THESIS

ASPEN MORTALITY IN THE COLORADO AND SOUTHERN WYOMING ROCKY MOUNTAINS: EXTENT, SEVERITY, AND CAUSAL FACTORS

Submitted by

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ABSTRACT

ASPEN MORTALITY IN THE COLORADO AND SOUTHERN WYOMING ROCKY MOUNTAINS: EXTENT, SEVERITY, AND CAUSAL FACTORS

Quaking aspen *(Populus tremuloides* Michx*)* is a deciduous hardwood tree widely distributed throughout North America. In Colorado, quaking aspen is found on a wide variety of sites, from the lower-elevation foothills of the eastern edge of the Rockies to moderate- and high- elevation montane sites throughout the Rocky Mountains. Aspen dieback has been documented throughout western North America over the past decade, resulting in stands that have either elevated proportions of overstory mortality or thin crowns, or both. Stands experiencing dieback may or may not produce regeneration cohorts. In this study, we surveyed aspen in the north-western corner of Colorado on the White River and Routt national forests, along the front range of Colorado on the Pike-San Isabel national forests, and in the south-central region of Wyoming on the Medicine Bow national forest during 2009 - 2010.

We established 573 random roadside survey plots in stands that contained at least 50% aspen cover type. From these random plots, we found average standing aspen tree mortality ranged from 3.3 to 23.7 % on the four national forests and 11% on the east side of the continental divide and 4 % on the west side. Low elevation stands had significantly less mortality (7%) vs. high elevation (8%). The roadside plot data suggests that Colorado's aspen on these four national forests overall were healthy; mortality rates

among aspen were fairly low (~3 – 8%) among all stems, and average percent live crown among adults was high (~85 – 90%), in spite of nearly ubiquitous presence of disease (~97 – 99%) and high incidence of insect damage (~50 – 75%).

We also established 98 aspen stand assessment plots with half of the plots in damaged stands, as defined by U.S.D.A. Forest Service aerial detection surveys (ADS), and half in healthy aspen stands. Damaged stands were defined as those stands with (1) thinning crowns among at least 25% of adult aspen, (2) stands with moderate (<50% of stems) levels of overstory mortality, or (3) stands with high (>50% of stems) levels of overstory mortality. Healthy aspen stands were defined as having (1) a maximum mortality rate of 5 - 7% among all aspen, and/or (2) more than 75% of adult aspen with full crowns.

Adult aspen in damaged stands tended to be less vigorous, based a health score index from 1 to 5, with higher scores indicating less healthy conditions (where 1=0-25% damage; 2 = 25-50% damage; 3 = >50% damage; 4 = recent dead; 5 = >5 years dead). Health scores averaged 1.7 in healthy stands, compared to 2.3 in damaged stands. Saplings in damaged stands tended to be healthier with a score of 1.7, compared to 2.2 in healthy stands. Further, there was no difference in the proportion live or total numbers of saplings per hectare between healthy and damaged stands. The prevalence of damaging organisms, such as *Cytospora* canker (20% in damaged, 13% in healthy), wood-boring insects (27% in damaged, 10% in healthy), and aspen bark beetles (16% in damaged, 7% in healthy) was considerably greater among damaged stands. Site conditions also influenced the prevalence of some of these damage agents: bark beetles were most common among stands at low elevations (18%, compared to 11% and 6% at moderate and high elevations, respectively); *Cytospora* canker was most common among stands on south- or west-facing aspects (20% and 19%, respectively); both aspen bark beetles and *Cytospora* canker were also most common among stands in the southernmost section of the survey area, the Pike-San Isabel national forest (41% and 36%). There was no difference in the severity of canker or decay fungal infection between healthy and damaged stands. *Cytospora* canker infestations were more severe on the Medicine Bow NF compared to the other three national forests, and *Marssonina* foliar blight infection appeared to be most severe on slope summits, concave sites, and sites with either no to low percent slope or moderately steep slopes.

Based on the general state of aspen health within the study area, it appears that aspen in damaged stands were experiencing more severe environmental stress (e.g., late frost, drought, defoliation) and coupled with disease and insect infestations, resulted in greater mortality when compared to healthy stands. The severity of such conditions appears to be regional in scale, and it remains to be established that long-term or acute drought is the major factor influencing the observed conditions. Since no differences were detected in regeneration density between damaged or non damaged stands, it is possible that there will be no long-lasting effects on aspen longevity on these sites with the relatively low incidence of overstory mortality throughout all four national forests.

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Chapter 1: Biology of *Populus tremuloides* Michx. and Associated Damage Agents

Biology and Growth

Populus tremuloides Michx. is a deciduous hardwood tree widely distributed throughout North America, with a broader geographic range than any other native tree species (Little, 1971). This tree assumes a clonal growth habit, and vegetative propagation is its primary method of reproduction. Root suckers originate from shoot meristems that occur within the cork cambium (Scheier, 1973). Apical dominance of the adult ramets is maintained by a steady flow of the plant hormone auxin, which is produced in the phyllosphere and transported to the roots (Eliasson, 1971). Removal, wounding, or death of the adult trees results in rapid declines in root auxin levels, which initiates suckering (Eliasson, 1971, 1972). Suckering is suppressed by the interaction between auxin and cytokinin, two phytohormones produced in the rhizosphere (Winton, 1968 and Wolter, 1969). Low ratios of cyokinins to auxins inhibit shoot initiation; high ratios promote shoot initiation (Winton, 1968 and Wolter, 1969). This species is dioecious, and both male and female flowers form as catkins (Jones, 1985).

Barnes (1966) determined that aspen seedlings may initiate suckering soon after establishment. The number of original seedlings (or 'ortets') in an aspen stand has been found to be inversely proportional to the clone size, regardless of site conditions (Barnes, 1966). Other differences, such as varied width: length ratio and serration patterns of leaves may vary with genotype (Barnes, 1975). Grant and Mitton (1979) observed major distributional differences between male and female aspen; female aspen dominated lower elevations (to 2,450 m) but were in the minority at high elevation sites (> 2,900 m). Female clones also appear to have a higher annual radial growth rate than males, regardless of elevation (Grant and Mitton, 1979).

Genotype also appears to influence the levels of defensive foliar compounds, such as phenolic glycosides, and thus the susceptibility of the phenotype to defoliating insects (Donaldson and Lindroth, 2007). Similarly, recent work by Stevens and Esser (2009) indicates that there are gender differences in the amounts of two allelochemicals produced relative to growth. The production of condensed tannins, which are important protective compounds against phytopathogenic fungi and bacteria, appears to be more costly for female aspen than for males (Stevens and Esser, 2009). Phenolic glycosides, another major allelochemical, did not appear to be more costly to the females compared to the males (Stevens and Esser, 2009). Phenolic glycosides (PGs) are effective in deterring herbivory and defoliation by many foliage-feeding insects (Stevens and Esser, 2009). Overall, male and female aspen produce similar amounts of both defensive compounds (Stevens and Esser, 2009). A similar study by Smith, et al (2011), shows that phenolic glycoside concentrations are highest among young aspen, with the largest reduction in PGs occurring in young trees between ages 10 and 20 (Smith, E.A., et al, 2011). The same study showed that condensed tannin (CT) concentrations increase as trees age (Smith, E.A., et al, 2011).

Responses to drought tolerance (Griffin, et al, 1991), elevated ozone (Berrang, et al, 1991), and elevated carbon dioxide (Lindroth, et al, 2001), have all been shown to be phenotypically variable.

Soils

In Colorado, aspen grows in soils with a wide variety of textures (Jones, unpublished data). In Wisconsin, aspen grow best on sites with at least 3-4 feet of well drained topsoil (Fralish and Loucks, 1967). Saxton and Rawls (2006) determined that there is a strong relationship between the silt content in a particular soil and its water-holding capacity. However, Hancock, et al, (2008), showed that aspen grown in soils with a high sand and low clay content produce significantly more total biomass than do individuals grown in soils with high clay content.

Soil nutrient deficiency can have variety of impacts on aspen. For example, aspen tend to respond to nitrogen deficiency by producing smaller leaves, which results in a decrease in net photosynthesis (Greitner, et al, 1994). Burks (1994) theorizes that nitrogen deficiency may also increase the severity and incidence of cankers caused by *Cytospora chrysosperma* (Pers.:Fr.) Fr. Daubenmire (1953) found that aspen leaf litter contained higher levels of nitrogen, phosphorus, potassium, and calcium in comparison with a variety pine and fir species.

Drought & Climate Change

Acute Drought

Studies indicate that, like most other tree species, growth rates of aspen are a function of climatic factors combined with various site and soil characteristics (Hogg, et al, 2008). The impacts of drought on *P.tremuloides* includes a decrease in leaf area index (LAI), which continues to be affected up to two years following the drought event (Krishnan et al, 2006). The same study determined that ecosystem respiration rates respond more quickly to drought onset, and are more sensitive to the end of a drought period than are ecosystem photosynthesis rates. This can be attributed to the fact that respiration rates are influenced by near-surface water content in soils, whereas photosynthesis rates are influenced by soil water content deeper in the rhizosphere (Krishnan, et al, 2006). In aspen, the severity of drought stress impacts the degree to which root water flow properties are altered (Siemens and Zwiazek, 2003). Severely-stressed individuals display an inhibition of root hydraulic conductivity, as a result of an increase in the ratio of apoplastic to cell-to-cell water transport (Siemens and Zwiazek, 2003).

Drought also impacts the susceptibility of aspen to canker-causing fungi. A 1996 study showed that aspen inoculated with *Cytospora chrysosperma* (Pers.:Fr.) Fr. and exposed to drought conditions had significantly larger cankers one week after inoculation than did non drought-stressed trees (Guyon, et al, 1996). The same study also tested host susceptibility to *Cytospora* canker under waterlogging and defoliation conditions. Only trees that had been subjected to 75-100% defoliation showed increased canker size, relative to control trees (Guyon, et al, 1996).

Climate Change & Atmospheric Composition

In their 2009 study, Rehfeldt, et al, utilized several different General Circulation (GCM) and emissions models to predict the range of 74 western U.S. forest species in 2030, 2060, and 2090. Based on these models, the authors predict a reduction in the current range of *P. tremuloides* by 6-41% by 2030, and 46-95% by 2090 (Rehfeldt, et al, 2009). The authors also note that the future range of aspen is likely to occur on sites with elevations as much as 1000 meters higher than those found today (Rehfeldt, et al, 2009).

Changes in atmospheric composition are known to affect affect the health and growth rate of aspen. For example, tropospheric ozone, O_3, has been shown to alter leaf surface characteristics in *Populus tremuloides* Michx., and increased concentrations of ground-level ozone may make trembling aspen more susceptible to fungal attack (Karnosky, et al, 2002). Like many other tree species, ozone accelerates maturation and foliage senescence in *P. tremuloides* (Greitner, et al, 1994).

Experiments featuring elevated carbon dioxide (CO_2) have indicated initial increases in relative growth rates (RGR) in aspen, although growth rates subsequently decrease, possibly due to limited plant available nutrients (Brown, K.R., 1991). Lindroth et al (2001) found that aspen genotype strongly influences how an individual responds to an atmosphere of enriched CO_2. More specifically, researchers noted the differential response of aspen clones with respect to relative growth rates, including root: shoot ratio, and stem growth (Lindroth, et al, 2001). In an environment of enriched ozone and carbon dioxide, the initial positive influence of CO_2 on growth did not completely offset the negative influence of tropospheric ozone on tree physiology (Percy et al, 2002).

Disturbance & Regeneration

Aspen is known to regenerate prolifically following a stand-replacing fire (Scheier and Campbell, 1978). Fire intensity impacts sucker production; deeper parent roots tend to produce more suckers in areas where fire intensity was high, as compared to sucker production from shallower parent roots (Scheier and Campbell, 1978). Similarly, Perala (1995) found a 28% decrease in productivity after parent roots were injured during high-intensity burns. However, studies by Kulakowski, et al (2006) and others have shown that severe fires on Colorado's western slope generally result in a temporary 'pulse' in aspen covertype. Therefore, some caution should be taken in generalizing fire effects on aspen over different ecosystems (Kulakowski, et al, 2006). It has been hypothesized that with the recent, massive die-off of Lodgepole pine (*Pinus contorta* Douglas ex. Louden) due to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) infestation, will result in increased aspen covertype throughout the area. At this time, it is uncertain to what degree aspen will populate areas formerly occupied by lodgepole pine stands, though a recent study of post-outbreak forest structure within Rocky Mountain National Park indicates that there has been a slight increase in aspen covertype (Diskin, et al, 2011).

Fungi

A wide variety of necrotrophic and decay fungi attack aspen. These organisms range in pathogenicity; some, like *Cytospora chrysosperma* (Pers.:Fr.) Fr. (telemorphic form, *Valsa sordid*), are ubiquitous, existing as weak saprophytes on the bark surface, and cause damage only when the host is experiencing stressful environmental conditions (Sinclair, et al, 2005). When such favorable conditions do exist, *Cytospora* rapidly kills cambial tissue, effectively girdling and killing the host tree over several years (Bloomberg, W.J., 1962a; Bloomberg, W.J., 1962b). Others, such as sooty bark canker (*Encoelia pruinosa*)¸ is an aggressive and lethal pathogen on aspen, which gains access to the phloem through small breaks in the cork cambium (Hinds and Ryan, 1985). Black canker (*Ceratocystis fimbriata*), is common throughout Colorado aspen stands (Worrall, et al, 2011; field observation, M. Dudley). This phytopathogenic fungus causes rough-edged, target-shaped cankers on aspen as it kills newly-formed cambium while the host tree is dormant (Hinds, 1972b). Though not as common on aspen in the western United

States, *Hypoxylon mammatum* (Wahl.) Mill. is a canker-producing fungus, which may significantly reduce yield in silvicultural settings (Enebak, et al, 1996). Cankers caused by this fungus spread rapidly among drought-stressed aspens (Bagga and Smalley, 1969). Finally, *Cryptosphaeria lignyota* forms narrow, elongated cankers on host trees, and is usually associated with large wounds to the cork cambium (Hinds, 1981).

Of the many decay fungi found on the bole of aspen, *Phellinus tremulae (*Bond.) Bond. and Borisov is a major cause of wood volume loss in Colorado aspen stands (Hinds and Wengert, 1977). This fungus causes a white rot of the heartwood and sapwood of the tree, but rarely spreads below the root crown (Ross, 1976a). Another decay fungus affecting the stem of aspen trees is *Peniophora polygonia* (Pers.), which enters through wounds or other openings in the cork cambium and develops into a yellowish, stringy (Etheridge, 1961). Decay fungi commonly found in the roots of quaking aspen include *Flammulina velotipes, Ganoderma applanatum* (Pers.) Pat., and *Armillaria ostoyae* (Vahl.: Fr) Kummer. *F. velotipes* is generally associated with basal wounds, and forms a white and brown mottled decay in the roots (Hinds and Wengert, 1977). *Ganoderma applanatum* (Pers.) Pat. also enters the host through wounds, and subsequently attacks many parts of the butt, including the sapwood, heartwood, and cambium (Ross, 1976a). This rot, which is whitish in appearance, eventually rots larger roots and may cause extensive windthrow (Ross, 1976b). *Armillaria ostoyae* (Vahl.: Fr) Kummer is found on a wide variety of forest trees, and has often been described as a saprophyte (Basham, 1958). However, Armillaria is also known to kill roots and decrease sprouting (Basham, 1958). Although this pathogen has long been considered a secondary pest, a 2003 study by Brandt, et al, found *Armillaria* to be a primary pathogen of aspen in the boreal forests of Canada. To date, there is little to no data on *Armillaria* occurrence on aspen in Colorado.

Numerous pathogenic fungi colonize the foliage of *P. tremuloides*. Among the most common is *Marssonina populi* (Lib.) Magnus, which causes black spot of aspen (Spiers, 1984). Affected foliage displays irregular brownish patches surrounded by a yellowish 'halo' (Spiers, 1984). Each brown patch often include up to several acervuli (Spiers, 1984). Ink spot of aspen is caused by two or more species of the fungus *Ciborinia* (Groves and Bowerman, 1955). Affected foliage turns brown, and black spots form (sclerotia) (Baranyay and Hiratsuka, 1967). The sclerotia may fall out of the leaf, leaving circular to ellipsoid- shaped holes (Baranyay and Hiratsuka, 1967). This disease tends to be more severe on smaller trees (Baranyay and Hiratsuka, 1967). Shepherd's Crook of aspen, caused by *Venturia moreletii* (anamorph *Pollacia radiosa*), causes a blight of leaves and twigs (Holeski, et al, 2009). Under wet conditions, this pathogen may kill many to all regenerating terminal shoots in an aspen stand (Sinclair and Lyon, 1987). Symptoms include small black spots on foliage, which enlarge and eventually kill the leaf as it spreads downward through the petiole (Sinclair and Lyon, 1987). As the fungus spreads further, the terminal shoot blackens and curls, forming the characteristic 'shepherd's crook' shape (Sinclair and Lyon, 1987). Leaf rust of aspen is caused by *Melampsora medusae* Thumen, a fungus which requires two hosts: a conifer (Douglas fir, *Pseudotsuga menzesii* (Mirb.) Franco) and aspen (Sinclair and Lyon, 1987). On aspen, this fungus is found as teliospores (found on the abaxial leaf surface as yellow spots) and urediospores (Ziller, 1974). Aspen are (usually) not seriously impacted by *M. medusa*, although studies conducted at the Free Air Carbon Enrichment (FACE) experimental site in Rhinelander, Wisconsin showed that hosts subjected increased tropospheric ozone levels have shown to be more susceptible to attack by *M. medusa* (Karnosky, et al, 2002).

Insects

Many insect species feed on the bole, stem, and twigs of aspen, including species in the orders *Coleoptera* and *Lepidoptera*. Commonly-found insects in aspen of the western U.S. include two bark beetles (*Trypophloeus populi* Hopkins and *Procryphalus mucronatus* (LeConte)), several borers (*Agrilus liragus* Barter & Brown, *Poecilonota cyanipes* (Say), and *Saperda calcarata* (Say) among others), and an assortment of foliar insects, including leafminers, tiers, and rollers (Jones, Debyle, and Bowers, 1985; Jacobi, W.R., personal communication).

