Historic Range of Variability for Aspen in the Sierra Nevada and South Cascades

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1 Introduction

1.1 Physical setting

1.1.1 Geographic distribution

Aspen (*Populus tremuloides*) is one of the most widespread broadleaf species in North America (DeByle 1990, Potter 1998). It can be found throughout the assessment area in the Sierra Nevada and the Southern Cascades in addition to the Modoc Plateau, occurring both east and west of the crest (Fig. 1). In the Sierra Nevada, aspen is found in stands from the Kern Plateau on the Sequoia National Forest north to the Lassen National Forest. Here aspen occurs from 1,618 m to 2,682 m at the crest of the Sierra Nevada and drops to 1,719 m as it grades into the Great Basin (Shepperd et al. 2006). The largest stringer of pure aspen occurs along Hwy 395 around Conway Summit just north of Mono Lake on the eastside of the crest. In the Southern Cascades, aspen can be found ranging from 1,676 m to 2,438 m on the western slope and1,828 m on the eastern slope (Shepperd et al. 2006). On the Modoc Plateau aspen is abundant in the Warner Mountains and surrounding higher elevations.

1.1.2 Climate

Climate throughout the assessment area is characterized by warm, dry summers and cool, wet winters typical of a Mediterranean climate. Within the assessment area differences exist between the climate on the East and the West sides of the Sierra Nevada and along the North to South transition. Precipitation on the eastern slope is less than precipitation received on the west slope. In addition, precipitation varies on a South/North gradient with precipitation increasing as one moves north through the assessment area. Typically, the mixed conifer forests on the west slope can receive 76 -152 cm of rainfall with the highest elevations receiving up to 254 cm. Local topography can alter the temperature and precipitation in the assessment area. Average temperatures in this area ranges from 42 – 62 °F (Shepperd et al. 2006). The Modoc Plateau is considerably drier than the rest of the assessment area with precipitation less than half of what falls in the Southern Cascades and the Sierra Nevada. Snowfall in the assessment area is approximately 60% of precipitation while the Modoc Plateau only receives 30% (Shepperd et al. 2006). Temperatures are also slightly warmer on the Modoc Plateau than the rest of the assessment area.

1.1.3 Geology and glaciation

The modern geology within the assessment area was a product of the collisions of tectonic plates over the last 200 million years. During this time granite intrusions of Jurassic and Cretaceous (70-180 million years YBP) and volcanic extrusions that originated in the Tertiary Period (26-66 million YBP) were common and now can be found throughout the range (Shepperd et al. 2006) Aspen that is found growing in these locations are usually free from competition from adjacent community types. Glaciation was also common during the Quaternary (1,000 – 1.5 million YBP) with seven glacial periods occurring during the Pleistocene and one during the Holocene (Little Ice Age). The landscape that is left after glacial retreat would have met all of the criteria for aspen germination and establishment (Baker 1918, Barnes 1975). It has been hypothesized that most of the existing clones were introduced at the end of the last glacial period (10,000 YBP) and no new genetic varieties have been introduced since then (Jones and DeByle 1985).

1.2 Ecological setting

Aspen stands cover less than 1% of the assessment area, but provide important ecological functions and support a high diversity of plants and animals (Rogers et al. 2007) (Fig. 1, Table 2). The aspen vegetation type throughout the Sierra Nevada ecoregion is dominated by the shade intolerant pioneer species quaking aspen tree at mid to upper montane elevation zones within the greater matrix of the mixed conifer and red fir (*Abies magnifica*) forests.

Several adaptations have allowed aspen to maintain a large current geographic distribution and persist for long periods of time. Aspen has a high stress tolerance with the ability to occupy environmental conditions that most trees cannot. Aspen is a pioneer species that readily seeded in following the retreat of the glaciers (Barnes 1975). Aspen also have the ability to regenerate either through sexual (seeding) or reproduction asexual (vegetation) with the latter allowing for the inheritance of extensive root systems that allow a greater tolerance to climate stress (DesRochers and Lieffers 2001). The leaves of aspen are also highly adaptable becoming smaller under conditions xeric thereby reducing water stress. Leaves can also flutter which cools them more efficiently than other hardwoods. Aspen also have a higher photosynthetic rate as they are able to photosynthesize in low light and through their bark. This “live” bark allows trees to recover quicker from injuries and insects and allows them to photosynthesize during the winter (Shepperd et al. 2006).

Aspen can occupy any topographic position and aspect, but are usually more vigorous on those with a high solar radiation index (Potter 1998) (Table 1). Aspen can be found in areas where precipitation exceeds evapotranspiration and temperatures are relatively cool, however extensive stands on the eastside of the assessment area may not track with moisture conditions. These areas have deep soils with a high water holding capacity. The soil is also high in pH because of the more basic soil reactions typical of hardwood species (Potter 1998). Compared to adjacent conifer dominated stands aspen soils are higher in organic matter, decomposition rates, nitrogen and a lower C:N ratio (Bartos and DeByle 1981). As conifer encroachment increases the soil components also change which results in soils becoming more acidic and eventually unfavorable for aspen growth (Potter 1998).

Aspen stand types can be early seral and successional to conifers or exist in a stable state. The aspen stands that are stable usually occur in landscapes where conifers are unable to attain dominance. In addition, aspen vegetation differs as to its reliance on disturbance, primarily fire, to initiate the next age class (Shinneman et al. 2013). One classification scheme developed by (Shepperd et al. 2006) separates aspen stands into those that are reliant on riparian areas or watercourses and dry meadow fringes both of which are seral to conifers (Table 1). Other aspen types are often not closely associated with water such as upland aspen that are seral to conifers, but at a slower rate (Table 1). Other upland sites are considered stable state because they occur on areas that conifers would typically not be able to encroach into (tallus, moraines, upper topographic positions or ridgelines) (Table 1). A classification of aspen in montane habitats was completed by Potter (1998) identifying two main aspen classes – aspen/pennyroyal and aspen/

California corn lily. The aspen/pennyroyal class are particularly small (< 2 hectares) in size occurring on middle and lower slopes with some stands found in upland settings. These stands have a very diverse understory and are tracking on a successional pathway to replacement is larger in size but still less than 4 hectares. Typically, these stands are found at lower elevations on the lower slope positions and are associated with riparian or meadow areas. Understory diversity is high and the stands will naturally succeed to conifers in the absence of disturbance or the continued pressure from grazing.

The aspen vegetation type has been described as an oases of plant and animal diversity in the matrix of conifer forest types (Shepperd et al. 2006). According to a study by (Kuhn et al. 2011) aspen stands are more diverse than meadows and adjacent conifer stands harboring a number of unique species (Table 2). Not only is plant diversity high, but aspen also supports a wide array of wildlife, particularly birds and invertebrates. A number of focal bird species (ground nesters and cavity dwellers) are common to the aspen vegetation type (Table 2). Heath and Ballard (2003) and Matson (2000) identified the warbling vireo (*Vireo gilvus*) and the Orange-crowned warbler (*Vermivora celata*) as indicator species in the Sierra Nevada. Reduction in aspen extent as identified in the NRV section may be indicative of similar declines observed in both of these bird species in the assessment area. One explanation of the observed declines in plant and bird diversity is the increase in conifer cover (Richardson and Heath 2004, Kuhn et al. 2011). As conifer cover increases, studies have noted that bird and plant species richness declines (Richardson and Heath 2004). This would have large implications for the plants and wildlife in aspen stands if conifer cover increases to a point that it places increased pressure on these dependent species.

1.3 Cultural and socioeconomic setting

The association of aspen with water has attracted humans from the time of their initial presence in the assessment area. During pre and post European settlement, Native Americans and Europeans shaped the aspen forest type directly by use and indirectly by altering disturbance patterns. In addition, Europeans used the aspen vegetation type and adjacent meadows and riparian areas as prime grazing for sheep and livestock (Fig. 2). This common practice continues to occur in existing conditions placing additional pressure on an already stressed vegetation type.

1.3.1 Pre-Settlement (prior to 1849)

Before Native American migration to the assessment area the region was largely influenced by a combination of natural processes and climate change which is described in detail in the section on the natural range of variation of aspen composition. Humans have lived in the assessment area for the past 10,000 years (Anderson and Moratto 1996). During this time, the population of the Native Americans ranged from 90,000 to 100,000 (Parker 2002). These population numbers varied throughout time resulting in variable influence on land and resource use.

The majority of the Native Americans were organized into major settlements that were located on the West slope of the assessment area at lower elevations (Parker 2002). Some authors suggest that the permanent settlements would have been heavily influenced by their inhabitants (Shepperd et al. 2006). In the summer months the permanent camps were abandoned for higher elevations where the indigenous people would have located adjacent to water which most likely would have included some percentage of aspen stands (Anderson and Moratto 1996).

Native Americans in the assessment area modified landscapes to promote hunting, fishing and gathering as well as to provide protection and cultivation of native plants. These practices were sustained though different management that included burning, irrigation, pruning, harvesting, sowing and weeding (Anderson and Moratto 1996). Presently, there are still a number of plants that are unique to the aspen and riparian vegetation types that remain important to Native Americans.

Although the majority of these practices occurred in areas where aspen was not common, the burning practices that the Native Americans employed most likely impacted the adjacent aspen vegetation types. Native Americans burned for a number of reasons such as to remove brush and young trees, maintain patches of edible species and improve forage for wildlife (Anderson and Moratto 1996). It is largely unknown how the Native American burning practices modified the Sierra Nevada ecosystems (Skinner and Chang 1996). Physical evidence of burning by Native Americans is generally rare, particularly in the aspen vegetation type where it is difficult to establish an accurate fire history because aspen trees tend to burn at intensities that consume the entire tree (Skinner and Chang 1996, Parker 2002). In one study of Woski Pond in Yosemite Valley, Anderson (1991) was able to link a spike in charcoal accumulation, an indicator of fire occurrence, with the arrival of the Miwok culture around AD 1300; however they were not able to ascertain whether the source of ignition was human-related or lightning caused. Taylor and Beaty (2005) attributed 90 percent of ignitions from 1650 to 1850 to climatic variations (late summer weather and dry conditions during La Nina) in a study of pre-settlement fires in the Lake Tahoe basin. Although some changes were likely, it is assumed that these were within the natural range of variation of the aspen vegetation type fire regime resulting in negligible effects (Parker 2002).

1.3.2 European-American Settlement (after 1859)

Euro-Americans began to appear in the assessment area at the end of the pre-settlement period (1780 – 1850) as exploration began (Fig. 2). At this time, European influence on the landscape was minimal. However, initial contact between Native Americans and Europeans decreased their population as the result of disease and confrontation. This decrease in number would have been reflected in altered human disturbance processes. By 1850 the supposed impacts Native Americans had on vegetation was erased as their populations plummeted and their permanent settlements became isolated (Shepperd et al. 2006).

European influence on the aspen vegetation type began in the mid-19th century with the Gold Rush. This time period brought intensive and abusive extraction of natural resources and water diversion. This most likely changed the hydrologic regime of water dependent vegetation types and impacted the roots of aspen that were washed away or buried under sediment (Shepperd et al. 2006). Fortunately, sedimentation from hydrologic mining limited irrigation supply to valley farmers and was eventually stopped.

