The Status of Quaking Aspen (*Populus tremuloides*) in the Sierra Nevada

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BACKGROUND

In this review, I summarize the existing general knowledge of aspen in the western United States, focusing specifically on the Sierra Nevada whenever possible (although see Shepperd et al. 2006 for an extensive report on this topic), and reviewing the current understanding of climate effects on aspen, including sudden aspen decline (SAD).

Quaking aspen (*Populus tremuloides*) is the most widespread tree species in North America (Little 1971, Mueggler 1988). In western North America, aspens are primarily clonal, reproducing by root sprouting (Schier et al. 1985). They are adapted to high resource environments, specifically high light and nutrient levels (Kinney et al. 1997). As a result, many western aspen stands are seral, giving way to conifers that gradually overtop and shade out aspen starting after about 80 years (Mueggler 1985, Rogers 2002). Until then aspen stands can be very hardy, since stems destroyed by pathogens, insects, or fire are replaced by root sprouts. Moreover, about one third of western aspen stands, including most of California's aspen, may be stable, lacking invading conifers and persisting in the absence of disturbance (Sawyer & Keeler-Wolf 1995, Kay 1997). Some studies have indicated that aspen may be particularly vulnerable to precipitation and temperature levels (Hogg et al. 2002, Worrall et al. 2008).

Value

Associated with high levels of biodiversity, water conservation, livestock forage, and aesthetic value, aspen can be managed for multiple uses (DeByle & Winokur 1985, Bartos & Campell 1998).

Aspen is considered a "keystone species" (Bartos 2001), aspen stands a biodiversity "hotspot" (Stohlgren et al. 1999). Aspen stands have the highest vascular plant species richness in the southern boreal forest (Reich et al. 2001), second only to the western juniper/sagebrush association in the upper montane zone of the Sierra Nevada (Potter 1998). Aspen stands support some of the highest bird diversity in the U.S. (Griffis-Kyle & Beier 2003), and the greatest number of bird species in the Sierra Nevada specifically (Richardson & Heath 2004), including providing nesting sites for goshawks. Over 100 vertebrate and invertebrate herbivore species can be found among aspen trees (Lindroth 2008). A Colorado study showed that aspen habitat contains more plant and butterfly species by area than any of the other major vegetation types (Chong et al. 2001), although this depends on soil moisture (Weixelman et al. 1999). Aspen stands provide habitat for wildlife in the form of structural diversity, a dense understory, decay among live stems, and nesting cavities. For example, aspen habitat is important for beavers (Shepperd et al. 2006).

Net water consumption by aspen trees in terms of groundwater and surface water flow is considerably less than by conifers (Jaynes 1978, LaMalfa & Ryle 2008). Researchers have reported decreases of 5% (Harper et al. 1981) and 3-7 inches (Gifford et al. 1984) in water yield to the watershed when conifers replace aspen. This is due in part to their low water use efficiency and also to greater snow accumulation under aspen (LaMalfa & Ryle 2008). As a result, in addition to their high moisture content and herbaceous understory, aspen stands act as fire breaks (Fechner & Barrows 1976, van Wagner 1977, Peet 2000). Aspen-dominated landscapes are less likely to ignite from lightning fire than spruce-dominated landscapes (Krawchuk et al. 2006); in fact, aspen stands have been found to be 200 times less likely to burn than spruce-fir stands (Bigler et al. 2005). However, aspen will burn under very dry conditions (Jones & DeByle 1985). Aspen also retain more nutrients, such as nitrogen, potassium, and calcium, on the landscape compared to conifers (St. Clair 2008).

Physiology

Aspen have high resource requirements. They are shade intolerant (Baker 1949). They have lower water use efficiency and are associated with higher air temperatures, humidity, nutrient-rich soils, and lush undergrowth compared to spruce and fir stands (Ponton et al. 2006, Shepperd et al. 2006). Recruitment is optimal at pH 6 and salinity less than 1000 ppm (Barry 1971). In the Sierra Nevada, aspen are found in sites with a seasonally high water table (Barry 1971).

Sierra Nevada aspen are primarily found mixed in conifer stands, although the eastern Sierra have certain types of pure aspen stands that may perpetuate without major disturbance (Shepperd et al. 2006). Sierra Nevada aspen are found in seven major habitats (Ryel & Bartos 2008): meadow fringe, riparian, upland/conifer, lithic (including talus), snowpocket (with short growing seasons and harsh winter conditions), upland (pure aspen), and krummholz (i.e., stunted, shrub forms). In the southern Sierra, aspens seem to occur most abundantly between 1800 and 3000 m. They occur in pure stands fringing moist meadows (meadow fringe) and in rocky areas with adequate water (Rundel et al. 1988).

Once aspen trees reach maturity, they produce a hormone that prevents young new shoots from suckering. When a tree is killed or stressed, the flow of the suppressing hormone auxin from the crown down to the root system is disrupted and the release of the hormone cytokinin stimulates suckering (Schier 1976, Frey et al. 2003). Some estimate that aspen stands deteriorate around 80 to 120 years, often quite quickly (Shepperd et al. 2006); this likely has a genetic as well as an environmental component.

Western aspen are mostly reliant on clonal reproduction and rarely reproduce from seeds (Barry 1971). Until recently, there were no documented reports of seedling establishment in the Sierra Nevada (Shepperd et al. 2006). Aspen seeds are short-lived with very specific temperature and precipitation requirements (Maini 1968, Fechner et al. 1981). This seems to occur after severe fires, such as after a wildfire in southeast Arizona (Quinn & Wu 2001) or after the 1988 Yellowstone fires. Aspen regeneration from seed may be most effective in marginal stands or in areas with suitable habitat but no living aspen roots. It may become more important with changing climates (Mitton & Grant 1996); aspen seedlings could provide new genetic diversity upon which natural selection can act.

Soil

Appropriate soil condition is one of the most important requirements for aspen establishment and persistence (Mainie & Horton 1966, Renkin & Despain 2001). A study in the Greater Yellowstone Ecosystem (Brown et al. 2006) found that aspen "occurred more often on shale, glacial till, and sandstone parent materials than expected and was less common than expected on calc-alkaline, alluvium, volcanic, and granitic parent materials, based on the abundance of parent material classes in the GYE." Aspen trees grow best in mesic (not too wet or too dry) soil moisture conditions (Frey et al. 2004). They grow poorly in soils that hold too much or not enough water, including sandy soils with poor water-holding capacity (although others have stated that aspens grow best on sandy, welldrained soils (Perala 1990)), on slopes exposed to high light conditions, and in soils that restrict rooting depth (Shields & Bockheim 1981, Landhäusser et al. 2003). Aspen trees are five times more likely to be found on mineral soil than deep organic substrate (Lieffers and Landhäusser 2008).