Both species of bark beetle that attack aspen prefer hosts which are dying or otherwise stressed (Petty, 1977). *Trypophloeus populi* Hopkins and burrows a small (2 cm in length) egg gallery just beneath the bark surface (Petty, 1977). One to one and a half generations are produced each year, and individuals overwinter in the larval stage (Petty, 1977). Invasions by this beetle are often followed by *Procryphalus mucronatus* (LeConte). However, unlike *T. populi*, *P. mucronatus* targets dead, softened and fermenting aspen bark (Furniss, 1987). The egg galleries formed by this species are narrower and placed deeper within the bark than those of *T.populi*. *P. mucronatus* is known to produce one and a half to two generations per year (Petty, 1977).

There is one species of Ambrosia beetle found on trembling aspen, *Typodendron retusum*, which is found throughout the western U.S. (Hinds and Davidson, 1972). The beetle, which is dark brown or black with a yellow stripe across each elytra, tunnels into the sapwood of the host tree to a depth of about 1 cm and then turns at a right angle to its point of entry and forms a tunnel around the entire circumference of the tree (Hinds and Davidson, 1972). This species attacks both healthy and dying trees, and creates patches of dead tissue on the host tree (Kuehnholz, et al, 2001).

Two species of wood borers, *Agrilus liragus* Barter & Brown (the bronze poplar borer) and *Saperda calcarata* (Say) (the poplar borer) are commonly found on aspen. *A. liragus* is a Buprestid beetle native to North America and has been observed feeding on five species of *Populus* (Barter, 1965). The adults emerge in late spring and feed on aspen foliage (Barter, 1965). Females lay their eggs in small lots (5-8 eggs/ lot) in bark crevices (Barter, 1965). The larvae emerge about two weeks later and begin to bore into the cambium, and eventually bores a pupal cell in the outer xylem of the host tree before overwintering (Barter, 1965).

Similarly, *Saperda calcarata* (Say) is known to attack many species of *Populus* throughout North America (Broberg and Borden, 2005). *S. calcarata* appears to favor weakened hosts (Hanks, 1999). The females of this cerambycid lay their eggs in chewed furrows in aspen bark (Kukor and Martin, 1986). Larvae emerge and tunnel into the sapwood of the tree to feed (Kukor and Martin, 1986).

Of the many insects that feed on the foliage of *P. tremuloides*, the majority are of the order Lepidoptera, along with a few species of sawfly (order Hymenoptera) and leafhoppers (order Cicadellidae).

Choristoneura conflictana (Walker) is commonly known as the large aspen tortrix, and can be found feeding on aspen buds and leaves (Beckwith, 1973). Although it may cause branch death when populations are dense, it rarely kills its host (Beckwith, 1973). *Malacosoma disstria* Hubner also feeds preferentially on aspen foliage, although it is found on other deciduous trees throughout the west besides quaking aspen (Furniss and Carolin, 1977). *M. disstria* overwinters as eggs, and the larvae emerge as aspen buds open in the spring (Stehr and Cook, 1968). Pupation occurs after 30-40 days, after which the moths mate and lay their eggs (Stelzer, 1968, 1971). Outbreaks of this insect are not uncommon, and may occur within the same aspen stand for several years in a row (Stelzer, 1968). Hogg, et al (2002), demonstrated that past annual defoliation events could be identified in tree cores by light-colored bands of growth resulting from the outbreak period. The larvae of *Sciaphila duplex* (Walsingham) (known as the aspen leaftier), feed on the inter-veinal tissues of aspen leaves (Furniss and Carolin, 1977). As they feed, the larvae roll up the skeletonized leaves and secure them (Furniss and Carolin, 1977). The aspen leaftier is capable of completely defoliating a tree over one season, and widespread in Canada, the Northern Rockies, Nevada, and California (McGregor, 1967). *Alsophila pometaria* (Harris) is one of several species of foliage-feeding geometrid moths, and is commonly known as the fall cankerworm (Furniss and Carolin, 1977). The cankerworm may be found feeding on the foliage of many deciduous shrub and tree species throughout the western U.S. (Furniss and Carolin, 1977).

Phyllocnistis populiella Chambers, also known as the aspen leafminer, forms a serpentine mine as it feeds on inter-cuticular leaf tissues (Davidson and Prentice, 1968). In general, this species does not cause severe damage to the host tree (Davidson and Prentice, 1968). The aspen blotchminer, *Lithocolletis tremuloidiella* Braun, like the aspen leafminer, also feeds on the inter-cuticular leaf tissues of aspen (Furniss and Carolin, 1977). The feeding patterns of these two species are quite different; while the leafminer forms a meandering mine, the blotchminer forms a rounded, irregularly-shaped patch in the leaf (Furniss and Carolin, 1977).

Three species of leafhoppers (*Idiocerus* sp.) are commonly found in Colorado, including *I. formosus*, *I. lachrymalis,* and *I. suturalis* (Graham, et al, 1963). These insects feed on juices from aspen leaves and other succulent tissues, and lay eggs in young twigs (Jones et al, in Debyle and Winokur, 1985). Finally, many species of common sawfly (*Tenthredinidae*) may be found feeding on aspen foliage (Graham, et al, 1963).

Conifer Encroachment

Aspen is the primary pioneer tree species in forest succession in forests throughout the Rocky Mountain region (Mueggler, 1985). Following a disturbance event (e.g., a stand-replacing fire), aspen colonize the area, either by seed or through sprouting from existing roots (Mueggler, 1985). Numerous studies have established that changes in fire regimes from the early twentieth century onward have clearly altered forest succession (Beaty, et al, 2008; Kaye, et al, 2003; Kurzel, et al, 2007), and favor conifer-dominated landscapes, especially among current aspen/mixed conifer stands (Smith and Smith, 2005; Minnich, et al, 2000).

Wildlife

Aspen also serves as a food source for many ungulate and rodent species, including elk (*Cervus canadensis* Erxleben), moose (*Alces alces*), mice (*Perognathus* spp.), voles (*Microtus* spp.), and porcupines (*Erethizon dorsatum* (Linn.)). In areas of high elk densities, aspen may be heavily browsed (Kaye, et al, 2003). One study conducted in Colorado's Rocky Mountain National Park indicated that over 70% of the Park's aspen stands showed evidence of elk browsing, particularly in areas identified as elk winter range (Kaye, et al, 2003). Similarly, a study by Romme, et al (1995) in Yellowstone National Park found that elk browsed aspen indiscriminately of age class; unbrowsed stems apparently escaped unscathed due to snow cover (Romme, et al, 1995).

Regeneration Failure

A variety of biotic and abiotic factors may contribute to the failure of an aspen stand to produce regeneration (i.e., 'suckers'). Jacobi, et al (1998), found two scenarios under which aspen regeneration failure could occur on the western slope of Colorado. Under very wet spring conditions, waterlogging predisposes trees to infection by canker-causing fungi (Jacobi, et al, 1998). Aspen exposed to drought conditions were likewise predisposed to phytopathogenic fungi (Jacobi, et al, 1998). In areas where elk (*Cervus canadensis*) densities are high, regeneration may be decreased due to winter browsing (Suzuki, et al, 1999). Similarly, MacIsaac, et al (2006) determined that regeneration gaps in post-harvest aspen stands were attributable to grazing (by moose, *Alces alces*) and heavy herbaceous vegetation cover. The effect of vegetation cover may suppress regeneration in two ways: by increasing competition for available growing space and soil moisture; by lowering soil temperatures beneath heavily-vegetated areas, which in turn may prevent auxin levels in underlying aspen roots to be altered, and thus fail to initiate suckering (MacIsaac, et al, 2006). This is supported by the findings of Lavertu, et al, (1994), who showed that litter removal enhanced regeneration production in aspen stands in northwestern Quebec. Late spring frost may also suppress regeneration (Wolken, et al, 2009).

Aspen Dieback and Sudden Aspen Decline

Aspen dieback has occurred throughout western North America over the past decade. Forest health researchers have documented stand damage in southern Utah (Bartos, 2008), Arizona (Fairweather, et al, 2008), and the boreal aspen forests of Alberta and Saskatchewan (Hogg, et al, 2008). Worrall, et al (2008) first observed this phenomenon in Colorado during 2005, and coined the term 'Sudden Aspen Decline' (SAD), based on their observation that affected stands underwent rapid mortality (Worrall, et al, 2008). Among affected stands, mortality increased from an average of 10% to between 280-567% (Worrall, et al, 2008). Stands experiencing significant mortality rates also lacked a regeneration cohort, suggesting that they may not persist on the landscape (Worrall, et al, 2008). There were three hypothetical effects that were suggested that may be acting synergistically to speed the rates of aspen damage. These include: drought conditions; stand aspect and elevation, and clone susceptibility to disease and damage agents (Worrall, et al, 2008; Bartos, 2008; Hogg, et al, 2008; Fairweather, et al, 2008). Biological agents that may be affecting survivorship of stands include *Cytospora* canker, the poplar borer, the bronze poplar borer, and two aspen bark beetle species (Worrall, et al, 2008). Though these agents are generally considered to be of secondary importance to stand health, stands which are already stressed may experience increased mortality from these disease and damage agents (Worrall, et al, 2008, 2010).

Chapter 2: Aspen Health in Four National Forests in Colorado and southern Wyoming, USA

Introduction

Populus tremuloides Michx. is a deciduous hardwood tree widely distributed throughout North America, with a broader geographic range than any other native tree species across the continent (Little, 1971). In Colorado, aspen covers approximately 1.2 million hectares, and is one of the few hardwood tree species in the state.

This tree assumes a clonal growth habit, and vegetative propagation is its primary method of reproduction. Aspen is an important successional tree species throughout the forests of the Rocky Mountains and the western United States and Canada (Mueggler, 1985). Root suckers originate from shoot meristems that occur within the cork cambium (Scheier, 1973). Apical dominance of the adult stems, 'ramets', is maintained by a steady flow of the plant hormone auxin, which is produced in the phyllosphere and transported to the roots (Eliasson, 1971). Removal, wounding, or death of the adult trees results in rapid declines in root auxin levels, which initiates suckering (Eliasson, 1971, 1972; Sandberg, 1951). Aspen clone size has been shown to be inversely proportional to the number of original seedlings (or 'ortets'), regardless of site conditions (Barnes, 1966). Other clonal differences, such as varied width: length ratio and serration patterns of leaves vary with genotype (Barnes, 1975). Genotype also appears to influence the levels of defensive foliar compounds, such as phenolic glycosides, and thus the susceptibility of the phenotype to defoliating insects (Donaldson and Lindroth, 2007).

Studies indicate that, like most other tree species, growth rates of aspen are a function of climatic factors combined with various site and soil characteristics (Hogg, et al, 2008). The impacts of drought on aspen includes a decrease in leaf area index (LAI), which continues to be affected up to two years following the drought event (Krishnan et al, 2006). The same study suggested that ecosystem respiration rates respond more quickly to drought onset, and are more sensitive to the end of a drought period than are ecosystem photosynthesis rates. In aspen, the severity of drought stress impacts the degree to which root water flow properties are altered (Siemens and Zwiazek, 2003).

Widespread aspen dieback has been observed throughout western North America over the past decade (Bartos, 2008; Hogg, et al, 2008) Forest health researchers have documented stand mortality in southern Utah (Bartos, 2008), Arizona (Fairweather, et al, 2008), and the boreal aspen forests of Alberta and Saskatchewan (Hogg, et al, 2008). Worrall, et al (2008) first coined the term 'Sudden Aspen Decline' (SAD), in Colorado during 2005. SAD is distinguishable from aspen dieback based on the rapid rate of stand death with SAD; affected stands experience dramatic increases in overstory mortality and lack a regeneration cohort (Worrall, et al, 2008).

Several factors are hypothesized to be acting synergistically to increase the occurrence of aspen dieback and mortality. These include: drought conditions; stand aspect and elevation, and clone susceptibility to disease and damage agents (Worrall, et al, 2008; Bartos, 2008; Hogg, et al, 2008; Fairweather, et al, 2008). Biological agents that may affect survivorship of stands include *Cytospora* canker (*Cytospora* spp), poplar borer (*Saperda calcarata*), the bronze poplar borer (*Agrilus liragus*), and two aspen bark beetle species (*Trypophloeus populi* and *Procryphalus mucronatus*) (Worrall, et al, 2008; Jacobi, W.R., personal communication). Though these agents are generally considered to be of secondary importance to stand health (primary disease and damage agents include sooty bark (*Encoelia pruinosa*) and *Cryptosphaeria* (*Cryptosphaeria lignyota*) cankers and forest tent caterpillar (*Melacosoma disstria*), stands which are already stressed may experience increased mortality from these disease and damage agents (Worrall, et al, 2008, 2010). The area where Sudden Aspen Decline has been documented includes the national forests of southwestern Colorado (i.e., the Gunnison, Grand Mesa, and Uncompahgre National Forests). The U.S. Forest Service Forest Health Management group has conducted aerial surveys of aspen damage on national forests in Colorado and southern Wyoming since 2006. Thus, prior to this study, it was not known whether the mortality observed among aspen stands throughout the areas beyond the extent of the SAD study area was attributable to Sudden Aspen Decline, or to some other factor.

The overall objectives for this project were two-fold: to determine the overall health of aspen stands on U.S.D.A. Forest Service lands in Colorado and southern Wyoming. We achieved this through the establishment of random rapid roadside survey plots and a field assessment of damaged and healthy aspen stands on U.S.D.A. Forest Service lands in Colorado and southern Wyoming, based on the Forest Service's aerial survey data to determine the causes of damage. The specific hypotheses for the overall health survey were: that basal area and stand density would be similar in all forests sampled east and west of the Continental Divide; that aspen stand structure would be similar in all national forests sampled; the proportion of aspen dieback would be uniform among sampled forests, and is not related to site and stand factors. For the field survey (i.e., determining the cause of aspen dieback), our specific hypotheses were as follows: the observed aspen dieback was not related to site or stand characteristics; incidence of diseases or insects among aspen was not related to any one site, stand or abiotic factor; aspen dieback was not related to damage incurred by a particular disease or insect.

Methods

Study Areas:

Four study areas were used to assess aspen stands for health and to determine the causes of aspen mortality. Two of the study areas (Pike-San Isabel and Medicine Bow National Forests) were east of the Continental Divide and two were located west of the Divide (White River and Routt National forests). The four study areas represent the drier, aspen stands that occur along the eastern slopes of the Colorado Front Range of the Rocky Mountains and the wetter, western slope areas. Sampling areas were selected because they had the most aspen area, based on a remotely-sensed vegetation data layer (downloaded from the Colorado Vegetation Classification Project website, http://ndis.nrel.colostate.edu/coveg/) in a Geographic Information System (GIS) (Tables 21 and 22). Aspen stands in two or three districts per forest were sampled.

Roadside Survey Plots

During 2009-2010, we installed 573 survey plots along roads in eleven ranger districts on the four national forests (Table 1). GIS was used to show areas where aspen stands and forest roads intersected, and survey points were generated using the 'Create Random Points' tool in ArcToolbox® (ESRI, Redlands, CA, USA). One survey point was generated for each potential roadside survey plot. Potential survey points were loaded onto GPS units (Garmin Etrex Legend H). We utilized the survey points to begin a survey; subsequent roadside plots were placed 160 m (0.10 miles) apart from each other. In areas where the aspen vegetation type was extensive, we increased plot spacing to 804 m (0.5 miles).

Site and Tree Data

Rectangular roadside plots (25 x 5 m, 0.0125 ha) were placed 10 - 50 m from the road edge, and contained at least 50% aspen, based on visual estimation. Data recorded included: location via GPS (Garmin Etrex Legend H), elevation (from GPS or topographical map), aspect (degrees), percent slope, slope position (e.g., summit, shoulder slope, backslope, footslope, toeslope, or valley bottom), slope configuration (e.g., concave, convex, broken, undulating or linear), a visual estimation of percent stand mortality and percent crown dieback, presence or absence of regeneration (i.e., those trees with DBH < 12 cm), the stand structure (i.e., open or closed canopy, with single or multiple cohorts), understory and shrub species, other tree species, presence of obvious insect or disease damage, and presence of other damage agents (such as ungulate bark browsing, human-caused damage, etc). Percent stand mortality was the estimated overall mortality of the stand, including saplings, poles, and adult-sized aspen.

Aspen Stand Assessment Plots

Plot Selection

We randomly selected damaged and healthy aspen stands to assess stand health based on aerial survey information. The U.S. Forest Service conducts yearly aerial surveys of forest pests in Colorado and southern Wyoming. To do so, aerial survey technicians observe affected stands from fixed-wing aircraft, and digitize polygons onto georeferenced maps displayed on a laptop computer (https://fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_038662.pdf). In 2006, the

Forest Service began to survey aspen stands across Colorado, due to reports of aspen mortality on many national forests. Four categories of affected stands were mapped: (1) aspen stands currently undergoing an apparent defoliation or foliage discoloration event (though not to the extent to be labeled as aspen mortality and dieback); (2) stands with thinning crowns among at least 25% of adult aspen; (3) stands with moderate (<50% of stems) levels of overstory mortality; or (4) stands with high (>50% of stems) levels of overstory mortality (Howell, unpublished methods).