Timber extraction was another local and widespread activity throughout the 19th century. It had severe impacts on the landscape as whole hillsides were left void of all vegetation. A study by

Kim and Rejmankova (2001) showed that a distinct decrease in pollen during the late 19th century and increased sedimentation in the Lake Tahoe basin (Central subregion) coincided directly with the time period of heavy timber removal. Although timber extraction and mining were widespread, there effects on the aspen vegetation was negligible and mostly a result of indirect consequences.

Grazing throughout the assessment area directly impacted aspen stands and most likely altered their successional pathways. In the early 1860s, an era of intensive grazing throughout the assessment area began (Leiberg 1902) (Fig. 2). During this time period, sheep were allowed to graze without any restrictions and often numbered in the millions. The Basque sheepherders which were common during this time monitored their herds at high elevations. In the aspen stands they left behind arborglyphs or carvings in the trees which are now considered an important cultural resource. Domestic livestock most likely caused direct impacts to aspen through trampling and foraging, but the widespread practice of burning the pastures to improve forage was more far reaching (McKelvey et al. 1996). Unlike the Native Americans, the sheepherders were not selective about what they burned rather setting fire to all mesic landscapes and burning to consume large downed fuels to reduce obstacles to sheep movement. John Muir in 1877 attributed almost 90 percent of fires during this time to sheep herders although some feel this is an overestimate (McKelvey et al. 1996). What is clear is that the patterns of burning differed from the natural and native American fire regimes, differentially affecting dominant vegetation types.

There are mixed accounts on how this influenced aspen stand growth and vigor. Many accounts have recognized the ability of aspen to thrive in an environment dominated by frequent fire (Brown and DeByle 1989, Skinner and Chang 1996). Some have even hypothesized that aspen quite probably expanded during the end of the Little Ice Age which corresponded with an increase in human caused disturbance (Rogers et al. 2007). The potential residual effects from timber extraction and frequent fire were 1) a decrease in conifer competition 2) increase in disturbance initiated suckering and 3) creation of newly created forest openings (Shepperd et al. 2006).

Contemporary patterns of aspen forests were initially influenced at the beginning of the 20th century by the decrease in intensive grazing and implementation of fire suppression policies. Both cattle and sheep (Fig. 2) were regularly grazed throughout the aspen and adjacent vegetation types (e.g., meadows, riparian, red fir, mixed conifer) at the beginning of the 20th century. Grazing remained unregulated until the 1920s, when regulations helped bring livestock numbers within reasonable bounds (Kosco and Bartolome 1981). Current management practices have drastically reduced the number of allotments and stocking rates on Forest Service lands. In addition, fire suppression policies ended burning in and around aspen having continued to impact the existing stands today.

2 Methodology

Types of information used to reconstruct the time period prior to the 1800s, primarily the early and mid- Holocene epoch extent of aspen throughout the assessment area include records from pollen and macrofossils extracted from lake cores and macrofossils from pack rat middens. Only select variables were interpretable from this data, namely aspen extent and composition (Table

3). These long term records are important for determining climate-disturbance relationships and predicting response of existing vegetation types to future climate projections. Although these types of data provide a picture of the extent of the aspen vegetation type throughout the Holocene Epoch they are not without limitations. Important caveats to consider are the limited spatial extent of the lake and midden samples allowing only local conditions to be extrapolated. As a result, these may not be an accurate representation of the landscape scale (Romme et al. 2012).

There is continued difficulty determining an NRV for aspen due to limited historical information. Other variables (Table 3) were determined from historic accounts from the recent past (1880s – 1940s) including written accounts, cover type maps, and aerial photographs. In addition, conditions from current reference sites provide us with some indication as to the ecology of aspen under a more natural process regime. These data allow only interpretation to the most current period of the Holocene period namely the Anthropocene Epoch and provide a window into the potential shifts of aspen vegetation under the future projected climate.

Variables not assessed were not included in this discussion and may not be appropriate for determining trends in the range of variability.

3 The Natural Range of Variation and Comparison to Current Conditions

3.1 Function

The recession of the glaciers at the beginning of the Holocene created a niche for aspen to establish. Throughout the early to mid-Holocene essential disturbances such as fire, climate change and to a lesser extent landslides and avalanches maintained the function of the aspen (Table 4). In the late Holocene and current time, aspen function has been modified by more recent climate change, grazing and to a lesser extent insects and disease. However fire has been the most consistent influence on the extent and health of this vegetation type. The policy of fire suppression enacted in the past 120 years in combination with other biotic and abiotic factors have led to a notable decline in the aspen vegetation type.

3.1.1 Fire

There has been a large body of work that has been completed on the influence of fire on aspen in the Interior West (DeByle 1990, Rogers et al. 2007), but the fire regime in the aspen vegetation type that occupies California has not been well established. Additionally, very little work has been done trying to develop the natural range of variation of the function of fire within aspen.

3.1.1.1 NRV

Fire frequency in aspen is often difficult to determine as the aspen vegetation type is part of a highly complex matrix that ranges from low elevation mixed conifer zones with fire return intervals (FRI) ranging from 30 – 90 years and high elevation red fir zones with fire return intervals ranging from 50 -150 years (Shinneman et al. 2013). Van de Water and Safford (2011) conducted an extensive literature search and estimated that the mean FRI for the aspen vegetation type was 19 years with a range of 10 – 90 years. Additionally, Miller et al. (2001) conducted a fire history study in existing aspen stands in the Great Basin and found that a stand replacement disturbance occurred every 60 years with mixed replacement every 10-20 years. These estimates attempt to differentiate between the FRI on aspen sites that are located west and east of the crest. In addition, aspen can be either early seral or stable. Seral state aspen would have benefited from fires by decreasing competition from invading conifers and stimulating suckering. Stable state aspen would have been less tied to fire or other disturbances as competition from surrounding vegetation would have been less. Evidence has suggested these stands were capable of regenerating without any form of disturbance triggering a hormonal response (Shepperd et al. 2006, Shinneman et al. 2013). As a result, fire suppression has been more detrimental to seral state aspen (Shepperd et al. 2006, Pierce and Taylor 2010).

Aspen typically regenerate after stand replacing fire that opens up the canopy and triggers a hormonal response which stimulates sprouting. This would indicate that that the natural range of variation of fire severity would trend towards high. A review by (Shinneman et al. 2013) indicated that fire severity in the assessment area ranged from mixed to high severity. This information was only based on three studies, but further research in current fires verifies this conclusion. Fires conducted to achieve high severity effects reduced litter and increased the number of suckers as compared to low severity burns (Bartos 1979, Keyser et al. 2005). In addition, high severity fires are usually very effective at reducing invading conifers (Keyser et al. 2005).

3.1.1.2 Comparison to Current

Fire return intervals currently are different from the NRV established for the aspen vegetation type. Landscapes that are burning more frequently than they would have during pre-European settlement have a mean FRI of 6.3 years. Fire return intervals in areas burning 1.5 to 3 times less than the NRV have a mean FRI of 28.4 to 57.6 years (Safford and Van de Water In review) USA</title></titles><pages>In review.</pages><dates><year>In review</year></dates><pub-location>Albany, CA</pub-location><publisher>U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station</publisher><urls></urls></record></Cite></EndNote>. In addition, Safford and Van de Water (In review)USA</title></titles><pages>In review.</pages><dates><year>In review</year></dates><pub-location>Albany, CA</pub-location><publisher>U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station</publisher><urls></urls></record></Cite></EndNote> calculated the PFRID which is the percent difference between current fire frequencies and the frequencies that occurred prior to European settlement. The aspen vegetation type had a mean PFRID of 80 with a range of 7 to 89 percent. This index indicates that aspen is burning much less than this vegetation type would have done in a pre-European setting.

The fire perimeter dataset from 1904-2012 in the assessment area supports the above conclusion showing that fires that burned into the aspen vegetation type covered only 300 hectares which is about 5% of the extent of aspen (Fig. 3). The majority of hectares that did burn in a particular year were composed of many fires. For example, in 2001 there were 140 lightning ignited fires that burned into vegetation dominated by aspen had a mean of 2 hectares burned within each of the fires that had some effect on aspen. Overall, the aspen vegetation type is burning at a much lower frequency than would have been expected in the natural range of variation.

A decrease in fire occurrence in the aspen dominated vegetation as evidenced by the fire history records (Fig. 4) implies that fire severity is also departed from the natural range of variation (Ko 2001). Quantitative evidence throughout the past 150 years is lacking making a definitive determination difficult. However, considering the Regional Monitoring Trends in Burn Severity dataset from 1984 – 2012, only 24% of the aspen dominated landscape burned at severities that resulted in a > 50% change in canopy cover (Fig. 4). Of this only 10% burned at high severity consuming > 75% of the canopy (Fig. 4). Although fire is clearly occurring in the aspen vegetation type throughout the assessment area, only those that were of sufficient intensity would be beneficial. This intensity would have to be great enough to consume a substantial portion of the canopy to trigger a hormonal suckering response.

Shinneman et al. (2013) developed a framework based on the fire regimes of aspen types using the probability of fire occurrence and fire severity (Fig. 5). From this framework he identifies stable state and seral state aspen. Based on NRV and current conditions, the fire independent stable aspen types such as those in krummholtz, snowpockets or lithic zones could be considered to be within the natural range of variability for fire, while the fire dependent seral conifer-aspen would likely be out the natural range of variability (Table 1). The fire dependent montane and subalpine stand types that occur in riparian and meadow fringes would likely still be within the range of variability, but trending towards outside of the range.

3.1.2 Grazing

Wild ungulates as well as domestic cattle and sheep have been closely associated with the aspen community for the past 10,000 years because of its proximity to water and increased biomass (Potter 1998). Grazing influences mesic habitats by recycling nutrients, influencing primary productivity, reducing competition, and altering disturbance regimes (Hobbs 1996). In order to thrive in regularly disturbed sites, many species that are found within the aspen vegetation type including aspen have developed adaptive responses to allow for rapid recovery. Aspen in particular has developed specific traits to respond favorably following disturbance such as: 1) rhizamatous clonal sprouting, 2) high density sprouting, 3) deciduous leaves, 4) extensive carbohydrate storage in belowground root systems, and 5) rapid growth (Shepperd et al. 2006).

3.1.2.1 NRV

Large herbivores were common in the assessment area prior to Euro-American arrival and were likely abundant throughout the Sierra Nevada as evidenced in sediment cores (Davis and Shafer 2006). Following the megafauna extinctions, aspen continued to be grazed by a number of native ungulates that were common throughout the Holocene such as mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and antelope (*Antilocapra americana*) (Ratliff 1985). Most of the native herbivores in the assessment area have been reduced in number or have been extirpated from the area with the exception of the mule deer (Shepperd et al. 2006). It remains an important herbivore throughout the aspen vegetation type primarily as it moves to higher elevations in the spring to feed on the forage and utilize the cover in aspen for fawning (Loft et al. 1991).