Aspen stands have more nutrient-rich and warmer soils than conifer stands. Specifically, aspen soil has higher organic matter (due to denser herbaceous layer), higher litter decomposition rate, higher nitrogen, and lower carbon: nitrogen ratio (Amacher 2008).

As aspen age and deteriorate, the soil components change; a study on the Wasatch National Forest in Utah found that concentrations of phosphorus and percent silt were significantly lower on soils with deteriorating clones than on soils with healthy clones (Schier & Campbell 1978). One of the possible causes of conifer succession is that as aspen age and conifers establish, the soil loses its organic layer, leaches nutrients, and becomes more acidic and thinner. Aspen grow much better on their own nutrient-rich soil than on conifer soil, whereas subalpine fir shows no preference (St. Clair 2008).

Recent historic extent

There has been some controversy over the historical extent of aspen in the west over the last several hundred years. Some experts found a 50-96% decline in aspen throughout the western US (Bartos 2001) since the 19th century. In Colorado, which has 50% of the aspen in the western U.S., several studies have given evidence of aspen decline over the last century (Rogers 2002). One study showed that conifers in the Rocky Mountain watershed have increased over threefold since the 1850s, with a 75% reduction of aspen (Gallant et al. 2003; Fig. 1). Others (Wirth et al. 1996) found a nearly 50% decrease in aspen in the Gravelly Mountains of southwestern Montana from 1947 to 1992, primarily from conifer invasion. A tree-ring study in the Sierra Nevada (Potter 1998) showed that aspen was more extensive before 1850. However, some researchers

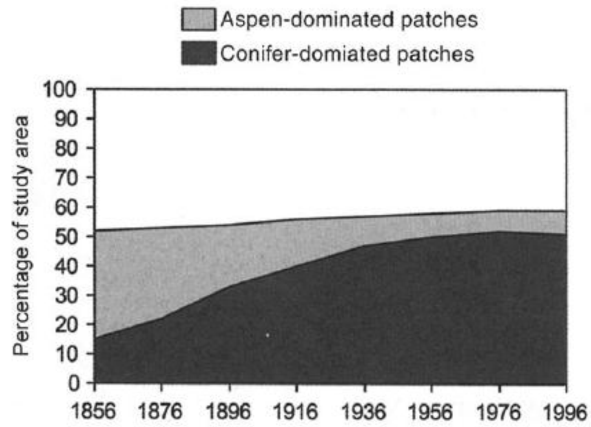

Figure 1. Changes in area of conifer-dominated patches vs. aspen-dominated patches, as modeled through time. (From Gallant et al. 2003)

believe this decline is within the historic range of variability of the species over the last several centuries (Smith & Smith 2005).

Other studies indicate that aspen are not actually in decline. One study showed that much of the Greater Yellowstone Ecosystem (MT, ID, and WY) has only minimally lost aspen or gained conifer cover (Brown et al. 2006). Increased disturbance rates through logging have resulted in a huge increase in aspen dominance in the Great Lakes region (Friedman & Reich 2005) and aspen are very common in Colorado and Utah. Some recent studies found that Rocky Mountain National Park has more aspen than previously thought (6.4%), 25% of that pure aspen, and aspen are still regenerating despite some elk browsing (Kaye et al. 2003, Kaye et al. 2005). Researchers (Manier & Laven 2001) analyzed photographs over time and showed that aspen and conifer cover has increased, and meadows decreased, across Colorado over the last 80-100 years, although many aspen stands are starting to show succession to conifers. Other data show that 90% of trees in Rocky Mountain National Park are younger than 80 years old (Binkley 2008), contradicting evidence that most modern aspen established during the disturbances and fires of the late 19th century and before (Shaw 2008). Some researchers hypothesize that the late 19th century fires, particularly in Colorado, may have unusually increased aspen extent (although slightly decreased aspen density), which may now just be getting back to historical values and are faring well at mid-elevations (Kulakowski et al. 2004, Kulakowski et al. 2006).

Aspen in California have had a slightly different history. Currently, aspen only comprise 1% of the Sierra Nevada forest cover (compared to nearly 10% in Rocky Mountain National Park), although they are disproportionately important due to their biodiversity and physical environment benefits (Thorne 1977, Barbour 1988), and consequently have been studied less than other plant communities. Historic studies have indicated that late 19th century climate and/or disturbance led to more extensive aspen cover than currently exists in the Sierra Nevada (Potter 1998). Mining and logging caused extensive clearing during the late 19th century, as well as sheep grazing, the most widespread disturbance for aspen in the Sierra Nevada (Shepperd et al. 2006). In some areas of the Sierra Nevada, such as Conway Summit in Mono County, the release from intensive grazing has caused a large increase in aspen cover over the last century (Shepperd et al. 2006). The age of most aspen in the Sierra Nevada correlates with the timing of increased fire suppression, conifer encouragement, and grazing (Potter 1998). Likewise, using lodgepole pine, a species that responds comparably to climate and disturbance, as a reference, researchers estimate that aspen increase at the end of the 19th century was due to human disturbance. They extrapolate that climate conditions at the end of the Little Ice Age further increased aspen extent (Shepperd et al. 2006). Although these different causes (human disturbance and changing climate) are difficult to separate (Millar & Woolfenden 1999), genetic and other evidence indicates that aspen were more prevalent throughout the Sierra Nevada in the recent past than they are now (Shepperd et al. 2006).

MANAGEMENT CONCERNS

Disturbance and Succession

Apical dominance, through hormonal control, prevents regeneration in a healthy stand, whereas a disruption in hormonal flow leads to high rates of sprouting. Vegetative reproduction by suckers generally requires a disturbance or dieback that alters the hormonal balance within the system (Schier et al. 1985, Bancroft 1989). Without disturbance such as a fire or mechanical cutting to kill the old trees, some argue (Jones & DeByle 1985, Fites-Kaufman et al. 2007), aspen trees are replaced by grass, shrubs, or conifers and the root system eventually dies out. Although they do not decrease aspen growth or increase mortality, once present conifers prevent aspen establishment until a disturbance (Kaye et al. 2005). According to a study in the central Rocky Mountains, conifer establishment occurs most often early in stand development and after 100 years, although it can occur at other times (Kaye et al. 2005).

Conifer succession is an issue because aspen stands are much more diverse than conifer forests (DeByle 1985) and soil fertility is higher and less acidic underneath aspen than under conifers (Gallant et al. 2003). Further, a study in South Dakota showed that presence of some pine trees in aspen stands does not increase (or decrease) bird diversity (Rumble et al. 2001).