Approximately half of our survey plots were established in aspen stands classified as ‘damaged’ (categories 2-4 in the 2008 and 2009 aerial surveys) and half in unaffected stands (though not as a paired-plot design). For a stand to be designated as ‘damaged’, it must have been mapped by aerial surveyors as showing significant mortality, (i.e., the moderate to heavy or light to moderate mortality categories listed above), widespread defoliation, or significant crown thinning (as described above). Prior to conducting field work, GIS software (ArcMap® 9.2, ESRI) was used to create a set of random points within the damaged and unaffected aspen cover types. The aspen damage datasets were obtained from the U.S. Forest Service’s Region 2 Aerial Sketchmapping website (http://www.fs.usda.gov/wps/portal/fsinternet/). An aspen vegetation covertype was utilized to place survey plots in healthy aspen stands. The vegetation dataset was produced by the Colorado Vegetation Classification Project (CVCP) (http://ndis.nrel.colostate.edu/coveg/). This state-wide vegetation type map is based on data from the Landsat Thematic Mapper ™ satellite. Data from CVCP were downloaded by watershed, and areas containing at least 50% aspen coverage were selected from the larger dataset. Individual watershed-area shapefiles of aspen covertype were then compiled into one large shapefile using the ‘Union’ tool in the ‘Overlay’ toolset in ArcToolbox (ESRI, 2008). Total area of aspen covertype and yearly mapped damage areas within each of the national forests and ranger districts surveyed can be found in Tables 18 & 19.

The set of randomized points (generated using the ‘Create Random Points’ tool within the Data Management toolset in ArcToolbox) were uploaded onto a GPS unit (Garmin Etrex Legend H®). However, we encountered significant difficulties locating these stands in this way, due to either surveyor error, or incorrect identification of vegetation type, so we utilized orienteering skills to correctly identify the randomly selected stand. Potential stands had to be at least 50% aspen stems, and be at least 120 x 20 m in size, or another potential site was located.

Transect Data

In order to gain a general overview of site and stand conditions, a transect of not more than 100 meters was established, in a direction which bisected the aspen stand. Stand-level data collected included: transect bearing; percent slope; aspect (degrees); elevation (meters); slope position (e.g., summit, shoulder slope, backslope, footslope, toeslope, or valley bottom); slope configuration (e.g., linear, undulating, broken, convex, or concave); evidence of disturbance (e.g., fire scar, evidence of grazing, thinning, avalanche, or other major disturbance event); stand structure (e.g., an open or closed stand, with one or more stories); tree species (other than aspen) present, and the dominant shrub and herb species present. These data were obtained during transect establishment.

The presence of *Armillaria* root disease on aspen was determined by sampling three recently dead or dying trees randomly located along each transect for the presence of mycelial fans. We utilized methods developed by Blodgett, Allen and Burns, 2007 (INT-EM-07-01). We excavated a 12-cm deep trench around the base of the tree, starting at the tree's northern-facing aspect. Bark was removed, and the roots and root crown were examined for mycelial fans and rhizomorphs. If mycelium was found on the first or second tree examined, we stopped searching for *Armillaria* sign on dead trees, and examined up to two living trees with thin crowns or small, yellowing leaves for presence of mycelium.

Plot Data

Three circular, fixed-area subplots with an area of 200 m^2 and a radius of 8 m were randomly established along the 100 m transect (Fig. 1). Within each of the three subplots, adult trees (DBH > 12 cm) were tallied, and diameter recorded at breast height (1.37 m, DBH height) (Fig. 2). At the center of each sub-plot, a smaller, concentric subplot of 6.2 m radius, and area of 30.1 m^2 was established for the purpose of quantifying and measuring large and small pole-sized regeneration (with small poles having a DBH 0.1 – 2.9 cm, and large poles a DBH of 3.0 – 11.9 cm) (Fig. 2). Sapling-sized individuals (0.30 m to 1.37 m tall) were tallied and measured in three circular (1.3 m radius) smaller subplots centered at the edge of the adult subplot at 100, 200, and 300 degrees from plot center (Fig. 2). In the case that regeneration was prolific (i.e., more than 5 stems/ m^2), the subplot was divided into quarters and two of these sections were tallied for an estimate of overall stand regeneration density.

Tree Data

Within each subplot type, all aspen were tallied by the four size classes and given a health status of 1 through 5. The health status index was based on the apparent overall health of the tree. Factors included in the estimation of the health index score included presence of disease, insect, or abiotic damage, crown fullness, and apparent health of the vascular cambium. More specifically, status scores represented the following conditions: a score of a '1' indicated that the tree had little or no obvious disease or damage agents present (i.e., damage covering 0-25% of the bole or crown); a '2' indicated that the tree had minor to moderate damage to the crown or bole (i.e., damage covering 25-50% of the bole or crown); a '3' indicated that the tree had incurred severe damage to the crown or bole (i.e., damage covering >50% of the bole or crown); a '4' indicated a recently dead tree (the tree was dead but the majority of the bark was intact, and fine twigs were present); a '5' indicated that the tree had been dead for more than five years (portions of the bark and fine twigs were absent). The first ten adult aspen in each plot were assessed for percent live crown, and the first ten individuals for all four size classes were assessed for disease and damage agents. In order to quantify the amount of insect or disease damage present, the bole and crown were carefully evaluated for percent extent of defoliation, cankers, conks, wounds, or any other disease or damage agents. When a disease or damage agent was detected, it was recorded as present and then assigned a severity score from 1 to 3. A severity score of '1' indicated that the agent affected less than 25% of the crown or bole circumference; a '2' indicated that the agent affected between 25-50% of the crown or bole circumference; and a severity score of '3' indicated that the agent affected more than 50% of the crown or bole circumference. We also tallied by size class all non-aspen tree species in the plot, and noted whether they were living or dead.

Tree age was determined by coring at DBH height one adult dominant or co-dominant aspen in each sub-plot. One individual from each of the three regeneration size classes was also selected and destructively sampled and a cross section collected at ground level to determine age. Cores were placed in paper straws and regeneration cross-sections placed in a paper bag and processed in the laboratory.

Tree Cores & Cross-sections

Sample Processing

All cores and cross-sections were air-dried, sanded, and examined under a dissecting microscope to determine pith date. Cross-dating using the skeleton plot technique (Stokes and Smiley, 1968; Swetnam, et al, 1985), a graphical technique for comparing ring-width was used to determine relative growth and determining the narrowest rings.

Tree Ring Measurements

Annual rings widths, to nearest 1/100 millimeter were measured using an increnometer (Velmex, Inc, Bloomfield, NY, USA). The associated software program (J2X software, Velmex, Inc, Bloomfield, NY, USA) produces an rwl file as an output. This raw data was then checked using COFECHA, a simple DOS-based computer program that describes the accuracy of the chronology, or the correlation of each series (i.e., each core) with the master chronology (i.e., the average of individual dated cores for a specific area or region). Those series with correlations of less than 0.40 were separated into another file, and then re-run as ‘undated’ series against the group which had correlation values greater than 0.40. The series with low correlations were corrected, and the two groups of measurements were combined and converted into a single dataset using the computer program YUX (Publisher).

Drought Index Data

To estimate the effect of drought conditions in Colorado and southern Wyoming for the period 1999-2008, we utilized a 4-km spatial drought index from the Forest Health Technology Enterprise Team (FHTET) with the U.S. Forest Service. These datasets were developed by Frank Koch and Bill Smith (U.S.F.S.) (manuscript in preparation), and utilized PRISM temperature and precipitation data, as well as calculations of potential evapotranspiration rates. PRISM datasets (The PRISM Climate Group, http://prism.oregonstate.edu/) are developed using weather station data and algorithms. Weather data from precise locations are extrapolated mathematically to predict weather conditions up to 4 km away, creating a gridded data set.

To obtain drought index conditions for each of our roadside and stand health survey locations for the years 1999-2008, we utilized the ‘Sample’ tool within the Spatial Analyst toolbox of ArcToolbox in ArcMap® (ESRI Inc., Redlands, CA). From this operation, an INFO table (non-spatial table) was produced, listing the UTM coordinates of each survey point, along with a drought index value from the gridded drought data set. This procedure was repeated for each annual dataset through 2008. Each INFO table was exported to a DATABASE format table, which is compatible for use with Microsoft Excel® (Microsoft Corp., Redmond, WA). Finally, individual files were compiled into a single spreadsheet for statistical analysis.

Statistical Analysis

All analyses were conducted using SAS 9.2 software (The SAS Institute Inc., Cary, NC). Data were analyzed based on whether it was considered plot- , transect-, or tree-level. For example, site conditions (such as slope and elevation) were analyzed at the transect- or plot-level, and disease and damage agent presence was analyzed at the tree level. Tree and plot data were averaged across the three survey plots for analysis.

Roadside Survey Plot Data

Data collected from roadside plots were analyzed using the PROC GLM and PROC GLIMMIX procedures in SAS to fit general linear models using an analysis of variance (ANOVA) and least-square means comparisons. In the PROC GLM procedure, both categorical and continuous variables were included as independent variables. Categorical variables used included: elevation, which was divided into four categories (by dividing the original elevation by 400); percent slope, which was divided into three categories, 0-9%, 10-20%, and > 20%; aspect was divided into the four cardinal directions. A single continuous variable, drought index, was also analyzed. The response variable used in this model was the square-root of the estimated stand mortality (i.e., the proportion of standing dead aspen within the stand).

In the PROC GLIMMIX procedure, the same four independent variables (elevation, slope, aspect, and drought index) were modeled. Response variables included: the presence of each of the three regeneration size classes; the presence of disease or insect damage; average percent live crown; and average stand mortality.

Transect and Plot Data

Site variables were analyzed as mixed linear models using the PROC GLIMMIX procedure. The response variables used included the proportion of live stems by size class, quadratic mean diameter (QMD), average tree health score, stand density, and trees per hectare (Eq 1-4).

Categorical variables (i.e., those used in the 'class' statement) used in all analyses included forest (or ranger district), healthy or damaged stand, and transect and plot number. Additional categorical variables used in the various statistical models included elevation, aspect, drought index, and select disease and insect presence and severity. Continuous variables included core increment widths, regeneration and adult tree ages, stand size (in hectares), and site index. Site index was calculated using the equation listed in the Appendix (Eq. 5). Survey plot elevation, measured in meters, ranged from 2200-3400 m. The effect of elevation was analyzed as a categorical variable by dividing elevation by 400 and rounding the outcome off to the nearest integer (i.e., 6, 7, or 8). Survey plot aspect was categorized by degrees into the four cardinal directions. Drought index values for each transect were grouped into two periods, where values for 1999-

2004 represented period one, and values for 2005-2008 represented period two. Values were grouped based on the assumption that the most recent episode of aspen dieback, if related to drought, is most likely related to the drier period, which occurred between 1999-2004, rather than the wetter period, which occurred between 2005-2008. Drought data was also analyzed yearly, with core increment data either matching yearly drought index data, or was staggered by one year (i.e., such that drought data was pared with core increment data from the following year). Core increment data was averaged across plots to the transect level, and merged with the drought index dataset prior to analysis. Regeneration and adult tree age was calculated by subtracting the pith date from 2008. Age was then average by size class across plots to the transect level.

Due to differences in sample sizes (not all plots had core increment and regeneration sample data associated with them), the drought index/increment data was analyzed separately from the complete datasets (e.g., elevation, aspect). Random variables were transects within ranger districts (or forests) and plots within transects and ranger districts (or forests).

Tree Data

Tree data were also analyzed as mixed linear models using the PROC GLIMMIX program. The response variables used included: the proportion of stems with a particular disease or damage agent present; average health status among adult aspen; average percent live crown among adult aspen. Categorical variables included ranger district (or forest), healthy or damaged stand, disease or damage agent, and transect and plot number. Random variables were the same as those used in transect and plot data analysis.

Results

Roadside Survey Plots

During 2009 and 2010, we established 573 road survey plots (i.e., rapid aspen health assessment plots) on eleven ranger districts within four national forests (Table 1). During analysis, a number of these plots were excluded due to insufficient data, recording errors, or other problems, resulting in a sample size of 500 (for the percent live analysis) and 573 (for the percent mortality, presence of regeneration, and presence of disease and insect damage). The Pike-San Isabel and White River national forests had the greatest numbers of survey plots (over 200 plots per forest), with fewer plots on the Routt and Medicine Bow national forests (Table 1). Fewer plots were established on the Routt and Medicine Bow national forests due to time and weather constraints.

Average stand mortality for a combination of all four size classes of aspen was generally less than 10% for most sites examined (Table 2). Average mortality was greatest at sites with moderate elevations (2400-2800 m), and those on north-facing aspects. Stands growing on sites located on toeslopes or valley bottoms had the lowest mortality among slope position categories. Among slope configuration categories, those sites with convex configurations had the highest mortality rates, as did sites with low (0 – 9%) or gentle (10 – 19%) slope categories. Stands located east of the continental divide showed significantly higher mortality (11%) than did those stand located west of the divide (4%).

Average percent live crown was greatest on moderate- and high-elevation sites, contrary to percent stem mortality rates (Table 2). Percent live crown was also greatest among aspen stands located on toeslopes or valley bottoms, and on sites with gentle to moderate slopes (Table 2). Differences in percent average live crown among stands east and west of the continental divide were not significant, nor were the differences among ranger districts or national forests (omitting data from the Medicine Bow national forest) (Table 2).

Most aspen stands had at least three size classes. For example, sapling-, and large-pole sized aspen were ubiquitous among all sites (Table 3); for this reason, no differences were detected in stem presence among the site variables. There were detectable differences among plots with respect to small pole-sized aspen stems. These were more likely to occur among stands in valley bottoms or on toeslopes (Table 3). Among ranger districts, stands on the South Park (Pike-San Isabel N.F.) and Blanco (White River N.F.) districts were least likely to contain small poles, and the Salida, San Carlos (both Pike-San Isabel N.F.), Yampa, Hahn's Peak, (both Routt N.F.), and Rifle (White River N.F.) districts were most likely to contain small poles (Table 3).

Insect damage among aspen stands (e.g., entrance holes of wood-boring insects, crown defoliation by various foliage-feeding species) was more occurred more frequently on sites east of the continental divide (Table 4). Insect damage was also more common among stands located on the Pike-San Isabel and White River National forests (Table 4). Evidence of disease agents (e.g., *Cytospora*, sootybark cankers) was very common among sites, with nearly 99% of sites visited showing evidence of infection (Table 4).

Aspen Stand Assessment Plots

During the 2009 field season, we established 49 transects on five ranger districts (South Park, Salida, Blanco, and Hahn's Peak ranger districts) within the Pike-San Isabel, White River, and Routt National Forests. We established an equal number of transects during the 2010 field season, on seven ranger districts (the San Carlos, Aspen-Sopris, Rifle, Yampa, Brush Creek-Hayden, Laramie, and Douglas ranger districts) within the Pike-San Isabel, White River, Routt, and Medicine Bow National forests. We collected tree density and size data and utilized three measures of aspen tree health including the percent live standing aspen (percent live aspen, Table 5)- a measure of current survival, a health index of 1 – 5, and percent live crown- a continuous scale of standing live adult aspen crown density.

Aspen density varied significantly among the four national forests for small pole-sized and adult aspen; we found that more pole-sized trees were on the east vs. the west side of the continental divide, and we found fewer small poles on the Pike-San Isabel, Routt, and White River national forests than on the Medicine Bow (Table 5). The site factors that impacted aspen density included site aspect and slope configuration. Small pole-sized aspen were most common among stands on south- and west- facing aspects, and significantly more large pole-sized aspen among stands on east- and south-facing aspects (Table 5). The effect of slope configuration was significant with respect to stems per hectare among adult aspen; stands located on sites with a linear slope configuration had the most adult aspen stems (Table 5). In addition, we found that the average number of large pole-sized aspen was negatively correlated with average adult aspen age.

The least-squares means of the quadratic mean diameters for adult aspen (>12 cm DBH) ranged from 20 – 28 cm over the four national forests. There was a significant difference between the diameter of adult aspen east and west of the divide (Table 6). Mean diameter of adults on the east side of the divide was less (20.3 cm) than those on the west (25.1 cm). The effect of stem age by size class with respect to quadratic mean diameter (QMD) was significant among adult aspen (Table 6). The QMD of adult aspen was positively correlated with adult age .

The least-squares means of percent live adult aspen was fairly uniform among the four national forests, ranging from 73 – 84%, while taking into account the effect of various other factors, including district, stand type (i.e., healthy or damaged), continental divide position, and site factors (Table 7). There were significantly more live stems among 'healthy' stands, (82%), than among 'damaged' stands (74%). Aspect and elevation significantly affected the percent of live stems in the four aspen size classes. There were more living small pole-sized stems on low elevation sites than on moderate- to high-elevation sites. There was a higher percent of live adult aspen stems on sites with north-facing aspects than those with west-facing aspects (Table 7). The effect of stem age in each size class with respect to the proportion of live stems per hectare was significant and negative among small- and large-sized poles and adult aspen (Table 7).

Average health index score (1 – 5 rating) of adult aspen was 1.7 among trees in healthy stands, and 2.3 among trees in damaged stands; health scores did not differ with respect to continental divide position (Table 8). The pattern was reversed among aspen saplings, which were healthier in damaged stands. Saplings differed in health status by the four national forests, with the healthiest on the Medicine Bow and White River national forests. Site factors that affected health status included elevation, aspect, and average adult aspen age (Table 8). Small pole-sized aspen were less healthy among stands on high elevation sites, and large pole-sized aspen most healthy among stands on low and high elevation sites. Overall, adult aspen among stands on west-facing slopes were less healthy than those growing on north- east-, and south- facing aspects (Table 8).

This effect was not significant when adult aspen health was assessed with respect to percent live crown (see below).

The average percent live crown among adult aspen was fairly consistent among national forests and continental divide position (Table 9). Average live crown was higher among trees in healthy stands (86%) than among those in damaged stands (62%). Site variables that affected percent live crown included elevation and percent slope. Trees in stands on high elevation sites tended to have fuller crowns than trees on lower-elevation sites. Percent live crown was lowest among trees on sites with little to no slope, and greatest on sites with mild to moderate slopes (Table 9). The effect of stem age of aspen regeneration with respect to average percent live crown of adult aspen was significant among pole-sized aspen (Table 9). Average live crown among adult aspen was negatively correlated to average age of pole-sized aspen (i.e., the fuller the crown of the adult aspen, the younger the pole-sized regeneration).

