

Aspen's Ecological Role in the West



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William H. Romme¹, Lisa Floyd-Hanna², David D. Hanna²,
and Elisabeth Bartlett³

Abstract—Aspen exhibits a variety of ecological roles. In southern Colorado, the 1880 landscape mosaic contained a range of stand ages, of which half were >70 years old and half were younger. Pure aspen stands in southern Colorado are widespread and may result from previous short fire intervals that eliminated local conifer seed sources. Aspen regeneration in northern Yellowstone Park is controlled by ungulate browsing pressure and fire, so it has been limited since 1920. However, an episode of aspen seedling establishment occurred after the 1988 fires. We urgently need additional detailed, local case studies of aspen ecology to inform management decisions.

Introduction

As the most widely distributed tree species in North America (Fowells 1985), quaking aspen (*Populus tremuloides*) exists within a great diversity of ecological settings and exhibits a similar diversity of ecological roles. Generalizations about aspen's ecological role are therefore difficult—and potentially dangerous. Nevertheless, several key questions about aspen ecology need to be answered to help guide our decisions about sustainable aspen management today and in the future.

In this paper we address three basic questions about the ecological role of aspen in the Rocky Mountain West. For each question, we offer more than one answer, based on several case studies that reflect the wide range of ecological settings in which aspen occurs. One important outcome of this comparative analysis is the recognition that we urgently need additional detailed, local case studies of aspen ecology. The questions are:

1. What was the range of variability that existed prior to EuroAmerican settlement in the late 1800s, with respect to aspen disturbance regimes and landscape patch dynamics?
2. What are the major factors, biotic and abiotic, that control aspen successional dynamics and responses to disturbance?
3. Do aspen's life history traits and reproductive mechanisms provide adequate resilience to impending climatic and environmental changes?

Question 1: Pre-1900 Aspen Disturbance Regimes and Landscape Patch Dynamics

Aspen disturbance regimes and landscape patch dynamics have been highly variable in both time and space. We illustrate this range of variability by examining two very different case studies. The first comes from the southern Rocky Mountains, in the western San Juan National Forest. Here aspen is the dominant cover type, creating the landscape matrix over thousands of hectares. In this area fire clearly was a major disturbance agent in the past, but ungulate

¹Fort Lewis College, Durango, CO.
²Prescott College, Prescott, AZ.
³University of Wyoming, Laramie, WY.

browsing apparently was of minimal importance. The second case study is from the northern Rocky Mountains, specifically the winter ungulate range of Yellowstone National Park. Aspen stands in this area exist as relatively small patches within a matrix of other vegetation types, and both fire and ungulate browsing have been important components of the disturbance regime.

Aspen Fire History and Patch Dynamics in the San Juan National Forest

Aspen forest is a dominant cover type over extensive areas at middle elevations in the western San Juan National Forest, where individual patches of aspen forest may cover hundreds of hectares (Jones and Schier 1985; Romme et al. 1992). The most important agent of disturbance in aspen forests of the southern Rocky Mountains before 1900 was fire, although other natural disturbances were locally important including windthrow, fungal diseases, tent caterpillars and other insects, snow damage, hail, lightning, and sunscald (Jones and DeByle 1985a; Jones et al. 1985; Romme et al. 1999; Veblen 2000).

Jones and DeByle (1985b:77) observed that "... almost all even-aged aspen stands in the West appear to be the result of severe fire, whether or not the aspen type is climax on the site." Yet despite this widespread recognition of the importance of past fire in aspen forests, we have little specific information on aspen fire history in the southern Rockies. Baker (1925) studied fire scars in Ephraim Canyon in central Utah and concluded that light fires had occurred every seven to 10 years within the general region of his study area (actual extent of the study area not specified). Meineke (1929) determined that fires had occurred in every decade of the nineteenth century at the Great Basin Range Experiment Station in the Wasatch Range, Utah, but that the only severe fire was in 1867. Harniss and Harper (1982) found that the conifers were older in subalpine fir-aspen stands at higher elevations than in white fir-aspen stands at lower elevations. They suggested that this may reflect longer fire intervals at the higher elevations, but their study provided no estimates of actual fire intervals in the aspen zone. To obtain more detailed and quantitative estimates of past fire intervals and landscape dynamics within the aspen forest type, we studied fire history in an aspen-dominated landscape on the western flanks of the La Plata Mountains in the San Juan National Forest.

Methods

Reconstructing fire history is more difficult in aspen forests than in some other forest types, because aspen are easily killed by fire and few fire-scarred trees can be found with which to date past fires. Therefore, we used a less precise method of determining fire history that was based on the statistical distribution of current stand ages, i.e., the time since the last lethal fire (Johnson and Gutsell 1994). To develop this method, we began by sampling five aspen stands in 1995 within the Lime Creek burn, an area near Silverton, Colorado, where an extensive fire in 1879 was documented by written records. In two aspen stands, we removed an increment core from every stem within a circular plot at a height of about 1 meter. The cores were glued to slotted boards, air dried, sanded, and stained. The number of annual rings was counted under 20-power magnification using a dissecting microscope. Additional years were added to the estimate of stem age for cores that had missed the center of the tree, based on the radius of curvature of the innermost rings, and three years were added to the age of each stem as an estimate of the time required to grow to coring height.

The age structure of aspen stems in the 1879 Lime Creek burn was constructed from all readable cores in the two stands (about 20% of the sampled increment cores were rotten, lacking centers, or otherwise unreadable). The post-fire aspen that which resprouted after the documented 1879 burn was clearly detectable in the current age structure of the stands (figure 1). Nearly 60% of the aspen trees in our sample had established between 1880 and 1890, even though many individuals of younger age classes were present due to continued recruitment of stems into the canopy for several decades following the fire. The Lime Creek data also revealed that very few aspen trees had survived the fire in 1879, as would be expected in such a fire-sensitive species. Next, we collected increment cores only from 15–20 of the largest and oldest appearing stems in three additional stands within the Lime Creek burn area. The age structure of these stands similarly contained a prominent cohort of stems that had established within a decade after 1879, plus numerous younger stems from the 1890s–1910s (data not shown). From this preliminary analysis of current age structure in stands of known fire history, we determined that in subsequent analyses of stands with unknown fire history, we could assume that the oldest cohort of 2+ living aspen stems dating to a single decade in any stand today represents the initial postfire cohort.

Landscape-scale fire history

Once we had verified that postfire aspen cohorts could still be detected in aspen stands that burned >100 years ago, we determined fire history in a 76 km² area of unknown fire history at an elevation of 2,650–3,310 m in the western portion of the San Juan National Forest (Romme et al. 1999). A 1 km² grid was overlaid on the 7.5-minute topographic quadrangles for the study area based upon the UTM 1,000 m grid tics. A sample point was randomly chosen within each 1 km² grid cell such that each unit of the total study area had an equal probability of being sampled (Johnson and Gutsell 1994). The sampling sites identified on the map then were located in the field. If the sampling point appeared to have been logged, we randomly selected another point within the 1 km grid cell. At each point we collected an increment core at breast height from the 20 largest sound aspen trees. Cores were glued to boards, sanded, stained, and dated as described above.

We then summarized the ages of dominant aspen stems in each of the 76 sampled stands, and estimated the decade in which the most recent lethal fire

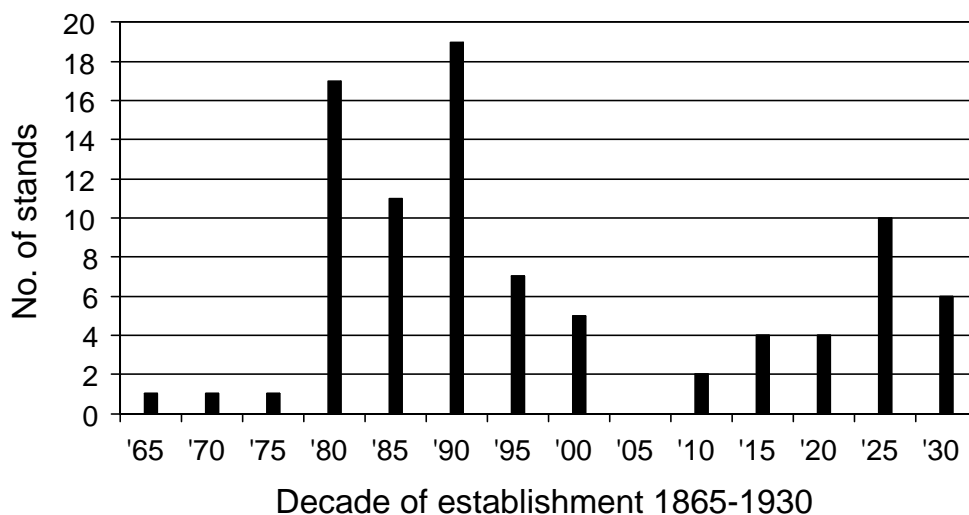


Figure 1—Age structure in 1995 of all aspen stems >5 cm d.b.h. within two aspen stands known to have originated after a lethal fire in 1879, Lime Creek burn, San Juan National Forest, Colorado.

had occurred. The oldest postfire cohort detected was from the 1760s, and we found cohorts in other stands representing fires in every decade from the 1810s through 1870s (figure 2). Twenty-seven stands did not contain any set of 2+ trees established within the same decade that was old enough to represent a postfire cohort, but these stands did contain individual old aspen trees (>150 yr). In these stands, we assumed that the stand had originated long ago and that most or all of the original postfire cohort had died through natural causes such as disease. We could not assign a precise age to these stands but called their date of origin “pre-1760s” since the oldest recognizable postfire cohort was from the 1760s. Some of these stands may have originated more recently than the 1760s and had simply lost their postfire cohort, but we think that most actually did date from before the early 1800s because of their all-aged, all-sized canopy structure. Another 19 stands contained no apparent postfire cohort but no old trees either; time since fire in these stands could not be determined and they were listed as “unknown” and deleted from the statistical analysis. See Romme et al. (1999) for additional details of sampling and determining stand ages.

Fire History and the Landscape Mosaic During the Reference Period

Table 1 summarizes the number of aspen stands that became established in each decade from the 1870s to the 1760s, as well as the number of old stands of uncertain origin date (“pre-1760s”). None of the stands that we sampled had originated later than 1880, apparently because no extensive fires occurred in our study area after this time. However, small fires have occurred elsewhere in the San Juan Mountains during the 20th century, and small patches of younger aspen stands can be found in those areas. Extensive fires occurred in our study area in the 1870s and 1860s. Fewer stands date from the early to mid 1800s, either because there were fewer or less extensive fires during that time, or because evidence of these early fires has been destroyed by the fires of the later 1800s. Approximately 45% of the sampled stands appeared to have last burned at some time prior to the early 1800s (“pre-1760s” in table 1).

What kind of a landscape mosaic existed in the aspen zone prior to the grazing, logging, and fire control efforts of the 20th century? Figure 2 summarizes the distribution of stand ages as they must have existed in the mid-1880s. These ages were determined by subtracting the decade of stand origin (table 1) from 1880. For example, the 10 stands that originated in the 1870s (table 1) would have been about 10 years old in the mid-1880s (figure 2). We determined in this way

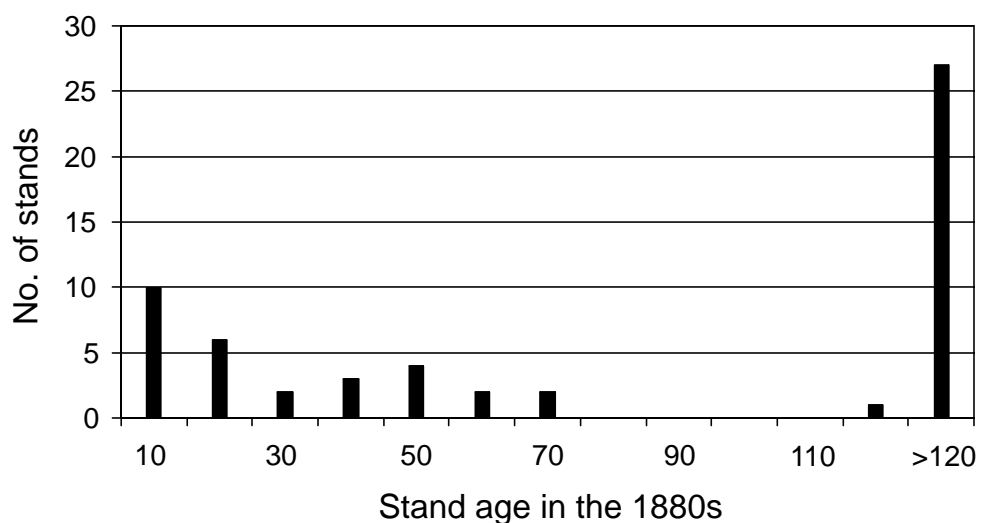


Figure 2—Distribution of stand ages in the 1880s within a 77-km² study area within the San Juan National Forest, Colorado, estimated by subtracting the decade of stand origin (table 1) from 1880.

Table 1—Number of stands within a 77-km² study area in the western San Juan National Forest, Colorado, that established after lethal fires in each decade since the 1760s.

Decade of last fire	Number of sampled aspen stands
1870s	10
1860s	6
1850s	2
1840s	3
1830s	4
1820s	2
1810s	2
1800s	0
1790s	0
1780s	0
1770s	0
1760s	1
Pre-1760s	27
Unknown	19
Total	76
Total, exc. unknown	57

that the median stand age in the 1880s was about 70 years. This means that about half of the stands in the landscape were >70 years old and half were <70 years old. If half of the landscape had burned within the previous 70 years, then it would require about twice this length of time, or 140 years, for an area equal to the entire landscape to burn. Thus, our best estimate of the fire rotation period in an aspen-dominated landscape during the period of indigenous settlement is about 140 years.

We conclude from this analysis that within this aspen dominated landscape during the period from the mid-1700s to the late 1800s, approximately half of the aspen forest consisted of relatively young stands developing after fires within the preceding 70 years, and that half of the stands had escaped fire for more than about 70 years. Fires occurred somewhere within the 76 km² study area nearly every decade, but it required more than a century for an area equal to the entire study area to be burned. Some stands probably were re-burned at relatively short intervals (<70 years), but many others persisted for more than a century without burning.

Caveats

Three important weaknesses of this fire history study should be acknowledged. First, we cannot say in which exact years fires occurred, because dating fires from postfire age cohorts is inherently less precise than dendrochronological dating based on fire-scarred trees. However, because fire scars are so rare in aspen forests, the decade-level precision that we achieved is probably about the best that can be done in aspen-dominated landscapes of the southern Rocky Mountains. A second weakness of our method is that it cannot distinguish between two or more fires within the same decade, nor can it depict actual sizes or shapes of patches created by individual fires. Finally, it is important to note that we probably detected only the relatively large fires that occurred in the past. Many smaller fires undoubtedly occurred in places between the locations of our sample points and were not detected. This may not be a serious error from the standpoint of interpreting past fire effects, however, because a few large fires

probably were responsible for most of the burned area; this is the case today in boreal forest and several other types of fire-dominated landscapes (Johnson 1992; Moritz 1997; Romme et al. 1998).