Many experts support this idea that disturbance is required to maintain aspen stands (Bartos & Mueggler 1981, Jones & DeByle 1985, Smith & Smith 2005). For example, the low elk herbivory hypothesis for the Rocky Mountains proposes that anthropogenic burning combined with predation effects on elk has allowed long-term aspen persistence and the suppression of burning and predators has now precipitated aspen decline (White et al. 2003).

On the other hand, researchers (Shepperd et al. 2001, Kulakowski et al. 2004) have found aspen regenerating and stems of various age-classes in the interior west in the absence of fire or other large disturbances. Some (Kurzel et al. 2007) have argued that fire may just eliminate competition but that it is not necessary to trigger sprouting, showing as evidence that some stands lacking conifers regenerate without disturbance. The replacement dieback hypothesis (Mueller-Dombois 1986) predicts that cohort senescence leads to episodic aspen regeneration. Similarly, although a Quebec study showed that aspen volume decreased at about 60 years of age, the exact age of stand decline could not be predicted (Pothier et al. 2004) and a tree-ring study showed no decline apparent by the time aspen reached 120 years old (Kaye et al. 2005).

The resolution of this issue may include both explanations. Bartos and Campbell (1998) characterize three different types of western aspen: stable, seral (successional to conifers), and decadent (dying). Thus, stable aspen stands, e.g., found in riparian areas where wet conditions limit fire and conifer encroachment, may not require major disturbance for continued subsistence, whereas aspen stands in dryer areas may require disturbance to prevent conifer succession (Strand et al. 2009).

Fire

Seral aspen stands are fire-dependent; they increase readily after a severe burn and then gradually turn over to another vegetation type (Bergeron 2000). Fire events every 50 years in an area with just a few aspen can stimulate stand replacement. Although there is some discussion about which aspen ecosystems are seral, there is little debate that fire suppression in the last century in environments where fire is naturally common has led to an increase in conifer extent and decrease in aspen trees across the western United States (Loope & Gruell 1973, Gruell & Loope 1974, Mueggler 1985, Bartos & Campbell 1998). This idea that reduced fire frequency has allowed conifer succession and led to a long-term decrease in aspen extent exacerbated by ungulate browsing, particularly in the Intermountain West, is known as general aspen decline. However, as stated earlier (see "Recent historic extent"), it is argued that this decrease is just a return to historical conditions after excessive widespread disturbance in the late 1800s and early 1900s.

Research in California found that conifers are replacing aspen stands due to less frequent fire and grazing pressures (Jones et al. 2005). In the San Juan Mountains, elevation appears to be the most important correlate with conifer succession; researchers hypothesize that there are more conifers in higher elevations because frequent fire has caused the depletion of the conifer seedbank at lower elevations (Romme et al. 2001).

Pathogens and insects

Many fungal diseases affect aspen, with different levels of lethality and other attributes (Anderson & Anderson 1968, Hinds 1985, Johnson et al. 1995). For example, vulnerability to white trunk rot differs by clone (Jones and Ostry 2008). Genetic variability also affects susceptibility to *Hypoxylon* canker, an important killer of aspen in the Great Lakes area that also appears to depend on site and stand characteristics. Neither of these diseases appears to be stress-related. On the other hand, *Cytospora* canker (Fig. 2), the most common aspen fungus, can cause death in weak, injured, or stressed trees. Black canker is the second most common aspen canker and surrounds trunk wounds, causing deformity but not mortality. Sooty-bark canker, however, is the most frequent cause of aspen mortality in parts of the western U.S. This canker can be seen when dead bark sloughs off the tree, exposing inner black bark; it mainly affects old, large trees at mid-elevation.

Many types of insects interact with aspen as well (Jones et al. 1985a). Outbreaks of western and forest tent caterpillars are notable as they can entirely defoliate an aspen stand. Large aspen tortrix outbreaks can also strip entire canopies, although they are uncommon in California and rarely cause tree mortality, except potentially in high-use areas such as campgrounds. Other defoliators include aspen leaftier, geometrid moths (loopers/panworms/

inchworms), and leafrollers. Aspen leafminers are among the most common insects on aspen throughout much of the West, although they rarely cause mortality. Poplar borers infest all age-classes but especially disturbed stands or stressed trees (Graham & Harrison 1954, Ewan 1960, Hinds 1976) and are apparent from signs of ejected frass and dried sap that accumulate around the hole. Poplar twig borers have a similar effect as poplar borers. Poplar butt borers primarily attack tree bases and have previously caused massive mortality in high elevations in Colorado and Utah. The aspen root girdler mostly infests lightly stocked sucker stands, though it has also been reported to cause root damage in the Midwest (Benson & Einspahr 1967), and is apparent because affected suckers keep their dead leaves over winter. Bark beetles affect dead bark or stressed trees fairly commonly, mining the bark on the trunk and large branches; finally, aphids occasionally are found feeding on aspen.

Figure 2. *Cytospora* canker with bleeding and orange discoloration in dying aspen on Uncompahgre Plateau, CO.
(Photo Courtesy of Jim Worrall, US Forest Service)

Although aspen trees are attacked by many fungal diseases (e.g., cankers) and insects (e.g., stem borers), few are normally lethal. These infestations are more an issue when the trees are stressed by environment or herbivores, such as droughts or elk stripping bark. Furthermore, insects and fungal infestations can have secondary negative effects, such as leading to tree weathering. Also, aspen produce phenolic glycosides to reduce herbivory by gypsy moths, ungulates, etc., at a cost of lower growth. Moreover, at peak infestation, aspen are unable to defend against gypsy moths (Lindroth 2008).

Mammal Impacts

Elk

Elk (*Cervus elaphus*) have been shown to have the most detrimental impact on aspen stand health of any herbivore in North America. For example, elk have been found to be the primary inhibitor of aspen regeneration in Rocky Mountain National Park, much more than fire suppression, natural succession, climatic fluctuations, or other factors (Baker et al. 1997, Binkley 2008). Elk in the central Rocky Mountains decrease aspen establishment and stand-level growth, although they do not appear to affect stem growth or mortality (Kaye et al. 2005). Elk impacts depend somewhat on stand characteristics; aspen density, for instance, is an important determiner (White et al. 2003). A study in Canada (White & Feller 2001) showed that open stands provide a positive feedback loop on elk impact that is difficult to disrupt (elk feed more on open stands, making the stands more open), even when elk numbers are brought down.