Biotic Effects: Presence of Insects and Diseases

A total of fourteen different insect varieties or damage types were detected in the study. Of these, ten were present at very low levels (i.e., overall incidence of $n < 15$) and were not subjected to in-depth analysis. Insects with low occurrence included: ambrosia beetles (*Typodendron retusum*), forest tent caterpillar (*Malacosoma disstria*), aspen leafminer (*Phyllocnistis populiella*), aspen blotchminer (*Lithocolletis tremuloidiella*), sawflies (Suborder Symphyta), leafhoppers (*Idiocerus* spp.), eriophyid mites (*Eriophyes* spp.), and aphids (Family *Aphidae*). Additionally, we lumped the bronze (*Agrilus* liragus) and poplar borer (*Saperda calcarata*) into a single category (‘wood borers’), combined all foliage-feeding insects (e.g., the large aspen Tortrix (*Choristoneura conflictana*) into one general category ('foliage feeders'), and combined all leaf-tying insects into a single general category ('leaf tiers').

Fourteen phytopathogenic fungal agents were detected in the survey. Six of the fungal pathogens were present at very low levels and were not subjected to in-depth analysis and included the decay fungi *Peniophora polygonia* and *Armillaria ostoyae*; the root disease *Ganoderma applanatum*; the foliar fungi *Ciborinia* spp., *Melampsora medusa*; and the canker fungus *Dothiora polyspora* . Likewise, thirteen types of animal damage were detected, and seven types of abiotic damage. Of these two categories, sixteen were present at very low levels and were not subjected to in-depth analysis. The low incidence damage included antler rubbing, moose feeding, rodent feeding, porcupine feeding, beaver damage, birds feeding, birds nesting, human damage, lighting, sunscald, drought stress, and frost crack. Note that some damage categories were combined (e.g., rodent feeding, bark and stem). See Table 16 for a complete list of disease and damage agents.

Insect Damage Agents

We found wood-boring insects and bark beetles to be the most commonly-occurring insects, with 5 – 41% of the trees on the four national forests showing evidence of wood borers or bark beetles(Table 12).

The presence of wood boring insects on aspen was significant with respect to elevation, stand type, national forest, percent slope, and slope configuration (Table 12). In general, trees on sites that were of moderate elevation (2600-2900 m), located on steep

(>50%) slopes with concave or undulating configurations had the highest prevalence of wood-boring insects (Table 12). Furthermore, trees on the Pike-San Isabel and Medicine Bow national forests had the greatest rate of wood borer evidence, followed by the White River and Routt national forests (Table 12).

The presence of bark beetles on aspen differed significantly among all four national forests, stand types, continental divide position, and the five site parameters (Table 12). There were significantly more trees with bark beetles in damaged stands than in healthy stands (16% and 7%, respectively) (Table 12). There were also significantly more beetles among aspen on the Pike-San Isabel national forest (41%) than on the Medicine Bow, Routt, or White River National forests (0%, 10%, and 5%, respectively) (Table 12). Beetle-infested trees were more prevalent on low-elevation sites, sites positioned on summits or shoulder slopes, on sites with no or low slopes, on sites with concave slope configurations, and on sites east of the continental divide (Table 12).

The prevalence of foliage-feeding insect damage (i.e., foliage feeders and leaf tiers in Table 12) was significantly influenced by elevation, aspect, stand type, continental divide position, site percent slope, and site slope configuration (Table 12). Foliar damage was more common among trees in damaged stands, on stands west of the continental divide, on sites with gentle slopes, moderate-elevation sites, and those with north- or east-facing aspects (Table 12).

Disease Damage Agents

Cytospora canker, *Marssonina* foliar blight, and the decay fungus *Phellinus tremulae* (Bond.) Bond. and Borisov were the only diseases that occurred with enough frequency among all four size classes of aspen (i.e., $n \geq 100$ trees) to be included in the final analysis. The prevalence of *Cytospora* canker on aspen was significantly influenced by stand type, continental divide position, national forest, percent slope of the site, and slope configuration (Table 10). In general, trees in 'damaged' stands east of the continental divide, with slopes of 10% or less and having slope configurations of broken, concave, or convex had the highest prevalence of *Cytospora* canker. The average severity rating of *Cytospora* canker was generally high (> 2.5), and did not vary significantly by site variables (Table 14). Canker severity differed only among national forest, and was less severe on the Medicine Bow compared with the other three forests (Table 14).

The presence of *Marssonina* leaf blight was influenced by all parameters except for site slope position (Table 10). It should be noted that symptoms of this foliar blight become evident in late summer, and that during each of our field seasons, we surveyed the northern-most forests at the end of the season. Thus, *Marssonina* could well have been present in stands in the southern part of our survey area, and was not detected due to the time of year that those areas were surveyed. Nonetheless, *Marssonina* was most common among trees on sites with low elevation, north- or west-facing aspects, on sites west of the divide, on sites with concave slope configuration, and among trees on damaged stands (Table 10). The severity of *Marssonina* leaf blight infestation among aspen was influenced by elevation, stand type, divide position, and site percent slope (Table 14). Trees in high elevation sites tended to have more severe blight infection than those on moderate or low sites; conversely, trees on north-facing sites had the least severe outbreaks, as did trees on sites with undulating slope configuration.

The presence of *Phellinus tremula* (white trunk rot) on aspen was influenced by elevation, aspect, continental divide position, national forest, and site slope configuration (Table 11). White trunk rot was generally more prevalent trees on sites west of the divide, on north- or west-facing aspects, and on sites with concave slope configurations. The severity of white trunk rot on aspen was not significantly influenced by any of the eight parameters included in the analysis (Table 14).

The three other canker diseases subjected to complete analysis-*Ceratocystis*, *Cryptosphaeria*, and *Encoelia*- and the one other blight disease (*Venturia*) occurred at a rate of 1 – 2% among all size classes of aspen (Tables 10 and 11). Although there are some statistically significant differences in the prevalence of these diseases, prevalence remained very low.

Black canker (*Ceratocystis fimbriata*) prevalence was low overall, but was influenced by elevation, aspect, stand type, divide position, slope position, and percent slope (Table 10). Overall, black canker was more frequently observed on trees on high-elevation sites on toeslopes or valley bottoms. The Routt and White River national forests had the lowest incidences of this disease (Table 10). Sooty bark canker (*Encoelia pruinosa*) prevalence was low overall, but greater among trees in ‘damaged’ stands (Table 10). The prevalence of *Cryptosphaeria* canker among aspen was influenced by national forest (Table 10). Virtually no *Cryptosphaeria* canker was detected on the Medicine Bow and White River national forests. The presence of Shepherd’s Crook (*Venturia tremulae)* was influenced by aspect and site percent slope (Table 11). Trees on sites with north-facing aspects and on sites of moderate to steep slopes were more likely to have Shepherd’s Crook.

We detected *Armillaria* root rot on dead aspen in 64% of plots (Table 17). Among stands where *Armillaria* was detected on dead trees, it was also detected on live trees 11% of the time (Table 17). There was no apparent relationship between presence of this disease and site or stand characteristics (data not shown).

Abiotic and other damages:

The prevalence of fire scars among aspen was infrequent, though fire scars were more common among trees on moderate- and high-elevation sites (Table 13). Although analysis indicated significant influence of other parameters, estimates were too small to be useful.

The prevalence of fire scars among aspen was influenced by elevation, Continental Divide position, national forest, slope position, percent slope, and slope configuration (Table 13). Wounds of unknown origin were more common on trees in high-elevation sites, sites west of the divide, and sites with steep slopes, toeslopes, and undulating or broken slope configurations (Table 13).

The prevalence of branch galls among aspen was influenced by elevation, Continental Divide position, national forest, and percent slope (Table 13). Although analysis indicated significant influence of other parameters, estimates were too small to be useful.

The prevalence of ungulate bark browsing was influenced by elevation, stand type, Continental Divide position, national forest, slope position, percent slope, and slope configuration (Table 13). Trees on sites east of the divide were more likely to have evidence of bark browsing, as were trees in ‘damaged’ stands, and those on the Pike- San Isabel national forest.

Three environmental factors were analyzed with respect to average stem age by size class. There were no significant factors in any of the analyses performed (Table 15). Age of large and small poles were not different from each other, and were about 28 years old, whereas saplings averaged 5 years old, and adult aspen averaged 91 years old (Table 15).

Tree Growth and Drought:

Drought index data was analyzed for the period of January 1999 through December 2008 with respect to adult aspen annual increment data for the same period. No significant relationships were detected. We also analyzed the same two datasets by calculating the relative drought and increments between 2002 and the average of 1999 and 2000. This was based on the observation of the graphed drought index data, which indicated a moderate drought in 2002. We hypothesized that the trees would respond quickly to the drought, and that they would likewise show a significant decrease in growth for 2002 compared with the 1999 and 2000 growing seasons. There were differences in increment growth between national forests (data not shown), but the relationship between increment and drought index was not significant. More work is needed to determine whether the lack of relationship between growth increment and drought index is due to small sample size (of increment cores), errors in increment measurement, or drought index data resolution.

Stand site index was analyzed for most transects, where adult aspen age had been determined. There were no significant relationships between any of the stand density (proportion live stems, QMD, stems per hectare) or tree health (average health status, percent live crown) variables tested against site index (data not shown).

Discussion

Roadside Survey

Overall, analysis of the data collected from the roadside survey portion of this study does not clearly indicate any single factor influencing stand health. Analysis of data collected during the aspen health survey indicates that the structure of stands throughout the four national forests surveyed is consistent. There were, however differences in the prevalence of small pole-sized aspen at the district level. These differences may point to specific site and environmental factors not detected at the forest-level scale. Based on survey plot data from the same districts, such factors could include heavy grazing of young aspen by elk or cattle; a particularly dense understory, which could prevent regeneration from occurring keeping soil temperatures low; lack of a disturbance event in recent history that would have triggered a regeneration cohort.

Average stand mortality over all four size classes was consistent across national forests (if data from the Medicine Bow are assumed to be fundamentally different from data collected on the other three national forests), and ranged from 3 – 4%. This rate is lower than mortality rates noted by aerial survey, where the area impacted ranged from 0.05 – 14% of the total aspen covertype (Table 19). The mortality rate is also lower than that found by Steed and Kearns (2010) in Montana and Idaho, and consistent with those found by Hogg, et al (2008) in western Canada. Among ranger districts, there were significant differences in average stand mortality; districts surveyed in 2009 tended to have higher mortality estimates, which could be attributed to either (1) that these districts experienced more aspen damage than did the other districts in the survey, (2) surveyor error or inexperience. Specifically, mortality data collected from the Medicine Bow national forest is higher by nearly a factor of ten, so caution should be used in including it in final conclusions. Among ranger districts, stands located on the South Park and Blanco districts showed the highest average mortality (Table 2).

We found that stands occurring on high-elevation sites, on sites with convex slope configurations, and those on sites east of the continental divide experience higher levels of stand mortality than those occurring on other site types. At the same time, stands on moderate- and high-elevation sites had fuller crowns, as did stands occurring on sites located on toeslopes and valley bottoms, and those with no to low slopes. Considering that stands experienced both increased morality and fuller adult aspen crowns at moderate- and high-elevation sites, it may be that these stands are simply more mature; the understory aspen cohorts are undergoing natural dieback as the adult cohort thrives. It's very possible that the observed increased mortality rates may simply be due to better growing conditions; stands in which adult aspen are growing vigorously will tend to have more morality in the understory as the canopy fills out and regeneration receives less light.

Other results from this analysis point to possible water relations: areas east of the continental divide are generally drier than those on the west; toeslopes and valley bottom sites (and low percent slopes) most likely are wetter than those on backslopes or summit areas with greater percent slopes; sites with convex slope configurations may well experience drier conditions than those with other configurations. Analysis of insect and disease presence among the aspen we surveyed with roadside survey plots did not indicate any significant relationships between any of the environmental or site conditions

-except for disease prevalence among national forests and continental divide position, which we attribute to differences in surveyor perception, and are thus not true effects.

Aspen Stand Assessment Plots:

Contrary to our initial hypothesis, analysis of survey data indicated that there were significant differences among stands east and west of the continental divide. Adult aspen west of the divide tended to have larger diameters and fuller crowns than adult aspen east of the divide. However, stands east of the divide had on average more adult stems per hectare, more live saplings per plot, and healthier saplings than did stands west of the divide. A study of aspen in Montana and Idaho by Steed and Kearns (2010) did not show any difference in aspen mortality or stand density east and west of the continental divide.

Analysis of stand survey data indicated that, although there were significant differences in adult aspen mortality and insect and disease prevalence among aspen in ‘healthy’ vs. ‘damaged’ stands, it appears likely that aspen will persist on most sites. The main differences between the two stand types (i.e., healthy and damaged) included: proportions of live adults; average health status among sapling- and adult-size aspen; presence of ungulate browsing; presence of bark beetles, wood borers, leaf-tying insects and general foliage feeding insects; presence of canker-causing fungi, especially *Cytospora*; and the damage severity rating of *Marssonina* leaf blight. Observed prevalence of *Cytospora* canker in this study was much higher than in a recent survey of aspen health in the Northern Rocky Mountains (Steed and Kearns, 2010). We observed

Phellinus conk at a rate of about 4%, where stands in the northern rocky mountain area have infection rates of 10 – 11% (Steed and Kearns, 2010).

In general, damaged aspen stands contained fewer total adult aspen stems, and fewer live adult aspen stems. Further, average health status and proportion live crown was lower among adult aspen in damaged stands. This was expected because 'damaged' stands were identified from aerial surveys based on stand mortality and crown dieback. Likewise, during surveying, damaged stands were selected because they were clearly less healthy than adjacent stands. Disease prevalence among damaged stands was not detected during aerial surveys, and thus was not used in stand classification. Survey data indicates that damaged stands contained significantly more *Cytospora* (*Valsa* spp), sooty bark (*Encoelia pruinosa*), and black (*Ceratocystis*) cankers, wood-boring insects (*Agrilus* liragus Barter & Brown and *Saperda calcarata*), aspen bark beetles (*Trypophloeus populi* and *Procryphalus mucronatus* (LeConte)), and leaf-tying insects than healthy stands. Three diseases, Shepherd's Crook (*Venturia tremulae*), *Phellinus* conk, and *Cryptosphaeria* canker, were not significantly more prevalent among damaged stands. Prevalence of *Cytospora* canker was greater among stands east of the Divide, but *Phellinus* decay, branch galls, leaf-tying insects, damage from foliage-feeding insects, and Shepherd's Crook shoot blight were more common among stands west of the Divide. These findings support the hypothesis that stands east of the Divide are more likely to experience drought conditions, and thus, the prevalence of disease and damage agents frequently found on drought-stressed trees (e.g., *Cytospora* canker) would likely be greater under such conditions. Conversely, stands west of the Divide are likely to be wetter than those on the east, and thus the prevalence of diseases associated with wet conditions (e.g., Shepherd's Crook blight) would be greater west of the Divide. Compared with the current study, Brandt et al (2003) found much lower rates of wood borer damage (~3% vs. 20%) and comparable rates of *Armillaria* root decay (14% vs. 11%) in their survey of aspen stands across central and western Canada.

Among aspen stands in the national forests surveyed, there were several significant differences. Saplings and small pole-sized stems occurred at the highest densities and were healthier overall on sites in northern-most forests, including the Medicine Bow and Routt national forests. Since regeneration class was based solely on diameter or height, it's possible that small poles were more common on the Blanco and South Park districts than recorded, but were growing at a faster or slower rate than other sites, putting them in the large pole or sapling size classes.

Among adult aspen, crowns were fullest on sites located in the Routt and White River National Forests, which are located west of the Continental Divide, and among stands on moderate- and high-elevation sites. This may be due to the wetter conditions generally found on these sites. Likewise, stands located on flat sites may be subject to flooding events, and the root systems among trees in these stands could be shallower than those on steeper slopes, making them more vulnerable to periods of drought. Stands with higher live crown percentages also tended to have higher mortality rates (Table 2). This apparent discrepancy is most likely due to the fact that aspen stands with fuller crowns tend to have more understory mortality. Aspen self-thin as the stand ages; adults fill the canopy and reduce the amount of light reaching the forest floor. Any regeneration present eventually dies.

Overall, our data suggests that aspen stands throughout Colorado experience varying degrees of environmental stress and disease and insect damage. This is indicated by the increased rates of adult stem mortality among stands east of the continental divide (which tends to be drier than the west) and the increased presence of such stress-related organisms as *Cytospora* canker aspen bark beetles, and poplar borers among damaged stands. Other recent studies of aspen mortality throughout western North America have attributed the observed mortality to acute drought conditions (Worrall, et al, 2008 & 2010; Fairweather, 2008; Hogg, et al, 2008). Acute drought is most likely the main inciting factor, though further analysis is required to definitively link the marked increase in select damage agents with moisture deficit. In spite of this, many stands recently classified as damaged will likely persist on the landscape, as indicated by the high proportions of live regeneration among both damaged and healthy stands, and the low proportion of damaged aspen stands to total aspen area.

This is not surprising, because aspen self-thin as the stand ages; adults fill the canopy and reduce the amount of light reaching the forest floor. Any regeneration present eventually dies.

Table 1. Numbers of roadside survey plots[1] established in aspen stands in Colorado, 2009 – 2010

National Forest	Ranger District	Number of Roadside Plots	Year Surveyed
Pike-San Isabel		216	
	South Park	48	2009
	Salida	52	2009
	Pike	70	2010
	San Carlos	46	2010
White River		203	
	Blanco	45	2009
	Rifle	50	2010
	Aspen-Sopris	108	2010
Routt		114	
	Hahn's Peak	54	2009
	Yampa	60	2010
Medicine Bow		88	
	Laramie	78	2010
	Brush Creek-Hayden	10	2010
	Brush Creek-Hayden	10	2010

[1] During analysis, between 48-121 plots were excluded due to insufficient data or other problems, resulting in a sample size of 500 (for the percent mortality analysis) and 573 (for the percent live crown, regeneration occurrence, and disease and insect occurrence analyses).