The introduction of domestic sheep and cattle in the mid-1800s significantly increased the number of grazing animals in the assessment area (Fig. 6). In some locations, the abundance of livestock during this historic period has been estimated to equal or exceed the abundance of large herbivores during the late-Pleistocene (Davis and Shafer 2006). Grazing was most intense during the 19th century with sheep grazing reaching a peak between 1880 and 1900 in one study in the North subregion (Fig. 6). The numbers of sheep gradually decreased but certain areas likely had sheep grazing until the 1920s (Taylor 2008). Cattle grazing reached its peak on USFS lands in the assessment area around 1920 with around 2,400 head of cattle. Since then permitted cattle has been slowly decreasing to current numbers of around 700 – 1,000 individuals (Fig. 6). These levels of livestock and there effects on aspen reproduction was well noted throughout the assessment area in the early 1900s (Sampson 1919).

Following the period of intensive grazing and prior to fire suppression (≈ 1910) some anectodal evidence suggests that aspen conditions improved as fires were still occurring but grazing pressure on suckers was minimal. In one study, Taylor (2008) recorded the year that stems originated in the North subregion (Lassen National Forest, Eagle Lake Ranger District). He showed an increase in aspen regeneration occurring around the time that sheep grazing was reduced from 2,500 to around 1,000 individuals. Increased trends in aspen suckering that coincided with the end of intensive grazing and beginning of fire suppression have been noted in the Sierra Nevada (Potter 1998) and the Lake Tahoe basin management unit (Ko 2001) in the Central subregion as well.

3.1.2.2 Comparison to Current

The number of sheep and cattle grazing in the assessment area peaked around 1920 and gradually decreased to numbers below 1000 and 500 head for cattle and sheep, respectively (Fig. 6). Although the numbers of permitted livestock allowed to graze in aspen stands has dramatically decreased, domestic sheep and cattle continue to utilize many of the mesic areas in the assessment area. Contemporary foraging and habitat use patterns of native grazers suggest that grazing intensity and utilization during the Holocene was much lower than that of current time periods (Hobbs 1996). Studies comparing foraging behavior and habitat preferences in native and domestic ungulates have shown that native grazers, such as deer, have a more dispersed grazing pattern avoiding congregating in large herds in mesic areas (Loft et al. 1991).

A decline in aspen has been noted throughout the Western United States (Bartos 2001) and more particularly in the assessment area (Shepperd et al. 2006). A number of studies throughout the assessment area have noted excessive browsing on all seedling and sapling stage aspen (Loft et al. 1991, Potter 1998, Taylor 2008). Excessive grazing depletes aspen stands of suckers shifting them from multi-age to even-aged altering the successional patterns (Jones and DeByle 1985, Kay and Bartos 2000). Excessive grazing also causes a reduction in the terminal leader growth leading to a decline in aspen productivity (Jones et al. 2009). Physiological effects can also occur from excessive grazing such as increased cavitation which results in mortality of young seedlings (Galvez and Tyree 2009). All of these effects reduce the successful recruitment of aspen to large sapling stages reducing the overall vigor of the stand. This is further complicated by conifer encroachment.

Contemporary management practices, such as fencing, range improvements, mineral supplementation, and predator control, often result in higher densities and concentrations of livestock, particularly in mesic sites (Shepperd et al. 2006). Fencing has been used effectively in many resprouting aspen stands to reduce livestock use or eliminate livestock use until the saplings reach a height that is above browse line (Kota and Bartos 2010). A recent study conducted in Oregon showed the importance of excluding ungulates from recently treated aspen stands. They noted a three times higher density of suckers in recently fuel treated aspen stands when native and domestic ungulates were excluded from the sites (Endress et al. 2012).

3.1.3 Insects/Disease

3.1.3.1 NRV

No published literature was identified establishing the NRV for insects or disease. There is probably little reason to believe that any of the current insects and diseases are outside of the NRV for the aspen vegetation type.

3.1.3.2 Comparison to Current

Aspen is susceptible to a variety of foliar diseases, stem decays and cankers and defoliating and wood boring insects (Shepperd et al. 2006). Aspen is susceptible to a number of fungal cankers that enter through wounds in its sensitive living bark. These fungi can attack, girdle and eventually kill the tree by blocking translocation of photosynthates. Aspen is also susceptible to root diseases such as *Armillaria* which are spread from root to root contact. This disease usually doesn't cause entire stands to die rather small pockets of trees will contract the disease and usually fall over from weakened root systems. Insects also can cause damage to both the bark and the foliage of aspen although aspen isn't susceptible to common conifer insects such as the mountain pine beetle (*Dendroctonus ponderosae*). Other stress factors such as climate change, ungulate browsing and conifer encroachment can accelerate the rate of stand decline by increasing crown dieback and mortality of individual stems. A list of the current insects and disease present in aspen can be found in Table 5.

3.1.4 Invasive Species

3.1.4.1 NRV

Non-native invasive plants are beyond their natural range and historic distribution through human activities (Schwartz et al. 1996). By definition, non-native species in California are those that were introduced after European contact in 1769. It was likely that few invasive species existed in aspen prior to this. Following this period, settlement led to building of modern roads and other development that has acted as a vector for a number of non-native invasive plants.

3.1.4.2 Comparison to Current

Aspen are very conducive to spread of invasive plants because of their fertile soils, moist habitats within and adjacent and their dependence on disturbance. Currently, there are a number of non-native invasive plants associated with high elevations. Of such (Shepperd et al. 2006) listed a number that could be potential threats to aspen such as St. Johnswort (*Hypericum perforatum*) and bull thistle (*Cirsium vulgare*). Both of these species have been observed in aspen stands in the Lake Tahoe Basin Management Unit located along roads and riparian corridors. Although few non-native invasive plants in aspen are found at high cover they do occur in great numbers (Shepperd et al. 2006). Care must be taken to decrease the probability of spread, particularly when planning restoration activities with machinery that can act as vectors. A significant spread of non-native invasive plants could alter the distribution of resources placing significant stress on aspen and its associated understory. It would be a safe assumption that any of non-native invasive species in highly valued aspen stands is outside of the natural range of variability (Shepperd et al. 2006).

3.1.5 Hydrological pathways

3.1.5.1 NRV and Comparison to Current

Water balance is an important consideration in the aspen vegetation type. As disturbance has decreased and aspen has declined conifer density has increased potentially shifting the water balance. It is hypothesized that a conifer dominated landscape will use more water than a similar landscape dominated by aspen due to 1) the ability of conifers to transpire water from soil anytime of the year if temperatures are above freezing and 2) the increase in surface area of conifers which allows for more transpiration than the broadleaf aspen (Kaufmann 1985). Additionally, aspen has a greater snow water equivalent because aspen stands are able to accumulate more snow than similar conifer dominated stands (Fig. 7). Because ablation, evapotranspiration and sublimation are low there is a greater annual water yield than adjacent conifer dominated stands. This increase in greater annual water yield is important for the assessment area where 75-90 percent of water is allocated for some downstream purpose (LaMalfa and Ryle 2008). Few studies have attempted to quantify these changes but Gifford et al. (1984) noted that the impacts of conifer encroachment into aspen dominated stands is indeed reducing water yields. If conifer encroachment persists in the assessment area, the water yield from the aspen vegetation type may continue to trend to outside of the natural range of variability.

3.1.6 Conifer encroachment – Disruption of the Successional pathways

3.1.6.1 NRV and Comparison to Current

Aspen can either be early seral state that is successional to conifers or be maintained in a stable state. Regardless, aspen is a shade intolerant species that relies on some form of disturbance to renew the stand (Shepperd et al. 2006). There are stable aspen stand types, mostly in the eastern portion of the assessment area and on substrates that inhibit conifer growth, that do not need disturbance to perpetuate, rather they continue to establish through suckering (Table 1) (Ko 2001). Most of the aspen types in the assessment area are classified as early seral and are increasingly affected by encroaching conifers.

The main form of reproduction is asexual following a hormone response triggered by a disturbance (Baker 1918). The suckers (ramets) arise from underground root systems and self-thin in the first few years following establishment (Shepperd et al. 2006). Aspen ramets can range in age from 5 – 140 years in mixed age class stands and are known to decline after 120 years (Shepperd et al. 2006, Taylor 2008). Genets or the aspen clones have been documented as being well over 1,000 years in age and most likely much older potentially dating back to the end of the last glacial period (Mitton and Grant 1996, Shepperd et al. 2006). Sexual reproduction is extremely rare in aspen (Mitton and Grant 1996). It is more likely to observe sexual reproduction following conditions that foster primary succession such as the recession of glaciers or large fires such as those that occurred at Yellowstone National Park (Turner et al. 1999) that would have produced the environment necessary to foster seedling establishment.

In 1934, when Wieslander conducted his surveys in California he noted the seral stage of all encountered vegetation types (Wieslander 1935). In the Central Sierra Nevada, Wieslander noted that only 4 percent of aspen was in the early seral stage due to fire or logging (Thorne et al. 2006). The remaining landscape had no indication of disturbance. Since fire suppression policies were enacted in the early to mid-1900s, there has been little recorded disturbance in aspen stands throughout the assessment area. Simulation models show that aspen with conifer encroachment that persist under the current fire regime (>100 years) will see an 80 percent decline after 200 years as a result of transition to conifer dominated stands (Strand et al. 2009a). Likewise, successional estimates in the Great Basin aspen and juniper dominated stands predicted that 80 years after a stand replacing event junipers will retain dominance (Miller et al. 2001).

The decline in aspen can be attributed to the disruption of the successional processes as a result of disrupted fire cycles (DeByle 1990) which has led to conifer encroachment. On the Eagle Lake Ranger District on the Lassen National Forest (Taylor 2000) noted that only 24% of aspen stands had been affected by a wildfire since 1910 where the normal fire return interval was 14.4 – 25.6 years in the surrounding forest matrix. As a result, 82% of the stands are highly susceptible to being overtopped by conifers which would result in aspen declines (Taylor 2000). Likewise, 30% and 54% of aspen stands on the Lake Tahoe Basin Management Unit and the Modoc National Forest have been rated as high risk to conifer dominance (Di Orio et al. 2004, Shepperd et al. 2006).

Although the early seral aspen stands may be outside of the natural range of variation in successional pathways, stable aspen stands may still be within the natural range of variability. (Ko 2001) identified certain sites in the Lake Tahoe Basin Management Unit that appear to be stable aspen stands with 13 out of 20 having stable structures with only 3 appearing to have severe issues with conifer encroachment. This may indicate that certain types of aspen stands adopt other modes of regeneration besides disturbance to mediate continuous regeneration.

3.2 Structure

3.2.1 Patchiness and connectivity

Most studies that have reported on the spatial structure and connectivity of aspen stands do not distinguish between clonal patches and stand patches. Aspen stands vary in size throughout their range in North America. For example, stands in the eastern United States are small and usually less than a few hectares in size (Wyman et al. 2003). In the Interior West, stands of aspen can be quite large covering hundreds of hectares with thousands of stems, but can also be found in small stands less than 10 hectares in size (DeWoody et al. 2008). Not every aspen stand or patch is an isolated clone nor are they monoclonal with some stands having a complex intermingling of multiple clones (Shepperd et al. 2006). Aspen stand structure is variable throughout the assessment area. Westside stands are widely scattered and small (1-5 hectares) and can often finger along mesic sites forming a contiguous matrix (Fig. 9). Stands on the eastside of the assessment area are widely separated south of Mono lake and large and quite common northwards. The structure of this aspen type is more closely associated with the Rocky Mountain aspen stands (Potter 1998). There is little published information detailing the natural range of variation of aspen structure in the assessment area, however current aspen structure provides a snapshot of past recruitment over the past 150 years.