In some areas, elk browsing rates are high enough that wildfires or controlled burns without protection of the stand from grazing after fire can lead to the elimination of aspen stands. Studies of the 1988 Yellowstone National Park fires show that extent of burn is irrelevant if the elk density is very high; Yellowstone had no successful aspen regeneration due to ungulate browsing. This is in part due to the trophic cascade effect of removing wolves from the area and thus releasing elk from predation pressure: with wolves gone, elk increased, and aspen decreased (Hebblewhite et al. 2005, Halofsky & Ripple 2008). An historical view makes a strong case: 85% of aspen in Yellowstone NP originated between 1871 and 1920, with only 5% after 1921, coinciding with the removal of wolves from the ecosystem (Ripple & Larsen 2000).

Deer and livestock

Although there are no free-ranging elk populations in the Sierra Nevada, deer may have similar impacts there (Loft et al. 1993). Because mule deer do not feed in such high densities they are not as much of a problem as elk, but deer and cattle together may be (Smith et al. 1972). Deer, sheep, cattle, and wild horses can reduce or eliminate regeneration by destroying suckers (DeByle 1985). Livestock grazing can negatively affect aspen regeneration (White et al. 1998). Effects of wild ungulates and livestock can be reduced by managing around seasonal use patterns and at local scales (Weisberg & Coughenour 2001). Certain areas will be more highly impacted due to browse availability (e.g., snow depths prevented ungulate herbivory on northeast aspects in Wyoming; Kilpatrick & Abendroth 2001, Kay 1990). Similar concerns, and potential solutions, exist for packstock.

Sudden Aspen Decline (SAD)

One issue of major concern for aspen managers is sudden aspen decline, or SAD (Worrall et al. 2008), the rapid death of some or all of a mature aspen stand with little or no regeneration (Shepperd 2008). Although unusual aspen mortality has been seen periodically over the last four decades in the Great Lakes region, Canada, and the interior western U.S, this phenomenon was brought into focus in Utah and Arizona starting in 2002, and soon after in Colorado.

Characteristics

SAD occurs rapidly and simultaneously across a stand, in one to three years (Peterson & Peterson 1992, Worrall et al. 2008). It appears on the landscape as standing defoliated trees that look white (bark still remains), indicating that they died recently. Large trees appear to die first and effects may start at the edge of a stand (Ciesla 2008). Younger cohorts are often not affected (Shepperd & Guyon 2006).

SAD can be distinguished from insect defoliation or frost damage because of complete defoliation in addition to dieback of tree branches (Worrall et al. 2008). There is some concern that roots are dying first (Worrall et al. 2008). This would explain the lack of regeneration that has been seen, although this response may be delayed for a season (Campbell et al. 2008). With complete root death, the aspen stand will eventually succeed to a non-aspen vegetation type. A 2007 study found 0-90% of root volume dead in several stands in Colorado (Worrall et al. 2008).

Incidence

SAD has occurred recently and most noticeably in southwestern Colorado, northern Arizona, and parts of Utah and Canada, but it has also been seen in Idaho, Nevada, Montana, and Wyoming. Data from permanent plots analyzed using remote sensing indicated that the average mortality of aspen in Utah, Nevada, and western Wyoming in 2006-2007 was 31%, two-thirds of that occurring within two years (Hoffman et al. 2008). An aerial survey spotted 56,091 ha of SAD in Colorado (Worrall et al. 2008). In three to four years, mortality increased in four study stands by up to 566%. An estimated 13% of Colorado's aspen cover showed effects of SAD by 2007 (Rodebaugh 2008), with a total of 140,000 acres of aspen lost in the San Juan area alone by 2009 (Sudden Aspen Decline FY 2009 President's Budget Rocky Mountain Research Station 2009).

Outside of the Intermountain West and the Rocky Mountains, SAD extent is unclear. A recent survey in eastern Washington showed no sign of SAD in two national forests

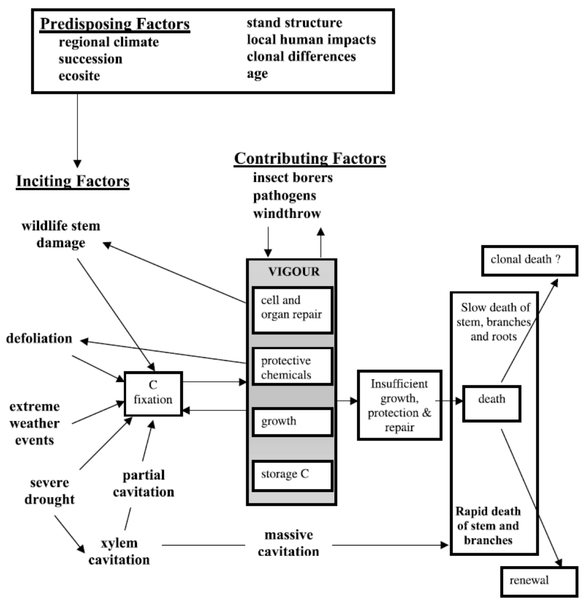

Figure 3: Conceptual model of aspen dieback at the stand level as governed by carbon (C) production and allocation. (Frey et al. 2004)

(Hadfield & Magelssen 2004). Very little survey work has been done to explore the incidence of SAD in the Serra Nevada.

Causes

SAD appears to have a strong climate correlation; most occurrences can be related to high temperatures and drought (Worrall et al. 2008). In addition, SAD-like events seem to occur earlier in areas with higher annual temperatures and/or drier climates (Shields & Bockheim 1981, Hogg & Hurdle 1995). A hypothesis for SAD in the Intermountain West is that drought and hot weather in the early 2000s put stress on aspen stands. A related cascade of events was seen at the same time in western Canada (Hogg et al. 2008). Similarly a drought in 1961 caused ubiquitous mortality in the grasslands of western Canada a few years later, causing direct deaths or secondary deaths from *Cytospora* (Zoltai et al. 1991). Some researchers developed a decline disease hypothesis (Frey et al. 2004, Worrall et al. 2008; Fig. 3): defoliation or a severe drought plus high temperatures during the growing season incite, stand and site factors predispose, and certain insects and pathogens finally contribute to the death of the aspen. Other factors have been implicated, including herbivore impacts and freeze-thaw events (Cayford et al. 1959, Cox & Malcolm 1997, Frey et al. 2004); fine root damage caused by extreme winter freeze followed by drought could cause SAD by reducing water and nutrient uptake (Frey et al. 2004). A similar winter exposure mechanism was implicated in the sudden decline of yellow-cedar in southeastern Alaska (Beier et al. 2008).