Table 2. Average percent mortality and live crown of aspen from a roadside survey, in Colorado, 2009 - 2010

Independent Variable		y = Average Stand Mortality n = 573[2] LS Mean[1]	Lower C.I.	Upper C.I.	y = Average Live Crown n = 500[2] LS Mean[1]	Lower C.I.	Upper C.I.
Elevation							
	Low	7.1a	6.22	8.05	85.8a	83.90	87.80
	Moderate	6.6ab	5.81	7.43	90.2b	88.33	92.01
	High	8.1b	6.94	9.33	93.9b	91.18	96.57
Aspect							
	North	7.9	6.96	8.88	85.7a	83.71	87.70
	East	7.3	6.43	8.25	90.0b	88.00	92.13
	South	6.7	5.90	7.57	92.1b	90.18	93.97
	West	7.1	6.20	8.11	92.0b	89.85	94.10
Slope Position							
	Summit- Shoulder Slope	8.3b	7.22	9.37	88.0a	85.68	90.26
	Backslope-Footslope	8.5b	7.70	9.40	87.0a	85.28	88.64
	Toeslope- Valley Bottom	5.2a	4.38	6.13	95.0b	92.70	97.27
Slope Configuration							
	Broken	5.0ab	2.61	8.15	93.1ab	85.97	100.00
	Concave	6.7a	6.07	7.41	90.3b	88.72	91.95
	Convex	10.1c	9.22	10.94	87.0a	85.26	88.68
	Linear	7.0ab	6.41	7.72	90.3b	88.85	91.83
	Undulating	7.9b	7.18	8.66	88.9ab	87.33	90.53
% Slope							
	0 - 9%	8.4b	7.43	9.36	87.6a	85.55	89.58
	10 - 19%	7.6ab	6.70	8.50	91.8b	89.87	93.76
	20 - 29%	6.7a	5.79	7.58	91.0abc	88.87	93.08
	30 - 39%	6.7a	5.78	7.71	89.6bc	87.35	91.88
	≥ 40%	7.0ab	5.65	8.55	89.7b	86.53	92.98
Continental Divide							
	East	11.2b	10.07	12.35	89.3	87.25	91.31
	West	4.2a	3.56	4.83	90.6	88.76	92.41
Forest (Divide)							
East	Med. Bow	23.7c	21.32	26.22	85.2a	82.32	88.04
	Pike-San Is.	3.3a	2.75	3.92	93.5c	91.53	95.47
West	Routt	3.8ab	3.10	4.47	92.0bc	89.87	94.07
	Wht River	4.6b	3.94	5.33	89.2ab	87.34	91.11
District (Forest * Divide)							
Med. Bow	BCH*	30.8f	26.55	35.43	91.7bd	87.07	96.48
	Laramie	17.5e	15.75	19.38	78.8a	76.47	81.23
Pike-San Is.	Pikes Peak	3.3bc	2.68	4.07	89.9b	87.67	92.10
	Salida	2.0a	1.41	2.66	-	-	-
	Sa n Carlos	2.4ab	1.80	3.06	97.2d	94.73	99.66
	South Park	6.2d	4.78	7.83	-	-	-
Routt	Hahn's Pk	4.6cd	3.78	5.56	88.5b	86.15	90.92
	Yampa	3.0ab	2.30	3.73	95.5d	92.97	97.98
White River	Aspen-Sopris	3.3bc	2.68	3.97	89.7b	87.64	91.79
	Blanco	7.6d	6.48	8.84	85.7b	83.26	88.13
	Rifle	3.5b	2.67	4.40	92.3bd	89.58	95.10

[1]Least-squares means are presented as they were analyzed against eight site and environmental parameters.
[2] During analysis, between 48-121 plots were excluded due to insufficient data or other problems, resulting in a sample size of 500 (for the percent mortality analysis) and 573 (for the percent live crown analysis).
Average mortality was estimated based on the proportion of dead standing aspen in all size classes compared to the approximate total standing aspen within the plot. Average percent live crown was estimated based on the approximate mean live crown of all standing aspen with DBH >11.9 cm within the plot.
*BCH = Brush Creek-Hayden ranger district.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Table 3 A-D. Average percent frequency[1] of three regeneration size classes of aspen from roadside survey plots[2], in Colorado, 2009 – 2010

3A.

		Elevation*			Aspect			
Size Class	**n**	**Low %(SE)**	**Moderate %(SE)**	**High %(SE)**	**North %(SE)**	**East %(SE)**	**South %(SE)**	**West %(SE)**
Saplings	573	97 (253.5)	99 (99.0)	99 (52.5)	98 (139.2)	98 (117.8)	99 (71.9)	99 (125.1)
Small Poles	573	80 (2.1)	83 (1.7)	86 (2.0)	84 (1.8)	88 (1.4)	80 (2.0)	78 (2.6)
Large Poles	573	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)

3B.

Slope Position*			Slope Configuration				
Summit-Shoulder %(SE)	**Backslope-Footslope %(SE)**	**Toeslope-Valley %(SE)**	**Broken %(SE)**	**Concave %(SE)**	**Convex %(SE)**	**Linear %(SE)**	**Undulating %(SE)**
98 (155.4)	99 (87.3)	99 (98.9)	100 (0.0)	78 (1.9)	88 (1.3)	84 (1.6)	83 (1.6)
72a (2.8)	78a (1.8)	93b (1.2)	64 (9.5)	87 (0.04)	85 (1.5)	88 (1.2)	85 (1.5)
100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)

3C.

% Slope					Continental Divide Position*		National Forest*			
0 - 9% %(SE)	**10 - 19% %(SE)**	**20 - 29% %(SE)**	**30 - 39% %(SE)**	**≥ 40% %(SE)**	**East %(SE)**	**West %(SE)**	**Medicine Bow %(SE)**	**Pike-San Isabel %(SE)**	**Routt %(SE)**	**White River %(SE)**
99 (82.3)	99 (90.9)	99 (119.3)	97 (215.2)	99 (84.1)	99 (62.4)	98 (193.2)	100 (17.3)	97 (219.4)	98 (146.7)	97 (253.8)
81 (1.9)	85 (1.6)	84 (1.8)	81 (2.2)	83 (3.0)	84 (1.8)	82 (1.8)	90 (2.0)	76 (2.2)	83 (2.1)	80 (1.9)
100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)

3D.

Ranger District (Forest * Divide)*										
BCH %(SE)**	**Laramie %(SE)**	**Pike's Peak %(SE)**	**Salida %(SE)**	**San Carlos %(SE)**	**South Park %(SE)**	**Hahn's Peak %(SE)**	**Yampa %(SE)**	**Aspen-Sopris %(SE)**	**Blanco %(SE)**	**Rifle %(SE)**
99 (54.6)	100 (5.4)	99 (53.8)	97 (264.2)	99 (96.3)	82 (127.2)	99 (124.4)	98 (172.2)	98 (201.8)	94 (452.0)	98 (175.5)
92bcd (2.8)	88bcd (2.0)	76bcd (2.5)	89bcd (1.9)	78bcd (2.6)	50ad (5.1)	58abcd (3.4)	95bc (1.1)	87bc (1.6)	54abd (3.6)	90bcd (1.9)
100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)

[1]Percent frequency of sapling- and pole-sized aspen among eight site and environmental factors.
[2] During analysis, between 48-121 plots were excluded due to insufficient data or other problems, resulting in a sample size of 500 (for the percent mortality analysis) and 573 (for the percent live crown, regeneration occurrence, and disease and insect occurrence analyses).
*Some standard errors are very large due very low occurrence within some factor levels.
**BCH = Brush Creek-Hayden ranger district
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Table 4. Average incidence[1] of insect- and disease damage among four size classes of aspen from a roadside survey, in Colorado, 2009 - 2010

	Insects		Disease	
	n = 573[2]			
Independent Variable	**LS Mean**	**Std Error**	**LS Mean**	**Std Error**
Elevation				
Low	68	7.6	99	99.6
Moderate	64	7.2	99	77.5
High	60	9.2	99	87.8
Aspect				
North	63	7.8	99	8.3
East	69	7.0	99	65.3
South	63	7.5	99	98.3
West	61	8.4	98	112.2
Slope Position				
Summit- Shoulder Slope	70	7.7	99	85.8
Backslope-Footslope	64	6.5	98	149.9
Toeslope- Valley Bottom	57	9.4	99	68.6
Slope Configuration				
Broken	83	15.8	100	0.0
Concave	63	6.1	89	3.2
Convex	59	5.7	85	4.4
Linear	50	6.0	88	3.3
Undulating	59	6.3	91	2.9
% Slope				
0 - 9%	66	7.5	99	65.7
10 - 19%	62	7.6	98	116.3
20 - 29%	65	7.8	98	135.8
30 - 39%	65	8.6	99	92.2
≥ 40%	62	9.5	99	54.3
Continental Divide				
East	79 b	6.1	99	76.7
West	44 a	7.1	99	100.5
Forest (Divide)				
Medicine Bow	88c	6.6	99	47.9
Pike-San Isabel	67b	6.5	98	122.4
Routt	34a	7.7	98	134.4
White River	55b	7.4	99	75.0
District (Forest * Divide)				
Brush Creek-Hayden	89	11.1	99	46.7
Laramie	87	5.1	99	49.0
Pike's Peak	57	8.6	98	169.7
Salida	66	9.8	98	172.5
San Carlos	73	7.8	99	61.5
South Park	72	10.1	98	123.8
Hahn's Peak	29	8.4	98	107.2
Yampa	41	9.7	98	168.2
Aspen-Sopris	68	6.9	98	116.8
Blanco	59	9.8	97	243.3
Rifle	38	10.6	100	14.8

[1]Average percent values are least-squares means of evidence of major insect or disease damage (e.g. wood borer symptoms, canker symptoms or decay fruiting bodies on stems) modeled with the eight site and environmental parameters. [2] During analysis, between 48-121 plots were excluded due to insufficient data or other problems, resulting in a sample size of 500 (for the percent mortality analysis) and 573 (for the percent live crown, regeneration occurrence, and disease and insect occurrence analyses). Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Table 5. Average live aspen stems per hectare (stems/Ha) among four size classes in Aspen Stand Assessment Plots in Colorado, 2009 - 2010

	Saplings		Small Pole		Large Pole		Adults	
	n = 82		n = 62		n = 70		n = 92	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation								
Low	1860	804.0	766	483.7	248	360.0	703	126.8
Moderate	2294	664.1	1006	349.0	1032	271.2	767	100.9
High	2995	950.4	1015	546.6	1044	387.4	693	155.0
Aspect								
North	1873	866.1	465a	539.8	586ac	362.0	647	141.1
East	3206	816.0	588a	423.6	1405d	357.4	671	130.8
South	2547	66.4	1618b	403.4	940acd	301.8	709	104.1
West	1907	921.1	1042ab	456.5	165a	368.5	857	139.1
Stand Type								
Damaged	2550	721.3	997	390.6	645	288.0	655	108.9
Healthy	2215	698.2	860	374.4	905	290.2	786	112.0
Divide Position								
East	2926	720.7	881	376.6	1151b	285.1	800	110.8
West	1840	762.4	977	444.3	398a	324.3	642	119.5
Forest (Divide)								
Medicine Bow	3959	994.8	1608d	594.8	2178b	433.0	944	157.2
Pike-San Isabel	1894	723.1	152ab	412.1	123a	294.9	656	115.2
Routt	2244	959.3	1534cd	603.2	153a	433.2	683	146.7
White River	1436	795.0	420ab	428.9	643a	346.1	600	122.9
Slope Position								
Summit - Shoulder	1765	1041.3	560	660.0	545	505.2	587	140.6
Backslope - Footslope	2933	588.0	1176	268.2	1031	217.9	819	85.8
Toeslope - Valley	2450	923.1	1051	514.4	747	373.5	757	140.6
% Slope								
0 - 9%	1751	792.4	589	461.7	640	351.3	666	123.4
10 - 19%	2138	723.4	743	404.4	790	300.2	721	114.0
20 - 29%	3262	793.7	1380	467.9	1445	364.1	615	124.3
30 - 39%	2649	1058.1	554	570.4	328	428.4	893	162.9
≥ 40%	2114	1070.4	1378	603.3	670	464.6	709	167.9
Slope Configuration								
Concave	2534	698.3	1607	521.6	243	775.9	442a	116.4
Convex	1521	607.2	1068	375.9	539	357.3	588a	97.9
Linear	4042	749.7	950	454.1	1249	313.0	978c	140.8
Broken	1861	2340.0	209	984.6	243	776.0	947abc	317.7
Undulating	1957	675.4	810	418.8	654	305.1	647b	110.0
Age								
	Paramete r Est	Std. Err	Paramete r Est	Std. Err	Paramete r Est	Std. Err	Paramete r Est	Std. Err
	40.08	205.220	-13.58	19.65 7	3.45	12.481	2.82	2.040

Average stems per hectare are least-squares means as modeled with the eight site and environmental parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level. N = the number of transects with size classes present.
Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 6. Quadratic Mean Diameter (QMD) among three size classes of aspen, from Aspen Stand Assessment Plots in Colorado, 2009 - 2010

	Small Pole n = 62[1]		Large Pole n = 74[1]		Adults n = 114[1]	
Parameter	**Mean (cm)**	**Std. Error**	**Mean (cm)**	**Std. Error**	**Mean (cm)**	**Std. Error**
Elevation						
Low	1.2	0.23	8.2	0.65	24.5	1.59
Moderate	1.3	0.16	7.3	0.49	22.5	1.26
High	1.4	0.26	7.8	0.70	21.1	1.94
Aspect						
North	1.4	0.25	7.9	0.65	21.8	1.76
East	1.1	0.20	8.1	0.64	22.6	1.64
South	1.3	0.19	7.8	0.54	21.6	1.30
West	1.4	0.21	7.3	0.66	24.7	1.74
Stand Type						
Damaged	1.3	0.18	7.8	0.52	22.6	1.36
Healthy	1.3	0.18	7.7	0.52	22.8	1.40
Divide Position						
East	1.4	0.18	7.7	0.51	20.3a	1.39
West	1.2	0.21	7.9	0.58	25.1b	1.49
Forest (Divide)						
Medicine Bow	1.4	0.28	7.1	0.78	20.0	1.96
Pike-San Isabel	1.4	0.19	8.2	0.53	20.6	1.44
Routt	1.1	0.28	7.9	0.78	26.3	1.83
White River	1.4	0.20	7.9	0.62	23.8	1.54
Slope Position						
Summit - Shoulder	1.1	0.31	7.4	0.91	24.4	2.28
Backslope - Footslope	1.6	0.13	7.6	0.39	21.8	1.07
Toeslope - Valley	1.3	0.24	8.3	0.67	21.8	1.76
% Slope						
0 - 9%	1.1	0.22	8.0	0.63	23.1	1.54
10 - 19%	1.2	0.19	8.3	0.54	22.6	1.43
20 - 29%	1.3	0.22	7.3	0.66	22.7	1.55
30 - 39%	1.5	0.27	7.7	0.77	22.9	2.04
≥ 40%	1.4	0.28	7.6	0.84	22.1	2.10
Slope Configuration						
Concave	1.5	0.25	8.1	0.64	24.3	1.45
Convex	1.2	0.18	7.2	0.56	22.7	1.22
Linear	1.5	0.21	7.8	0.55	22.0	1.76
Broken	1.0	0.46	8.9	1.40	21.1	3.97
Undulating	1.3	0.20	6.9	0.55	23.5	1.37
Age						
	Parameter Est	Std. Err	Parameter Est	Std. Err	Parameter Est	Std. Err
	0.00	0.007	0.03	0.017	0.06*	0.021

Quadratic Mean Diameters are least-squares means as modeled with the eight site and environmental parameters. QMD was calculated using equation 2 in the appendix.
[1] Sample size (n) is the number of trees averaged by ranger district, stand type, transect, and size class.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the P ≤ 0.05 level.
*Indicates significance at the P ≤ 0.05 level.
Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 7. Average percent of live aspen stems among four size classes, in Aspen Stand Assessment Plots, 2009 - 2010

	Saplings n = 83[1]		**Small Pole n = 62[1]**		**Large Pole n = 74[1]**		**Adults n = 114[1]**	
Parameter	**LS Mean (%)**	**Std. Error**	**LS Mean (%)**	**Std. Error**	**LS Mean (%)**	**Std. Error**	**LS Mean (%)**	**Std. Error**
Elevation								
Low	78	13.1	71	20.0	71	15.8	75	6.2
Moderate	93	10.8	63	14.5	82	11.9	77	4.9
High	94	15.5	51	22.7	64	17.0	83	7.6
Aspect								
North	95	14.1	41	22.4	53	15.8	84	6.9
East	94	13.3	48	17.6	87	15.6	82	6.4
South	76	10.9	76	16.8	78	13.2	81	5.1
West	87	15.0	82	19.0	72	16.1	67	6.8
Stand Type								
Damaged	95	11.8	59	16.2	60a	12.6	70a	5.3
Healthy	81	11.4	65	15.6	84b	12.7	86b	5.5
Divide Position								
East	94	11.8	55	15.6	77	12.5	75	5.4
West	82	12.4	68	18.5	67	14.2	81	5.9
Forest (Divide)								
Medicine Bow	115	16.2	69	25.0	81	18.9	77	7.7
Pike-San Isabel	78	11.8	42	17.1	74	12.9	74	5.6
Routt	78	15.6	67	25.1	62	19.0	78	7.2
White River	86	13.0	69	17.8	72	15.1	85	6.0
Slope Position								
Summit - Shoulder	77	17.0	65	27.4	78	22.1	84	8.9
Backslope - Footslope	91	9.6	56	11.1	55	9.5	74	4.2
Toeslope - Valley	96	15.0	64	21.4	83	16.3	76	6.9
% Slope								
0 - 9%	77	12.9	78	19.2	74	15.4	67	6.0
10 - 19%	79	11.8	76	16.8	62	13.1	81	5.6
20 - 29%	103	12.9	51	19.4	55	15.9	82	6.1
30 - 39%	107	17.3	35	23.7	72	18.7	85	8.0
≥ 40%	74	17.5	69	25.1	99	20.3	77	8.2
Slope Configuration								
Concave	91	11.4	86	21.7	72	15.6	80	5.7
Convex	80	9.9	74	15.6	79	13.7	74	4.8
Linear	91	12.2	42	18.9	69	13.4	87	6.9
Broken	98	38.0	50	40.9	59	34.0	71	15.6
Undulating	81	11.0	56	17.4	82	13.4	80	5.4
Age								
	Parameter Est	Std. Err	Parameter Est	Std. Err	Parameter Est	Std. Err	Parameter Est	Std. Err
	0.00	0.016	-0.01*	0.005	-0.01*	0.003	0.00*	0.001

Average percent values are least-squares means as modeled with the eight site and environmental parameters.