3.2.1.1 NRV and comparison to current

No information is available on the structure of aspen beyond the past 60 years. More recently, Di Orio et al. (2004) documented the structure of 3,033 hectares of aspen from a 1946 aerial photo set in the North subregion in the Warner Mountains on the Modoc National Forest. Mean patch size was 4 hectares with a range of 0.02 to 458 hectares. In addition to documenting patch size, they provided an estimate of fragmentation in 1946 with a unitless measure called Mean Proximity Index. In 1946, this number was relatively high indicating less likelihood of fragmentation. Presently, Di Orio et al. (2004) found that mean patch size had decreased to 3 hectares with a range of 0.04 – 141 hectares. They also noted a higher measure of fragmentation as conifer encroachment has increased the number of stands by 8% and once continuous aspen patches were now completely absent of suckers (Di Orio et al. 2004).

Other studies also reported on current aspen stand structure throughout the assessment area. The only landscape level information on patch size for aspen/conifer stands encompassed the area from Carson Pass in the Central bioregion to the Eagle Lake Ranger District in the North bioregion. Here patch size in 2005 ranged from 0.3 to 4.4 hectares with a relatively small mean of 0.9 hectares (Kuhn et al. 2011). Another study in Lassen National Forest in a montane zone in the North subregion, found that over the extent of the area sampled aspen patches ranged from 1 to 10 hectares in size (Taylor 2008). Within these stands, 98% were occupied with aspen seedlings and 73% were occupied with conifer seedlings (Taylor 2008). In contrast stands on the Eastside of the crest in the Northwest Great Basin had stands that currently ranged well up to 71 hectares in size (Miller et al. 2001). Of the landscapes presented above, all had variable age structures and were representative of a multi-age and sized structure which is discussed further in the section on conifer encroachment (for example, Fig. 9) (Ko 2001, Taylor 2008).

It would be difficult to interpret the difference between the NRV and current conditions of structure in the assessment area. This can be attributed to two main issues: 1) there are limited reports of NRV and none were prior to pre-European presence and most originated from post fire suppression and after intensive grazing management and 2) there are distinct differences between aspen types that affects the structure of these stands (e.g., some stands persist as even aged until a stand replacing disturbance occurs while others maintain a mixed stand structure throughout stand development). The patchy and isolated nature of most aspen stands in portions of the assessment area is probably outside the range of NRV. This change has been attributed to excessive grazing, fire suppression and conifer encroachment.

3.2.2 Productivity – Herbaceous Biomass

3.2.2.1 NRV and Comparison to Current

Productivity in aspen stands is robust due to the high incidence of light reaching the forest floor and the association with water (Potter 1998). Some studies have reported as much as 3,200 kg/ha of understory herbage in the Western United States and in the assessment area levels are equally as high (Bartos et al. 1994, Richardson and Heath 2004). This quality of herbage benefits a number of wildlife species as forage and hiding cover and supports grazing by domestic livestock.

Decreased productivity in aspen stands is attributed to increases in conifer encroachment and excessive grazing or a combination of the two. Conifer encroachment and excessive grazing have been shown in the previous section to be outside the range of variability. Stam et al. (2008) noted a negative relationship between conifer cover and understory biomass. Understory production in aspen stands began to decline under very low levels (10% to 20%) of conifer encroachment. Management implications include loss of forage production capability and wildlife habitat and potential overstocking of livestock grazing allotments if the associated loss of forage is not considered (Loft et al. 1991, Stam et al. 2008). Decreases in breeding bird densities are also reflected in these vegetation differences, as ground-nesting species and riparian specialists will likely decrease (Richardson and Heath 2004).

3.3 Composition

3.3.1 Geographic distribution and plant species diversity

3.3.1.1 NRV

There is little information on the extent of aspen in the early to mid-Holocene. However, aspen were most likely one of the first species to colonize the previously glaciated landscape as these environments were good for seedling establishment (Baker 1918) (Table 3). The receding glaciers would have left behind vegetation free areas with plenty of water and rich soils (Shepperd et al. 2006). A study in Alaska where *Populus* pollen is common in the historical records indicated a peak of invasion occurring around 11,000 – 9,500 YBP (Ager 2003). A similar study in the Central/Southern bioregion indicates similar high rates of pollen after the glacial period (Fig. 10) (Anderson 1991, Morris et al. 2012). In the mid-Holocene (8,000 – 1,100 YBP) aspen pollen remained constant in the record (Fig. 10) during warmer temperatures and a shift from dry to moist conditions (Table 3). In the time period from 1,100-650 YBP temperatures were warmer which most likely encouraged the growth of tree species that were resistant to drought and recurring low intensity fire (Table 3). In the early Holocene during the transition from the Medieval Warm Period (MWP) to the Little Ice Age (LIA) (650 YBP) a peak in *Populus* pollen grains at several lake basins was observed (Table 3, Fig. 10). Aspen has been shown to track parallel shifts in lodgepole pine (*Pinus contorta*) as both favor full sunlight characteristic of immediately after stand replacing fires (Skinner and Chang 1996). During this time period when fires were infrequent, but potentially more intense increases in such subalpine species as lodgepole pine were evident (Millar and Woolfenden 1999). This suggests that aspen would have had a similar response. In the late Holocene an increase in disturbance (Table 3) in the late 19th century (180 YBP) favored an additional pulse of aspen regeneration in stands that established in the previous Little Ice Age (650 – 100 YBP) (Shepperd et al. 2006). Current ages of aspen average about 100 – 150 years support this pulse of regeneration during the late 19th century when human disturbance was at its highest (Fig. 10).

Most helpful in determining the NRV for distribution of aspen is a better understanding in what climate conditions aspen seedling/resprouting establishment occurred. One study in southwestern Colorado attempted to determine when aspen seedlings established at treeline (Elliott and Baker 2004). They found that in climates with low mean maximum summer temperatures and high mean spring precipitation seedlings established. Aspen asexual reproduction, on the other hand, was correlated with warm temperatures and low precipitation. These patterns may be closely tied to the disturbance regime of the particular climate (Table 3).

3.3.1.2 Comparison to Current

Distribution of aspen today is confined to areas that established prior to European settlement but were previously occupied. There is some evidence that aspen has been in the assessment area for the past 8,000 years establishing after the retreat of the glaciers (Strain 1964). Aspen sexual regeneration requires distinct environmental conditions that are often met following a stand replacing event where bare mineral soil is exposed. Even with these conditions the probability that aspen will regenerate is rare and observed infrequently within the areas in the Sierra Nevada (Krasnow et al. 2012). Given these limitations, aspen primarily regenerate through clonal sprouting making their distribution centered on existing stands and the report of current conditions a record of the expansion or shrinking of these patches.

Little to no information on the extent of aspen prior to European settlement is available for comparison with the present distribution. There are historical accounts that document the changes in the extent of aspen, but these are limited to the past 100-200 years. Some of the more recent mapping efforts identified an increase in aspen following the period in the 19th century when human disturbance was at its highest (Fig. 2). The Wieslander VTM surveys did account for some of this change in the Central bioregion. Thorne et al. (2006) showed that the aspen dominated areas had decreased by 73%. Of these areas, 92% had no indication of recent fire. At the time of the Wieslander surveys, it appears that the aspen stands at least in the Central bioregion had stagnated with a lack of disturbance. In addition, a number of studies have shown declines in smaller regions. Di Orio et al. (2004) used 1940s photo interpretation in the Northern bioregion to find that 24% of aspen was declining. Aspen was also observed to be declining in the Lake Tahoe Basin Management Unit (2%) (Ko 2001) and in the Eastside forests (Bates et al. 2006), but to a lesser extent as these aspen dominated stands tend to continue to regenerate without disturbance.

Aspen understory are unique and harbor a diverse plant assemblage that are quite often distinct from the adjacent conifer/meadow matrix habitat with aspen and meadows far exceeding the conifer stands in species richness, diversity and eveness (Kuhn et al. 2011). In addition, aspen stands support a high site-to-site (beta diversity) heterogeneity across the Northern bioregion in the assessment area (Di Orio et al. 2004, Kuhn et al. 2011). In a study that covered the central and north subregion, (Kuhn et al. 2011) found 316 plant species in aspen of which 63 were unique to the aspen plant community. The majority of all species observed were graminoids and forbs. (Kuhn et al. 2011) also found a weak relationship between aspen/conifer combined cover and Shannon-Wiener diversity index indicating that as total canopy cover increased diversity decreased. This could be adverse to total diversity in aspen stands as conifers continue to encroach in the absence of disturbance. Among the losses would be a decrease in ecological function, decrease in available biomass for grazing ungulates and a decrease in the occurrence of indicator plant species. Limited information about composition in the assessment area throughout the Holocene and even in the past 150 years is available with the exception of direct observations by surveyors in the area. Barlow (1901) remarked on the diversity of plant and bird species in the aspen stands located in the Central bioregion.

Little comparison can be made between the pre-European aspen distribution and composition and the current conditions. It appears that throughout the Holocene, aspen fluctuated directly with changes in climate. This was true until the early 19th century where increased disturbance most likely increased aspen distribution. This most likely would have continued until the initiation of fire suppression which resulted in marked decreases in aspen across the assessment area. Composition of aspen is strongly influenced by fire (Brown and DeByle 1989) with more forb species occurring following high severity fire. Because little or no fire has occurred in the aspen stands in the assessment area it would be safe to assume that composition has begun to decrease.

3.3.2 Genetic diversity

Information on the genetic variability and clonal distribution of aspen within the assessment area can help to determine the past extent of our current aspen stands and help to guide restoration strategies to preserve aspen genetic resources. It was long believed that each stand represented an individual clone and these clones could be easily distinguished by phenotypic characteristics (Shepperd et al. 2006). In addition, it was assumed that since sexual reproduction was rare that vegetative reproduction alone accounted for the range of aspen in the assessment area (Shepperd et al. 2006). Recent genetic information within the assessment provides spatial information that the extent of aspen throughout the Holocene was greater than the existing conditions.

Aspen primarily reproduces vegetatively through the production of sprouts following a disturbance. Auxin which is normally produced to suppress the development of shoots decreases following a stem losing its apical dominance allowing pre-existing buds and meristems to develop into shoots (DeByle 1990). Under good environmental conditions, clones can spread anywhere from 15 to 100 feet (Jones and DeByle 1985) and have upwards of 100,000 ramets sprout following a disturbance (Bartos 1979). Although the spread rates can be quite large natural barriers to expansion such as bedrock and riparian areas would have inhibited the spread of clones throughout the assessment area.