Some stands and sites appear to suffer more from SAD: 1) low elevation (Baker & Shaw 2008, Worrall et al. 2008, Brandt et al. 2003); 2) south and southwest aspects (Worrall et al. 2008); 3) and low slope areas. Over 90% of aspen stems have died on some low elevation sites in Arizona, with 16-43% mortality in mid and high-elevation sites (Fairweather & Geils 2008). These factors further indicate a climate component; low elevation sites and southern aspects are generally drier and warmer in the summer. Aspen stands on sloped areas may be better adapted to moisture stress and thus not as affected by acute drought events (Worrall et al. 2008). Further, with changing climates low elevation sites may be receiving less snow and thus may be increasingly less insulated and more vulnerable to freeze-thaw events during the winter. There may also be a correlation with conifer competition, since conifers may not be as present at high elevations.

Although there has been some debate on the issue (Frey et al. 2004), the latest results indicate that SAD vulnerability does not increase with age once trees are physiologically mature (Brandt et al. 2003, Worrall et al. 2008). There is further debate on whether or not size is correlated with SAD; some researchers have shown high DBH trees to be more susceptible (Worrall et al. 2008), whereas others hypothesize that tall thin trees in exposed xeric sites would be most vulnerable (Frey et al. 2004). Just as a drought cause for aspen dieback hypothesizes narrow DBH trees would be most affected, water stress should increase water tension and xylem cavitation and cause dieback in the upper crown first (e.g., in cottonwoods-Rood et al. 2000). It is also unclear whether stand density has an effect (Hogg et al. 2002, Worrall et al. 2008).

Different pathogens and insects appear to be more commonly associated with SAD than with other aspen death (Worrall et al. 2008). Although no single biotic factor appears to be responsible for SAD, five were found to be common in Colorado (Worrall et al. 2008): *Cytospora* canker, poplar borer, bronze poplar borer, and two aspen bark beetle species. These are species that do not normally kill aspen.

ASPEN AND CLIMATE

Preferred Climate

The productivity of aspen appears to be limited by temperature, precipitation, and radiation; ideal conditions are mesic with high light levels, snowfall, and potential evapotranspiration (Brown et al. 2006). Aspen function poorly in hot, dry conditions (Jones et al. 1985b); photosynthesis declines at temperatures greater than 25° C (Lawrence & Oechel 1983), especially when the humidity is low (Dang et al. 1997). Moreover, although aspens can tolerate extremely cold air, they cannot live in cold soils (6° C or less). This is one of the reasons that conifers overtake aspen, since leaf litter cools soil and makes it uninhabitable for aspen. Thus, aspen fare better at lower elevation in northern aspects, but at higher elevations better at southern aspects. However, distinctive aspen features like their clonality and root systems do make them fairly stress-tolerant (Lieffers et al. 2001). In addition, the size and motion of the leaves that give quaking aspen its name are an adaptation to prevent overheating as stomata close to avoid water stress during dry periods (Roden & Pearcy 1993).

A study (Brown et al. 2006) in the Greater Yellowstone Ecosystem (Montana, Idaho, and Wyoming) showed that aspen (1.4% of mapped land area) is found at an average elevation of 2300 m (range=1559-2921), annual precipitation of 70.6 cm (range=33.8-153.4), and temperature of 2.1° C (range=2.2°-6.1° C). In western Colorado, similar to the Sierra Nevada in that fire is rare historically and at present, aspen do better at mid-elevations (2200-3000m) than higher elevations (Romme et al. 2001, Kulakowski et al. 2004). Where solar radiation is high, aspen are found where the growing season PET < 119.7 cm, annual maximum temperature > 6.9° C, and slope > 2.5 deg; where light levels are low, aspen inhabits the converse conditions (PET > 119.7 cm, annual Tmax < 6.9° C, and slope < 2.5 deg). Another study in Manitoba, Canada, found that a hot June led to low radial growth and also found that aspen trees do not depend on early-season water availability, with no effect of temperature in the previous October, unlike bur oak (Boone et al. 2004).

Seedlings require high precipitation for several years to establish (Romme et al. 2001). Seedling establishment may be particularly important in a changing climate since it will offer genetic diversity upon which natural selection can act. There is debate over the age of clones, but if current aspen stands were established in centuries past they may be genetically adapted to cooler climates such as occurred during the Little Ice Age (Barnes 1966, Tuskan et al. 1996).

How Will Aspen Respond To Future Climates?

Precipitation

Aspen is a water-limited, drought-intolerant species (Niinemets & Valladares 2006). Severe droughts have caused the death or decline of aspen in Canada (Zoltai et al. 1991, Hogg et al. 2002). In the western Canadian interior, for example, researchers have found that moisture deficits have a more negative effect on boreal aspen than insects, even severe forest tent caterpillar outbreaks (Hogg et al. 2005, Hogg et al. 2008).

Pathogens and herbivores seem to interact with environmental stress to cause tree mortality. For example, drought conditions in spring and the following summer, or deep late spring snow packs plus summer drought, can cause aspen death through canker infections (Cryer & Murray 1992, Johnston 2001). In Canada, drought does not seem to be a problem except in combination with pathogens or insects. Moreover, drier, warmer conditions may favor gypsy moth invasions (Logan 2008) and forest tent caterpillar outbreaks (Hogg et al. 2002). Drought could also reduce sprouting after a disturbance because of higher susceptibility to insects and pathogens (Sexton et al. 2006).

Mammal impacts can exacerbate drought effects as well, such as in areas of the interior western U.S. (e.g., Rocky Mountain National Park), where the combination of drought, chronic heavy browsing, and the absence of fire seem to be leading to aspen decline (Romme et al. 2001). Climate change may have the strongest effect on areas where aspen are patchily-distributed on marginal habitat and ungulate browsing is heavy (Romme et al. 2001). A study of the Book Cliffs in Utah suggests that the combination of drying climates, displacement by conifers through shading and soil and microclimate effects, and ungulate browsing will decrease aspen cover in the future (Sexton et al. 2006).

Winter precipitation can also have a strong impact on aspen growth and survival. Since aspen stands require warm soil conditions, snow cover is important to protect roots from extreme winter temperatures (Frey et al. 2004), as well as to inhibit ungulate browsing in winter (Martin 2007). However, one analysis of aspen extent showed that, compared to gain or stable plots, aspen cover had decreased in areas with less summer precipitation and more winter precipitation/snowfall (higher potential and actual evapotranspiration, transpiration of ground water, and runoff), fewer annual growing degree-days (cooler), and higher light levels. In other words, mild winters and warmer wetter summers favored aspen, and snowy cold winters and dry bright summers were detrimental to aspen, leading to grasslands and conifer succession (Brown et al. 2006).