It is also important to recognize that we have created a “snapshot” of the structure of the aspen forest mosaic at a single time at the very end of the period preceding extensive EuroAmerican land use changes, viz., the 1880s. We do not know just how representative this particular decade was of the period of several centuries before the 20th century. The landscape mosaic in 1880 probably was similar in its broad features to earlier mosaics, but there must have been fluctuations over time. Thus, in earlier periods, the median stand age probably was greater or less than the 70 years that we determined for the mid 1880s. Note, for example, the period in the late 1700s and early 1800s, a time when apparently few aspen stands were regenerated by fire in our study area (table 1). This was a period of reduced fire activity throughout the Southwest (Swetnam and Betancourt 1998; Swetnam et al. 1999), when the age structure of aspen forest mosaics in many areas probably shifted toward a predominance of older stands. In contrast, the middle and late 1800s was a time of greater fire frequency throughout the Southwest, when the aspen landscape mosaic may have been dominated by younger stands. Therefore, in evaluating today's age structures and developing desired future conditions, the 70-year median stand age that we determined for the 1880s should be viewed only as an approximate characterization of the conditions during the pre-1900 reference period.

Finally, we note that our study area in the western San Juan Mountains is located on a broad expanse of gently sloping terrain, with little topographic complexity and therefore few barriers to extensive fire spread under dry windy conditions. In other parts of the Rocky Mountains, where the terrain is more rugged or dissected, pre-1880 fire intervals probably were longer and the 1880 landscape structure probably contained a higher proportion of older stands than is depicted in figure 2.

Comparison of current conditions

Patch clearcutting now has replaced fire as the dominant disturbance agent in our study area (Crouch 1983; Shepperd 1993). However, the landscape mosaic still resembles the pre-1900 mosaic in its broad features, and overall, aspen appears to be thriving. Important practical questions remain about the optimal size and shape of logging units, and about differences between postfire and post-logging habitats (e.g., snags and coarse woody debris; Romme et al. 2000). However, aspen shows no serious decline and is in no danger of disappearing from this ecosystem (cf. Kay 1997).

In portions of the southern Rocky Mountains where no logging is allowed, the distribution of aspen stand ages is gradually shifting toward a preponderance of older age classes (Mueggler 1989). From an ecological standpoint, this is probably not a cause for concern, at least not in many areas (cf. Johnson 1994). Note in the age structure data from the Lime Creek burn (figure 1) that canopy stems are continuing to regenerate in most old stands, even after the original postfire cohort has largely disappeared. Nor is there evidence of replacement by conifers in many aspen stands of the San Juan Mountains (see below). Old aspen stems, especially those with decay, are extremely important for wildlife (DeByle 1985), and we see no obvious signs of diminished ecosystem function (e.g., gross productivity, decomposition, biodiversity) as these aspen stands age. Fire frequency likely will increase in the next century because of global warming (Graham et al. 1990), regardless of current management policies, and many old stands will be lost to wildfire. Therefore, rather than regarding late-successional

aspen stands as a problem that needs to be fixed by returning them to younger states via logging or prescribed burning, we suggest that late-successional stands be regarded as valuable components of aesthetics and biodiversity, and worthy of preservation.

This case study may be representative of other areas on the western slope of Colorado and perhaps also portions of Utah and northern New Mexico, where aspen dominates mid-elevation portions of the landscape and fire was the principal agent of disturbance prior to EuroAmerican settlement.

Aspen, Elk, and Fire in Northern Yellowstone National Park

Only about 2% of the 140,000-ha ungulate winter range in northern Yellowstone National Park is classified as an aspen cover type (Hessl 2000). Aspen stands are mostly small, discrete patches within a landscape dominated by sagebrush (*Artemisia tridentata*) steppe and conifer forests of Douglas-fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta* var. *latifolia*). Aspen is largely restricted to a narrow elevation zone near the forest/steppe ecotone (Despain 1990).

Unlike the situation in southern Colorado, where stands have usually regenerated prolifically after disturbance, the extent and density of aspen stands in northern Yellowstone have clearly decreased during the 20th century (Wagner et al. 1995; Kay 1997; White et al. 1998). The current aspen decline is due largely to chronic heavy elk browsing. However, reconstructions of aspen age structures reveal that aspen overstory regeneration in northern Yellowstone may have been episodic even before the ecological changes that began with park establishment and EuroAmerican settlement of adjacent lands in the late 1800s. Most of the mature aspen found today in northern Yellowstone became established between 1871 and 1920 (Ripple and Larsen, in press[a]). A reanalysis of Warren's (1926) aspen data set indicates that aspen overstories were successfully regenerating, at least in places, from the 1750s through 1920s (Ripple and Larsen in press[a]). However, canopy regeneration may have been less widespread before 1870 than it was afterward, e.g., some photographs from the late 1800s show mostly sapling aspen stands apparently resprouting after recent fire. The late 1800s was a unique period in the ecological history of this area, when a combination of low elk numbers, recent fires followed by fire suppression, wolves, and moist weather allowed aspen stems to grow into large size classes over most of the ungulate winter range (Romme et al. 1995). This unique combination of conditions has not recurred since the early 20th century, and no significant aspen tree regeneration has occurred since that time (Ripple and Larsen, in press[a]). It is even possible that mature aspen were more abundant in the early 20th century, following the unique conditions of the late 1800s, than at any time in the previous century or centuries. As Singer et al. (1998) emphasize, the northern Yellowstone ungulate range must be viewed as a nonequilibrium system that exhibits wide variation in response to variability in climate and herbivore pressures (more on this below).

Question 2: Controls on Aspen Succession and Responses to Disturbance

Aspen stands may exhibit a variety of successional trajectories following disturbance. These trajectories are determined by local climate, soils, browsing

pressures, and seed sources. Also, as we suggest below, contingent historical events that occurred before the most recent disturbance may have a powerful influence on successional dynamics. We examine two case studies that illustrate responses to two very different kinds of disturbance regimes, local histories, and successional responses. The first study is from the San Juan National Forest, Colorado, where past fires were followed almost always by aspen regeneration, but with highly variable densities of associated conifer species. The second study is from northern Yellowstone National Park, where the success of postfire aspen regeneration is strongly influenced by ungulate browsing pressure.

Seral Versus Stable Aspen Forests in the San Juan National Forest, Colorado

Aspen may be found in pure stands, without any other tree species, or as a seral species in stands going through succession toward eventual domination by conifers. The conifers that gradually replace aspen in seral stands of the southern Rocky Mountains usually are Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at higher elevations, white fir (*Abies concolor*) and Douglas-fir at middle elevations, and ponderosa pine (*Pinus ponderosa*) at the lowest elevations. There is some controversy regarding the successional status of pure aspen stands. Some investigators argue that such stands really are not “climax,” but have been disturbed in the past and conifer replacement simply occurs over very long time periods (centuries or millennia). Other investigators suggest that pure aspen stands do in fact represent a stable vegetation type, independent of disturbance.

Regardless of the long-term successional status of pure aspen stands, it probably makes sense to regard them as a stable vegetation type within the intermediate time scales that managers have to deal with (Fetherolf 1917; Baker 1925; Langenheim 1962; Morgan 1969; Severson and Thilenius 1976; Mueggler 1985). For the remainder of this paper, we refer to pure aspen stands having little or no conifer component as “stable aspen.” We refer to aspen stands having enough conifers to dominate the stand once the current aspen canopy has died as “successional aspen.”

Stable aspen stands have an uneven age structure and lack conifers (Mueggler 1976, 1989; Betters and Woods 1981). They tend to be associated with certain combinations of elevation, topography, and substrate, but the patterns of association are weak. Baker (1925) reported that “heavy-soiled flats” are not favorable for conifers and support primarily aspen, whereas rocky soils favor conifers. Pfister (unpublished dissertation, cited in Mueggler 1976) reported that stable aspen stands were common at lower elevations, but that higher-elevation aspen stands tended to be seral to conifers. Similarly, K. T. Harper (personal communication, cited in Mueggler 1985) has observed that stable aspen communities are commonly found at mid-elevations and on southerly exposures, but that successional aspen communities predominate at higher elevations and on northerly exposures. Soils under stable aspen stands usually are richer than soils under a mix of aspen and conifers, but this may be a result of aspen dominance rather than a cause (Parker and Parker 1983; Cryer and Murray 1992). To better understand the environmental controls on aspen forest succession, we studied successional versus stable aspen stands in the San Juan National Forest, Colorado.

Methods

We located 65 mature aspen stands in a study area centered on the fire history study area described above, but also including some surrounding lands in the

western portion of the San Juan National Forest. The stands were selected from topographic maps and field observations to represent the full range of elevation, substrate, topographic conditions, and conifer densities found in this portion of the San Juan Mountains. In each stand (about 1 ha in extent) we measured conifer density in a belt transect placed through the center of the stand, collected 10 increment cores from dominant canopy aspen trees, measured soil pH and hue at five points along the central transect, and recorded elevation, substrate, slope aspect, slope position, and steepness. After computing conifer densities in all stands, we defined stable stands as those having <200 conifer stems/ha and successional stands as those having 200 or more conifer stems/ha. In fact, most of the stands classified as stable had no conifers at all, but the broader definition was necessary to provide adequate sample sizes for chi-square analyses.

Results

The observed frequency of stable stands was significantly greater than expected at elevations below 8,000 feet, and was less than expected above 8,000 feet (chi-square test, $P = 0.02$, table 2). Thus, stable aspen stands in the western San Juan Mountains tend to be associated with lower elevations, consistent with other observations (cited in Mueggler 1976), although successional stands also are common at lower elevations. Aspen stands at higher elevations tend to be successional, although we found some stable stands at all elevations up to 10,500 feet.

Stable aspen stands also were significantly ($P < 0.05$) associated with shale substrates rather than sandstones or igneous rocks, consistent with Baker (1925), but the pattern in our San Juan National Forest study area was weak and probably not ecologically meaningful (data not shown). Chi-square tests revealed no significant patterns in frequency of stable versus successional aspen stands with respect to soil hue, soil pH, aspect, slope position, or slope steepness. There was a significant association between stable versus successional aspen stands and stand age, i.e., older stands tended to be successional and younger stands tended to be stable (data not shown). However, older stands also were significantly associated with higher elevations and younger stands with lower elevations, so elevation appears to be the most important underlying variable associated with aspen successional patterns in this area.

Interpretation

These results suggest that the occurrence of stable versus successional aspen forests in the western San Juan National Forest is explained not by deterministic climatic or topographic gradients, but by local historical contingencies. Many of the stable aspen stands are located adjacent to a zone of ponderosa pine that

Table 2—Frequency of stable aspen stands (<200 conifers/ha) in relation to elevation in the western San Juan National Forest, Colorado. The pattern is significantly different from the null model (chi-square = 10.27, 3 degrees of freedom, $P = 0.0164$, $n = 65$).

Elevation	Observed	Expected
<i>feet</i>		
6,000–7,000	21	15
7,001–8,000	16	10
8,001–9,000	21	29
9,001–10,500	7	11

covers an extensive plateau area just to the west and at lower elevations than the aspen zone. Median fire intervals before 1880 in the ponderosa pine zone were five to 15 years (Romme et al. 1999), because of frequent summer dry periods and highly flammable litter. Fires that were ignited in the ponderosa pine zone probably often spread into the adjacent aspen forests. The resulting fire intervals in the low-elevation aspen forests probably were longer than in the pine forests, because of the low flammability of aspen fuels, but were shorter than the time required for conifer seedlings to reach reproductive age. Consequently, conifer seed sources were locally eliminated in many stands. However, the aspen responded to frequent fire by resprouting from the roots, thus maintaining its local dominance.

In contrast, median fire intervals in aspen forests at the higher elevations, remote from the ponderosa pine zone, were substantially longer than in aspen at lower elevations. For example, median fire intervals prior to 1900 were >150 years in spruce-fir forests of the San Juan Mountains (Romme et al. 1999). Hence, conifer seed sources persisted at the higher elevations, and most aspen stands remained successional. Baker (1925) similarly suggested that recurrent fires (at about a 50-year rotation) may help maintain pure aspen forests by eliminating conifer seedlings and saplings. Thus, we hypothesize that many stable aspen stands in the southern Rocky Mountains and perhaps elsewhere, especially those at lower elevations, developed primarily in response to very short fire intervals in the past. These stands now persist without conifer invasion even in the absence of fire, because local conifer seed sources have been eliminated.

Effects of Fire and Ungulate Browsing on Aspen in Yellowstone National Park

The large fires of 1988 burned nearly a quarter of the northern Yellowstone winter range. However, even though the fires stimulated abundant sucker production in most of the burned aspen stands, almost none of those suckers are growing into new canopy stems today (Romme et al. 1995; Kay 1997). Why is aspen responding to this recent disturbance by fire in a fundamentally different manner than it did a century ago? The principal reason appears to be chronic heavy browsing by elk. The browsing is clearly preventing the aspen sprouts from growing taller than about 0.5 m and also may be gradually reducing the density and overall vigor of the sprouts and of the underlying aspen root system (White et al. 1998). Whereas fire formerly stimulated aspen tree regeneration in this region, current heavy browsing pressure has “uncoupled” the beneficial effect of recent fires on aspen (Hessl 2000). The warmer and drier climatic conditions of the 20th century also may have stressed the aspen and made them less resilient to browsing (Coughenour and Singer 1991).

We suggest that Yellowstone's northern winter range is representative of other areas in the West where aspen has always been a somewhat marginal species, because of suboptimal climate and soils coupled with heavy ungulate browsing pressures. A similar 20th century decline in aspen has been documented on elk winter ranges in Rocky Mountain National Park, Colorado (Olmsted 1979; Baker et al. 1997), in the Jackson valley, Wyoming (Krebill 1972; Bartos et al. 1991; Hessl 2000), and in Banff, Jasper, Yoho, and Kootenay National Parks in Canada (White et al. 1998). Aspen probably is most vulnerable to decline in this kind of ecological setting—in response not only to chronic heavy browsing, but also to drought and changes in the fire regime.

However, it is premature to predict a certain loss of aspen even in these landscapes where it is most vulnerable to decline. In the same national parks listed above, but outside the ungulate winter ranges, and in places like southwestern Colorado where climate and soils apparently are optimal for aspen, there is little or no evidence of aspen decline (Suzuki et al. 1999; Romme et al. 1999). Even within the elk winter range of the Jackson valley, Wyoming, Hessl (2000) found some stands that were regenerating adequately after prescribed fires, perhaps because of unique genetic characteristics or other subtle factors not immediately obvious. Moreover, aspen clones can persist for a very long time, even when subjected to intense browsing or competition from conifers (Despain 1990; Peterson and Peterson 1992). White et al. (1998) observed in Jasper National Park that aspen began to regenerate again after wolves were reestablished in the 1970s. With the recent reintroduction of wolves in Yellowstone, it is possible that predation pressure will reduce elk densities and modify elk foraging behavior in such a way that aspen will be able to escape browsing pressure and regenerate in portions of the northern range where no significant regeneration has occurred in the last 80 years (Ripple and Larsen, in press[a]). Ripple and Larsen (in press[b]) also report that “jackstraw piles” of fallen conifers killed by the 1988 fires provided aspen sprouts with at least partial protection from elk browsing in northern Yellowstone National Park.