Aspen are dioecious with clones being either male or female (DeByle 1990). Trees flower several weeks before the trees leaf out and seed is produced in abundance every 2 to 5 years. The narrow range of conditions necessary for germination has limited seedling establishment across the region. Aspen seed are only viable for a short time (2- 4 weeks) (Barry and Sachs 1968) and require exposed mineral soil, above freezing temperatures and adequate moisture for germination (McDonough 1979). In recent years, major disturbances such as the Yellowstone fires have resulted in numerous seedlings establishing supporting the hypothesis that seeding is more common than previously recognized (Romme et al. 1997). Sexual reproduction in the assessment area has been considered to be rare with only a few known cases of seedlings reported by (Krasnow et al. 2012) found in areas that were recently severely burned. Despite the rare occurrence of seedling establishment, adequate male and female clones are present in the assessment area as was evidenced by a study in the Central subregion (Eldorado National Forest) that documented a ratio of 2 males to every 1 female clone (Burton 2004).

Genetic diversity is a rough measure of the reproductive health of aspen. Two ways in which high levels of genetic diversity can be accounted for in aspen is through rare seedling establishment and clonal (somatic) mutations (Shepperd et al. 2006). In order for clonal mutations to occur the clones must be permanent on the landscape which a trait very common in the arid Western aspen where clones are estimated to be several thousand years old (Mitton and Grant 1996). In the assessment area two studies documented high levels of genetic variability with a high degree of polymorphic loci across the studies but low within stands because of the monoclonal nature of many stands (Hipkins and Kitzmiller 2004, DeWoody et al. 2009). This and many other studies in the Western United States have led researchers to believe that aspen is one of the most genetically diverse plant species (Mitton and Grant 1996).

Studies that have looked at the spatial distribution of clones within stands suggests that clones were at one time larger as evidenced by disjunct populations of clones with the same genetic makeup (Fig. 11). One study in the Central subregion (Eldorado National Forest) (Hipkins and Kitzmiller 2004) and another study in the North subregion (Lassen National Forest) (DeWoody et al. 2009) concluded that small stands tended to be monoclonal (<3.2 hectares) while large stands were composed of multiple clones.

4 Projected Future Conditions and Trends

4.1 Climate Change

Although aspen is a widely distributed broadleaf tree in the Western United States little research has been conducted to assess the affects climate may have on its growth, vigor and reproduction. Aspen typically occupy the fringes between different vegetation types. These marginal habitats are often more susceptible to climate stress. Declines in aspen have been noted in the Western United States over the last century, but the agent of change is largely unknown (Frey et al. 2004). Two probable agents are an absence of disturbance which has led to encroachment of conifers and climate change. Climatic variation has been shown to be strongly associated with the growth and mortality of aspen in the Intermountain West (Hanna and Kulakowski 2012), but this trend has not been established for decreases in aspen the assessment area. This decrease in growth has been largely attributed to increasing temperatures and extended periods of drought (Rehfeldt et al. 2009, Hanna and Kulakowski 2012). As these abiotic stresses are coupled with ongoing biotic stress it may lead to a more pronounced decline of aspen.

Aspen has a wide current range which indicates it ability to adapt to varying environmental conditions. The extent of aspen will likely track with changes to the prevailing climate similarly to the trend that was observed throughout the Holocene. It is likely that a similar decrease in aspen and other high elevation conifers was experienced in the Medieval Warm Period (1100-650 YBP) where temperatures were 3°C warmer than existing conditions (Table 3). During this time, various species were found growing at higher elevations than they are found now (Millar et al. 2006) and many subalpine species shifted upslope. In California, aspen has been projected to be restricted to higher elevations under climate change scenarios (Rehfeldt et al. 2009).

Projected climate models in the assessment area show an increase in average temperature of 2-4°C (Safford et al. 2012). This could potentially result in a 20-90 percent decrease in snowpack and an earlier snow melt that could increase water stress for aspen and other high elevation conifers (Safford et al. 2012). Predicted decreases in aspen across the West are 23% (6.7-41%) in 2030, 51% (39.7-74.1%) in 2060 and 69% (46.2-94.4%) in 2090 (Rehfeldt et al. 2009). Future distributions of the aspen vegetation type have been assessed for vulnerability in the South bioregion. Using a GFDL climate model (35% decrease in precipitation and a 4.5°C increase in temperature), Schwartz et al. (2013) scored 57% of existing aspen distribution as at a moderate or high exposure (Fig. 12). This indicates that aspen is projected to decrease in distribution in 2070-2099. A similar contraction was observed in the PCM climate model (no change in precipitation, 2.5°C increase in T) which showed only 30% of aspen scored at moderate or high exposure (Fig. 12). The most at risk aspen types according to the vulnerability assessment would be those located in the ecotones of wet habitats. It is largely unknown whether aspen will be able to migrate to appropriate locations to accommodate a rapid change in climate with asexual reproduction as its only mechanism for spread (Rehfeldt et al. 2009).

Climate may also change the function and structure of the aspen vegetation type indirectly by altering disturbance processes. Strand et al. (2009a) did indicate that if disturbance is limited aspen stands will remain even aged and offer little recruitment for replacement. This could decrease the structural diversity of the aspen and reduce the likelihood that these stands will continue to persist. Other studies report similar declines in aspen with no change in the current management structure. Strand et al. (2009b) simulated the loss of aspen under certain scenarios in the Western US. They found that under the current fire regimes (an FRI of 340 to 450 years) and no management the loss of seral aspen will continue to occur. However, a return to the pre-European FRI would result in only a 12-14% decrease across the landscape over the next 70-80 years. This scenario would maintain early and mid seral aspen allowing for continue sprouting after a disturbance.

5 Summary

A complete description of the determinations of NRV is included in Table 6. Below is a summary of the major NRV for the aspen vegetation type in the assessment area.

- Limited data are available to determine the natural range of variability of the fire regime in aspen stands throughout the Holocene. Information from several studies indicates a fire return interval of 10-90 years dominated by mixed to high severity fires. Because of the dependency of aspen on the fire regime of the surrounding forest matrix, a determination that the fire return interval of mixed conifer or red fir forests is outside the range of NRV will likely have an effect on the interspersed aspen stands.

- Grazing intensity and utilization is outside the NRV; however some sites may recover with successful exclusion and rotation practices.

- There is only anecdotal evidence on the pre-European structure of aspen forests in the assessment area. A decrease in disturbance events may be converting historical multi-age and multi-structured forests to more even-aged single canopied forests.

- Species diversity and the extent of the aspen vegetation type remains within the NRV throughout the time period of the Holocene. There is some evidence that in the assessment area competition from encroaching conifers may be facilitating the contraction and fragmentation of the aspen vegetation type.

- Genetic diversity is high among the few studies that have been completed within the assessment area. This is corroborated by studies in aspen throughout the interior West.

6 Table and Figures

Table 1. Common aspen stand types and their location, and seral stage (Shepperd et al. 2006, Shinneman et al. 2013).

Stand type	**Location**	**Fire dependence**	**Seral stage**
Riparian	Permanent/seasonal water course	Dependent	Early
Meadow fringe	Dry meadow fringes	Dependent	Early
Upland aspen/ conifer	Located away from any surface moisture regimes	Dependent	Early
Lithic	Lateral/terminal moraines, tallus, rock	Independent	Stable
Upland pure	Variable site locations	Independent	Stable
Snow pocket	Topographic positions where snow accumulates	Influenced	Stable
Krummholtz	Ridgelines	Independent	Stable

Table 2 Common tree, herbaceous and terrestrial species associated with the aspen vegetation type (Richardson and Heath 2004, Shepperd et al. 2006, Kuhn et al. 2011).

Tree species	**Herbaceous species**	**Terrestrial species**
Trembling aspen *opulus tremuloides*	Douglas' sagewort *Artemisia douglasiana*	red-breasted sap-sucker *Accipiter gentilis*
white fir *Abies concolor*	cutleaf Indian paintbrush *Castilleja lacera*	red-naped sapsucker *Sphyrapicus nuchalis*
red fir *Abies magnifica*	fireweed *Chamerion angustifolium* *(L.) Holub ssp. Angustifolium*	Empidonax flycatcher *Empidonax oberholseri*
Jeffrey pi*ne* *Pinus jeffreyi*	twinleaf bedstraw *Galium bifolium*	Swainson's thrush *Catharus ustulatus*
ponderosa pine *Pinus ponderosa*	cleftleaf ragwort *Packera moresbiensis* *(Calder & Roy L. Taylor) J.F. Bain starry*	MacGillivray's Warbler *Oporornis tolmiei*
	false lily of the valley *Smilacina stellate*	warbling vireo *Vireo gilvus*
	bugle hedgenettle *Stachys ajugoides v. ajugoides*	Oragne-crowned warbler *Vermivora celata*

Table 3. Indicators assessed in the natural range of variability of aspen with reference to the source of information and the time frame of the data source.

Variables Assessed	Source of Information	Time Frame
Geographic distribution	Pollen and macrofossils from lake cores, macrofossils from pack rat middens, mapping efforts in early 1900s, historical photographs	Paleoecological and reference conditions
Plant species diversity	Pollen and macrofossils from lake cores, macrofossils from pack rat middens	Paleoecological conditions
Structure	National Park Service lands (Yosemite National Park, Sequoia/ Kings Canyon National Park, Lassen Volcanic National Park), Research Natural Areas (Cub Creek Research Natural Area), historical photographs	Reference conditions
Disturbance	Limited fire scar information, National Park Service lands (Yosemite National Park, Sequoia/ Kings Canyon National Park, Lassen Volcanic National Park), Research Natural Areas (Cub Creek Research Natural Area)	Reference conditions

Table 4. Climate, fire frequency, and aspen and lodgepole extent throughout the early Holocene (12,000 -650 YBP).

Temporal Scales (YBP)	**Temperature** (difference from current)	**Precipitation** (difference from current)	**Charcoal Concentrations/ Fire Frequency**	**Aspen Extent**	**Lodgepole Pine Extent**
650-present	Low[4]	Moist[4]	Low[3,4,7,11,12]	Change in aspen extent potentially due to alteration of disturbance patterns	Gradual expansion[14]
1,100-650	Moderate[1, 7, 8]	Dry[7, 8]	Low[3,4,7,11,12]	Gradual decrease in aspen and other subalpine species dominance[13]	Unknown
4,000 – 1,100	Moderate[1, 2]	Moist[4]	Moderate[3,4, 5,7,11,12]	Modern aspen forests were dominant in 2200 ybp and increased through the Little Ice Age[13]	Gradual expansion[14]
8,000 – 4,000	High[1, 4]	Dry[10]	High[2,3,4, 5, 7,9,11,12]	Unknown	Disappeared from low elevation sites[14]
12,000 – 8,000	Low[4, 5]	Moist[5]	Low[3,7,11,12]	Unknown, but likely abundant	Widely established throughout modern expasion[14]

[1] (Potito et al. 2006)
[2] (Anderson 1990)
[3] (Beaty and Taylor 2009)
[4] (Anderson 1996)
[5] (Smith and Anderson 1992)
[6] (Woolfenden 2003)
[7] (Anderson et al. 2008)
[8] (Millar et al. 2006)
[10] (Anderson and Smith 1994)
[11] (Brunelle and Anderson 2003)
[12] (Daniels et al. 2005)
[13] (Anderson 1991)
[14] (Anderson 1996)

Table 5. Significant insects and disease in the aspen vegetation type.