[1] Sample size (n) is the number of trees averaged by ranger district, stand type, transect, and size class.

Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

*Indicates significance at the $P \leq 0.05$ level.

Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 8. Average health status of four size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009 - 2010

	Average Health Status							
	Saplings n = 83[1]		Small Pole n = 62[1]		Large Pole n = 74[1]		Adults n = 114[1]	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation								
Low	2.0	0.26	1.4a	0.49	2.2ab	0.45	2.1	0.19
Moderate	1.9	0.21	2.4a	0.35	1.6a	0.34	2.1	0.15
High	1.9	0.30	3.3b	0.55	2.6b	0.49	1.8	0.24
Aspect								
North	1.8	0.28	2.9	0.55	2.2	0.46	1.8a	0.22
East	2.0	0.26	2.6	0.43	2.0	0.45	1.9ab	0.20
South	2.1	0.21	1.9	0.41	2.0	0.38	1.9ab	0.16
West	1.9	0.29	2.1	0.46	2.3	0.46	2.4b	0.21
Stand Type								
Damaged	1.7a	0.23	2.4	0.40	2.3	0.36	2.3b	0.17
Healthy	2.2b	0.22	2.4	0.38	2.0	0.37	1.7a	0.17
Continental Divide Position								
East	1.8	0.23	2.6	0.38	2.1	0.36	2.1	0.17
West	2.0	0.24	2.2	0.45	2.1	0.41	1.8	0.18
Forest (Divide)								
Medicine Bow	1.4a	0.32	2.5	0.60	1.8	0.54	2.1	0.24
Pike-San Isabel	2.2b	0.23	2.7	0.42	2.5	0.37	2.2	0.18
Routt	2.3b	0.30	1.9	0.61	2.2	0.55	1.9	0.22
White River	1.8ab	0.25	2.5	0.44	2.1	0.44	1.8	0.19
Slope Position								
Summit - Shoulder	2.3	0.33	2.5	0.67	2.0	0.64	1.8	0.28
Backslope - Footslope	1.7	0.19	2.5	0.27	2.5	0.27	2.0	0.13
Toeslope - Valley	1.8	0.29	2.1	0.52	1.9	0.47	2.1	0.22
% Slope								
0 - 9%	1.8	0.25	1.8a	0.47	2.0	0.44	2.2	0.19
10 - 19%	1.9	0.23	2.5ab	0.41	2.6	0.38	1.9	0.17
20 - 29%	1.7	0.25	2.6ab	0.47	2.1	0.46	2.1	0.19
30 - 39%	1.7	0.34	3.3b	0.58	2.1	0.54	1.7	0.25
≥ 40%	2.5	0.34	1.7a	0.61	1.9	0.58	2.0	0.26
Slope Configuration								
Concave	1.9	0.22	1.8	0.53	2.2	0.45	2.0	0.18
Convex	2.2	0.19	2.2	0.38	2.1	0.39	2.2	0.15
Linear	2.1	0.24	3.2	0.46	2.6	0.39	1.7	0.22
Broken	1.3	0.74	2.2	1.00	2.1	0.98	2.1	0.49
Undulating	2.2	0.21	2.5	0.43	1.7	0.38	2.0	0.17
Age*								
Parameter Est	Std. Err	Paramet er Est	Std. Err	Paramet er Est	Std. Err	Parameter Est	Std. Err	Paramet er Est
	-0.03	0.053	0.03	0.016	.03	0.011	0.11	0.095

Health status is based on a 5-point index, where 1 = healthy, 2 = 5 – 50% damaged, 3 = >50% damage, 4 = recent mortality (< 5 years since death), 5 = old mortality (>5 years since death). Average health status is least-squares means as modeled with the eight site and environmental parameters.

[1]Sample size (n) is the number of trees averaged by ranger district, stand type, transect, and size class.

*Age means are parameter estimates. Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 9. Average percent live crown of adult aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

n = 116[1]	Adults	
Parameter	**Mean**	**Std. Error**
Elevation		
Low	75ab	6.0
Moderate	67a	4.8
High	80b	7.3
Aspect		
North	77	6.7
East	78	6.2
South	76	4.9
West	65	6.6
Stand Type		
Damaged	62a	5.2
Healthy	86b	5.3
Divide Position		
East	70	5.2
West	78	5.7
Forest (Divide)		
Medicine Bow	65	7.4
Pike-San Isabel	76	6.9
Routt	77	6.9
White River	78	5.8
Slope Position		
Summit - Shoulder	83	6.6
Backslope - Footslope	70	4.1
Toeslope - Valley	69	6.7
% Slope		
0 - 9%	65a	5.8
10 - 19%	77bc	5.4
20 - 29%	70ab	5.9
30 - 39%	87c	7.7
≥ 40%	71ab	7.9
Slope Configuration		
Concave	71	5.5
Convex	68	4.6
Linear	81	6.7
Broken	78	15.0
Undulating	72	5.2
Age*		
	Parameter Est	Std. Err
	-0.018	0.0005

Least-squares means are the average adult percent live crown as modeled with the eight site and environmental parameters.

[1]Sample size (n) is the number of trees averaged by ranger district, stand type, transect, and size class.

*Age mean is a parameter estimate, and represents the relationship of regeneration age to average percent live crown of adult aspen.

Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Table 10. Percent incidence of canker diseases on four size classes of live aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Ceratocystis		*Cryptosphaeria*		*Cytospora*		*Encoelia*	
				n = 4241				
Parameter	LS Mean(%)	Std. Error	LS Mean(%)	Std. Error	LS Mean(%)	Std. Error	LS Mean(%)	Std. Error
Elevation								
Low	0a	1.1	1	0.4	19	3.2	2	1.4
Moderate	2b	1.1	1	0.4	16	3.0	1	1.3
High	2b	1.2	1	0.4	13	3.5	1	1.5
Aspect								
North	1a	1.2	1	0.4	14a	3.4	1	1.5
East	1a	1.2	1	0.4	12a	3.3	2	1.4
South	1a	1.1	0	0.4	20b	3.1	1	1.3
West	3b	1.1	0	0.4	19b	3.3	2	1.4
Stand Type								
Damaged	2b	1.1	1	0.4	20b	3.0	2b	1.3
Healthy	1a	1.1	1	0.4	13a	3.1	0a	1.3
Divide Position								
East	3b	1.1	1	0.4	23b	3.3	1	1.4
West	1a	1.1	0	0.4	10a	3.2	2	1.4
Forest (Divide)								
Medicine Bow	2	1.2	0a	0.4	9a	3.5	2	1.5
Pike-San Isabel	3	1.5	1b	0.5	36b	4.2	0	1.8
Routt	1	1.2	1b	0.4	14c	3.4	2	1.5
White River	1	1.2	0a	0.4	5a	3.2	1	1.4
Slope Position								
Summit - Shoulder	0a	1.4	1	0.5	24b	4.0	2	1.7
Backslope - Footslope	1b	1.0	0	0.4	12a	2.9	2	1.3
Toeslope - Valley	5c	1.2	1	0.4	13a	3.3	0	1.4
% Slope								
0 - 9%	0a	1.1	0	0.4	22d	3.2	2	1.4
10 - 19%	2b	1.1	0	0.4	18c	3.1	1	1.3
20 - 29%	2ab	1.2	1	0.4	17bc	3.3	1	1.4
30 - 39%	3c	1.2	7	0.4	16bc	3.5	3	1.5
≥ 40%	2abc	1.3	1	0.5	10a	3.6	1	1.6
Slope Configuration								
Concave	3	0.7	1	0.2	28c	1.9	2	0.8
Convex	3	0.6	1	0.2	20a	1.6	1	0.7
Linear	2	0.7	1	0.3	14ab	2.0	1	0.9
Broken	0	5.0	0	0.2	0a	14.3	1	6.2
Undulating	3	0.7	1	0.2	22a	1.9	2	0.8

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and environmental parameters.

Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level

Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 11. Percent incidence of decay and foliar blights among four size classes of live aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Phellinus tremula		*Marssonina Populi*		*Venturia tremulae*	
	n = 4241					
Parameter	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**
Elevation						
Low	4b	1.8	15c	2.9	2	1.1
Moderate	4b	1.7	11b	2.8	1	1.0
High	0a	2.0	8a	3.2	2	1.2
Aspect						
North	4b	1.9	15b	3.1	3b	1.2
East	2ab	1.8	6a	3.0	1a	1.1
South	1a	1.7	9a	2.8	1a	1.1
West	3bc	1.8	14b	2.9	1a	1.1
Stand Type						
Damaged	3	1.7	13a	2.8	1	1.0
Healthy	2	1.8	9b	2.8	2	1.1
Divide Position						
East	1a	1.8	3a	2.9	1	1.1
West	4b	1.8	19b	2.9	2	1.1
Forest (Divide)						
Medicine Bow	0a	2.0	2a	3.2	2	1.2
Pike-San Isabel	4b	2.3	5a	3.8	0	1.4
Routt	5b	1.9	26c	3.1	1	1.2
White River	4b	1.8	13b	2.9	3	1.1
Slope Position						
Summit - Shoulder	2	2.2	10	3.6	1	1.3
Backslope - Footslope	3	1.6	11	2.6	2	1.0
Toeslope - Valley	2	1.8	12	3.0	2	1.1
% Slope						
0 - 9%	4	1.8	12bc	2.9	0a	1.1
10 - 19%	4	1.7	11b	2.8	1b	1.1
20 - 29%	2	1.9	5a	3.0	3c	1.1
30 - 39%	2	1.9	16c	3.1	1b	1.2
≥ 40%	1	2.0	11b	3.3	3c	1.2
Slope Configuration						
Concave	4bc	1.0	18bc	1.7	1	4.8
Convex	3b	0.9	12bc	1.5	2	0.6
Linear	2a	1.1	10ad	1.8	1	0.5
Broken	0abc	8.0	13abcd	12.9	2	0.7
Undulating	5c	1.1	4a	1.7	3	0.6

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and environmental parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level

Table 12. Percent incidence of insect damage among four size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Wood Borers		Bark Beetles		Foliage Feeders		Leaf Tiers	
	n = 4241							
Parameter	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**
Elevation								
Low	13a	3.4	18c	2.4	1a	1.0	1a	1.1%
Moderate	21bc	3.2	11b	2.2	3b	0.9	3b	1.0%
High	20bc	3.7	6a	2.6	0a	1.0	2ab	1.2%
Aspect								
North	18	3.6	16c	2.5	2b	1.0	2ab	1.2%
East	18	3.4	5a	2.4	3c	1.0	1a	1.4%
South	20	3.3	14c	2.3	0a	0.9	1b	1.2%
West	18	3.4	10b	2.4	1b	1.0	3b	1.0%
Stand Type								
Damaged	27b	3.2	16b	2.4	3b	0.9	3b	1.1%
Healthy	10a	3.3	7a	2.3	0a	0.9	1a	1.1%
Divide Position								
East	22b	3.4	15b	2.4	0a	1.0	2	1.1%
West	14a	3.3	8a	2.3	2b	0.9	2	1.1%
Forest (Divide)								
Medicine Bow	21	3.6	0a	2.6	0	1.0	2ab	1.2%
Pike-San Isabel	24	4.4	41d	3.0	0	1.2	1ab	1.4%
Routt	12	3.6	10c	2.5	3	1.0	1a	1.2%
White River	16	3.4	5b	2.4	2	0.9	3b	1.1%
Slope Position								
Summit - Shoulder	18	4.1	19b	2.9	1	1.2	4b	1.4
Backslope - Footslope	17	3.1	9a	2.1	1	0.9	1a	1.0
Toeslope - Valley	20	3.4	7a	2.4	1	1.0	2ab	1.1
% Slope								
0 - 9%	13a	3.4	18c	2.4	1b	1.0	1	1.1
10 - 19%	17bc	3.3	13b	2.3	4c	0.9	2	1.1
20 - 29%	21bc	3.5	9a	2.4	0a	1.0	3	1.1
30 - 39%	16ac	3.6	8a	2.5	0a	1.0	2	1.2
≥ 40%	24d	3.8	9a	2.6	1b	1.1	3	1.2
Slope Configuration								
Concave	22b	2.0	21b	1.4	0a	4.2	2a	0.6
Convex	21bc	1.7	18bc	1.1	2c	0.5	2a	0.6
Linear	16a	2.1	9a	1.5	1a	0.6	2a	0.7
Broken	6abc	15.0	0a	10.5	3abc	4.2	0a	4.9
Undulating	26c	2.0	16c	1.4	0b	0.6	4b	0.6

Least-square means are percent occurrence of insect presence among four size classes of aspen analyzed with eight site and environmental parameters.

Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 13. Incidence of wounding, galls, and browsing among four size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Unknown Wound		Fire Scar		Branch Galls		Ungulate Browsing	
	n = 4241							
Parameter	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**	**LS Mean(%)**	**Std. Error**
Elevation								
Low	0a	1.2	0a	0.6	0a	1.1	3a	2.3
Moderate	1b	1.2	0bc	0.6	0b	1.0	10b	2.1
High	7c	1.4	0bc	0.7	7c	1.2	12bc	2.5
Aspect								
North	2ab	1.3	0	0.7	2b	1.1	8	2.4
East	3b	1.3	0	0.7	0a	1.1	10	2.3
South	2a	1.2	0	0.6	3b	1.0	7	2.2
West	2a	1.3	0	0.6	2b	1.1	9	2.3
Stand Type								
Damaged	2	1.2	0b	0.6	2	1.0	11b	2.2
Healthy	2	1.2	0a	0.6	1	1.0	5a	2.2
Divide Position								
East	1	1.3	0	0.6	1a	1.1	15b	2.3
West	3	1.2	0	0.6	2b	1.0	2a	2.2
Forest (Divide)								
Medicine Bow	3ab	1.4	0b	0.7	4bc	1.2	5b	2.5
Pike-San Isabel	0a	1.6	0abc	0.8	0a	1.4	25c	2.9
Routt	2a	1.3	0a	0.7	2b	1.1	2a	2.4
White River	4b	1.2	0bc	0.6	3c	1.1	2a	2.2
Slope Position								
Summit - Shoulder	0a	1.5	0	0.7	0a	1.3	9ab	2.8
Backslope - Footslope	3b	1.1	0	0.6	2b	1.0	6a	2.0
Toeslope - Valley	4b	1.3	0	0.7	4c	1.1	10b	2.3
% Slope								
0 - 9%	2bcde	1.2	0a	0.6	1b	1.1	5a	2.3
10 - 19%	1ab	1.2	0a	0.6	1b	1.0	10b	2.2
20 - 29%	4cf	1.3	1b	0.7	3c	1.1	8b	2.3
30 - 39%	1ad	1.3	0a	0.7	0a	1.1	10b	2.4
≥ 40%	4ef	1.4	0a	0.7	5d	1.2	10b	2.3
Slope Configuration								
Concave	2ad	0.7	0abc	0.4	2b	0.6	14b	1.3
Convex	2bd	0.6	1b	0.3	4c	0.5	17c	1.1
Linear	2bd	0.8	0a	0.4	0a	0.7	13b	1.4
Broken	1abcd	5.5	0ab	2.8	2abc	4.7	0a	10.0
Undulating	4abc	0.7	0a	0.4	1b	0.6	13b	1.3

Least-square means are percent occurrence of insect presence among four size classes of aspen analyzed with eight site and environmental parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.
Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 14. Severity of Cytospora canker, Phellinus decay, and Marssonina foliar blight among four size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Cytospora Canker		*Phellinus* Conk		*Marssonina* Blight	
	n = 611		n = 160		n = 488	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation						
Low	2.8	0.21	1.5	0.24	1.0b	0.08
Moderate	2.6	0.19	1.4	0.20	0.8a	0.08
High	2.7	0.26	1.1	0.32	1.2b	0.16
Aspect						
North	2.6	0.22	1.3	0.26	0.9	0.11
East	2.9	0.22	1.5	0.24	0.9	0.13
South	2.7	0.20	1.2	0.20	1.1	0.08
West	2.6	0.21	1.2	0.24	1.1	0.09
Stand Type						
Damaged	2.6	0.19	1.2	0.21	1.1	0.09
Healthy	2.7	0.21	1.3	0.20	0.9	0.09
Divide Position						
East	2.6	0.21	1.1	0.25	0.8a	0.11
West	2.8	0.20	1.5	0.18	1.2b	0.08
Forest (Divide)						
Medicine Bow	2.3a	0.23	1.1	0.30	0.8	0.11
Pike-San Isabel	2.9b	0.23	1.2	0.38	.	.
Routt	2.7b	0.22	1.4	0.24	1.2	0.08
White River	2.8b	0.21	1.5	0.18	1.2	0.09
Slope Position						
Summit - Shoulder	2.8	0.25	1.0	0.38	1.0ac	0.15
Backslope - Footslope	2.5	0.19	1.5	0.16	1.0bc	0.07
Toeslope - Valley	2.7	0.21	1.4	0.25	0.9a	0.10
% Slope						
0 - 9%	2.8	0.20	1.4	0.22	1.3c	0.09
10 - 19%	2.7	0.20	1.5	0.17	1.0b	0.07
20 - 29%	2.5	0.21	1.2	0.27	0.9ab	0.13
30 - 39%	2.7	0.23	1.2	0.31	1.3c	0.11
≥ 40%	2.8	0.30	1.1	0.36	0.6a	0.15
Slope Configuration						
Concave	2.6	0.11	1.3	0.21	1.2c	0.10
Convex	2.6	0.13	1.0	0.20	1.1b	0.09
Linear	2.5	0.14	1.4	0.32	1.0b	0.12
Broken	3.4	0.87	.	.	.	.
Undulating	2.4	0.13	1.4	0.21	0.7a	0.13