Question 3: Aspen Life History Traits, Reproductive Mechanisms, and Resilience

As a long-lived clonal species that reproduces primarily via vegetative sprouting, aspen responds very effectively to local disturbances that fall within the recent historic range of variation in disturbance kind and severity. Thus, in the San Juan Mountains study area, fire poses no serious threat to the long-term persistence of extensive aspen stands, even if fire frequency increases in the next century in response to global climate change. Similarly, aspen in the San Juan Mountains should be able to withstand reasonable logging and grazing programs, especially if those programs are designed to mimic the disturbance regime of the pre-1900 period as much as possible (Romme et al. 2000).

The situation is less clear in northern Yellowstone, where current browsing intensity may exceed historic levels—not with respect to acute browsing intensity (which must have been occasionally intense at many times in the past) but possibly with respect to the chronic heavy browsing pressure now occurring. Nevertheless, aspen's long genet life span, extensive root systems, and ability to produce new stems asexually have enabled it to persist throughout a century of heavy browsing pressure and may maintain the species well into the next century even under the current disturbance regime (Despain 1990).

However, asexual reproduction via root sprouting is not enough. To be able to cope with broad-scale climate change or habitat alterations that exceed the range of variation experienced during the last several centuries, aspen must be able to maintain genetic diversity through sexual reproduction and to produce new genetic individuals through seedling establishment (Eriksson 1992; Mitton and Grant 1996). Climate simulations under doubled-CO₂ scenarios suggest that climatically suitable geographic ranges for many species will shift substantially during the next century, and that conditions within species' ranges may be altered (Romme and Turner 1991; Bartlein et al. 1997). Moreover, most individual aspen genets that we see on the landscape today may have established

during cooler climates in the past, e.g., during the Little Ice Age or even in the early Holocene (Baker 1925; Cottam 1954; Barnes 1966; Tuskan et al. 1996), and hence may not be genetically well equipped to cope with the warmer climates and other environmental changes expected in the next century.

Aspen seedlings have been notoriously rare in the West throughout the 20th century, but genetic studies within mature populations indicate that occasional seedling establishment has occurred during previous centuries (Jelinski and Cheliak 1992). The most recent episode of sexual reproduction in aspen occurred following the 1988 Yellowstone fires (Kay 1993; Romme et al. 1997). The 1988 fires burned about 300,000 ha in and around Yellowstone National Park and were the largest fires in this region in the last 300 years (Romme and Despain 1989). Extensive surveys conducted in 1993 revealed that aspen seedlings were restricted to burned areas and varied greatly in local density, with maximum densities of >300 stems/ha (Romme et al. 1997). Notably, aspen seedlings were abundant in many areas well outside the pre-1988 distribution of aspen, as well as within the pre-1988 distribution. What does this unexpected response to the extensive fires of 1988 indicate about aspen's resilience to the environmental changes expected in the next century? We address this broad question by posing three smaller questions:

Why Did Extensive Aspen Seedling Establishment Occur After the 1988 Fires?

Establishment of new aspen genets in the West apparently has been infrequent and episodic (Jelinski and Cheliak 1992), principally because aspen seedlings are extremely intolerant of desiccation or competition (Moss 1938; McDonough 1979). A rare "window of opportunity" for seedling establishment occurred after 1988, due to a combination of unusually moist and cool weather in early summer, the occurrence of extensive bare substrate where competition from other plants was greatly reduced, and prolific seed production by mature aspen individuals that survived the fires. For instance, May precipitation in Yellowstone National Park was 139–197% of average in 1989–1991, and total plant cover in burned forests was 2–53% of cover in unburned forests (Romme et al. 1997).

The next century is likely to bring more extensive fires (Graham et al. 1990), which could mean more episodes of aspen seedling establishment if the concurrent weather conditions are cool and moist. However, if the fires of the next century are associated with drought and high temperatures, then aspen may be unable to establish new genets, and increased fire activity instead may lead to local extirpation of some old clones without establishment of new genets—especially in areas of chronic heavy ungulate browsing or other stresses on aspen.

What Are the Patterns of Genetic Diversity in the Aspen Seedlings?

Seedling populations sampled in 1993 exhibited greater overall genetic diversity than adult populations sampled on Yellowstone's northern range (Tuskan et al. 1996). However, as of 1997, there were no strong spatial patterns in the genetic structure of seedling populations across the Yellowstone Plateau (Stevens et al. 1999). This suggests that intense selection pressures have not yet occurred in the seedling populations, i.e., that we still see a more-or-less random distribution of genetic composition across the landscape reflecting vagaries of seed source and seed dispersal. Stevens et al. (1999) hypothesize that selective

mortality will occur over the next few decades, and that local genetic diversity in seedling populations will decrease as one or a few genotypes come to dominate individual sites.

It seems logical that this infusion of new individuals with unique genetic recombinations into the aspen populations of the Greater Yellowstone area will enhance the species' ability to survive or even thrive in the face of impending climatic and environmental changes. However, we are in only the earliest stages of what will be a long-term population process. The rare episode of aspen seedling establishment that occurred after the 1988 Yellowstone fires provides a unique opportunity to document the establishment of new aspen individuals and genetic structure in a natural setting.

What Will Be the Long-Term Ecological Role of the New Aspen Genets?

Based on the resampling of permanent plots from 1996–1998, aspen seedling densities are decreasing across most of the Yellowstone Plateau (M.G. Turner and W. H. Romme, in preparation). Causes of mortality appear to include heavy browsing by elk as well as locally adverse microclimate and soils conditions. Over much of Yellowstone National Park, many or even most of the new aspen individuals that appeared after 1988 seem destined to disappear over the next few decades, leaving no lasting ecological legacy.

However, some of the new aspen genets are thriving and appear likely to become well established and to persist indefinitely. For example, in one study area in west-central Yellowstone National Park, aspen genets that germinated in 1989 were >1 m tall in 1999 and had a single dominant stem. These individuals were growing in a dense tangle of fallen pine stems killed by the 1988 fires, which probably protected the aspen seedlings from excessive elk browsing. Thus, even though most of the aspen seedlings that established soon after the 1988 fires may perish, enough may survive to increase overall genetic diversity of the species and to establish new genets in new locations. Tuskan et al. (1996) suggest that episodes of new aspen genet establishment may typically exhibit just such a pattern of initially high seedling densities, followed by extensive mortality with survival of a few individuals that are best adapted to local conditions and which go on to produce clonal structures. Additional seedling establishment events of this kind in the future may be crucial to long-term survival of aspen in the Yellowstone region if climate change in the next century shifts the elevational zones of tolerance for plant species (Romme and Turner 1991; Bartlein et al. 1997) and if continued browsing pressure combined with drought and other stresses causes local extirpation of some old aspen clones.

Conclusions and Management Implications

1. Aspen plays a variety of roles in western landscapes, depending on the ecological context. We urgently need more detailed, local case studies of aspen ecology, disturbance regimes, responses to disturbance, landscape patch dynamics, and genetic and population structure to further illustrate its different roles and to provide a reliable basis for making useful generalizations. For example, our understanding of the very different pre-1900 disturbance regimes in aspen forests of the San Juan National Forest and northern Yellowstone National Park helps to explain the very different responses to recent disturbance that have been observed in the two systems.

2. Long-term persistence of aspen may be threatened, especially in the face of broad-scale global change, in settings like Yellowstone's northern range, where (a) aspen stands have always been patchy and restricted to limited portions of the landscape, probably due in part to locally marginal climate and soils conditions, and (b) ungulate browsing is intense, concentrated, and chronic.

3. Long-term persistence of aspen probably is not threatened, even in the face of global change, in settings like the San Juan National Forest where (a) aspen stands are extensive and cover a wide range of elevations and topographic positions, probably due in part to locally favorable climate and soils conditions, (b) fire was the principal disturbance agent in the past, and (c) ungulate use is relatively light or widely dispersed.

4. In settings like the San Juan National Forest, conifer invasion of aspen stands is a natural successional process that has always occurred in some stands during long fire-free intervals, and there have always been some long fire-free intervals. For example, the paucity of fire in the 20th century somewhat resembles the reduced fire activity of the late 1700s and early 1800s in the Southwest. The relatively high proportion of old aspen stands that we see in some unlogged landscapes today probably is not far outside the historic range of variability in landscape patch structure.

5. Old aspen stands in the southern Rockies, with or without conifer invasion, are extremely valuable for wildlife and aesthetics and show no obvious decline in ecosystem function. Because the next century is likely to bring increased fire frequency, similar to what occurred in the late 1800s or even exceeding the fire frequency of that period, old aspen stands probably will become less abundant in the future—regardless of current management decisions.

6. Although aspen reproduces primarily via asexual root sprouting, it also periodically produces new genetic individuals via sexual reproduction and seedling establishment. Seedling establishment is associated with large-scale disturbances (e.g., fire) that coincide with cool moist climatic conditions. The resulting genetic recombination and establishment of new individuals in new geographic locations may enhance aspen's ability to tolerate the broad-scale climate and habitat changes anticipated in the next century.

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Biodiversity: Aspen Stands Have the Lead, But Will Nonnative Species Take Over?

Geneva W. Chong^{1,2}, Sara E. Simonson², Thomas J. Stohlgren^{1,2}, and Mohammed A. Kalkhan²

Abstract—We investigated vascular plant and butterfly diversity in Rocky Mountain National Park. We identified 188 vascular plant species unique to the aspen vegetation type. The slope of the mean species-area curve for the aspen vegetation type was the steepest of the 10 types sampled, thus, an increase in aspen area could have much greater positive impacts on plant species richness than other vegetation types. Aspen plots contained the greatest number of butterfly species and ranked highest with all diversity indices tested. However, aspen plots were the most heavily invaded by nonnative plant species, which could have negative effects on native plant and butterfly species diversity.

The importance of aspen (*Populus tremuloides* Michaux) for maintaining biodiversity in western landscapes is well introduced in DeByle et al. (1985), where aspen stands are noted for their own genetic diversity, as well as providing habitat for insects, birds, and mammals. Stohlgren et al. (1997a,b) found a disproportionately high number of vascular plant species in aspen stands in relation to their coverage in the Beaver Meadows area (750 ha) of Rocky Mountain National Park, Colorado. There, aspen covered only 1.2% of the landscape, but it contained 45% of the plant species sampled.

Resource managers in Rocky Mountain National Park (the Park) are concerned that elk (*Cervus elaphus* Nelsoni) may be harming vegetation in portions of the Park (Berry et al. 1997). Localized studies have reported little or no aspen regeneration in elk winter range (Baker et al. 1997; Olmstead 1997), while a more extensive study did find successful regeneration at landscape scales in areas of low elk use (Suzuki et al. 1999). Similar concern and controversy over regeneration exists in the Greater Yellowstone Ecosystem (Barnett and Stohlgren 2000; Bartos et al. 1991; Gruell and Loope 1974; Krebill 1972; Romme et al. 1995; Weinstein 1979). Another potential harmful effect on aspen stands and the diversity that they support is invasion by nonnative plant species. Work in other species-rich habitat types has found that hotspots of native plant diversity are being invaded by nonnative plant species (Stohlgren et al. 1998b, 1999a,b,c). These invasions may have long-term, negative consequences for native diversity, especially in vegetation types such as aspen that are small, scattered, and rare on the landscape in parts of their range.

Our objective was to assess a variety of vegetation types' contributions to plant and butterfly species richness. We used species-log(area) curves (Gleason 1925; Rejmanek and Ejvind 1992; Shmida 1984) to compare the relative contributions to vascular plant species richness made by 10 different vegetation types in the Park. Species-area curves allow comparisons across vegetation types, and even other studies, because the slopes of the curves can be calculated and compared without the difficulties posed by other diversity indices that often require abundance data (for evenness) and vary greatly depending on study design (Ludwig and Reynolds 1988). In addition, species-area models allow one to estimate the number of species expected in an area larger than the area

¹Midcontinent Ecological Science Center, U.S. Geological Survey, Colorado State University, Fort Collins, CO.

²Natural Resource Ecology Laboratory, Colorado State University, Fort Collins.

sampled. These estimates may also be used as an index of diversity (richness). We also examine the number of species that only occur in one vegetation type (unique to a vegetation type) and the number of nonnative plant species found in a set of vegetation plots.

To test the use of plant richness to predict the diversity of other taxonomic groups, we investigated the significant contributions of aspen to butterfly species diversity and the relations between butterfly species richness and plants in the Beaver Meadows area (Simonson et al. 2000).

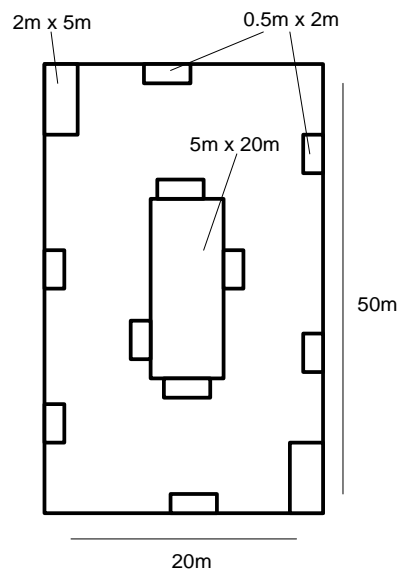
Our results should place renewed emphasis on the need to maintain aspen on the landscape to maintain landscape-scale biodiversity. In addition to managing natural processes such as elk herbivory and fire, resource managers may need to detect invasive species early, monitor their effects, and control nonnative plant invasions to maintain the native diversity supported by aspen.

Methods

Study Sites

From 1995 through 1998, 104 Modified-Whittaker plots (20 m x 50 m or 10 m x 25 m; figure 1) were established (using stratified, random sampling) in 10 vegetation types in a 54,000 ha portion of Rocky Mountain National Park, Colorado (after Stohlgren et al. 1997b). Vegetation cover types were identified on aerial photos (1987, color; 1:15840 scale) and included aspen (*Populus tremuloides* Michaux), willow (*Salix* spp.), dry meadow (various species), wet meadow (various species), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), lodgepole pine (*Pinus contorta* Dougl.), mixed conifer (various species), subalpine (various species), alpine tundra (various species), and spruce/fir (*Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt). Twenty of the aspen plots were located based on a previous bird study (stands were similarly randomly located; Natasha Kotliar, U.S. Geological Survey, personal communication). Butterfly data were collected in 1996 on the 24 Modified-Whittaker plots (four plots in each of six vegetation types: aspen, burned ponderosa, dry meadow, lodgepole pine, ponderosa pine, and wet meadow) in the 750 ha Beaver Meadows study area (Simonson et al. 2000).

Figure 1—The Modified-Whittaker plot (not to scale). The main plot is 20 m x 50 m and contains ten 1-m² subplots (0.5 m x 2 m, six inside the perimeter of the main plot and four outside the perimeter of the 100-m² subplot), two 10-m² subplots (2 m x 5 m, in opposite corners of the main plot), and one 100-m² subplot (5 m x 20 m in plot center). Sampling at multiple spatial scales (1-m², 10-m², 100-m², and 1000-m²) allows the construction of a species-area curve (figure 2). Plots that measured 10 m x 25 m (four vegetation plots) had the same plot design, but all dimensions were halved.