Agent Fungal pathogen	**Time to tree mortality**
black canker, *Ceratosystis* spp.	The second most common aspen canker that rarely results in mortality as it takes years to girdle the tree.
Cytospora canker, *Cytospora chrysosperma*	The fungus that causes this canker usually only attack stressed trees and occurs in combination with other more lethal pathogens.
sooty bark canker, *Encoelia pruinosa*	A lethal canker that occurs on large older trees causing rapid mortality.
snake canker, *Cryptosphaeria* spp.	A lethal canker that occurs on sprouts, saplings and trunk of older trees causing rapid mortality.
trunk rot fungus, *Phellinus tremulae*	Doesn't normally kill the tree but weakens live trees.
Armillaria	Can cause significant localized mortality but doesn't kill whole stands. It also can prevent suckering from occurring. Could *Armillaria* become more of an issue with the encroachment of fir into aspen stands?
Insect	
poplar borer, *Saperda calcarata*	Does not kill the tree but it can create entry wounds for pathogens.
bronze poplar borer, *Agrilus liragus*	Does not kill the tree but it can create entry wounds for pathogens.
satin moth, *Leucoma salicis*	Can cause defoliation events but do not kill the tree. It can also trigger a suckering response.
large aspen tortrix, *Choristoneura conflictana*	Can cause defoliation events but do not kill the tree. It can also trigger a suckering response.

Table 6. Summary of variables describing aspen characteristics within the assessment area relative to their estimated natural range of variability (NRV) in the Holocene with an indication of confidence in making each comparison.

Ecosystem Attribute	Indicator Group	Indicator	Variable	Within HRV	Confidence	Pages	Notes
Function	Disturbance	Fire	Fire return interval	no	moderate	7	Few fires have burned within USFS lands in the past 100 years. Those that have burned into aspen stands have been restricted to the eastside of the Sierra Nevada and within NPS lands. The FRI is clearly outside of NRV.
Function	Disturbance	Fire	Fire severity	no	low	8	Fire severity within aspen stands throughout the Western United States requires high severity fire to facilitate reproduction. Observations beginning in the 1920s showed very little area impacted by high severity fire. In addition, in the past 29 years only 16% of recorded fires in aspen stands were high severity.
Function	Disturbance	Insects/Disease	Insect/Disease Occurrence	yes	low	11	Little information is available on the background levels of insect and disease within the aspen. It appears that presently insects or disease alone does not cause mortality associated with sudden aspen decline rather a combination of stressors such as climate, grazing, and fire suppression leads to widespread dieoff.
Function	Disturbance	Grazing	Utilization	no	high	9	The introduction of livestock increased grazing beyond background levels that would have existed with native ungulates. Since the decrease in intensive grazing in the early 1900s some recovery has occurred within aspen stands.

Ecosystem Attribute	Indicator Group	Indicator	Variable	Within HRV	Confidence	Pages	Notes
Function	Disturbance	Hydrologic regime	Water balance	no	low	12	Replacement of aspen with conifers could be decreasing water yields as evidenced in studies throughout the Western US. Aspen's net water consumption is considerably than conifers due to low water use efficiency and greater snow accumulation.
Function	Succession	Successional patterns	Conifer density	no	moderate	12	Conifer densities have increased in seral state aspen as a result of fire suppression and excessive grazing. Although there is no information on conifer densities throughout the Holocene in the aspen vegetation, conifer density in the last 150 years is considered outside of NRV. Conifer densities within stable state aspen are still within NRV.
Structure	Understory cover	Percent of cover	Percent cover	yes	low	15	In most cases, percent cover of vegetation is within NRV levels. However, grazing may have caused substantial reduction in cover of select species.
Structure	Patchiness	Size and connectivity	Size of aspen stands	no	low	13	The patchy and isolated nature of most aspen stands in the assessment area is outside the range of NRV. This change has been attributed to excessive grazing, fire suppression and conifer encroachment.
Structure	Patchiness	Size and connectivity	Clone size	maybe	low	17	Genetic evidence does not cover the entire assessment area. However, evidence shows that the disjunct distribution of many clones indicates that aspen was more widespread.

Ecosystem Attribute	Indicator Group	Indicator	Variable	Within HRV	Confidence	Pages	Notes
Structure	Productivity	Biomass	Herbage	maybe	low	15	In most cases, percent cover of vegetation is within NRV levels. However, grazing and fire suppression may have caused substantial reduction in productivity.
Composition	geographic distribution of ecosystems	land cover	land cover	yes	low	15	Although there is little evidence from the Holocene on distribution in the assessment area it appears that patters of existing aspen are tracking along similar climatic fluctuations.
Composition	geographic distribution of major species	Species composition	Distribution of major species	yes	low	16	There is little information available for species composition in the Holocene but distribution of major species is still within NRV.
Composition	Proportion of growth forms	Clonal/genetic diversity	Polymorphic loci	yes	low	17	High genetic diversity was evident at one location within the Central subregion. This is corroborated by numerous studies in the Western aspen distribution.
Composition	Species diversity	Total number of species	Total number of species	maybe	low	16	This may be out of the range of NRV due to excessive grazing pressures. Some areas may be recovering due to more ambitious grazing practices focusing on exclosure of cattle and strict rotations.
Composition	Species assemblage	Species assemblage	Number of non-native species	no	moderate	11	Non-native invasive species are outside of the NRV with more non-native species found in aspen habitat.
Composition	Proportion of growth forms	Sexual distribution of aspen clones	Male:female clone ratio	maybe	low	17	It is most likely that with recurring disturbance the sexual diversity would be greater. A higher male to female ratio amongst clones would facilitate reproduction.

Figures

Figure 1. The current extent of aspen in the assessment area (CalVeg Regional Dominance).

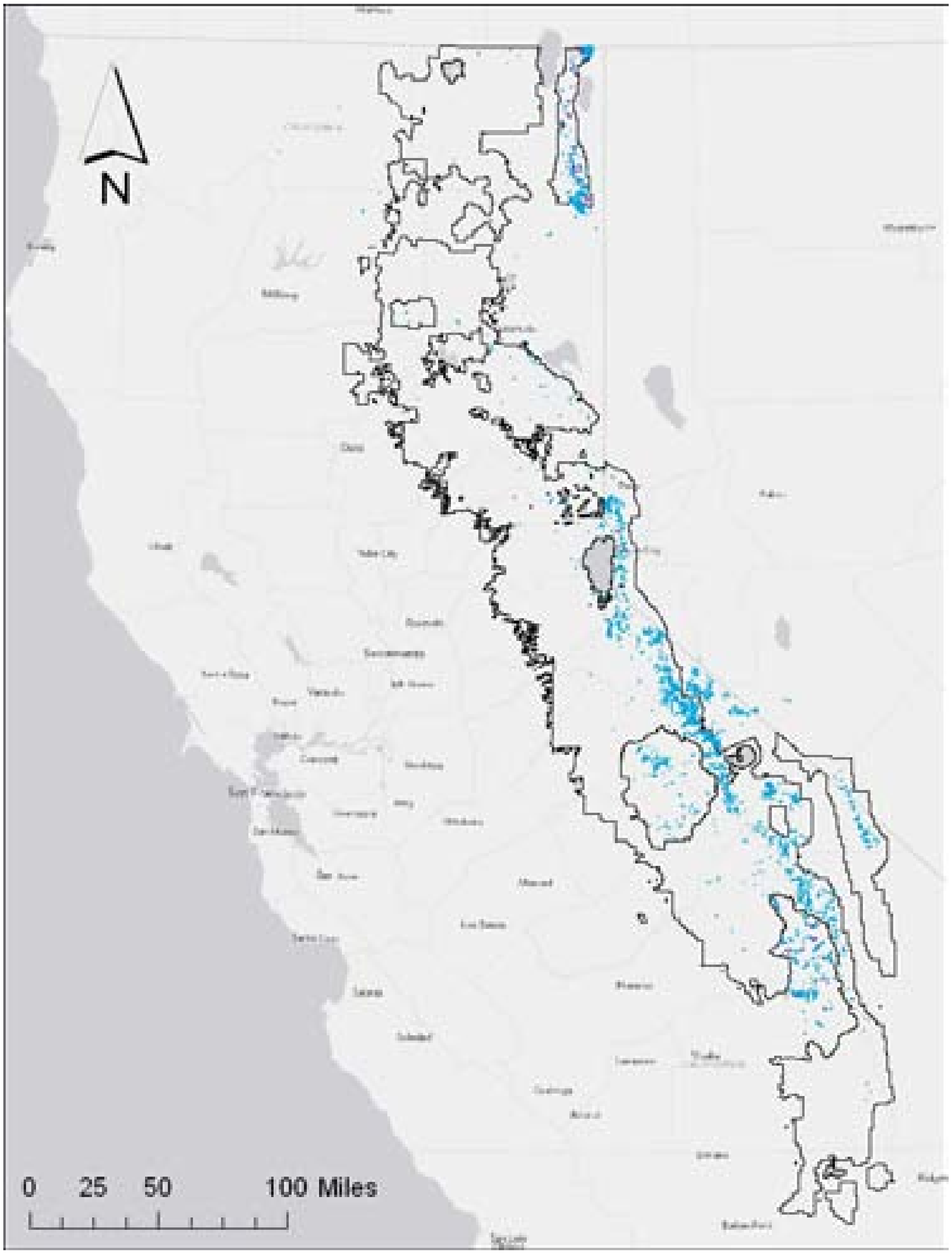


Figure 2. Human caused disturbances that occurred from 100 YBP - present (approx. 1850 – 1940) that influenced the extent of aspen in the assessment area.