Temperature

Future climate changes may bring increased disturbance via storms and fire, which would theoretically increase aspen on the landscape. However, interactions between different factors make the net effect of changing climates difficult to predict. If the climate warms and dries, and if there are other stressors present such as heavy ungulate browsing, aspen may be unable to resprout or establish new seedlings (Romme et al. 2001). One study modeled that aspen in the Canadian boreal will increase productivity for the next 200 years, acting as a large carbon sink; however, prolonged (6-year) droughts during this time would eventually cause severe dieback (Grant et al. 2006).

Fire

Fire frequency will also have an effect on aspen cover. A variety of authors have argued that increased temperatures and decreased precipitation would lead to more frequent fires, which would favor aspen regeneration through suckering (Jones & DeByle 1985, Graham et al. 1990, Schier et al. 1985, Rogers 2002, Elliot & Baker 2004). Moreover, frequent severe fires can deplete the conifer seedbank, leading to a pure aspen landscape (Hogg et al. 2005). In fact, in high-elevation forests with long fire intervals, the natural succession of aspen stands to conifers may be reversed by future stand-replacing fires, especially if the area burned by such fires increases due to climate change (Dale et al. 2001).

CO_2

As atmospheric CO_2 increases, longer roots and thus better nutrient uptake should increase aspen productivity (Pregitzer et al. 2000). One experimental study in Wisconsin showed that aspen growth increased 39% with elevated atmospheric CO_2; growth was especially accelerated with increased moisture (Norby et al. 2005). However, increased O_3 may cancel these positive effects. Moreover, the effects of more CO_2 may decrease over time (Kubiske et al. 2006). Therefore, some researchers stress that the results of elevated atmospheric CO_2 will be complex and difficult to predict (Lindroth et al. 2001, Hogg 2001).

Summary

Some research indicates that future climates will have a positive effect on aspen (Zoltai et al. 1991, Shepperd et al. 2006), while some models hypothesize that conditions will exceed the moisture tolerance of aspen (Nitschke & Innes 2008). Aspen might simply move upslope under future climate change (Ryel & Bartos 2008). However, many researchers see a complicated, unpredictable future, where increased drought and defoliation will vie with CO_2 fertilization and warmer soils to uncertain cumulative effects, likely different in different regions (Hogg 2001). For example, although many have predicted that climate change will increase aspen extent, a modeling analysis in Wisconsin showed that aspen will decline in the boreal forest of the Great Lakes region (He et al. 2002). Finally, the spread of SAD in the western U.S. and Canada may presage future negative effects of warming and drying climates.

MANAGEMENT

Most healthy aspen stands have stems mostly younger than 100 years, adequate sprouting, and an ample herbaceous layer underneath the canopy (Bartos & Campbell 1998). As stated by Campbell and Bartos (2001), with a focus on the Intermountain West, the five risk factors for aspen stands are: "conifer cover (understory and overstory) greater than 25%; aspen canopy cover less than 40%; dominant aspen trees greater than 100 years old; aspen regeneration less than 500 stems per acre (5 to 15 feet tall); and sagebrush cover greater than 10%." They recommend prioritizing treatments in stands where conifers are taller than aspen.

Because of their hormonally-determined apical dominance, many aspen stands require periodic disturbance to stimulate roots to increase sprouting and rejuvenate a new stand (Schier et al. 1985). Aspen stands that are dominated by conifers or that are breaking up and not naturally reproducing may require treatment to regenerate (Mueggler 1989). However, management can target stands with live aspen present in the overstory first to ensure adequate rootstock is available (Gallant et al. 2003).

To restore degraded or over-run aspen stands, managers have a number of options. A good first step is to determine the desired endpoint of the action (e.g., 2000-5000 stems/acre in 10 years and a height increase annually-Experiences and Recommendations from the Field 2008). This will allow an assessment of the effectiveness of the treatment as well the desired endpoint. An effective monitoring plan can be put in place to quantify growth and browsing. Random, non-permanent, circular-shaped plots are recommended (Kilpatrick et al. 2003).

Recommendations for aspen management, developed for the Sierra Nevada but applicable across the West, are to reintroduce natural process and species interactions to the landscape where possible (Shepperd et al. 2006). In other words, allow wildfire, carnivores, and reduce and rotate livestock. Where this is not feasible, there are several options for treatment; four are detailed here.

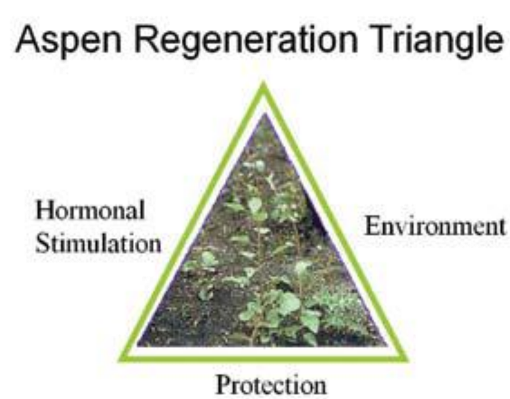

Figure 4. The aspen regeneration triangle illustrates the interdependence of factors that are crucial to aspen regeneration success. (From Shepperd et al. 2001)

Prescribed Burns

Fire is often considered the preferred treatment option for restoring aspen. For instance, the Walker Wildfire on the Santa Fe National Forest (NM) resulted in an average sprout density of 12,960 sprouts/acre, compared to only hundreds in comparable burned areas (Patton & Avant 1970). Fire has the added benefit of returning nutrients to the soil, especially important if conifers have been present for a long time and the soil is poor and acidic. Unfortunately, one of the central benefits of restoring aspen (reducing wildfire risk) makes prescribed fire a difficult option: aspen is hard to burn (Barrows et al. 1976). It also may take several years for trees to die (Brown & DeByle 1987). In mixed stands, one can fell conifers a year ahead to allow them to cure. The season of treatment does not seem to affect aspen restoration (Experiences and Recommendations from the Field 2008).

On the other extreme, it is important to be careful in stands with many conifers, since severe fires in stands with high fuel loads and on certain soil types can damage aspen root systems and reduce regeneration (Perala 1991, Kilpatrick & Abendroth 2001). The Umatilla National Forest in Oregon dealt with this issue effectively when using fire to restore aspen by employing heat-reflecting fire shields and pulling debris away from tree bases (Shirley & Erickson 2001). Another consideration is site characteristics; for example, aspen on slopes appear to be more vulnerable to fire damage than stands on flat areas. Some research has shown that, overall, severe fires actually produce more regeneration than moderate fires (Bailey & Whitham 2002), as long as roots are not damaged. In a similarly complex interaction, researchers showed that intermediate burns are better (result in higher regeneration and arthropod species richness) than severe burn areas where elk density is high since elk browsed most in severe burn areas.