Plot Designs

The Modified-Whittaker plot for vegetation sampling consists of ten 1-m² subplots, two 10-m² subplots (in opposite corners), and one 100-m² subplot (in plot center) all contained within the 20 m x 50 m plot (figure 1). The original plot design placed the ten 1-m² subplots around the inside of the plot perimeter (Stohlgren et al. 1995). However, after 1996, four of the 1-m² subplots were moved to the outside perimeter of the 100-m² subplot to decrease the linearity of the 1-m² subplots. The 1-m² subplots were placed to maximize the distance between them while allowing for easy relocation where long-term monitoring was an objective (Stohlgren et al. 1998a). Within each 1-m² subplot, we identified all vascular plant species, recorded their average height, and estimated their cover to the nearest percent. In the 10-m² subplots and the 100-m² subplot we recorded species presence. Finally, the entire 1,000-m² plot was surveyed and any previously unrecorded (in the subplots) species were recorded.

For butterfly sampling, the 20 m x 50 m plot contained six 10-m² subplots around the inside of the plot perimeter and one 100-m² subplot in the plot center (Simonson 1998). The butterfly plot was overlain directly on the vegetation plot. Butterfly diversity was measured based on systematic surveys of the subplots and plot, under minimum weather conditions (Simonson 1998). Butterflies were identified to species, and abundances were also recorded.

Analyses

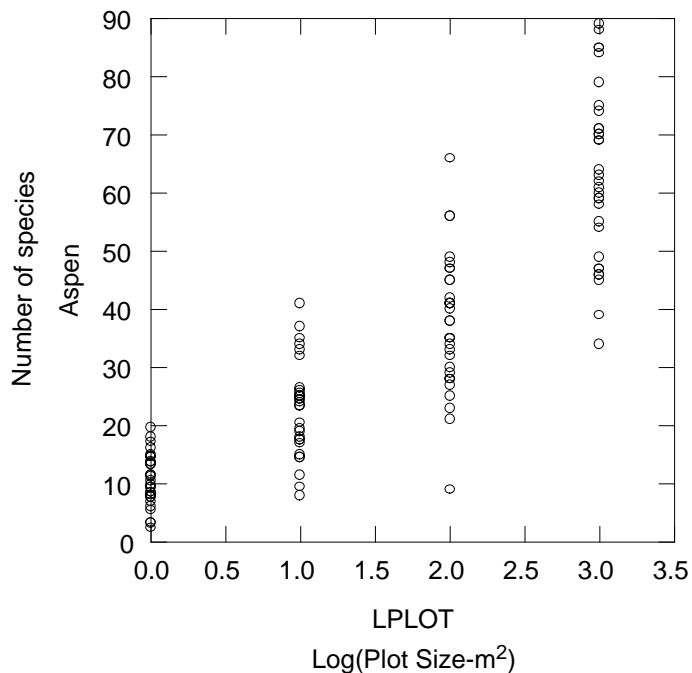
Species lists were compiled for plants and butterflies to determine the total numbers of species found in each vegetation type as well as the species unique to a vegetation type. Nonnative plant species were noted. All plant specimens identified to species follow the National Plants Database nomenclature (USDA NRCS 1999). Some plants could not be identified to species because of phenology or condition, so they were labeled with a unique identifier. If these “unknowns” could be identified to genus, then the genus was included in the descriptive name. For analyses, we erred on the side of caution by lumping difficult unknown species together (e.g., many grasses and small, basal rosettes of composites).

Species-log(plot size) curves, hereafter called species-area curves, were constructed using the mean number of plant species found in each subplot for the 1-m² and 10-m² subplots and the total number of plant species found in the 100-m² subplot and the full 1,000-m² plot. These curves are the result of linear regression where the number of species is dependent on the area sampled (figure 2). Thus, the curve rises more rapidly in species-rich habitat types because more species are encountered as area is increased (the slope of the line is steeper). Species-area curves were developed for each vegetation type based on all the plots sampled in that type. Butterfly data were analyzed using rarefaction curves, analysis of variance, diversity and evenness indices, and regression (Simonson et al. 2000).

Results

We identified 188 vascular plant species that occurred only in aspen plots (N = 32 plots) (appendix A). The remaining vegetation types (N = 72 plots) combined contained 264 species that only occurred in one vegetation type. The slope of the mean species-area curve for the aspen vegetation type was the steepest of the nine vegetation types sampled (table 1, figure 2). The slope indicates the rate of accumulation of new species as the area sampled is increased.

Figure 2—An example species-log(area) curve. Data are from 32 Modified-Whittaker plots placed in 32 aspen stands. The slope of the regression line is an index of species richness: the steeper the slope, the more new species are expected to be added as the area sampled increases. We used plot size (m²) for area. The equation of the aspen regression is: $N = 17.18(\log(\text{area})) + 7.85$ (adjusted $r^2 = 0.76$, $p < 0.01$), where N is the predicted number of species for a given area, the slope is 17.18, and the constant (i.e., intercept) is 7.85.



Aspen plots contained 38 of the 42 nonnative species identified in all plots, and 15 of the 38 were not found in any other vegetation type (appendix A).

In the Beaver Meadows portion of the Park, four plots were sampled for plant and butterfly diversity in each of six vegetation types. Aspen covered the smallest area with a total of 8.8 ha scattered throughout the 750-ha area. Thirty-three butterfly species, a total of 252 individuals, were recorded in aspen stands, and seven of those species were found only in aspen (Simonson 1998; appendix B). For both richness and diversity indices, aspen consistently ranked the highest of the vegetation types sampled for butterfly diversity (Simonson et al. 2000; table 2). Butterfly species richness was strongly positively correlated with native plant species richness ($r = 0.64$; $p < 0.001$), but the best predictors of butterfly species richness were exotic plant species richness ($r = 0.70$; $p < 0.0001$) and exotic plant species cover ($r = 0.70$; $p < 0.001$; Simonson et al. 2000).

Table 1—Species-area curves for vascular plant species in 10 vegetation types from a 54,000-ha portion of Rocky Mountain National Park, Colorado. We used SYSTAT (SPSS, Inc., 1998) for statistical analyses. We used the mean number of species in the 1-m² and 10-m² subplots and the total number of species in the 100-m² subplot and 1,000-m² plot. We used the log(plot size) for area. The equations follow the general equation of a line: $N = m(x) + b$, where N = the number of species; m = the slope of the line; x = log(plot size); and b is a constant (the intercept). Larger values of the slope (m) indicate a greater accumulation of species as area is increased. In all cases $p < 0.01$.

Vegetation	Equation	Adjusted R ²	# plots
Aspen	$N = 17.18(\log(\text{area})) + 7.85$	0.76	32
Willow	$N = 15.11(\log(\text{area})) + 6.31$	0.80	9
Dry meadow	$N = 13.14(\log(\text{area})) + 8.20$	0.75	9
Spruce/fir	$N = 12.81(\log(\text{area})) + 5.78$	0.74	4
Ponderosa	$N = 12.47(\log(\text{area})) + 3.70$	0.85	8
Tundra	$N = 11.69(\log(\text{area})) + 14.40$	0.86	4
Wet meadow	$N = 11.60(\log(\text{area})) + 6.55$	0.71	8
Mixed conifer	$N = 9.36(\log(\text{area})) + 1.33$	0.48	5
Lodgepole	$N = 9.23(\log(\text{area})) + 2.82$	0.74	8
Subalpine	$N = 9.02(\log(\text{area})) + 3.80$	0.66	8

Table 2—Richness and diversity indices for butterflies in aspen (A), wet meadow (WM), Ponderosa pine (PP), dry meadow (DM), burned conifer (BC), and lodgepole pine (LP) vegetation types in the Beaver Meadows study area, Rocky Mountain National Park, Colorado (Simonson et al. 2000).

Vegetation	A	WM	PP	DM	BC	LP
Richness						
Observed species	33	27	21	19	15	13
Estimated species ^a	19	15	14	11	14	13
Diversity						
Simpson's A	0.08	0.11	0.12	0.17	0.12	0.13
Shannon's H	2.92	2.56	2.29	2.10	2.32	2.16
Hill's N1	18.60	12.89	9.83	8.13	10.21	8.71
Hill's N2	12.27	9.54	6.45	5.96	8.55	7.80

^aBased on rarefaction, which allows the comparison of species numbers between vegetation types where sample sizes (number of individuals observed) were unequal. This estimate provides an index of richness.

Discussion

Although aspen stands cover a small proportion of Rocky Mountain National Park (2% based on one Park map or 5% based on recent work by Kaye et al., this proceedings), they contribute a disproportionate amount to plant and butterfly species richness. For example, aspen comprised only 1.2% of the vegetation cover in the Beaver Meadows study area, yet the four plots sampled in aspen contained 150 plant species (45% of the plants observed on all 24 plots). Of the plant species, 50 were unique to the aspen type (25% of the unique species observed in the six vegetation types in that study; Stohlgren et al. 1997b). Beaver Meadows aspen contained more unique butterfly species than any other vegetation type. Thirty-three of the 49 butterfly species observed were seen in aspen, and seven of those were recorded only in the aspen type. In the Beaver Meadows study area (750 ha; Stohlgren et al. 1997b) and the larger study area (54,000 ha, present study) the slopes of species-area curves for plants in aspen were steeper than those for any other vegetation type sampled. Using slope steepness as an index of a vegetation type's contribution to species richness, aspen stands are clearly important for maintaining landscape biodiversity. Resource managers are justified in their concern about aspen's persistence on the landscape.

Managers must add invasive, nonnative species to their list of potential threats to the integrity of aspen ecosystems. We observed 42 nonnative plant species in the Park; 38 of those occurred in aspen stands, and 15 of those were not found in the plots in any other vegetation type. This is partially explained by the large number of plots in aspen ($N = 32$ plots), but it is still extremely high compared to the 72 nonaspen plots. Especially alarming was the presence of noxious, agricultural, and urban weeds (e.g., field bindweed, *Convolvulus arvensis* L.) in seemingly remote, undisturbed aspen stands. None of our sites that appeared relatively undisturbed had high cover of nonnative species, but their presence indicates that seed sources are available. With seed available, any disturbance is likely to result in increased cover of nonnative plant species. The ability of the nonnative species to form dense stands can prevent native plants from persisting or establishing (Whitson et al. 1996).

Other potential negative effects involve pollinator interactions between native and nonnative plants. For example, we observed many butterflies on the flowers of musk thistle (*Carduus nutans* L.) and Canada thistle (*Cirsium arvense* L.). Even though these nonnative species provide nectar, they are not suitable host plants

for most butterfly larva, which often require specific native hosts. If nonnatives are being pollinated this may increase their invasion success. In addition, many native plants are believed to be pollinator-limited (Burd 1994) even without competition for pollinators from nonnatives. If pollination of natives is reduced and results in decreased reproduction, this will exacerbate their displacement and could impact butterfly diversity by reducing the populations of required host plants.

Attempts to manage for intact aspen stands as a component of forest ecosystems must consider the potential negative impacts of nonnative plant species on native species richness across taxonomic groups. Controlling invasive nonnative species in aspen stands must be carefully done because these areas contain more unique assemblages of native species. Researchers and managers must be especially attentive to processes that encourage aspen regeneration or establishment (e.g., fire, disturbance) because these processes also facilitate nonnative species establishment. Understanding the connectivity of aspen and other vegetation cover types in relation to nonnative plant species movement and establishment will be an essential component to proactive management of native species and aspen stands.

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Appendix A

Plant species listed were only found in aspen stands (32 plots), except for the nonnative species indicated by an “N*”, which were found in other vegetation types as well. We only list plants that were identified to species (47 unknowns were not included). Please note that a portion of these species certainly occurs in other vegetation cover types, but they were not found in our plots in other types (N = 72). Species noted as “Rare” are listed by Spackman et al. (1997).

Status	Family	Scientific name	Common name
N*	Poaceae	<i>Agrostis gigantea</i>	Redtop
N	Poaceae	<i>Alopecurus pratensis</i>	Meadow foxtail
N*	Brassicaceae	<i>Alyssum alyssoides</i>	Pale madwort
N*	Brassicaceae	<i>Arabis glabra</i>	Tower mustard
N	Brassicaceae	<i>Brassica juncea</i>	India mustard
N*	Poaceae	<i>Bromus tectorum</i>	Cheatgrass
N*	Brassicaceae	<i>Camelina microcarpa</i>	False flax
N	Apiaceae	<i>Carum carvi</i>	Caraway
N	Asteraceae	<i>Carduus nutans</i>	Musk thistle
N*	Chenopodiaceae	<i>Chenopodium album</i>	Lambsquarters
N*	Asteraceae	<i>Cirsium arvense</i>	Canadian thistle
N	Convolvulaceae	<i>Convolvulus arvensis</i>	Field bindweed
N*	Apiaceae	<i>Conium maculatum</i>	Poison hemlock
N	Poaceae	<i>Cynodon dactylon</i>	Bermudagrass
N	Boraginaceae	<i>Cynoglossum officinale</i>	Gypsy flower
N	Poaceae	<i>Dactylis glomerata</i>	Orchardgrass
N*	Brassicaceae	<i>Descurainia Sophia</i>	Flixweed
N	Poaceae	<i>Elytrigia repens</i> var. <i>repens</i>	Quackgrass
N*	Poaceae	<i>Festuca ovina</i>	Sheep fescue
N*	Apiaceae	<i>Heracleum sphondylium</i>	Eltrot
N	Brassicaceae	<i>Lepidium campestre</i>	Field pepperweed
N	Brassicaceae	<i>Lepidium perfoliatum</i>	Clasping pepperweed
N*	Poaceae	<i>Lolium pratense</i>	Ryegrass
N	Fabaceae	<i>Melilotus officinalis</i>	Yellow sweetclover
N*	Poaceae	<i>Phleum pratense</i>	Timothy
N	Poaceae	<i>Poa compressa</i>	Canada bluegrass
N*	Poaceae	<i>Poa pratensis</i>	Kentucky bluegrass
N*	Polygonaceae	<i>Rumex acetosella</i>	Sheep sorrel
N*	Polygonaceae	<i>Rumex crispus</i>	Curly dock
N	Caryophyllaceae	<i>Silene vulgaris</i>	Maidenstears
N*	Brassicaceae	<i>Sisymbrium altissimum</i>	Tall tumbled mustard
N*	Asteraceae	<i>Taraxacum officinale</i>	Common dandelion
N*	Brassicaceae	<i>Thlaspi arvense</i>	Pennycress
N*	Asteraceae	<i>Tragopogon dubius</i>	Salsify
N*	Fabaceae	<i>Trifolium hybridum</i>	Alsike clover
N*	Fabaceae	<i>Trifolium repens</i>	White Dutch clover
N	Scrophulariaceae	<i>Verbascum thapsus</i>	Common mullein
	Poaceae	<i>Achnatherum lettermanii</i>	None listed
	Asteraceae	<i>Achillea millefolium</i> var. <i>occidentalis</i>	Western yarrow
	Poaceae	<i>Achnatherum nelsonii</i> ssp. <i>dorei</i>	Needle-and-thread
	Ranunculaceae	<i>Actaea rubra</i>	Baneberry
	Rosaceae	<i>Amelanchier alnifolia</i>	Saskatoon serviceberry