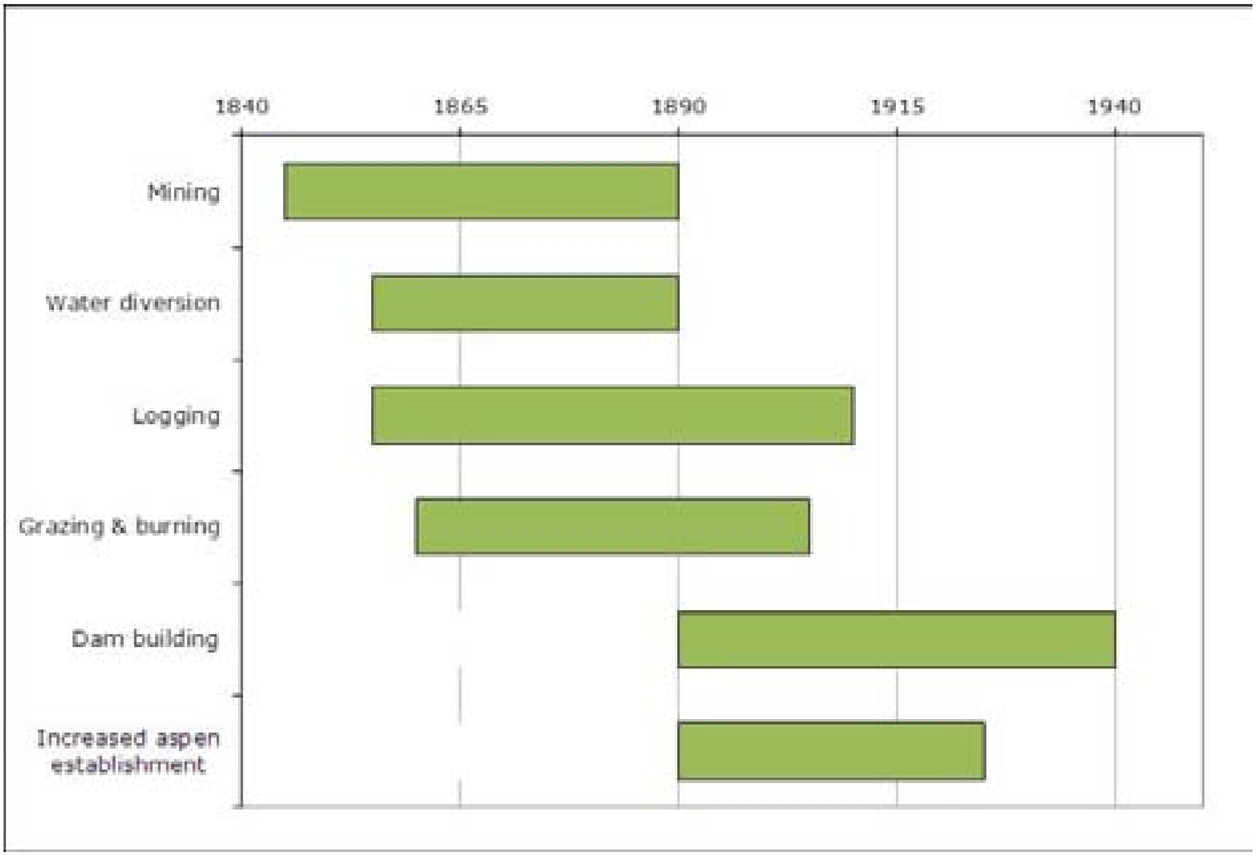


Figure 3. Hectares burned in the aspen vegetation type (identified using the CalVeg Regional Dominance) by human or lightning ignited fires derived from the FRAP database from 1904-2012.

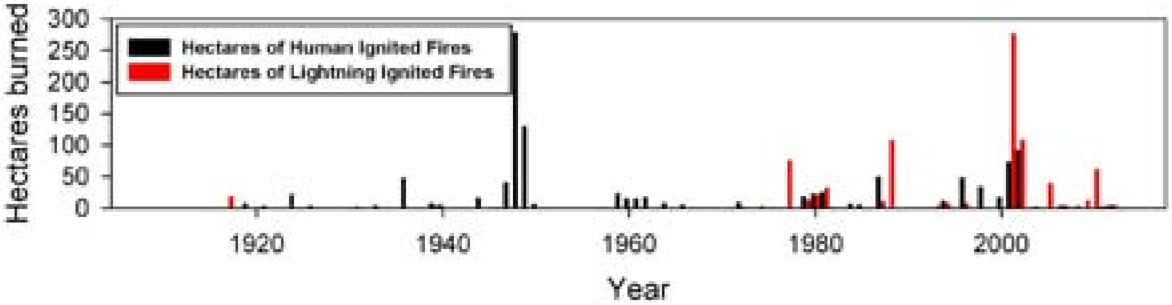


Figure 4. Fire severity (derived from the MTBS dataset) from fires that occurred from 1984-2012 within the aspen vegetation type (identified using the CalVeg Regional Dominance). Fire severity is defined as the percent change in canopy cover.

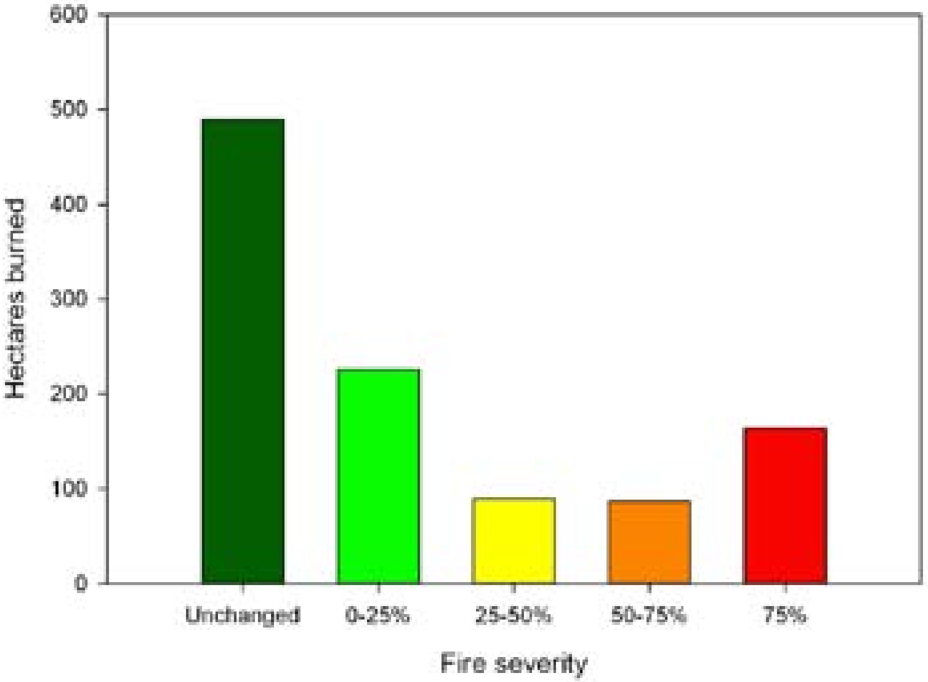


Figure 5. A framework of the fire regimes of the different aspen types found in the assessment area (refer to Table 1), 1 – fire independent, stable, 2 – fire-influenced, stable, 3 – fire dependent, seral, conifer-aspen mix, 4 – fire dependent, seral, montane aspen-conifer, 5 – fire dependent, seral, subalpine aspen conifer. Taken from (Shinneman et al. 2013).

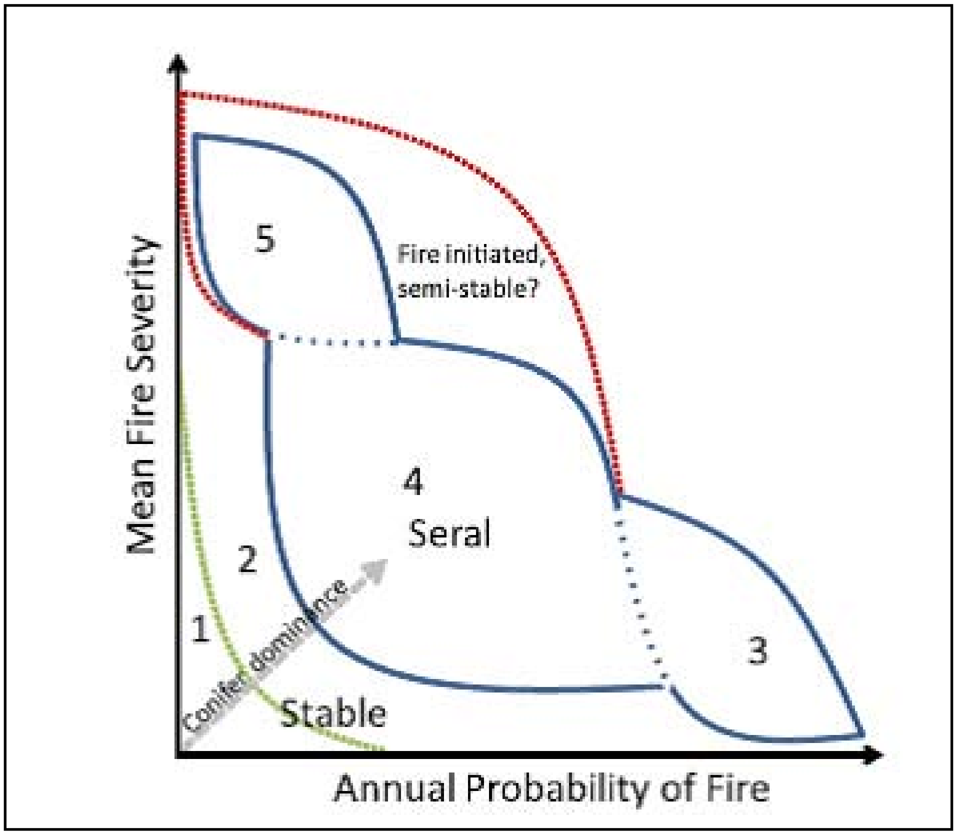


Figure 6. Sheep grazing records from 1905 to 1955 in the North subregion (Lassen National Forest, reproduced from Taylor 2008) and the number of permitted head of cattle on Forest Service Lands in California from 1910 to 2010.

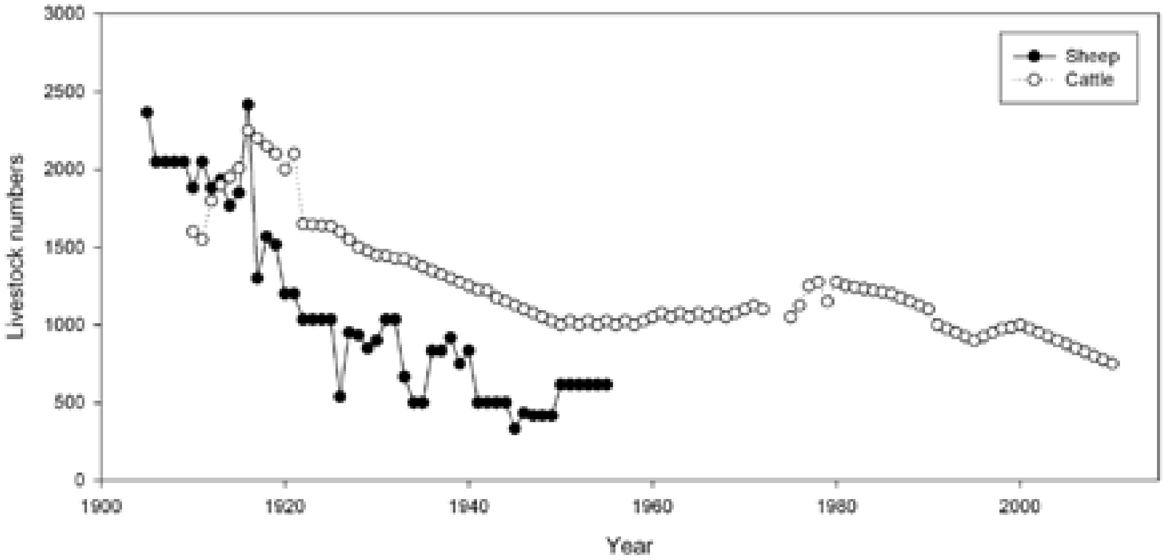


Figure 7. Aspen has the capability to capture more snow than adjacent conifer.

Figure 8. Frequency of aspen regeneration in 51 stands in the North subregion (Eagle Lake Ranger District, Lassen National Forest) by year. Reproduced from (Taylor 2008).