Logging/Cutting

Clearcutting stimulates release from hormone suppression (Patton & Avant 1970, Hungerford 1988) and is most effective in a stand with enough healthy stems to indicate a substantial root system (Shepperd et al. 2006). A study in Minnesota showed aspen stands had higher vascular plant species richness in southern boreal forest postlogging vs postfire (Reich et al. 2001). It can result in a sucker stand of 50,000-100,000 stems/ha (Howard 1996). However, there is a concern that if SAD is causing extensive root death, clones may not be able to regenerate and cutting may result in a cleared landscape (Schier 1975). Partial cutting will still increase the suckering response but much less than clearcutting since trees are still shaded and not as many roots are stimulated.

With heavy mechanical treatments, it is important to be careful of deep cutting or soil compaction (Lieffers & Landhäusser 2008). One study on the Uncompahgre Plateau showed that areas with 2 or more of the following could prevent resprouting (Johnston 2001): soils compacted by logging thin soils, heavy browsing pressure, and a seasonally high water table (e.g., low slope angle). As with burning, it is recommended to cut and remove logs in a single year to avoid damage to suckers.

Other Mechanical Treatments

Because of aspen's hormonal suppression system, one option to trigger sprouting is to sever or scrape roots via mechanical root stimulation (Fraser et al. 2004). This is done using a single-toothed ripper or similar equipment that cuts the connection between roots and shoots, thus releasing the plant from apical dominance. This is a particularly good method for meadow fringe aspen where roots are extending into potential habitat (Ryel & Bartos 2008).

If done correctly, bulldozing can yield great results: a project that used a rubber-tire skidder to simply push trees over obtained an average 37,888 stems/ha after slash was removed, over twice the density that resulted from clearcutting (Shepperd 1996).

Another option is to hand or mechanically thin conifers or aspen from stands. Thinning allows light through the canopy and stimulates aspen growth.

Herbivore Exclosures

The choice of exclosure will depend on browsing pressure, which varies by year and site. It is critical to measure ambient browsing pressure before conducting a burning or cutting treatment on aspen (Kay 1997). In some areas, particularly with elk present, a failure to protect aspen from browsing post-treatment will wholly prevent regeneration (Fig. 5). Even aspen suckers 4 meters high after being protected for 8 years were brought down (<1m) when exposed to elk browsing (Renkin & Despain 2001). Fencing can be a solution to this problem. It is important to fence immediately and for several years and to avoid early and late season livestock use. Smaller exclosures (e.g., <0.05-.25 ha) are recommended in order that ungulates try to move around, instead of through, them (Shirley & Erickson 2001, Bartos 2008). Eight foot net wire has been used effectively to keep out elk (Experiences and Recommendations from the Field 2008). Others recommend 6.5 foot buck-and-pole fences since they require little maintenance and last long enough for sprouts to grow above browse height. In some areas (e.g., Arizona), fences may need to be in place for as long as 15 years to prevent severe elk damage (Rolf 2001).

Creative methods of fencing have also been shown to be effective. Several conifers can be felled to create a small box around an area to act as natural refugia for suckers. Hinge fencing can reduce grazing by 40% with a cost of less than $500/ha, whereas wildlife fence may reduce grazing to 0% but at a high cost of more than $10,000/ha. Slash can also be used as livestock fencing (also known as jackstrawing). Both slash and hinge fencing might have other benefits of shading, water-retention, and wildlife habitat (Bartos 2008). Wherever possible, it is recommended that fences be set at least 50 feet outside the previous aspen edge, as the root system often extends further than is apparent (Experiences and Recommendations from the Field 2008).

In areas without elk or high density deer populations, it is still important to limit use of treated areas by domestic animals for several years (Campbell & Bartos 2001). This short-term reduction will lead to a long-term browse resource once the aspen stand is large enough. Another option is to treat a large area to swamp grazers and browsers, although in areas of high elk density (e.g., Yellowstone National Park) this has not worked in the past.

Trade-offs

Older aspen stands offer benefits to the landscape that are reduced, however temporarily, when stands are treated. Birds use dead and dying aspen stems and large conifer snags and logs. Some believe that conifer succession is a natural process and future natural disturbances will be sufficient (Knight 2001). Others have argued that since fire frequency may be increasing with climate change, and late-successional aspen have aesthetic and biodiversity benefits, no proactive measures may be required (Romme et al. 2001). Fire and other disturbances may also encourage invasives. Aspen in particular, with their moist habitat, rich soils, and exposure to light and disturbance, are conducive to promoting invasive species. In fact, nonnative species were found in aspen ecosystems much more commonly than other vegetation types in a study in Colorado (Chong et al. 2001), perhaps in keeping with their general increased biodiversity. In some cases, a solution could be to use targeted, smaller fires, which can still have desirable effects (Fule & Laughlin 2007). Fortunately, aspen, with its many benefits in terms of biodiversity, water conservation, and natural beauty, can be managed for many purposes at once.

