASTE  LAE  -----------------------------111----  1111
32 CIRS  ARV  -----------1-------------------11---  1111
83 BROM  INE  ---------------1-------------1-----1  1111

              000000000000000000000000000001111111
              000000000001111111111111111110000001
              00000111111000000011111111111000011
              01111011111000011100000011111
                    00001       00000100001
                                01111
```

Appendix IV: Conceptual soil profile descriptions for Elk Island study.

A. Orthic Gray Luvisol:

Horizon:	Thickness Range:	Comments:
LFH	2 - 9 cm	Scattered charcoal deposits.
Ah	0 - 6 cm	Variable in thickness, granular structure. Color: 10YR 1/1 to 3/2 (moist).
Ahe	2 - 12 cm	Salt & pepper or variable gray appearance. Color: 10YR 2/1 to 4/3 (moist).
Ae	7 - 20 cm	Fine blocky to platy, ashy, friable. Color: 10YR 3/2 to 5/4 (moist) and 10YR 8/1 to 6/3 (dry). May be a few fine mottles: 2.5Y 5/4.
AB	2 - 5 cm	Transitional horizon.
Bt		Prismatic macrostructure, medium to coarse blocky microstructure. Prominent darker colored clay skins. Color: 10YR 3/2 to 4/4 (moist). May be fine mottles: 10YR 4/6 to 5/6.

B. Gleyed Gray Luvisol:

Horizon:	Thickness Range:	Comments:
LFH	5 - 9 cm	Scattered charcoal deposits.
Ah	0 - 4 cm	Variable thickness, irregular border. Color: 10YR 1/1 to 2/2 (moist).
Ahe	3 - 8 cm	Variable border, patchy appearance. Color: 10YR 3/2 to 3/3 (moist).
Ae(g)	10 - 18 cm	Fine platy, silty/ashy when dry. Color: 10YR 3/2 to 5/3 (moist) and 10YR 8/1 to 7/2 (dry). May be mottles: 10YR 4/6 (One soil with a perched water table).
AB	2 - 6 cm	Transitional horizon.
Btgj		Prismatic macrostructure, medium to coarse blocky microstructure. Medium to very thick clay skins. Matrix Color: 10YR 4/2 to 5/3 (moist). Partial gleying evident. Mottle Color: 10YR 4/6 to 5/8 (moist).

Appendix IV (continued):

C. Luvic Gleysol:

Horizon:	Thickness Range:	Comments:
LFH	6 - 14 cm	Scattered charcoal deposits.
Ah	0 - 5 cm	Variable thickness. Color: 10YR 1/1 (moist).
Ahe(g)	6 - 15 cm	Fine blocky to platy, few mottles. Color: 10YR 2/1 to 3/4 (moist); 10YR 4/2 (dry). Mottle Color: 10YR 5/8 to 6/8 (moist).
Ae(g)	8 - 20 cm	Fine to coarse platy, ashy appearance. Color: 10YR 2/1 to 5/3 (moist) and 10YR 7/1 to 4/2 (dry). Mottle Color: 10YR 5/6 to 5/8.
AB(g)	2 - 6 cm	Transitional horizon.
Btg		Prominent gleying conditions and mottling, medium to coarse blocky structure, thick clay skins evident. Matrix Color: 10YR 3/2 to 5/2 (moist). Mottle Color: 10YR 4/6 to 5/8 (moist).

Appendix V: Soil horizon thicknesses, soil pH, and organic matter by disturbance and position.

	Horizon Thickness (cm):				Organic Matter:
	Ah	Ahe	Ae	pH	(%)
Disturbance:	P=0.189	P=0.159	P=0.259	P=0.406	P=0.021
Burned	2.33 a	5.58 a	13.83 a	5.86 a	5.56 a
Unburned	0.92 a	4.83 a	11.75 a	6.14 a	3.67 b
Control	2.08 a	7.25 a	13.33 a	6.22 a	6.41 a
Position:	P=0.167	P=0.070	P=0.188	P=0.015	P=0.035
Toe	2.89 a	7.56 a	14.78 a	6.36 a	5.77 a
South	1.78 a b	7.22 a	11.22 a	6.30 a b	5.99 a
Crest	1.33 a b	4.78 a b	11.89 a	5.73 c	5.02 a b
North	1.11 b	4.00 b	14.0 a	5.89 b c	4.08 b
Dist. x Position:	P=0.689	P=0.388	P=0.963	P=0.866	P=0.324
Toe x Burned	3.0 a	5.3 b	16.0 a	6.04 a	5.53 b
Toe x Unburned	3.0 a	6.0 a b	14.3 a	6.31 a	3.58 b
Toe x Control	2.7 a	11.3 a	14.0 a	6.73 a	8.21 a
South x Burned	2.7 a	7.0 a	11.3 a	6.15 a	7.02 a
South x Unburned	0 a	5.0 a	10.3 a	6.35 a	4.91 a
South x Control	2.7 a	9.7 a	12.0 a	6.39 a	6.03 a
Crest x Burned	1.3 a	5.0 a	13.3 a	5.48 a	5.61 a
Crest x Unburned	0.7 a	4.3 a	10.7 a	5.80 a	3.25 b
Crest x Control	2.0 a	5.0 a	11.7 a	5.90 a	6.20 a
North x Burned	2.3 a	5.0 a	14.7 a	5.75 a	4.08 a
North x Unburned	0 a	4.0 a	11.7 a	6.09 a	2.94 a
North x Control	1.0 a	3.0 a	15.7 a	5.83 a	5.22 a

Means represented by the same letter are not significantly different at P=0.05 using the Least Significant Difference test.

Interaction comparisons are between disturbances and within positions.