Appendix A, cont'd

Status	Family	Scientific name	Common name
	Ranunculaceae	<i>Anemone canadensis</i>	Meadow anemone
	Apocynaceae	<i>Apocynum androsaemifolium</i>	Spreading dogbane
	Ranunculaceae	<i>Aquilegia caerulea</i>	Colorado blue columbine
	Araliaceae	<i>Aralia nudicaulis</i>	Wild sarsaparilla
	Asteraceae	<i>Artemisia ludoviciana</i> ssp. <i>Mexicana</i>	Mexican white sagebrush
	Fabaceae	<i>Astragalus alpinus</i>	Alpine milkvetch
	Asteraceae	<i>Aster foliaceus</i> var. <i>parryi</i>	Parry's aster
	Asteraceae	<i>Aster laevis</i>	Smooth aster
	Asteraceae	<i>Aster novae-angliae</i>	New England aster
	Fabaceae	<i>Astragalus parryi</i>	Parry's milkvetch
	Asteraceae	<i>Aster porteri</i>	Porter's aster
	Fabaceae	<i>Astragalus sparsiflorus</i>	Front range milkvetch
	Asteraceae	<i>Brickellia californica</i>	California brickellbush
	Asteraceae	<i>Brickellia grandiflora</i>	Tasselflower brickellbush
	Poaceae	<i>Calamagrostis montanensis</i>	Plains reedgrass
	Cyperaceae	<i>Carex canescens</i>	Silvery sedge
	Cyperaceae	<i>Carex durinacula</i>	Needleleaf sedge
	Cyperaceae	<i>Carex foenea</i> var. <i>foenea</i>	Dryspike sedge
	Cyperaceae	<i>Carex lanuginosa</i>	Woolly sedge
	Cyperaceae	<i>Carex oreocharis</i>	Grassyslope sedge
	Cyperaceae	<i>Carex rostrata</i>	Beaked sedge
	Scrophulariaceae	<i>Castilleja miniata</i>	Scarlet paintbrush
	Rhamnaceae	<i>Ceanothus velutinus</i>	Snowbrush ceanothus
	Chenopodiaceae	<i>Chenopodium fremontii</i>	Fremont's goosefoot
	Asteraceae	<i>Cirsium canescens</i>	Prairie thistle
	Asteraceae	<i>Cirsium drummondii</i>	Dwarf thistle
	Ranunculaceae	<i>Clematis occidentalis</i>	Western blue virginsbower
	Scrophulariaceae	<i>Collinsia parviflora</i>	Smallflower blue-eyed Mary
	Orchidaceae	<i>Corallorhiza</i> sp.	Coral root
	Fumariaceae	<i>Corydalis aurea</i>	Golden smoke
	Pteridaceae	<i>Cryptogramma crispa</i>	Crisp rockbreak
	Boraginaceae	<i>Cryptantha fendleri</i>	Sanddune catseye
	Ranunculaceae	<i>Delphinium ramosum</i>	Mountain larkspur
	Brassicaceae	<i>Descurainia pinnata</i>	Western tanseymustard
	Primulaceae	<i>Dodecatheon pulchellum</i>	Darkthroat shootingstar
	Lamiaceae	<i>Dracocephalum parviflorum</i>	American dragonhead
	Poaceae	<i>Elymus elymoides</i>	Bottlebrush squirreltail
	Poaceae	<i>Elymus glaucus</i>	Blue wildrye
	Poaceae	<i>Elymus lanceolatus</i> ssp. <i>Albicans</i>	Montana wheatgrass
	Poaceae	<i>Elymus subsecundus</i>	Bearded wheatgrass
	Poaceae	<i>Elymus virginicus</i> var. <i>submuticus</i>	Virginia wildrye
	Onagraceae	<i>Epilobium brachycarpum</i>	Autumn willowweed
	Equisetaceae	<i>Equisetum laevigatum</i>	Smooth horsetail
	Asteraceae	<i>Erigeron subtrinervis</i>	Three-nerved fleabane
	Asteraceae	<i>Eucephalus engelmannii</i>	None listed
	Poaceae	<i>Festuca thurberi</i>	Thurber's fescue
	Rosaceae	<i>Fragaria vesca</i>	Woodland strawberry
	Polemoniaceae	<i>Gilia pinnatifida</i>	Sticky gilia

Appendix A, cont'd

Status	Family	Scientific name	Common name
	Orchidaceae	<i>Goodyera oblongifolia</i>	Western rattlesnake plantain
	Dryopteridaceae	<i>Gymnocarpium dryopteris</i>	Western oakfern
	Asteraceae	<i>Helianthella quinquenervis</i>	Five-nerve helianthella
	Asteraceae	<i>Heterotheca fulcrata</i>	Rockyscree false goldenaster
	Saxifragaceae	<i>Heuchera bracteata</i>	Bracted alumroot
	Asteraceae	<i>Hieracium albiflorum</i>	White hawkweed
	Rosaceae	<i>Holodiscus dumosus</i>	Rock spirea
	Juncaceae	<i>Juncus balticus</i>	Baltic rush
	Asteraceae	<i>Lactuca tatarica</i>	Large-flowered blue lettuce
Rare	Liliaceae	<i>Lilium philadelphicum</i>	Wood lily
	Orchidaceae	<i>Listera convallarioides</i>	Broadlipped twayblade
	Fabaceae	<i>Lupinus argenteus</i>	Silvery lupine
	Asteraceae	<i>Machaeranthera bigelovii</i> var. <i>bigelovii</i>	Bigelow's tansyaster
	Asteraceae	<i>Machaeranthera canescens</i>	Hoary aster
	Lamiaceae	<i>Monarda fistulosa</i>	Wild bergamot beebalm
	Poaceae	<i>Muhlenbergia asperifolia</i>	Alkali muhly
	Onagraceae	<i>Oenothera villosa</i> ssp. <i>Strigosa</i>	Hairy evening primrose
	Orobanchaceae	<i>Orobanche uniflora</i>	One-flowered broomrape
	Poaceae	<i>Oryzopsis asperifolia</i>	Roughleaf ricegrass
	Celastraceae	<i>Paxistima myrsinites</i>	Mountain-lover boxleaf myrtle
	Scrophulariaceae	<i>Pedicularis procera</i>	Grays lousewort
	Scrophulariaceae	<i>Penstemon rydbergii</i>	Rydberg's penstemon
	Solanaceae	<i>Physalis heterophylla</i>	Clammy groundcherry
	Rosaceae	<i>Physocarpus monogynus</i>	Mountain ninebark
	Orchidaceae	<i>Platanthera hyperborean</i> var. <i>hyperborean</i>	Northern green orchid
	Polygonaceae	<i>Polygonum aviculare</i>	Devils shoestrings
	Polygonaceae	<i>Polygonum douglasii</i> ssp. <i>Johnstonii</i>	Johnston's knotweed
	Rosaceae	<i>Potentilla nivea</i>	Snow cinquefoil
	Lamiaceae	<i>Prunella vulgaris</i>	Common selfheal
	Asteraceae	<i>Ratibida columnifera</i>	Upright prairie coneflower
	Asteraceae	<i>Rudbeckia laciniata</i>	Tall cone-flower
	Salicaceae	<i>Salix petiolaris</i>	Meadow willow
	Salicaceae	<i>Salix scouleriana</i>	Scouler's willow
	Apiaceae	<i>Sanicula marilandica</i>	Maryland snakeroot
	Selaginellaceae	<i>Selaginella densa</i>	Lesser spikemoss
	Selaginellaceae	<i>Selaginella underwoodii</i>	Underwood's spikemoss
	Asteraceae	<i>Senecio crassulus</i>	Thickleaf groundsel
	Asteraceae	<i>Senecio eremophilus</i> var. <i>kingii</i>	King's groundsel
	Asteraceae	<i>Senecio pudicus</i>	Bashful ragwort
	Asteraceae	<i>Senecio rapifolius</i>	Openwoods groundsel
	Asteraceae	<i>Senecio serra</i>	Butterweed
	Caryophyllaceae	<i>Silene drummondii</i>	Drummond's campion
	Caryophyllaceae	<i>Silene drummondii</i> var. <i>drummondii</i>	Drummond's campion
	Asteraceae	<i>Solidago simplex</i> ssp. <i>simplex</i> var. <i>simplex</i>	Mt. Albert goldenrod
	Rosaceae	<i>Sorbus scopulina</i>	Greene mountain ash
	Lamiaceae	<i>Stachys palustris</i>	Marsh hedgenettle
	Caryophyllaceae	<i>Stellaria calycantha</i>	Northern starwort
	Asteraceae	<i>Taraxacum officinale</i> ssp. <i>ceratophorum</i>	Fleshy dandelion

Appendix A, cont'd

Status	Family	Scientific name	Common name
	Caprifoliaceae	<i>Viburnum edule</i>	Mooseberry viburnum
	Violaceae	<i>Viola canadensis</i>	Canadian white violet
	Vitaceae	<i>Vitis riparia</i>	Riverbank grape
	Asteraceae	<i>Wyethia mollis</i>	Woolly wyethia

Appendix B

Butterfly species found in the aspen vegetation type in the 754-ha Beaver Meadows area of Rocky Mountain National Park (four 0.1-ha plots, each sampled four times; Simonson 1998).

Scientific name and authority	Unique to aspen plots
<i>Parnassius smintheus</i> Doubleday	
<i>Papilio rutulus</i> Linnaeus	
<i>Papilio multicaudatus</i> Kirby	X
<i>Pontia protodice</i> (Boisduval and Leconte)	X
<i>Pieris marginalis</i> (Scudder)	X
<i>Euchloe ausonides</i> (Lucas)	
<i>Colias eurytheme</i> Boisduval	
<i>Colias philodice</i> Godart	
<i>Colias alexandra</i> Edwards	
<i>Lycaena helloides</i> (Boisduval)	
<i>Lycaena rubida</i> (Behr)	
<i>Callophrys spinetorum</i> (Hewitson)	
<i>Callophrys eryphon</i> (Boisduval)	
<i>Everes amyntula</i> (Boisduval)	
<i>Celastrina ladon</i> (Cramer)	
<i>Plebejus acmon</i> (Westwood and Hewitson)	
<i>Plebejus saepiolus</i> (Boisduval)	
<i>Agriades glandon</i> (De Prunner)	
<i>Glaucopsyche lygdamus</i> (Doubleday)	X
<i>Speyeria atlantis</i> (Edwards) ^a	
<i>Speyeria aphrodite</i> (Fabricius)	
<i>Speyeria edwardsii</i> (Reakirt)	
<i>Phyciodes pratensis</i> (Behr)	
<i>Polygonia faunus</i> (Edwards)	X
<i>Polygonia gracilis</i> (Grote and Robinson)	
<i>Nymphalis antiopa</i> (Linnaeus)	
<i>Limentis weidemeyerii</i> (Edwards)	X
<i>Coenonympha tullia</i> (Edwards)	
<i>Cercyonis oetus</i> (Boisduval)	
<i>Oeneis chryxus</i> (Doubleday and Hewitson)	
<i>Erynnis persius</i> (Scudder)	
<i>Oarisma garita</i> (Reakirt)	
<i>Polites draco</i> (Edwards)	

^aComplex, including *Speyeria hesperis* (Edwards).

Adaptations of Quaking Aspen for Defense Against Damage by Herbivores and Related Environmental Agents

Richard L. Lindroth¹

Abstract—*Quaking aspen* (*Populus tremuloides*) employs two major systems of defense against damage by environmental agents: chemical defense and tolerance. Aspen accumulates appreciable quantities of phenolic glycosides (salicylates) and condensed tannins in most tissues and accumulates coniferyl benzoate in flower buds. Phenolic glycosides are toxic and/or deterrent to pathogens, insects, and small mammals, and coniferyl benzoate is toxic to ruffed grouse, but the functional significance of tannins remains unclear. Levels of secondary compounds are influenced by both genetic and environmental (e.g., resource availability) factors. Tolerance is less well understood but may play an important role as an adaptation to extensive damage during herbivore outbreaks. Critically needed is an assessment of the roles of chemical defense and tolerance in relation to the foraging ecology of large mammals such as cervids.

Introduction

If geographic range, population density, and capacity to flourish in a diversity of habitat types are indicators of “ecological success,” then quaking aspen (*Populus tremuloides* Michx.) must be considered one of the most successful of extant tree species. A primary contributor to such success has been the evolution of chemical and physiological defense systems that afford resistance or tolerance to a host of biotic and abiotic factors. The purpose of this paper is to provide a succinct summary of the defensive adaptations of aspen and how they are influenced by genetic and environmental factors, and to discuss implications for their efficacy against harmful environmental agents, particularly herbivores. (For more detailed information, refer to the review by Lindroth and Hwang [1996a].) One caveat must be stated up front: Nearly everything known about the defense systems of aspen is based on research conducted in Eastern North America. The same systems are likely important to Western aspen, although particular contexts will vary.

Plants have evolved arrays of chemical, physiological, and physical defenses against damage by environmental agents. For aspen, a growing body of literature has unveiled the critical importance of chemical defense mechanisms. Physiological defenses, such as tolerance, are less well understood but are generating increased interest. Physical defenses (associated with physical characteristics such as spines and silica) are unlikely of importance in aspen. In the context of this paper, secondary plant metabolites with demonstrated or putative protective roles will be considered “chemical defenses.” Tolerance—the capacity to sustain growth and reproduction following damage—will be considered a “physiological defense.”

¹University of Wisconsin, Madison, WI.

Chemical Defense

Secondary Metabolites

The dominant secondary metabolites of aspen are phenolic compounds, produced via the shikimic acid pathway. These include phenolic glycosides and condensed tannins, which occur in leaf, bark, and root tissues, and coniferyl benzoate, which occurs only in flower buds.

The signature secondary metabolites of aspen comprise a suite of salicylates generally known as phenolic glycosides (Lindroth et al. 1987; Palo 1984). The exact biosynthetic pathway is unknown, but the compounds are most likely derivatives of salicylic acid. They vary according to the type and position of benzoyl and similar functional groups, and these groups confer tremendous variation in terms of biological activity (Lindroth and Peterson 1988; Lindroth et al. 1988). Quaking aspen contains four phenolic glycosides, including salicin, salicortin, tremuloidin, and tremulacin (figure 1). Of these, salicin and tremuloidin generally occur in concentrations <1% leaf dry weight. Levels of salicortin and tremulacin, however, are much higher, typically 1 to 8% each, and occasionally attain 15% (Hemming and Lindroth 1995; Lindroth and Hwang 1996b; Osier et al. 2000a).

A second major class of phenolics produced in aspen is condensed tannins. These compounds are derived from 4-coumaric acid and accumulate to appreciable levels, up to nearly 30% of leaf dry weight (Hemming and Lindroth 1995; Lindroth and Hwang 1996b; Osier et al. 2000a). Aspen does not produce hydrolyzable tannins.

Coniferyl benzoate is a phenylpropanoid ester, also derived from 4-coumaric acid. Concentrations of this compound range from 0 to 7% dry weight in flower buds (Jakubas et al. 1993a,b).