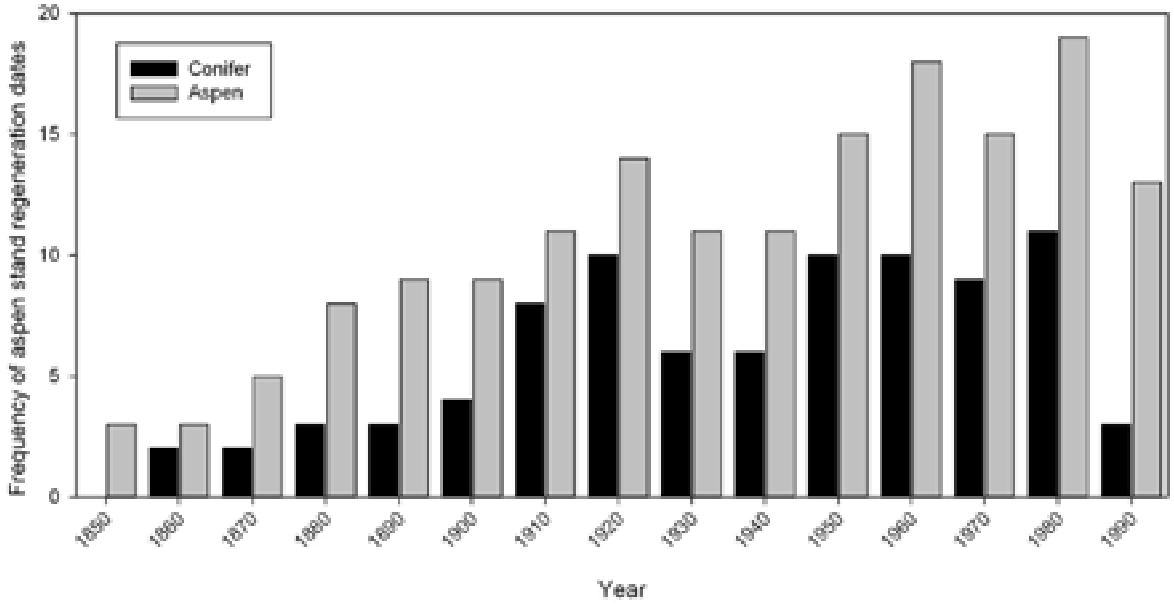


Figure 9. One mile east of Kit Carson Lodge Road Junction with highway. Stand of aspen and Jeffrey pine. Pyramid Lake. Taken by Albert Everett Wieslander on October 12, 1935.

Figure 10. Aspen pollen records from Woski Pond, Yosemite National Park and Southern Utah from the period of 8,000– 0 YBP (Anderson 1991, Morris et al. 2012).

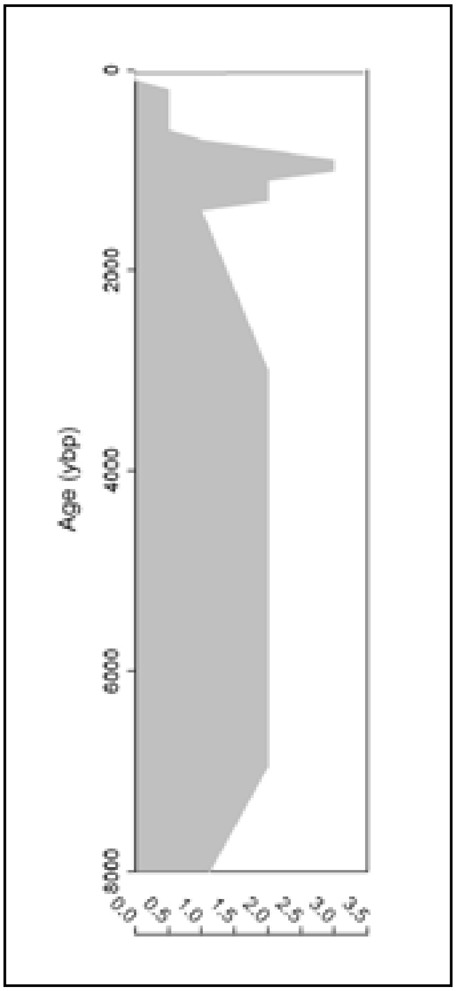


Figure 11. Genetic-Geographic classes of aspen stands on the Eldorado National Forest within eight HUC-7 watershed boundaries.

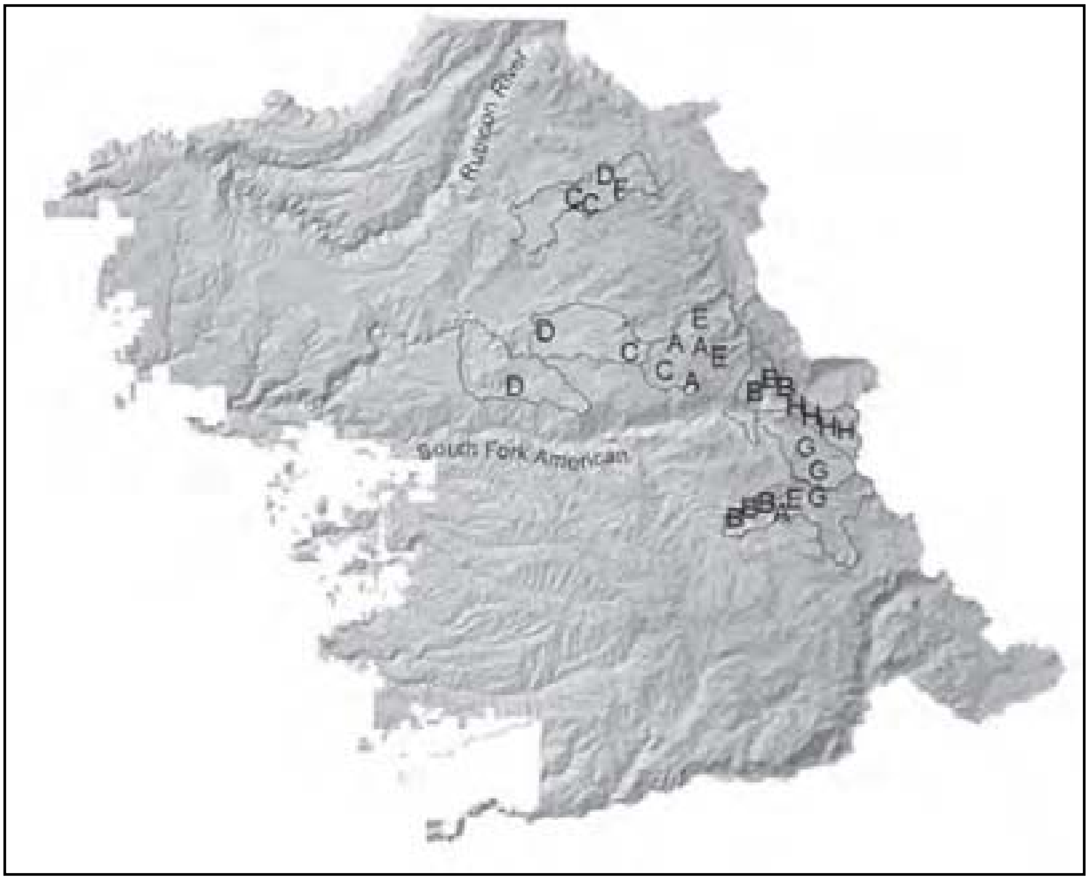
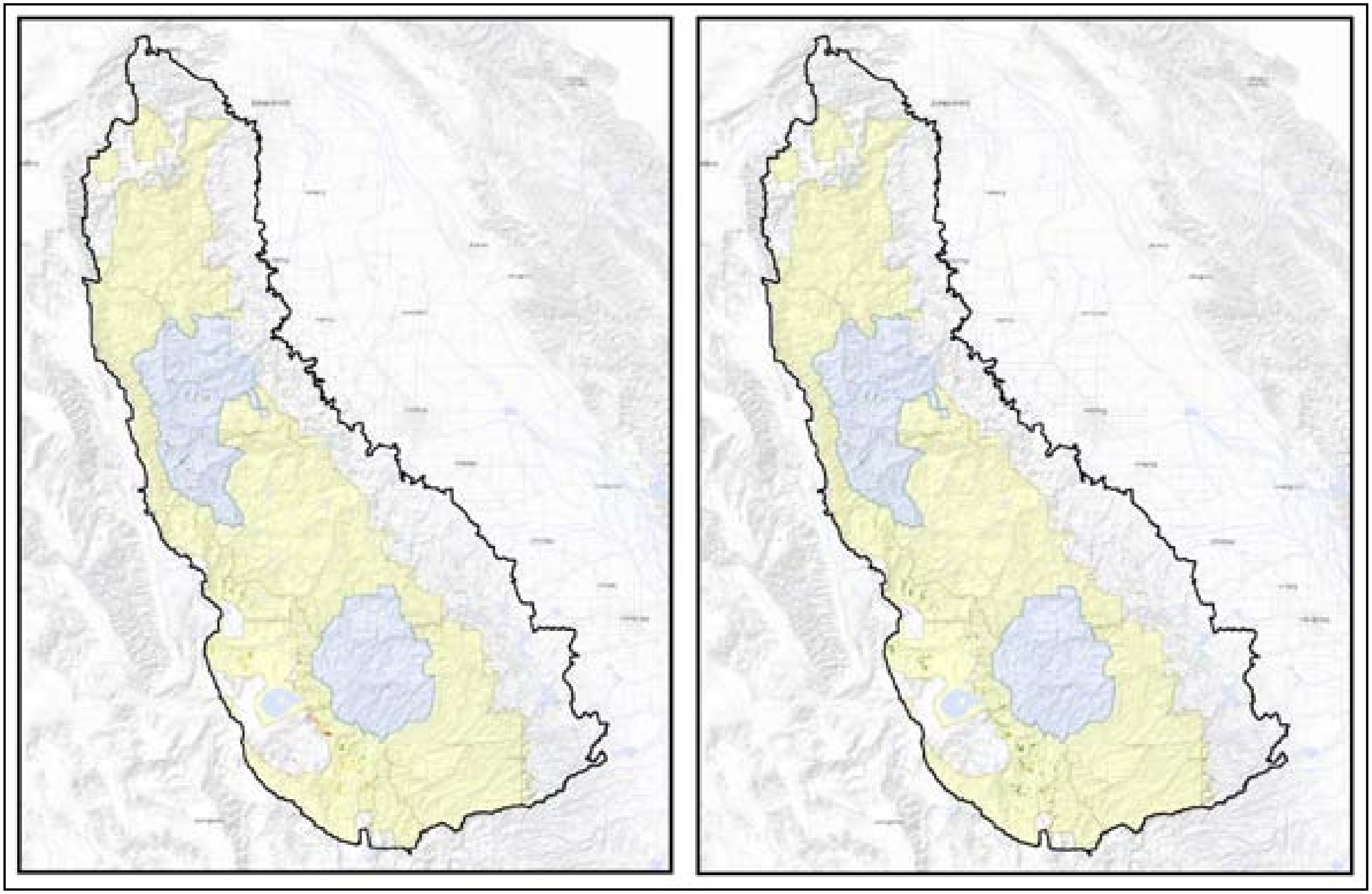


Figure 12. Climate vulnerability assessment for the Southern bioregion (including the Sierra, Sequoia and the Inyo) showing the exposure scores at 2010-2039 for the aspen type and the exposure scores at 2070-2099 using the GFDL climate model. Taken from (Schwartz et al. 2013).



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