Least-square means are severity (1 – 3) of each disease among four size classes of aspen analyzed with eight site and environmental parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.
Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 15. Average ages of four size classes of aspen in the Aspen Stand Assessment Survey in Colorado, 2009 – 2010

	Saplings n = 73		**Small Poles n = 36**		**Large Poles n = 41**		**Adults n = 83**	
Parameter	**LSMean, Years**	**Std. Error**	**LSMean, Years**	**Std. Error**	**LSMean, Years**	**Std. Error**	**LSMean, Years**	**Std. Error**
Divide Position								
East	5	0.4	34	6.5	35	8.3	87	4.5
West	6	0.5	23	3.2	28	3.5	95	4.7
Stand Type								
Damaged	5	0.4	27	4.4	28	5.6	95	4.6
Healthy	5	0.4	30	4.0	34	4.8	88	4.5
Forest (Divide)								
Medicine Bow	4	0.7	36	12.7	35	16.2	78	7.1
Pike-San Isabel	5	0.5	32	3.0	35	3.7	96	5.4
Routt	6	0.7	29	5.1	35	5.1	97	7.4
White River	5	0.6	17.3	3.8	21	5.0	93	5.9

Least-squares means are average ages of four size classes of aspen analyzed with three site parameters. Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table 16. List of all disease and damage agents included in the Aspen Stand Assessment Survey in Colorado, 2009 – 2010

Damage Agent Code	Agent Description
1.10	Wood Borers
1.20	Bark Beetles
1.21	Ambrosia Beetles
1.22	Bronze Poplar Borer
1.23	Poplar Borer
1.30	Foliage Feeders
1.31	Large Aspen Tortrix
1.32	Forest Tent Caterpillar
1.33	Aspen Leafminer
1.34	Aspen Blotchminer
1.35	Sawflies
1.36	Leafhoppers
1.37	Eriophyid mites
1.38	Unknown chewing
1.39	Blotchminer
1.40	Leaf Tier
1.50	Leaf Roller
1.80	Aphids
2.00	Fungal Agents
2.11	*Cytospora*, unknown
2.11.1	*Cytospora*, C. chrysosperma
2.11.2	*Cytospora*, other
2.12	*Cryptosphaeria lignyota*
2.13	Black Canker-*Ceratocystis fimbriata*
2.14	Sooty Bark-*Encoelia pruinosa*
2.20	Decay fungi- trunk
2.21	*Phellinus tremula*
2.22	*Peniophora polygonia*
2.30	Decay fungi- roots
2.31	*Armillaria* spp.
2.32	*Ganoderma applanatum*
2.40	Foliar Fungi
2.41	Ink spot- *Ciborinia* spp.
2.42	Shepherd's Crook-*Venturia moreletii*
2.43	*Marssonina populi*
2.44	*Melampsora medusae*
2.47	*Dothiora polyspora*
3.00	Animal Damage
3.10	Animal feeding-bark
3.12	Animal feeding- stems
3.13	Antler Rubbing
3.20	Moose feeding
3.30	Rodent feeding-bark
3.31	Rodent feeding- stems
3.40	Porcupine feeding
3.50	Beavers feeding-bark
3.51	Beavers feeding-stems/twig
3.52	Beavers-structural
3.60	Birds-feeding
3.61	Birds-cavity nesting
3.70	Humans
4.00	Abiotic
4.10	Lightning
4.20	Sunscald
4.30	Apparent drought stress
4.40	Frost crack
4.50	Fire scar
4.60	Unknown wound
4.70	Branch gall

Table 17. Percentage of established transects where *Armillaria* root rot was discovered on dead and live aspen in Aspen Stand Assessment plots in Colorado, 2009 - 2010

	Percent Transects with Armillaria	
	Dead aspen	Live aspen
Total	63.9	11.3
Forest		
Pike-San Isabel	51.4	2.6
Medicine Bow	58.8	11.8
Routt	62.5	12.5
White River	57.6	3.8
Stand Type		
Damaged	47.1	14.3
Healthy	52.8	8.0
Divide Position		
East	53.8	50.0
West	59.5	50.0

Table 18. Total hectares of aspen coverage[1] within the four national forests and eleven ranger districts included in this survey

Forest	R.D.	Ha	Pct Total
Medicine Bow		25874	
	Brush Crk-Hayden	20987	81.1
	Laramie	1414	5.5
	Douglas	3474	13.4
Routt		113120	
	Yampa	42370	37.5
	Hahn's Pk	70750	62.5
White River		136446	
	Blanco	45788	33.6
	Aspen-Sopris	67486	49.5
	Rifle	23172	17.0
Pike-San Isabel		123441	
	Pike's Pk	5570	4.5
	S. Platte	8894	7.2
	S. Park	31180	25.3
	Salida	27324	22.1
	San Carlos	50472	40.9

[1]Area calculation of aspen covertype based on remotely-sensed vegetation data for Colorado, courtesy the Colorado Vegetation Classification Project.

Table 19. Total hectares of remotely-sensed and mapped aspen damage[1] and percent annual change of aspen damage area within the four national forests for the years 2006 – 2009

Forest		2006	2007	2008	2009
Medicine Bow Damage (ha)		3422	1978	805	648
	Pct of Cover	13.2	7.6	3.1	2.5
	Pct Change	-	-5.6	-4.5	-0.6
Routt Damage (ha)		5740	15190	14793	9569
	Pct of Cover	5.1	13.4	13.1	8.5
	Pct Change	-	8.4	-0.4	-4.6
White River Damage (ha)		5528	18253	22608	20007
	Pct of Cover	4.1	13.4	16.6	14.7
	Pct Change	-	9.3	3.2	-1.9
Pike-San Isabel Damage (ha)		1104	10682	2593	5754
	Pct of Cover	0.01	0.1	0.01	0.1
	Pct Change	-	7.8	-6.6	2.6
	Total per Year	15794	46103	40799	35978
	Pct Cover	4.0	11.6	10.2	9.0
	Pct Change	-	0.1	-0.01	-0.01

[1] Area of annual aspen damage calculated based on aspen damage shapefiles, courtesy the U.S. Forest Service Region 2 Forest Health Protection. Areas mapped indicated thin crowns, dead standing aspen, or both.

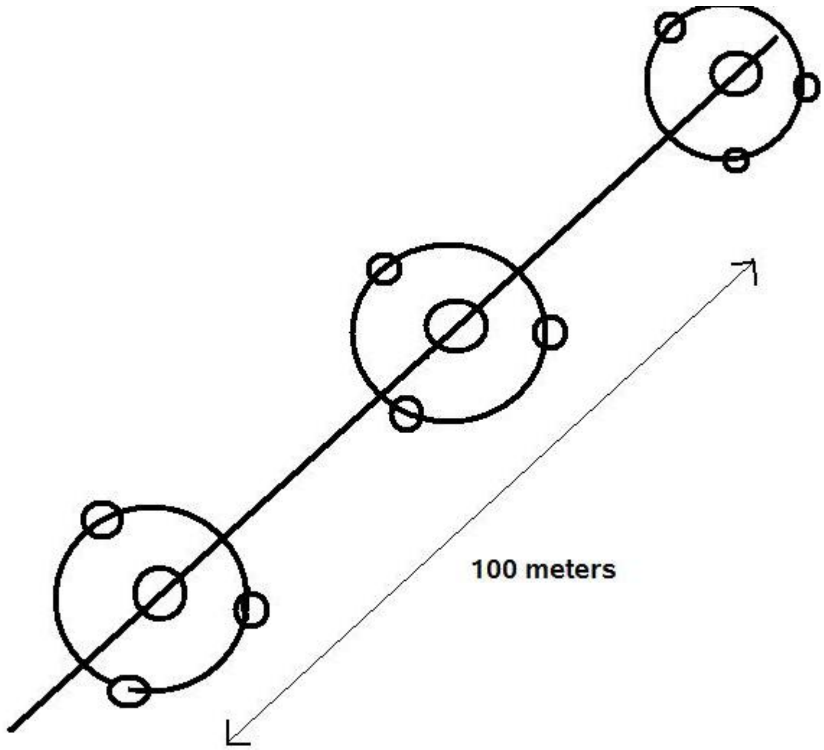

Figure 1. Diagram of 100-m transect and fixed-area circular plots utilized in aspen stand assessment plots in Colorado, 2009-2010.

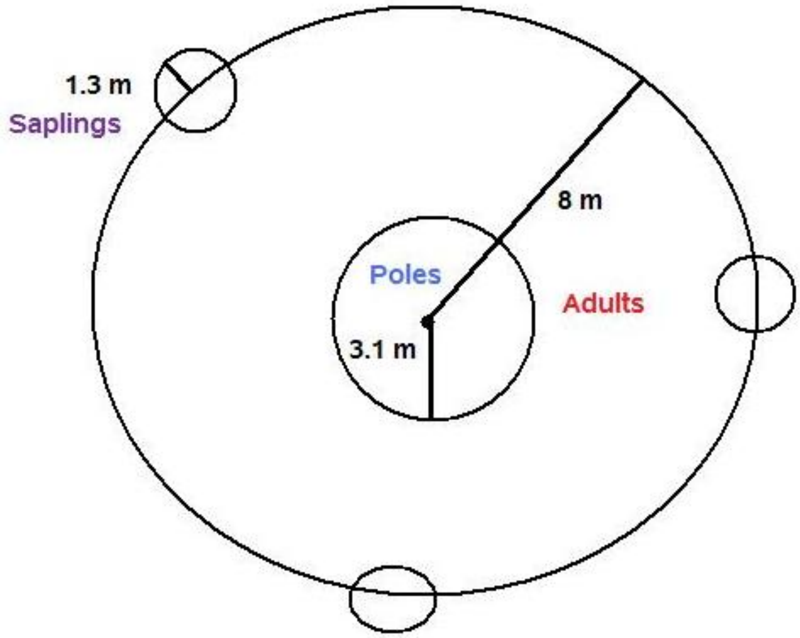

Figure 2. Detail of the fixed-area circular plot type utilized in aspen stand assessment plots in Colorado, 2009-2010.

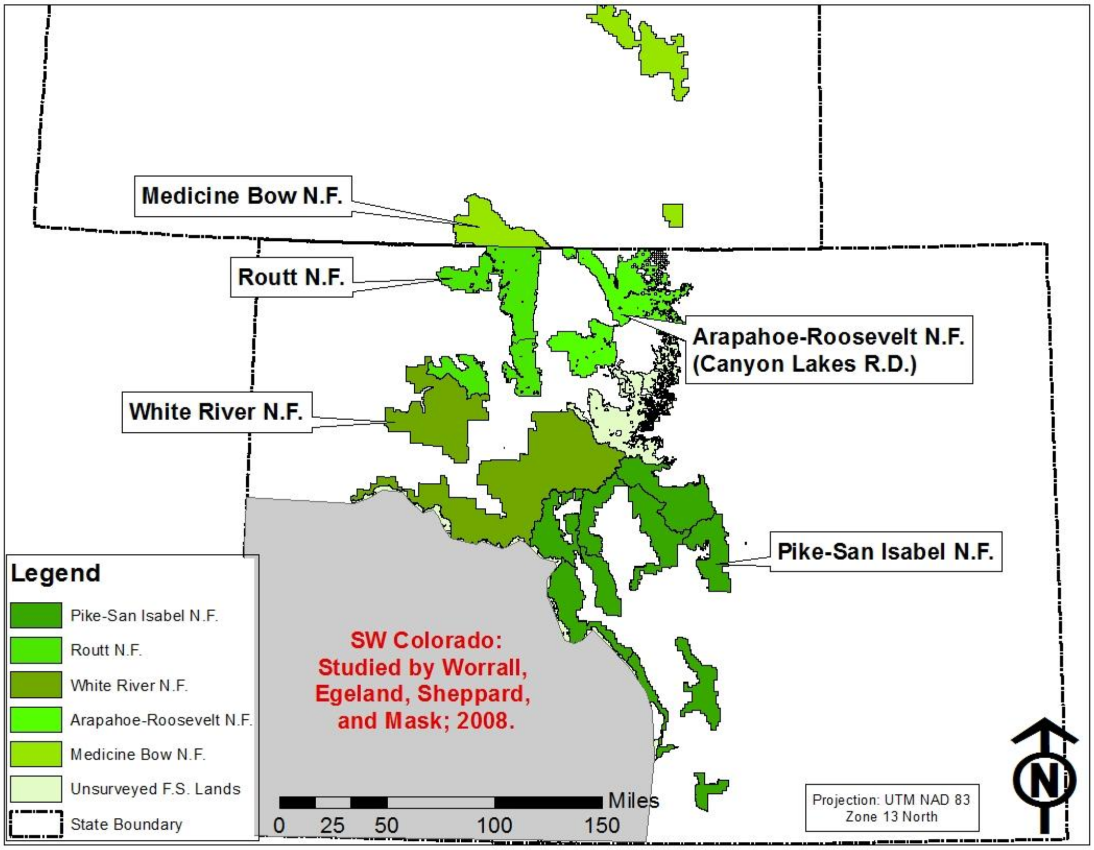

Fig. 3. Map of the National Forests surveyed in aspen stand assessment survey in Colorado, 2009-2010.

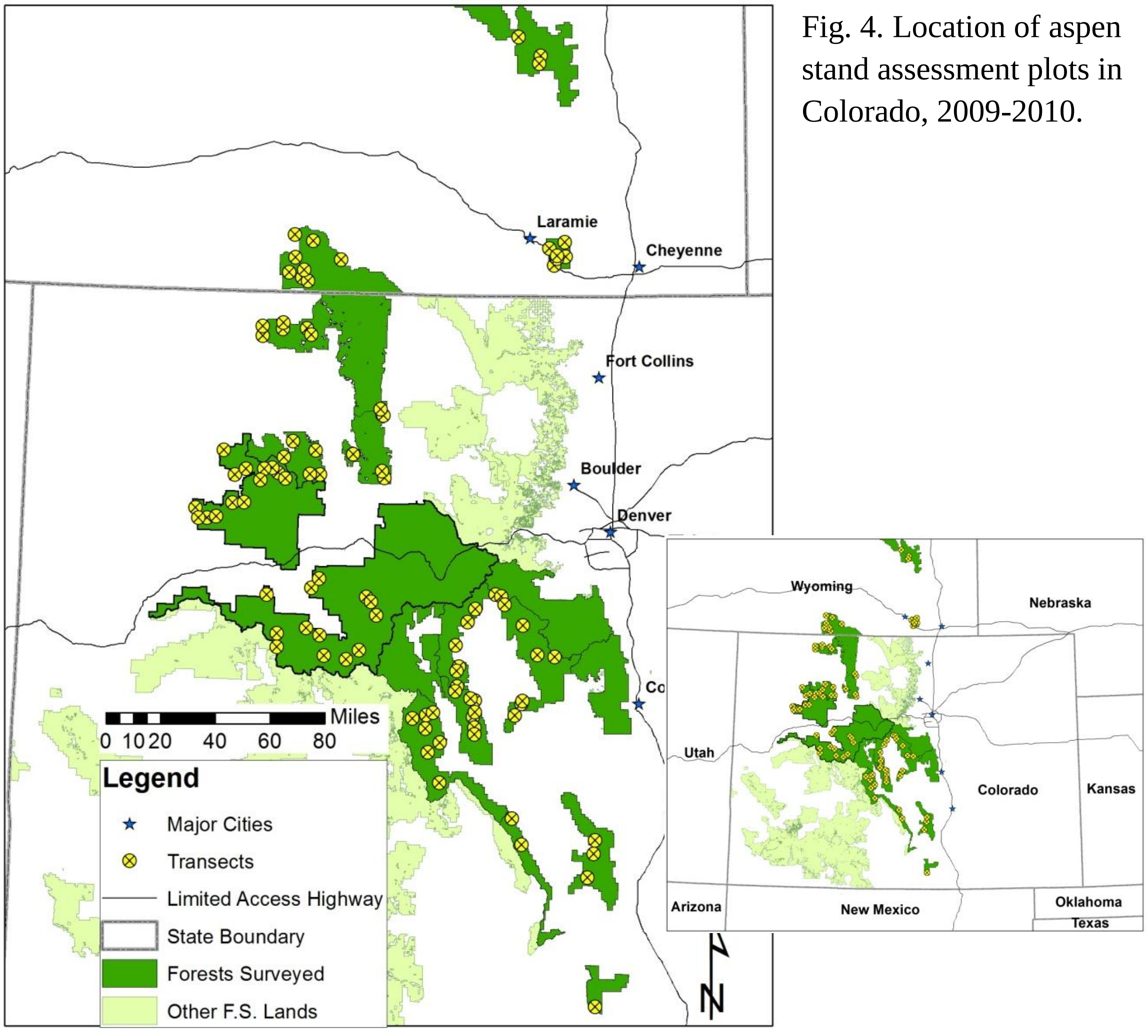

Fig. 4. Location of aspen stand assessment plots in Colorado, 2009-2010.