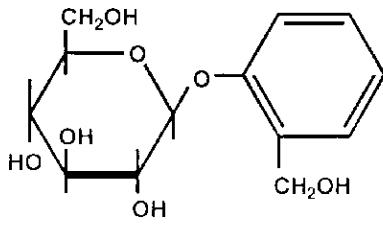
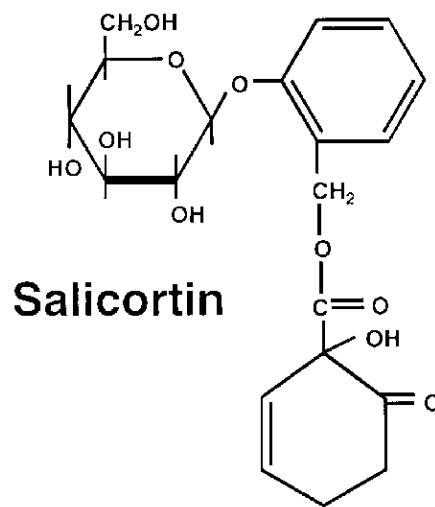
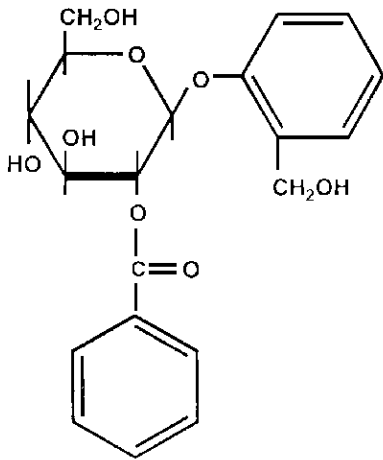
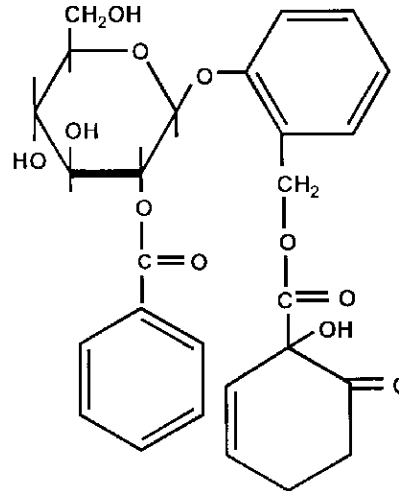
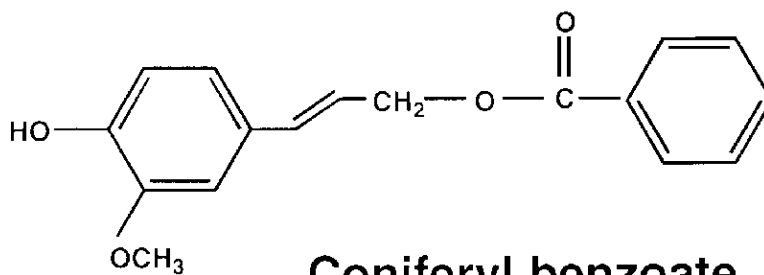
Phytochemical Variation

Aspen exhibits tremendous variation in levels of foliar chemical defenses (Lindroth and Hwang 1996a). Research over the last 10 years has identified a complex of genetic and environmental factors, and interactions among them, that contribute to such variation. Moreover, the magnitude of influence of genetics and environment varies among different secondary metabolites. In contrast to a large accumulated literature for leaves, we know almost nothing about quantitative chemical variation in stem, bark, or root tissues.

Genetic variation

Striking genetic variation among clones is a hallmark characteristic of aspen, and no less so for levels of foliar secondary metabolites. Among clones in a common field habitat, levels of total phenolic glycosides vary from <1 to 16% dry weight, whereas levels of condensed tannins vary from 3 to nearly 30% dry weight (Hemming 1998; Lindroth and Hwang 1996a,b; Osier et al. 2000a). Measurements of chemical variation among clones in the field do not indicate true genotypic variation, however, as they may be confounded with differences among local (clone) environments. Sorting out true genotypic variation requires growing trees in a common environment.

To that end, we have conducted several common garden experiments with trees propagated from root cuttings of field clones. Quantification of phenolic glycoside and condensed tannin concentrations revealed virtually the entire range of concentrations reported for field clones (Hwang and Lindroth 1997, 1998).

**Salicin****Salicortin****Tremuloidin****Tremulacin****Coniferyl benzoate****Figure 1**—Phenolic glycosides and coniferyl benzoate, characteristic secondary compounds of quaking aspen.

Interestingly, levels of secondary metabolites appear to be much more variable among aspen genotypes than are those of primary metabolites or mineral nutrients. Our studies have generally shown that although concentrations of water, carbohydrates, and nitrogen (an index of protein) may differ significantly among clones, the magnitude of variation (both relative and absolute) is minimal in comparison with that of secondary metabolites (Hwang and Lindroth 1997, 1998). We have not evaluated levels of macronutrients in aspen foliage. Jelinski and Fisher (1991), however, assessed nutrient content of winter twigs and reported similar low levels of clonal variation for all macronutrients except calcium. If aspen secondary metabolites are effective deterrents to feeding by particular herbivores, these results suggest that clonal variation in herbivore preference or performance may be more strongly determined by secondary than primary chemical composition.

Temporal variation

Levels of foliar defense compounds exhibit temporal variation with respect to both development (ontogeny) and seasonal progression (phenology). A preliminary survey of foliar defense chemistry in seedling, juvenile (burned or browsed), and mature aspen in Yellowstone National Park suggested that levels of phenolic glycosides decline as aspen mature (Erwin et al. 2000). These results are consistent with the hypothesis of ontogenetic development of chemical defense against herbivores, which purports that early successional trees have evolutionarily adapted to substantial herbivory during juvenile stages by the expression of high levels of constitutive defenses (Bryant and Julkunen-Tiitto 1995).

Within a growing season, changes in levels of foliar phenolic glycosides differ among clones; increases, decreases, and no significant changes have been reported (Hemming 1998; Hwang and Lindroth 1998; Lindroth and Hwang 1996a; Osier et al. 2000a). In contrast, levels of condensed tannins generally increase during a growing season, with the most pronounced increases occurring during the period of leaf expansion (Hemming 1998; Hwang and Lindroth 1998; Lindroth and Hwang 1996a; Osier et al. 2000a).

Resource availability

Numerous studies have investigated the effects of resource (light, water, nutrients, carbon dioxide) availability on the chemical composition of aspen. As would be expected for a fast-growing species (Bryant et al. 1987a), aspen exhibits considerable plasticity in chemical response to changes in nutrient availability. In general, these changes accord well with predictions of the carbon-nutrient balance (Bryant et al. 1983) and growth-differentiation balance (Herms and Mattson 1992) hypotheses. According to these hypotheses, environmental conditions that increase carbon availability (e.g., high light, high CO₂) or decrease nutrient availability (e.g., low soil fertility) lead to a relative excess of carbohydrates and an increase in C-based secondary or storage compounds.

Indeed, levels of phenolic glycosides, condensed tannins, and starch generally increase in aspen grown under conditions of high light, high CO₂, and/or low nutrient availability (Hemming and Lindroth 1999; Lindroth et al. 1993; McDonald et al. 1999). The various compounds are not, however, similarly responsive to changes in resource availability. Concentrations of condensed tannins respond much more strongly to environmental changes than do concentrations of phenolic glycosides. Moreover, the magnitudes of chemical responses differ among clones (significant gene x environment effects).

Induction

Damage by herbivores or pathogens can elicit a host of plant responses that alter the susceptibility of remaining tissues to further damage (Karban and Baldwin 1997). Several research groups have investigated short-term induction of chemical defenses in aspen leaves. Mattson and Palmer (1988) reported an 18% increase in total phenolics following artificial defoliation of 50% leaf area. Clausen et al. (1989) found that levels of salicortin and tremulacin, but not salicin and tremuloidin, increased (slightly) within 24 hours of mechanical defoliation. Work by my research group has shown slight to no increases in phenolic glycoside levels immediately following mechanical or natural defoliation (Lindroth and Kinney 1998; Roth et al. 1998; Osier and Lindroth 2000). In contrast, levels of condensed tannins generally increase following natural or artificial defoliation, and the magnitude of increase is influenced by resource availability (Lindroth and Kinney 1998; Roth et al. 1998; Osier and Lindroth 2000).

Less is known about long-term (interannual) induced defenses in aspen. Clausen et al. (1991) reported increases in only one (tremulacin) of four phenolic glycosides 1 year after 50 and 100% defoliation. Osier and Lindroth (unpublished data) investigated the effects of 90% defoliation on several aspen genotypes grown in nutrient-deficient or nutrient-rich soil. We found no increases in phenolic glycoside concentrations and a slight increase in condensed tannin concentrations 1 year after defoliation. Responses did not differ significantly across clones or nutrient treatments.

To date, virtually all work with induced defenses in aspen has focused on folivory. Almost nothing is known about the impacts of browsing on expression of foliar defense traits in aspen. According to the resource-based model of Bryant et al. (1991), however, defoliation and browsing may cause very different outcomes for the quality of subsequent leaf tissue. Severe defoliation contributes to mortality of fine roots, leading to reduced nutrient absorption, reduced nutrient concentration per leaf, decreased leaf growth, increased leaf carbohydrate pools, and an increase in carbon-based secondary metabolites. In contrast, browsing reduces leaf numbers, leading to increased nutrient concentration per leaf, increased leaf growth, decreased carbohydrate pools, and a decrease in carbon-based secondary metabolites. This model suggests that insect outbreaks on aspen may elicit changes in foliar quality very different from those of browsing mammals.

Costs of Chemical Defense

If levels of aspen defense compounds are strongly genetically determined, and if the compounds are effective deterrents against herbivores, the question arises as to why genetic variation persists in field populations. The classic answer to this evolutionary problem is that costs of defense must exist, such that expression of defense is not advantageous in all environments at all times.

Recent research by Osier and Lindroth (unpublished data) documented significant costs of resistance in aspen. These were exhibited as tradeoffs (negative genotypic correlations) between growth and phenolic glycoside concentrations among aspen genotypes. The tradeoffs were strongest in low-resource (low light, low nutrient availability) environments. In high-resource environments, however, the tradeoff disappeared. Thus, expression of high levels of constitutive defense (phenolic glycosides) appears to exact a cost in terms of plant growth, except in high-resource environments.

Tolerance

Historically, investigations of defensive strategies of plants have focused on chemical systems. Recently the concept of tolerance has begun to generate theoretical and empirical attention. Tolerance refers to the capacity of plants to maintain fitness through growth and reproduction after herbivore damage (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999). Tolerance is considered to be an especially viable form of defense in plants with high intrinsic growth rates, large storage capacity, and substantial physiological (e.g., photosynthetic) plasticity. All such traits are characteristic of aspen. Tolerance is advantageous in situations where herbivore damage is so uniform and severe that even chemically resistant genotypes are heavily damaged. Under such conditions, tolerance would confer a fitness advantage even though resistance does not. Tolerance may be selectively advantageous in forest ecosystems in which outbreak folivores cause extensive and uniform damage during peak periods of defoliation (Mattson et al. 1991). Examples include outbreaks of forest tent caterpillars (*Malacosoma disstria*), gypsy moths (*Lymantria dispar*), and large aspen tortrix (*Choristoneura conflictana*) on aspen.

Results from studies by Osier and Lindroth (unpublished data) suggest that aspen does exhibit tolerance to defoliation and that tolerance differs among aspen genotypes and resource environments. Under low nutrient availability, defoliation suppressed growth in each of four genotypes. Under high nutrient availability, however, two of the genotypes compensated nearly entirely for damage.

Defense Against Abiotic Agents

Lindroth and Hwang (1996a) reported that exceedingly little is known about the roles of aspen secondary metabolites with respect to protection from physical factors. Five years later, the same holds true. Phenolic glycosides may confer protection from ultraviolet (UV) radiation (Lindroth and Hwang 1996). Evidence in support of that function includes the fact that phenolic glycosides absorb UV radiation (especially at 200-320 nm) and that several clones of aspen propagated from cuttings collected in alpine environments in Colorado (high incident UV) continued to express very high levels of phenolic glycosides when grown in a common garden in Wisconsin.

Defense Against Biotic Agents

That the defense systems of aspen are based on fairly simple phenolic chemicals, coupled with physiological adaptations for tolerance, seem all the more remarkable given their apparent efficacy against a host of potentially damaging organisms. The phenolic glycosides, in particular, appear to have broad-spectrum activity, reducing the performance of organisms as variable as fungi, insects, and vertebrates (table 1).

Pathogens

Aspen is subject to diseases caused by viruses, bacteria, and most importantly, fungi (Ostry et al. 1988; Perala 1990). Although the nature of the defense mechanisms mounted against these pathogens is mostly unknown, secondary metabolites play a role in some cases.

Hypoxyylon mammatum stem canker is a serious fungal pathogen of aspen, particularly east of the Rocky Mountains (Perala 1990). Initially, Flores and Hubbes (1979, 1980) showed that phenolic glycoside “phytoalexins” (identity

Table 1—Organisms affected by secondary metabolites of aspen.

Species	Metabolite	Reference
Pathogenic fungi		
<i>Hypoxylon</i> (ascospores)	Unidentified “phytoalexin,” phenolic glycosides	Flores and Hubbes 1979, 1980; Kruger and Manion 1994
<i>Alternaria</i> (conidia and mycelia)	Unidentified “phytoalexin”	Flores and Hubbes 1979, 1980
Insects		
Gypsy moth (<i>Lymantria dispar</i>)	Phenolic glycosides	Hemming and Lindroth 1995; Lindroth and Hemming 1990; Hwang and Lindroth 1997; Osier et al. 2000b
Forest tent caterpillar (<i>Malacosoma disstria</i>)	Phenolic glycosides	Hemming and Lindroth 1995, 1999; Lindroth and Bloomer 1991; Lindroth et al. 1993
White-marked tussock moth (<i>Orgyia leucostigma</i>)	Phenolic glycosides	McDonald et al. 1999
Canadian tiger swallowtail (<i>Papilio canadensis</i>)	Phenolic glycosides	Hwang and Lindroth 1998
Big poplar sphinx moth (<i>Pachysphinx modesta</i>)	Phenolic glycosides	Hwang and Lindroth 1998
Large aspen tortrix (<i>Choristoneura conflictana</i>)	Phenolic glycosides	Bryant et al. 1987b
Aspen blotch leafminer (<i>Phyllonorycter tremuloidiella</i>)	Phenolic glycosides (?; marginal effect)	Auerbach and Alberts 1992
Vertebrates		
Ruffed grouse (<i>Bonasa umbellus</i>)	Coniferyl benzoate	Jakubas et al. 1993a,b
Snowshoe hare (<i>Lepus americanus</i>)	Unidentified “phenolic and terpene resin”	Bryant 1981
Beaver (<i>Castor canadensis</i>)	Unidentified “phenolic”	Basey et al. 1990

unknown) could be isolated from aspen twigs following inoculation with *Hypoxylon*; these compounds inhibited germination of *Hypoxylon* ascospores and *Alternaria* conidia, and growth of *Alternaria* mycelia. Later, Kruger and Manion (1994) showed that the phenolic glycosides salicin and salicortin, and the simple phenolic catechol, inhibit *Hypoxylon* ascospore germination.

Insects

Aspen serves as a host to over a hundred species of insects, including nine species of expansive outbreak folivores (Baker 1972; Furniss and Carolin 1977; Mattson et al. 1991; Perala 1990). Some of the latter defoliate trees on a scale rarely seen for other insect pests in North America. For example, annual defoliation by the forest tent caterpillar (*Malacosoma disstria*) and large aspen tortrix (*Choristoneura conflictana*) for the period 1957–1987 averaged 935,000 and 246,000 ha, respectively, with tent caterpillar outbreaks as large as 13.5 million ha observed (Mattson et al. 1991). With the exception of the gypsy moth (*Lymantria dispar*), all the major insect pests of aspen are native species.