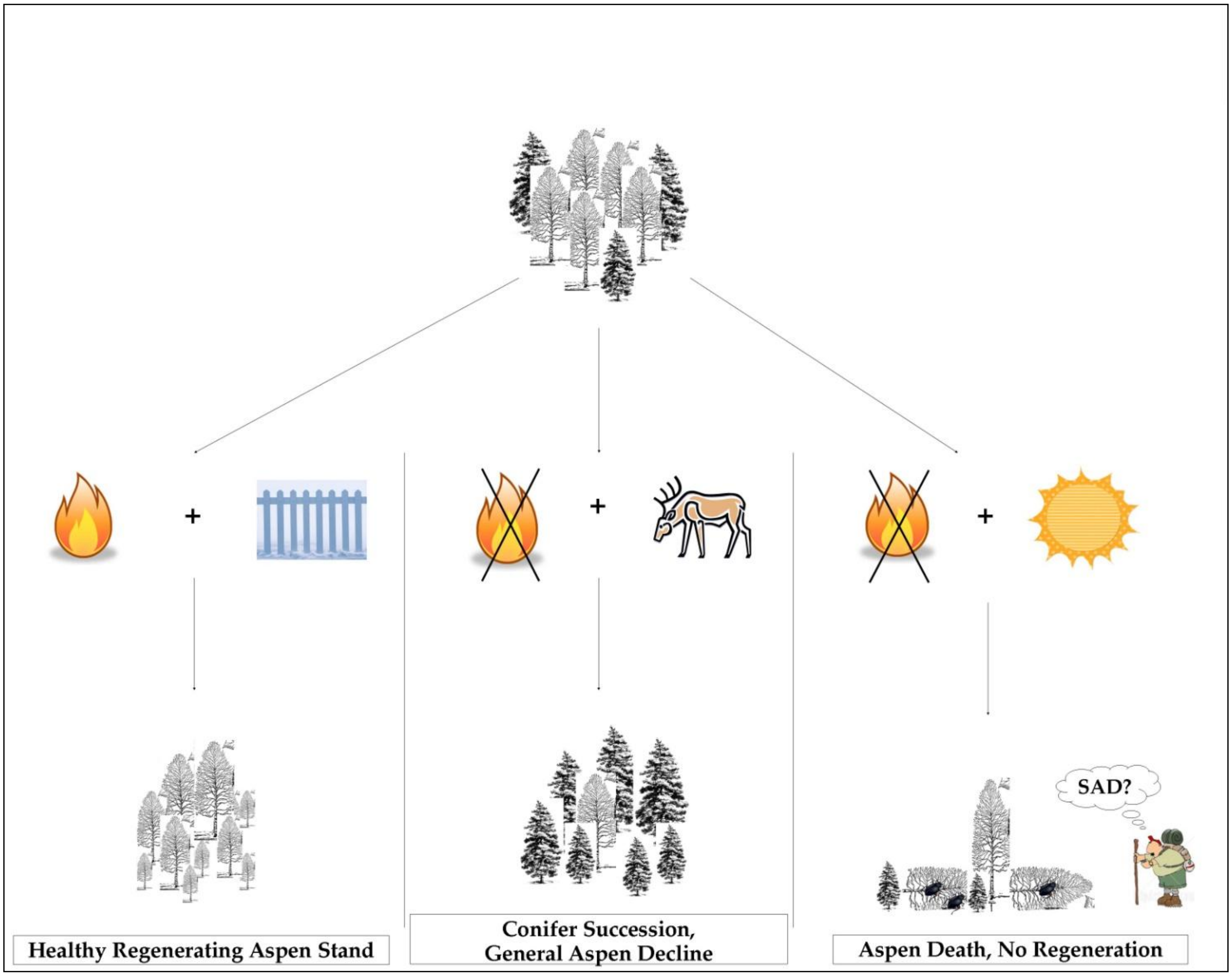

Figure 5. The distinction between the causes of general aspen decline and sudden aspen decline (SAD). Healthy regenerating aspen stands generally result from disturbance, such as fire, and protection from severe browsing effects. Lack of disturbance, exacerbated by intensive ungulate browsing, can lead to conifer succession, known as general aspen decline. Alternatively, increased temperatures and decreased precipitation, intensified by insects and pathogens, may be leading to SAD.

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Appendix I: Ongoing/Previous Projects

1. Lake Tahoe Basin Management Unit Aspen Community Restoration Project (2009)
    a. Lake Tahoe Basin Management Unit, CA
    b. To restore approximately 1,115 acres of aspen stands over the next ten years
    c. http://www.fs.fed.us/r5/ltbmu/projects/local/aspen-rest.shtml
    d. Contact Victor Lyon (Project Leader): 530-530-2749/vlyon@fs.fed.us

2. Sunflower Aspen Restoration Project (2007)
    a. Ochoco National Forest, Paulina Ranger District, OR
    b. Protect and enhanced 15 acres of habitat in 2 stands using buck and pole fence exclosures and removed pine and juniper.
    c. www.fs.fed.us/r6/nr/fp/Stewardship/sp_och_south_**aspen**.doc
    d. http://gis.fs.fed.us/r6/centraloregon/news/2008/06/20080604_aspen_restoration.pdf
    e. Contact Paul Smith (Biology Tech): 541-477-6920

3. Evaluation of Pine Creek Aspen Stand (2005)
    a. Eagle Lake Ranger District, Lassen National Forest, CA
    b. Surveyed a small aspen stand and recommended treatment
    c. http://www.fs.fed.us/r5/spf/publications/nessa/Pine_Creek_Aspen.pdf
    d. Contact Daniel Cluck (Entomologist): 530-251-2151/dcluck@fs.fed.us

4. Aspen Dahlgreen Prescribed Fire (2008)
    a. Evanston-Mt. View Ranger Districts, Uinta-Wasatch-Cache National Forest, WY
    b. Conducted a prescribed fire to regenerate aspen stands
    c. http://www.utahfireinfo.gov/rx/Aspen%20Dahlgreen/Aspen_Dahlgreen_NR_07_02_08.pdf
    d. Contact Kathy Jo Pollock (Public Affairs Specialist): 801-236-3409

5. Shoshone aspen restoration project (2003)
    a. Shoshone National Forest, Wind River Ranger District, WY
    b. http://www.fs.fed.us/r2/shoshone/news/2003/2003_0320_recovering_aspen_stands.htm
    c. Contact Ellen Jungck (Silviculturist): 307-455-4164

6. Harris Park Fuels Management Project (2005)
    a. Pike and San Isabel National Forests, Comanche and Cimarron National Grasslands, CO
    b. http://www.fs.fed.us/r2/psicc/spl/harrispark_fuels.shtml

7. Lassen National Forest Aspen Restoration
    a. Eagle Lake Ranger District, CA
    b. Successfully used timber harvest and hand thinning of conifers to regenerate aspen habitat
    c. Jones et al. 2005
    d. Contact Bobette E. Jones: 530-252-5816

8. Northern Colorado Front Range aspen survey (2006)
    a. Canyon Lakes District, Arapaho-Roosevelt National Forest, CO

   b. Kashian et al. 2007
   c. Contact Claudia Regan (Ecologist): 303-275-5004

9. Aspen Delineation Project (ongoing)
   a. Created to assess the state of knowledge and management efforts regarding aspen on public lands in the Sierra Nevada, Southern Cascades, and Great Basin
   b. http://www.aspensite.org/
   c. Contact David Burton: 916-663-2574/peregrines@prodigy.net

10. Quaking Aspen Stewardship Project
    a. PRBO Conservation Science Sierra Nevada Program
    b. http://www.prbo.org/cms/377
    c. Contact Stella Moss: 707-781-2555

Appendix II: Aspen Web Resources

- Aspen Delineation Project: www.aspensite.org/

- California Department of Fish and Game Aspen Delineation Project Data Center: http://www.dfg.ca.gov/rap/projects/aspen/

- Northern Rockies Aspen Working Group: www.aspensite.org/NorthernRockiesAspen.html

- Riparian Bird Conservation Plan: www.prbo.org/calpif/htmldocs/riparian.html

- US Forest Service PSW Sierra Nevada Research Center: www.fs.fed.us/psw/programs/snrc/

- US Forest Service RMRS Aspen Restoration Site: www.fs.fed.us/rm/aspen/

- Western Association of Fish and Wildlife Agencies (WAFWA) Habitat Committee: www.wafwa.org

- Western Aspen Alliance (WAA): www.western-aspen-alliance.org