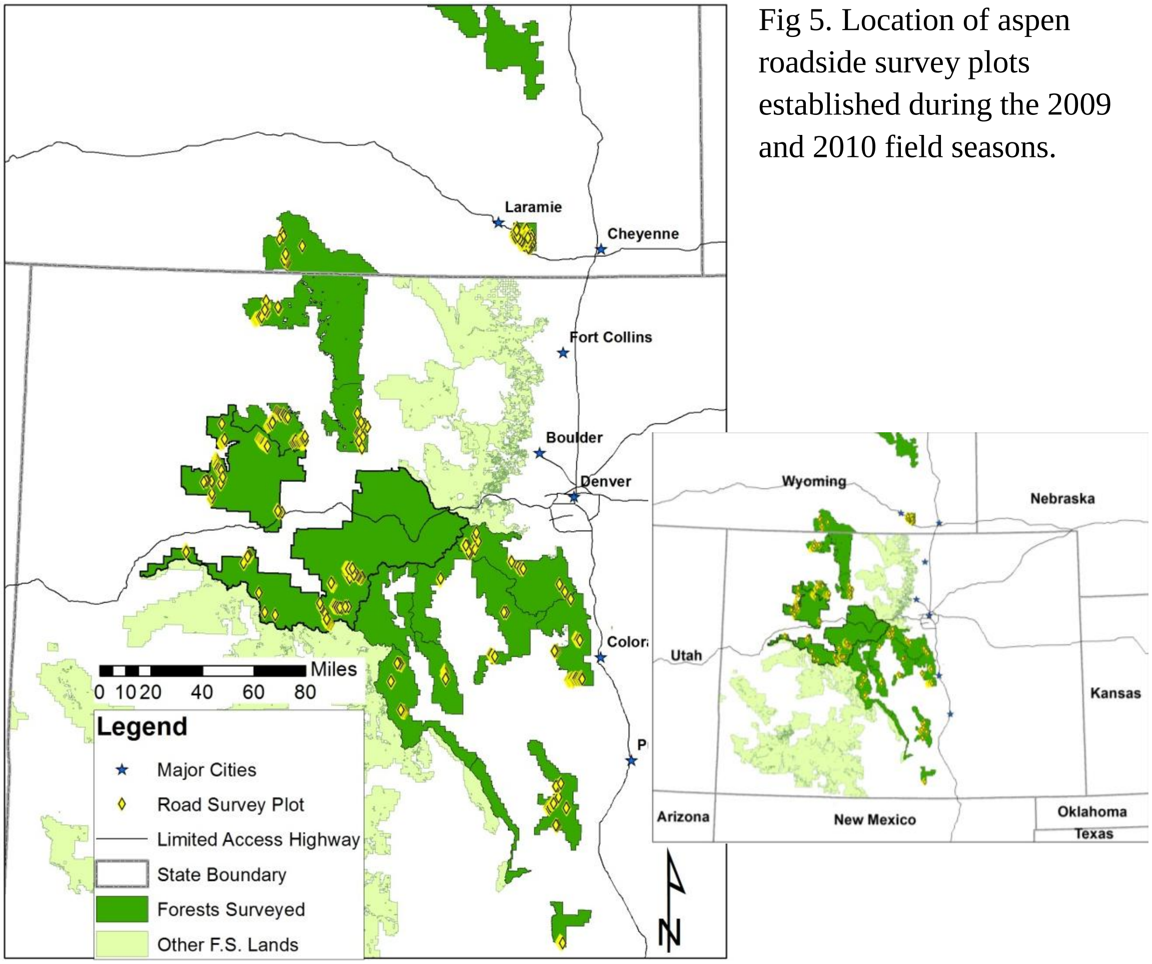

Fig 5. Location of aspen roadside survey plots established during the 2009 and 2010 field seasons.

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Appendix A.: Methods Details

Tree core and cross-section preparation

Cores were glued to a slim, grooved, wooden mounting block using white glue. Cores were aligned in the mounting block grooves such that the vascular tissues were perpendicular to the mounting block (i.e., faced up and down). Cores were then secured in the block groove to dry using tape. Samples were left to dry for at least twelve hours before sanding. Once the glue had completely dried, the top half (i.e., the rounded top edge) of the core was sanded off, first using a belt sander with 80-grit sandpaper, and then finished using 220-grit sandpaper. Cores were then hand-sanded using 400-grit sandpaper to produce a smooth surface with the tree rings clearly visible.

Regeneration cross-sections (or cookies) were given two flat, parallel surfaces to insure that the cross-section surface was flat and level. Samples were first cut using either a band saw or a reticulating saw and a vice, and then sanded using a belt sander with 80-grit sandpaper. Sample surfaces were further refined using either a belt or orbital sander with 220-grit sandpaper. Finally, the 'reading' surface was hand-sanded using 400-grit sandpaper.

Skeleton Plot Symbology and Construction

Standard dendrochronological symbology was used to indicate century (three dots in a line) and half-century (two dots) rings. In addition, decades were marked with a short line, and annual rings were each marked with a single dot. Skeleton plots were drawn for each sample using 1-mm square engineering paper. Such plots are graphic representations of tree age and relative growth, where the x-axis is time (in years), and the y-axis is an inverse scale of relative growth. Each sample was examined for the narrowest annual ring, and this was added to the skeleton plot as a 10-mm long line. All other rings were compared to the narrowest band, and graphed appropriately.

Equations used in data analysis

$$Proportion\ Live = \frac{number\ live\ stems}{total\ stems}$$, per size class, per plot.

Equation 1. The equation used to calculate the proportion of live aspen stems, by size class and plot.

$$\text{QMD} = \sqrt{(\frac{BA*Frequency}{k*TpHa})}$$

Equation 2. The equation used to calculate the quadratic mean diameter (QMD) per size class, per hectare. Where k = is a constant, 0.0000785; Frequency is the number of aspen per size class, per plot; TpHa is the number of aspen per size class, per hectare.

$$BA = \left(\frac{DBH}{2}\right)^2 * \pi$$

Equation 3. The equation used to calculate basal area, where DBH is diameter (in cm) at breast height (i.e., 1.37 m from the ground).

$$\text{TpHa} = \frac{Frequency(2-4)}{ha}$$

Equation 4. The equation used to calculate number of aspen stems per size class per hectare, where frequency (2-4) is the number of trees in each of the size classes 2-4, per plot; ha is hectares per plot.

$$\text{SI} = 4.5\ ft + 0.48274 * \left(\left(Tree\ ht * 3.23\frac{ft}{m}\right) - 4.5\ ft\right) * (e^{-0.07719*Age})\text{\^{}} - 0.93972$$

Equation 5. The equation to calculate Site Index, where Tree ht is average adult tree height and Age is average adult tree age.

Appendix B.: Analysis of Disease and Insect Prevalence by Aspen Size Class

Table B1. Percent incidence of *Cytospora* canker among four size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Saplings n =610		Small Pole n = 521		Large Pole n = 546		Adults n = 2564	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation								
Low	8	8.3	15	6.5	12	5.6	21c	3.5
Moderate	1	8.0	13	6.4	20	5.0	16b	3.2
High	5	9.1	11	9.5	23	6.4	10a	4.2
Aspect								
North	0	8.6	32b	8.7	14a	6.5	11a	3.7
East	8	8.3	6a	7.6	18a	6.1	13a	3.7
South	7	7.7	12a	5.8	10a	5.5	21b	3.4
West	4	8.3	3a	7.9	31b	6.1	17b	3.6
Stand Type								
Damaged	2	8.0	12	6.9	18	5.0	22b	3.3
Healthy	8	8.0	14	6.2	19	4.8	9a	3.4
Divide Position								
East	0	15.0	7	11.0	26	7.3	22b	3.5
West	16	3.1	19	4.9	11	4.3	10a	3.4
Forest (Divide)								
Medicine Bow	8a	6.3	13	7.3	28	6.3	8a	4.0
Pike-San Isabel	0ab	29.0	0	19.8	25	13.9	36b	4.5
Routt	22b	4.2	22	6.2	11	5.8	13a	3.8
White River	10a	3.5	17	5.0	10	4.1	7a	3.6
Slope Position								
Summit - Shoulder	4	7.5	9	6.3	18	4.0	11a	3.1
Backslope - Footslope	9	9.4	11	10.6	14	8.9	23b	5.0
Toeslope - Valley	1	8.3	20	7.9	24	6.4	13b	3.6
% Slope								
0 - 9%	0a	8.1	11	6.3	12	6.1	29c	3.6
10 - 19%	0a	8.0	13	6.4	26	5.0	19b	3.4
20 - 29%	0a	9.0	15	8.5	15	6.4	16b	3.8
30 - 39%	23b	8.7	23	8.2	21	6.7	10a	4.0
≥ 40%	7a	9.5	2	8.4	17	6.5	4a	4.1
Slope Configuration								
Concave	13	8.2	13	7.2	21ab	6.0	30d	2.4
Convex	16	7.8	10	6.3	15a	5.1	21bc	2.0
Linear	4	8.5	6	8.0	27b	5.4	7a	2.6
Broken	.	.	.	.	.	.	0ac	14.7
Undulating	2	8.5	23	7.2	11a	6.1	24a	2.4

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and location parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.
Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table B2. Percent incidence of Black canker (*Ceratocystis fimbriata*) among two size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Large Pole		Adults	
	n = 546		n = 2564	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation				
Low	0	1.5	1a	1.5
Moderate	2	1.3	3b	1.4
High	2	1.7	3ab	1.8
Aspect				
North	0	1.7	2a	1.6
East	1	1.6	1a	1.6
South	1	1.5	1a	1.4
West	3	1.6	5b	1.5
Stand Type				
Damaged	2	1.3	3b	1.4
Healthy	1	1.3	1a	1.5
Divide Position				
East	1	1.9	4b	1.5
West	1	1.1	1a	1.5
Forest (Divide)				
Medicine Bow	2	1.7	3	1.7
Pike-San Isabel	0	3.7	4	1.9
Routt	1	1.5	1	1.6
White River	1	1.1	1	1.5
Slope Position				
Summit - Shoulder	1	1.1	2b	1.3
Backslope - Footslope	0	2.4	0a	2.0
Toeslope - Valley	2	1.7	7c	1.6
% Slope				
0 - 9%	0	1.6	0a	1.6
10 - 19%	1	1.3	2b	1.4
20 - 29%	3	1.7	2ab	1.6
30 - 39%	1	1.8	4b	1.7
≥ 40%	1	1.7	2ab	1.8
Slope Configuration				
Concave	2	1.6	4	1.0
Convex	2	1.3	4	1.0
Linear	0	1.4	2	1.1
Broken	.	.	0	6.3
Undulating	1	1.6	4	1.0

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and location parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the P ≤ 0.05 level.
Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table B3. Percent incidence of Sooty Bark canker (*Encoelia pruinosa*) among two size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009 – 2010

	Large Pole		Adults	
	n = 546		n = 2564	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation				
Low	5	2.8	3	1.8
Moderate	2	2.4	2	1.6
High	0	3.0	2	2.1
Aspect				
North	2	3.2	1a	1.9
East	2	3.0	4b	1.8
South	1	2.7	1a	1.7
West	2	3.0	3a	1.8
Stand Type				
Damaged	2	2.5	4b	1.6
Healthy	1	2.4	0a	1.7
Divide Position				
East	0	3.6	2	1.8
West	3	2.1	2	1.7
Forest (Divide)				
Medicine Bow	0	3.1	4	2.0
Pike-San Isabel	1	6.8	0	2.2
Routt	2	2.8	3	1.9
White River	4	2.0	2	1.8
Slope Position				
Summit - Shoulder	2	2.0	4ab	1.5
Backslope - Footslope	5	4.4	2b	2.3
Toeslope - Valley	0	3.1	1a	1.8
% Slope				
0 - 9%	3	3.0	3	1.8
10 - 19%	2	2.5	1	1.7
20 - 29%	0	3.1	2	1.9
30 - 39%	1	3.3	4	2.0
≥ 40%	3	3.2	1	2.0
Slope Configuration				
Concave	4	2.9	3	1.2
Convex	2	2.5	1	1.0
Linear	2	2.6	2	1.3
Broken	.	.	2	7.3
Undulating	0	3.0	3	1.2

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and location parameters.

Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table B4. Percent incidence of Phellinus decay (*Phellinus tremula*) among two size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009-2010

	Large Pole n = 546		**Adults n = 2564**	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation				
Low	1	1.5	4ab	2.0
Moderate	1	1.3	5b	2.0
High	0	1.7	3a	3.0
Aspect				
North	0	1.7	5b	2.6
East	0	1.6	3ab	2.5
South	0	1.5	0a	2.3
West	1	1.6	5b	2.5
Stand Type				
Damaged	1	1.3	4b	2.3
Healthy	0	1.3	2a	2.4
Divide Position				
East	0	1.9	0a	2.4
West	0	1.1	6b	2.4
Forest (Divide)				
Medicine Bow	0	1.7	0	2.7
Pike-San Isabel	1	3.7	3	3.1
Routt	0	1.5	7	2.6
White River	1	1.0	5	2.5
Slope Position				
Summit - Shoulder	0	2.4	2	3.1
Backslope - Footslope	1	1.1	5	2.1
Toeslope - Valley	0	1.7	2	2.5
% Slope				
0 - 9%	0	1.6	6	2.5
10 - 19%	0	1.3	5	2.3
20 - 29%	0	1.7	3	2.6
30 - 39%	0	1.8	1	2.7
≥ 40%	2	1.7	1	2.8
Slope Configuration				
Concave	2	1.6	6b	1.7
Convex	0	1.3	3a	1.3
Linear	0	1.4	3ab	1.8
Broken	.	.	0ab	10.1
Undulating	0	1.6	6b	1.6

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and location parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.
Large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.

Table B5. Percent incidence of Shepherd's crook blight (*Venturia tremulae*) among three size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009-2010

	Saplings		**Small Pole**		**Large Pole**	
	n =610		**n = 521**		**n = 546**	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation						
Low	10b	5.9	17b	4.6	1	0.7
Moderate	0a	5.5	10b	4.5	1	0.7
High	10b	6.3	0a	6.6	0	0.8
Aspect						
North	13b	5.9	15b	6.1	0	0.8
East	3a	5.7	9ab	5.4	0	0.8
South	4a	5.3	4a	4.0	0	0.7
West	3a	5.7	7ab	5.5	0	0.8
Stand Type						
Damaged	3a	5.5	5a	49.0	0	0.7
Healthy	8b	5.3	12b	4.4	1	0.6
Divide Position						
East	0	10.2	7	7.6	1	1.0
West	13	2.1	10	3.4	0	0.6
Forest (Divide)						
Medicine Bow	6	4.3	4	5.1	0	0.8
Pike-San Isabel	0	20.2	11	13.8	2	1.8
Routt	11	2.9	7	4.4	0	0.8
White River	14	2.4	13	3.5	0	0.5
Slope Position						
Summit - Shoulder	6	6.5	4	7.4	0	1.2
Backslope - Footslope	5	5.2	7	4.4	1	0.5
Toeslope - Valley	6	5.7	14	5.5	1	0.8
% Slope						
0 - 9%	0a	5.6	0a	4.4	0a	0.8
10 - 19%	1a	5.5	8b	4.5	0a	0.7
20 - 29%	12b	6.2	12bc	6.0	0a	0.8
30 - 39%	3a	5.9	7ab	5.7	0a	0.9
≥ 40%	13b	6.6	18c	5.9	2b	0.8
Slope Configuration						
Concave	5a	5.6	11	5.1	0ab	0.8
Convex	12b	5.4	4	4.4	0a	0.7
Linear	1a	5.8	8	5.6	0ab	0.7
Broken	.	.	.	.	.	.
Undulating	4a	5.8	12	5.1	1b	0.8

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and location parameters.
Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.
Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm.

Table B6. Percent incidence of *Marssonina* leaf blight (*Marssonina populi*) among three size classes of aspen in Aspen Stand Assessment Plots in Colorado, 2009-2010

	Saplings n =610		Small Pole n = 521		Large Pole n = 546		Adults n = 2564	
Parameter	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**	**LS Mean**	**Std. Error**
Elevation								
Low	32c	10.4	33	7.3	21c	5.3	9	2.2
Moderate	2b	10.1	23	7.2	4b	4.7	6	2.0
High	0a	11.5	15	10.6	0a	6.1	3	2.6
Aspect								
North	26c	10.8	35b	9.7	2a	6.1	7b	2.3
East	0a	10.5	10a	8.6	0a	5.7	6b	2.3
South	17c	9.7	11a	6.5	13b	5.2	3a	2.1
West	0b	10.5	39b	8.8	7a	5.8	8b	2.2
Stand Type								
Damaged	5	10.2	26	7.8	5	4.7	6	2.0
Healthy	7	9.8	21	7.0	5	4.6	6	2.1
Divide Position								
East	0a	18.8	2a	12.2	0a	6.9	2a	2.2
West	40b	3.9	46b	5.5	17b	4.0	11b	2.1
Forest (Divide)								
Medicine Bow	0a	8.0	0a	8.1	0a	6.0	0a	2.4
Pike-San Isabel	0ab	37.1	5b	22.2	9b	13.2	3ab	2.8
Routt	56c	5.3	55c	7.0	28b	5.4	16c	2.3
White River	26b	4.5	37b	5.6	5b	3.9	5b	2.2
Slope Position								
Summit - Shoulder	20b	11.9	36b	11.9	2	8.4	0a	2.8
Backslope - Footslope	4a	9.5	26b	7.1	11	3.8	5b	1.9
Toeslope - Valley	0a	10.5	8a	8.9	1	6.0	14c	2.3
% Slope								
0 - 9%	36c	10.2	33cd	7.0	18c	5.8	2a	2.2
10 - 19%	11b	10.1	30c	7.2	9bc	4.7	7b	2.1
20 - 29%	0a	11.3	0a		0a	6.0	1a	2.3
30 - 39%	27c	10.9	49d	9.2	2b	6.3	7b	2.4
≥ 40%	0a	12.0	14b	9.4	4b	6.1	14c	2.5
Slope Configuration								
Concave	19b	10.4	38c	8.1	12	5.7	4be	1.5
Convex	34c	9.9	21b	7.0	6	4.8	9cd	1.2
Linear	0a	10.7	24b	9.0	4	5.1	7cd	1.6
Broken	.	.	.	.	.	.	9de	9.1
Undulating	0a	10.7	10ab	8.1	0	5.8	1ade	1.5

Least-squares means are the average percentage of infested stems among four size classes of aspen, as modeled with the eight site and location parameters.

Significant differences between means are indicated by letters; means with different letters are significantly different from each other at the $P \leq 0.05$ level.

Saplings were stems 0.3 – 1.37 m tall; small poles were those with DBH 0.1 – 2.9 cm; large poles were those with DBH 3.0 – 11.9 cm; adults were those with DBH >11.9 cm.