Numerous studies have evaluated the role of chemistry pertaining to the performance of aspen-feeding insects (table 1). These studies have included specialists and generalists, as well as outbreak and nonoutbreak species, and have been conducted under laboratory and field conditions. In nearly every instance, phenolic glycosides were of singular importance with respect to influence on insect performance (survival, development, growth, feeding, reproduction). Phenolic glycoside concentrations typically account for 60 to 98% of the

variation in insect performance parameters. Results from correlative studies have been substantiated by experimental studies in which purified phenolic glycosides were incorporated into insect diets (Hemming and Lindroth 1995; Lindroth and Bloomer 1991; Lindroth and Hemming 1990). The only study published to date that does not suggest a major role of phenolic glycosides in insect resistance in aspen is that of Auerbach and Alberts (1992) for aspen blotch leafminers (*Phyllonorycter tremuloidiella*).

Surprisingly, several studies have shown that condensed tannins have no deleterious effect on the performance of aspen-adapted insects (Ayres et al. 1997; Bryant et al. 1987b; Hemming and Lindroth 1995; Hwang and Lindroth 1997, 1998). Indeed, presence of moderate to high levels of tannins can actually increase consumption rates, perhaps as a consequence of the dilution of critical foliar nutrients (Osier and Lindroth 2000).

The efficacy of chemical defense appears to change during the course of insect (e.g., gypsy moth, forest tent caterpillar) outbreaks on aspen. At moderate to high insect population densities, aspen clones are not uniformly susceptible to defoliation; rates may vary from 20 to 90% of leaf area removed for clones in a common habitat (Lindroth, personal observation). Differential defoliation is likely due to genotypic differences in levels of phenolic glycosides, although this has yet to be confirmed experimentally. At very high population densities, however, all aspen are heavily defoliated, apparently irrespective of chemical variation. Traits conferring tolerance to damage would be particularly beneficial in these situations.

Vertebrates

Given the importance of aspen as a food source for a variety of vertebrate species, surprisingly little is known about the role of particular defense characteristics in mediating those interactions. The most detailed assessment of the impact of aspen chemistry on a vertebrate herbivore was conducted for ruffed grouse (*Bonasa umbellus*). A series of studies by Jakubas and colleagues (Jakubas and Gullion 1991; Jakubas et al. 1989, 1993a,b) revealed that coniferyl benzoate, rather than phenolic glycosides or tannins, strongly influences selection of buds and catkins. These tissues can comprise from much to nearly all of the diet of grouse during winter and spring. Ingestion of high levels of coniferyl benzoate causes loss of nitrogen, reductions in metabolizable energy, and acidosis from production of acidic detoxication products.

Less is known about the roles of aspen defenses with respect to herbivory by mammals. Winter browsing by snowshoe hares (*Lepus americanus*) may be influenced by aspen chemical composition, as adventitious shoots contain high levels of phenolic and terpene resins and are unpalatable to hares (Bryant 1981). 6-Hydroxycyclohex-2-ene-1-one and salicylaldehyde, derivatives of phenolic glycosides such as salicortin and tremulacin, protect internodes of juvenile balsam poplar (*Populus balsamifera*) from browsing by hares (Reichardt et al. 1990). Related work with other poplars and willows has shown that phenolic glycosides deter feeding by opossums (*Trichosurus vulpecula*) in New Zealand (Edwards 1978) and mountain hares (*Lepus timidus*) in Scandinavia (Tahvanainen et al. 1985).

Aspen chemistry also appears to play a role in defense against feeding by beaver (*Castor canadensis*). Aspen trees cut by beaver will resprout with a juvenile growth form, which is avoided by beaver when mature growth-form plants are available (Basey et al. 1990). Food selection is not influenced by phenolic glycoside levels, but by levels of an unknown phenolic constituent that occurs in high concentrations in juvenile tissue.

Almost nothing is known about the effects of aspen chemical composition on foraging by cervids. Given the importance of aspen as a browse species for deer (*Odocoileus hemionus*, *O. virginianus*), elk (*Cervus elaphis*), and moose (*Alces alces*), this represents a significant gap in our understanding of cervid foraging ecology. Because accessible aspen are heavily browsed by cattle and cervids (especially elk) throughout much of Western North America, the argument could be made that chemical defenses are ineffective in reducing herbivore damage. Although such may be the case now, it is likely an artifact of artificially sustained high densities of browsing mammals. Such high densities were likely rare throughout most of the evolutionary history of aspen (C. Kay, this proceedings). The potential error of the deduction of “ineffective defense” becomes clear as one considers the analogous situation with outbreak insects. At low to moderately high herbivore densities, marked differences in susceptibility to defoliation exist (advantages of chemical defense are obvious), but these differences disappear under conditions of exceptionally high herbivore feeding pressure. In situations during which chemical defenses are rendered ineffective, aspen likely relies on tolerance. But tolerance is a relatively short-term defense. It cannot be sustained during extended periods of heavy browsing, as now exist throughout much of the western range of aspen. Clearly, much remains to be learned about the roles of chemical and physiological mechanisms as mediators of aspen-mammal interactions in Western North America.

Conclusions

Much of the ecological success of aspen can be attributed to the defense systems it employs against potentially damaging agents in the environment. The dominant defense system is chemical, and phenolic glycosides are the signature compounds. Tolerance is also likely to be an important defense system, although less is known about this system than is known about chemical defenses. Commitment to chemical defense varies strikingly among aspen genotypes. Such variation is likely maintained due to the “costs” of defense; negative genetic correlations exist between growth and defense, and these are strongest under conditions of low resource availability. Chemical defense systems have been demonstrated to negatively affect the performance of a variety of aspen pathogens and herbivores. That work focused, however, on interactions between aspen and insect herbivores in the Great Lakes region. Critically needed is an evaluation of (1) the relevance of chemical defense and tolerance to herbivory by large browsing mammals and (2) implications thereof for the long-term health of aspen in Western North America.

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Mycorrhizal Fungi of Aspen Forests: Natural Occurrence and Potential Applications

Cathy L. Cripps¹

Abstract—Native mycorrhizal fungi associated with aspen were surveyed on three soil types in the north-central Rocky Mountains. Selected isolates were tested for the ability to enhance aspen seedling growth *in vitro*. Over 50 species of ectomycorrhizal fungi occur with *Populus tremuloides* in this region, primarily basidiomycete fungi in the Agaricales. Almost one-third (30%) were ubiquitous with aspen and were found on all three soil types. Over one-third (37%) were restricted to the acidic, sandy soil of the smelter-impacted Butte-Anaconda area, revealing a subset of fungi that tolerate these conditions. Mycorrhizal fungi were screened for their ability to enhance aspen growth and establishment. Of nine selected isolates, all but one increased the biomass of aspen seedlings 2–4 times. Stem diameter, height, and number of root tips increased with inoculation of some fungi. The native species *Paxillus vernalis*, *Tricholoma scalpturatum*, *Hebeloma mesophaem*, *Thelephora terrestris*, and *Laccaria* spp. were most promising for further study. *Pisolithus tinctorius* (available as commercial inoculum) formed prolific mycorrhizae and stimulated plant growth but does not occur with aspen in the Rocky Mountains.

Introduction

Over 80% of plant families are mycorrhizal, and this mutualistic association between plant roots and fungi are the rule in nature, not the exception (Malloch et al. 1980). Most terrestrial ecosystems depend on mycorrhizae, which promote the establishment, growth, and health of plants. Mycorrhizal fungi are particularly crucial in forest systems where they benefit trees by augmenting inorganic nutrient uptake and providing protection from heavy metals, drought, pathogens, grazers, and other organisms (Fogel 1980). Seven mycorrhizal “types” have been defined by the morphology of the root structures formed and the organisms involved (see Smith and Read 1997 for a review). The Pinaceae (pine family), Betulaceae (birch family), Salicaceae (willow and aspen family), Fagaceae (oak family), and Myrtaceae (eucalyptus family) are primarily *ectomycorrhizal* and associate mostly with basidiomycete fungi, which produce mushrooms as reproductive structures (Malloch et al. 1980). Mushrooms produced by mycorrhizal fungi can be observed near host trees at certain times of the year and are evidence of mycorrhizae in the soil. It should be kept in mind that not all mushroom-producing fungi are mycorrhizal, and forests also host a diverse array of large, fleshy fungi that are saprophytic, parasitic, or mutualistic in other ways (Pilz and Molina 1996).

Aspen (*Populus tremuloides* Michx.) is predominantly ectomycorrhizal (Cripps and Miller 1993; Fontana 1963; Vozzo and Hacksdaylo 1974). The prefix “ecto” refers to the intercellular nature of the fungal hyphae that remain external to the plant root cells. Hyphae form a layer over individual roots tips (mantle) and surround individual cortex cells (Hartig net) where nutrient exchange takes

¹Mycologist, Department of Plant Sciences, Montana State University, Bozeman, MT.

place, but they do not invade the root cells. The fungal mycelium proliferates into the soil, essentially extending the root system and enhancing the uptake of inorganic nutrients, primarily of phosphorus and nitrogen, which is considered a main benefit to the plant. In return, fungi subsist on carbohydrates from the plant, which are converted to fungal sugars. There are reports of *Populus tremuloides* associating with arbuscular mycorrhizal (AM) fungi that invade the root cells forming a type of endomycorrhizae, but we have found this to be rare. Other species of *Populus* are more likely to associate with AM fungi, and some are also ectomycorrhizal (Vozzo and Hacksaylo 1974).

There were two main objectives in the present study. The first was to survey the mycorrhizal fungi associated with aspen on three different soil types in the north-central Rocky Mountains and identify species with a narrow or broad range. The second objective was to evaluate the effectiveness of several mycorrhizal species in enhancing the growth of aspen seedlings. The second goal has potential application in mined-land reclamation.

In nature, an individual tree typically supports numerous species of mycorrhizal fungi simultaneously, and this mycoflora is dynamic, changing over the life of the tree. The potential number of fungal associates varies with the plant species. For example, Douglas-fir (*Pseudotsuga menziesii*) is capable of forming mycorrhizae with over 2,000 species of fungi (Trappe 1977), while alder (*Alnus* spp.) is limited to only a few (Brunner et al. 1990). In Montana and Idaho, we previously reported over 50 species of mycorrhizal basidiomycete fungi in aspen stands (Cripps and Miller 1993; Cripps 1997). That list has now been extended and refined with additional species determinations, particularly in the Cortinariaceae, a dominant family with aspen in terms of species richness. Ectomycorrhizal fungi exhibit various levels of specificity in plant-fungus interactions. Some fungi are restricted to one or a few hosts, while others have a preference for conifers or broad-leaf hosts. Some are known to occur with a wide range of trees. For example, *Suillus* occurs primarily with pine, occurs to a lesser extent with larch and Douglas-fir, and is rare with other trees. The genus *Gomphidius* appears restricted to pines, and *Lactarius controversus* to aspen and birch. The role that soil and other factors play in determining the mycobionts of a particular forest is only beginning to be understood. In Europe it is common to refer to a particular mycorrhizal fungus's preference for mull or mor soil, while in North America we know so little about the distribution of mycorrhizal fungi that patterns are yet to be completely discerned. Aspen occur in large, pure stands on many soil types and offer an opportunity to examine the role soil factors play in the distribution of mycorrhizal fungi on one host. Mycorrhizal fungi with aspen were surveyed on three very different soil types in Montana and adjacent areas of Idaho to determine if mycofloras varied or if the same subset of mycorrhizal fungi occurred in all stands. Some results have been reported in Cripps and Miller (1993). The updated list is given here along with the specifics of soil characteristics.

Potential Application of Mycorrhizal Fungi

The smelter-impacted area of Butte-Anaconda was of particular interest, because soils are acidic and high in concentrations of copper, iron, and zinc. Heavy metals such as cadmium have been found in aspen leaves on this Superfund site (Bissell 1982). The role of aspen as a pioneering tree in the recovery of smelter-impacted sites in this region is generally unrecognized, and reclamation efforts are typically focused on imported plants. The backside of the Anaconda smelter hill supports a vibrant aspen stand, and young aspen are

found within a few hundred feet of the smelter stack itself (Cripps 1996). Dotting the extensive moonscape of tailings waste, small isolated aspen appear to be healthy and thriving. Although their longevity is in question, the survival of even one is significant given aspen's clonal nature and potential to proliferate. At the smelter site in Kellogg, Idaho, a thriving natural aspen stand rises above the planted yellowing conifers. In Trail, British Columbia, where the smelter is still in operation, numerous *Populus* spp. line the banks of the Columbia River downwind of the smelter stack.

Whether aspen has seeded in or regenerated from protected pockets of aspen is an open question. It is difficult to account for the occurrence of isolated aspen trees located on tailings 10 m deep and surrounded by hectares of dumped tailings except by seeding, although this has not been verified. All of the roots examined at these sites were mycorrhizal and several species of fungi have been identified. Ectomycorrhizal fungi are crucial to aspen's survival in these areas, and their potential to expedite aspen colonization on these sites has not been examined. With this in mind, the effects of mycorrhizal fungi on early seedling growth of aspen were studied as an initial screening for native and nonnative fungi, which might be useful in aspen establishment and health and for mined-land reclamation. The parameters examined were the ability of the mycorrhizal fungi to (1) grow in vitro, (2) form mycorrhizae with aspen in vitro, and (3) affect biomass, height, stem diameter, and general health of aspen.

Methods

Sites

The three study areas are located in the north-central Rocky Mountains of southwestern Montana and southeastern Idaho at latitude 45° N, longitude 110–112° W, and elevations of 1,800 to 2,000 m (figure 1). The Butte-Anaconda (B) area lies near the towns of those names in Montana at an elevation near 1,800 m. Fumes from previously operating copper smelters killed much of the vegetation in the late 1800s and early 1900s, and aspen have colonized large areas within the last 70 years. The soil is a nutrient-poor sand (over 70%), with pH's from 4.3 to 5.7, and contains high concentrations of metals, particularly copper. The Cinnabar site (C) just north of Yellowstone National Park supports an older aspen stand with trees up to 114 years old that is gradually being invaded by conifers. The moist area is in a mountain basin, and the soil is a gravelly glacial till, high in P, Ca, and Mg. The large aspen stands of the Teton (T) area in SW Idaho lie on rolling uplands of well-drained soils formed from deep loess and composed of 75% silt. The soil is relatively fertile as attested to by adjacent agricultural land, and aspen tend to persist in this area without conifer replacement. Soil characteristics for the sites are shown in tables 1 and 2.

Mycorrhizal Synthesis and Growth Studies

Native and nonnative fungi that grew well in culture were selected for in vitro growth studies to examine the effects of individual fungal species on early aspen growth. Sterile technique was used to ensure that effects were due to the mycorrhizal fungi and not to extraneous organisms. Pot and field studies will be necessary to further examine effects of mycorrhizal inoculation under greenhouse conditions and for outplantings. Our purpose was to restrict each experimental unit to one mycobiont and one plant host (aspen). Sporocarp

Figure 1—Location of aspen forests in study. B = Butte-Anaconda smelter-impacted area. C = Cinnabar Basin north of Yellowstone Park. T = Teton foothills. I = the town of McCall, ID. Map courtesy of Ray Steiner, John Hopkins University.

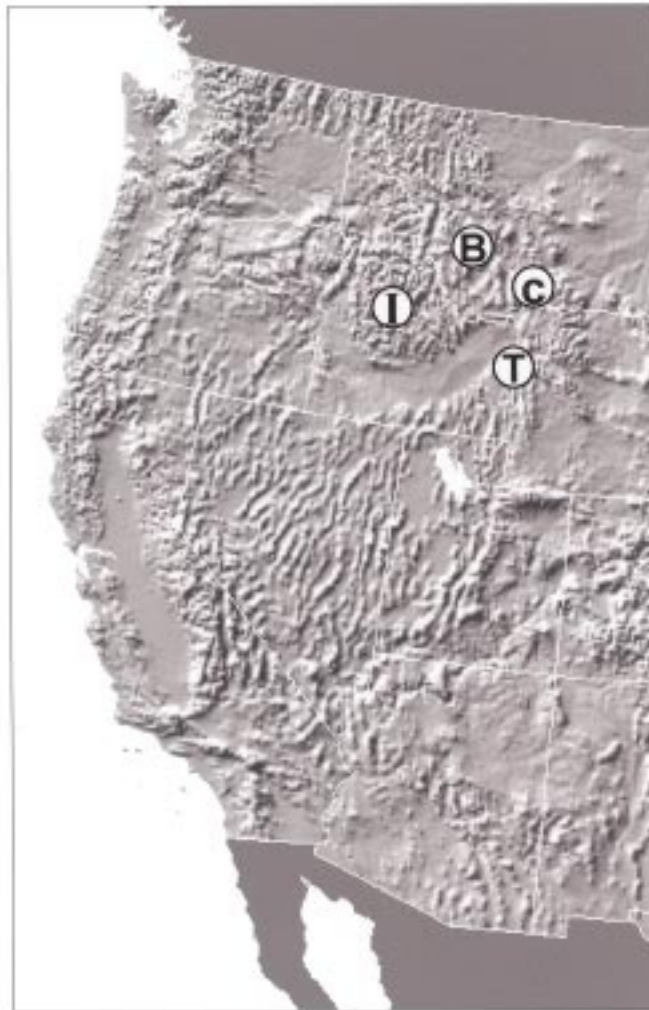


Table 1—Soil characteristics of aspen sites in relation to depth. OM = organic matter, CEC = cation exchange capacity.

Soil depth	Sand	Silt	Clay	pH	Exchangeable Ca in ppm	OM	Base saturation	CEC
<i>cm</i>	----- Percent -----					---- Percent ----		
Butte								
8	82	15	3	5.3	1.46	1.9	45	0.46
15	81	13	5	4.3	1.04	3.2	15	0.15
20	70	20	9	4.5	1.53	4.8	11	0.11
58	74	17	8	4.9	3.03	2.7	28	0.28
97	84	6	10	5.6	5.92	2.1	77	0.77
Cinnabar								
8	65	27	7	5.5	12.60	7.2	63	0.63
15	63	28	9	5.7	11.80	5.7	66	0.66
20	58	31	11	5.8	13.70	5.5	65	0.65
58	70	24	6	6.4	7.40	1.1	86	0.86
94	67	24	9	6.5	6.89	1.1	93	0.88
Tetons								
15	15	77	8	5.5	8.00	2.4	84	0.84
36	12	79	9	6.0	6.37	1.7	73	0.73
56	12	79	9	6.1	5.92	1.2	71	0.71
84	11	67	21	6.3	10.2	1.0	82	0.83
122	42	44	14	6.3	7.90	0.7	79	0.79

Table 2—Exchangeable macro- and micronutrients (ppm) of soil on aspen forest sites.

Soil depth	P	Ca	Mg	Zn	Fe	Al	Cu
<i>cm</i>							
Butte							
8	62	404	53	10.7	31.6	155	43
15	54	252	34	7.7	72.4	264	116
20	94	386	37	19.7	35.2	588	142
58	63	803	61	72.9	9.9	388	3.5
97	40	1,377	68	1.7	3.2	71	0.3
Cinnabar							
8	78	2,048	303	4.7	12.3	135	0.2
15	67	2,128	312	3.6	10.2	138	0.2
20	64	2,260	332	3.5	9.3	138	0.2
58	130	1,487	312	0.6	22.3	131	0.4
94	119	1,360	295	0.6	25.2	122	0.6
Tetons							
15	62	1,502	111	3.3	15.8	128	0.5
36	56	1,190	105	2.6	14.2	117	0.7
56	62	1,032	97	1.9	19.1	111	1.3
84	113	1,523	164	1.3	28.1	157	3.8
122	32	977	124	0.8	20.3	133	1.9

tissue of native fungi and mycelium of nonnative fungi was cultured according to the sterile technique described by Molina and Palmer (1982) and grown on Hagem's medium modified by Van Cotter (1987, unpublished): 4 g malt extract, 1 g yeast extract, 5 g d-glucose, 0.5 g NH₄Cl, 0.5 g KH₂PO₄, 0.5 g MgSO₄·7H₂O, 0.5 ml FeCl₃ (1% aqueous), 100 ml biotin (0.5 mg biotin/ml aqueous), and 100 ml thiamine-HCl (1 mg thiamine/ml aqueous) added to 1,000 ml of distilled H₂O. Eleven grams of agar/L were added to solidify the medium, which was autoclaved for 20 minutes. Cultures were incubated in the dark at 20 °C for a minimum of 1 month and used to inoculate 250 ml flasks containing 75 ml of liquid Cotter's modified Hagem's without agar.

Fresh aspen seeds were stored in a dry place at 0 to 5 °C. Seeds stored too long lose viability and the risk of contamination increases. Seeds were gently agitated in a 15% Clorox™ solution for 15 minutes and rinsed three times (10 minutes each) in double-distilled H₂O (Cripps and Miller 1995). Two drops of the detergent Tween™ were added to the first two solutions to reduce surface tension. Seeds were placed in petri dishes containing Cotter's modified Hagem's made with 11 g/L of agar and placed in a growth chamber under incandescent and fluorescent lights for 16 hours a day followed by 8 hours of dark. Seedlings that showed no signs of contamination were planted in synthesis tubes 23 days later.

Molina and Palmer's tube method of synthesis (1979) was followed using 10 ml peat, 90 ml of vermiculite, and 70 ml of Cotter's modified Hagem's (without agar) for each 200 ml synthesis tube. Five ml of mycelial slurry was added to each tube, which was autoclaved, and the lower part encased in aluminum foil. Ten replicates were used for each fungus and the uninoculated controls. After mycelium colonized the peat-vermiculite medium for 2 weeks, sterile seedlings were introduced and tubes were placed in a growth chamber. Tubes were periodically checked for mycorrhization and seedlings harvested after 3 months. At that time, the general condition of the aspen seedlings was noted, particularly leaf color. The stem diameter and height were measured. Roots were carefully washed and percent mycorrhization determined by counting the number of mycorrhizae per total number of root tips.

Seedlings were dried at 65 °C for 48 hours and weighed. The nonparametric Kruskal-Wallis *t*-test was used to compare responses in control seedlings versus those inoculated with individual fungi.

Results

Mycorrhizal Associates of Aspen

Over 54 species of ectomycorrhizal fungi occurred with aspen on the three study sites and additional aspen stands sampled in Montana and Idaho (table 3). The fungi are all Basidiomycota, primarily Agaricales (gilled mushrooms and boletes), and one Aphyllophorales (*Thelephora terrestris* Fr.). The fungi are distributed in seven families: Amanitaceae, Russulaceae, Tricholomataceae, Cortinariaceae, Paxillaceae, Boletaceae, and Thelephoraceae (figure 2). The dark-spored Cortinariaceae is the most diverse family, with 25 species of *Cortinarius*, *Inocybe*, and *Hebeloma* occurring in aspen stands. In casual observation, *Leccinum* species often dominate in terms of sheer biomass, with sporocarps occurring in large numbers. *Leccinum insigne* (orange-capped bolete) is considered one of the most characteristic species of aspen stands.

Two major categories of ectomycorrhizal fungi became apparent in the study. Nearly one-third (30%) of the ectomycorrhizal species occurred on all three soil types with *Populus tremuloides*. This percentage increased each year of the study as species fruited on additional sites, as is typical in fungal studies. In the second group, over 37% of the mycorrhizal species occurred only on the smelter-impacted, sandy, acidic soil of the Butte-Anaconda area, suggesting that there is a subset of mycorrhizal fungi more restricted to, or more tolerant of, these abiotic conditions.

Effect of Mycorrhizal Fungi on Aspen Seedling Growth

General condition of aspen

About half of the mycorrhizal fungi isolated grew in culture, and fewer grew well enough to be tested. Of the six native and three nonnative fungi selected for testing, all formed mycorrhizae with aspen, except *Chalciporus* (*Boletus*) *piperatus* (Bull.:Fr.) Singer. *Piloderma* formed a mantle, but no Hartig net. The general condition of plants at the end of the experiment is shown in table 4. None of the uninoculated control seedlings died, and leaves remained completely green throughout the experiment. This was also true for inoculation with four native fungi, *Amanita muscaria* v. *formosa* (Pers. Per Fr.) Bert., *Amanita pantherina* (DC Per Fr.) Krombh., *Paxillus vernalis* Watling, and *Tricholoma sculpturatum* (Fr.) Quel. In contrast, all plants inoculated with *Inocybe lacera* (Fr:Fr) Kummer became necrotic after forming a few mycorrhizae; the black leaves abscised and dropped off, and the plants died. *Chalciporus piperatus* inoculated plants did not form mycorrhizae, but leaf color was affected. Leaves of seedlings inoculated with *Paxillus vernalis* developed red, yellow, and black coloration, but plants remained in good condition. With the exception of *Inocybe lacera*, which produced 100% mortality in aspen seedlings, and one plant with *B. piperatus*, all plants inoculated with native mycorrhizal fungi were alive at the end of the experiment. However, mycorrhizae were slow to form under these conditions with native fungi.

Seedlings inoculated with nonnative fungi had a higher mortality rate (10–20%), and extreme leaf tips turned black. While *Cenococcium* and *Piloderma*-inoculated plants turned a pale yellow-green color, those with

Table 3—Ectomycorrhizal fungi occurring with *Populus tremuloides* in the north-central Rocky Mountains, U.S.A. B = Butte, C = Cinnabar, and T = Teton site.

Ectomycorrhizal fungi with <i>Populus tremuloides</i> in the north-central Rocky Mountains	State	Acidic, sandy infertile soil (Butte-Anaconda)	Calcareous, sandy loam (Cinnabar)	Calcareous silty soil (Tetons)	Soil types	Growth in vitro ^a
AMANITACEAE						
<i>Amanita alba</i> Gill.	MT, ID		+		C	–
<i>Amanita fulva</i> (Schaeff.) per Pers.	ID			+	T	–
<i>Amanita muscaria</i> v. <i>alba</i> Peck	ID				?	+
<i>Amanita muscaria</i> v. <i>formosa</i> (Pers per Fr.) Bert.		+	+	+	BCT	+
<i>Amanita pantherina</i> (DC. Per Fr.) Krombh.	MT, ID	+	+	+	BCT	+
<i>Amanita vaginata</i> (Bull. Per Fr.) Krombh.	MT, ID		+	+	CT	–
RUSSULACEAE						
<i>Lactarius controversus</i> (Fr.) Fr.	ID, MT	+	+	+	BCT	+
<i>Lactarius</i> cf. <i>zonarius</i> Fr.	MT, ID		+	+	CT	?
<i>Russula aeruginea</i> Lindbl.:Fr.	MT, ID	+	+	+	BCT	–
<i>Russula claroflava</i> Grove	MT	+			B	–
<i>Russula</i> cf. <i>krombholtzii</i> Kromb.	MT	+		+	BT	–
<i>Russula foetenula</i> Peck	MT	+	+		BC	–
<i>Russula</i> cf. <i>velenovskiyi</i> Mlz-Zv.	MT	+	+	+	BCT	–
<i>Russula xerampelina</i> (Schaeff.:Secr.) Fr.	MT		+		C	–
TRICHOLOMATACEAE						
<i>Laccaria laccata</i> v. <i>pallidifolia</i> (Peck) Peck	MT	+			B	+
<i>Laccaria proxima</i> (Boud.) Pat	MT	+			B	+
<i>Laccaria tortilis</i> (Bolt.) Cooke	MT	+	+		BC	?
<i>Tricholoma flavovirens</i> (Pers. Ex Fr.) Lun & Nan	MT	+			B	?
<i>Tricholoma populinum</i> Lge.	MT	+			B	+
<i>Tricholoma sculpturatum</i> (Fr.) Quel.	MT, ID	+	+	+	BCT	+
CORTINARIACEAE						
<i>Cortinarius alboviolaceus</i> (Pers.:Fr.) Fr.	MT		+		C	–
<i>Cortinarius hedyaromaticus</i> Cripps & Miller	MT		+		C	+
<i>Cortinarius ochrophyllus</i> Fr.	MT	+			B	–
<i>Cortinarius subbalaustinus</i> R. Hry.	MT, ID	+	+	+	BCT	–
<i>Cortinarius talus</i> Fr.		+			B	+
<i>Cortinarius trivialis</i> Lge.	MT, ID	+	+	+	BCT	–
<i>Cortinarius</i> cf. <i>stuntzii</i> Rehner and Ammirati	MT	+			B	?
<i>Cortinarius</i> cf. <i>sertipes</i>	MT		+		B	?
<i>Hebeloma insigne</i> Smith, Evenson & Mitchell	MT	+	+	+	BCT	+
<i>Hebeloma mesophaeum</i> (Fr.) Quel.	ID, MT	+	+		BC	+
<i>Hebeloma populinum</i> Romagn.	MT	+	+	+	BCT	+
<i>Hebeloma</i> spp. 1, 2, 3	MT				?	+
<i>Inocybe dulcamara</i> (Alb. & Schw:Pers) Kummer	MT	+	+		BC	+
<i>Inocybe flavella</i> v. <i>flavella</i> P. Karst	MT, ID	+	+	+	BCT	?
<i>Inocybe flocculosa</i> (Berk) Sacc. v. <i>flocculosa</i>	MT, ID	+	+	+	BCT	–
<i>Inocybe geophylla</i> (Fr.:Fr.) Kumm. v. <i>geophylla</i>	MT	+			B	–
<i>Inocybe griseoililacina</i> Lge.	MT		+		C	–
<i>Inocybe lacera</i> (Fr:Fr) Kummer v. <i>lacera</i>	MT, ID	+			B	+
<i>Inocybe longispora</i> Lge.	MT	+			B	–
<i>Inocybe mixtilis</i> (Britz.) Sacc.	MT	+	+		BC	–
<i>Inocybe nitidiuscula</i> (Britz.) Sacc.	MT	+	+		BC	–
<i>Inocybe phaeocomis</i> (Pers.) Kuyper v. <i>major</i>	MT	+			B	–
<i>Inocybe rimosa</i> (Bull:Fr.) Kummer	MT, ID	+			B	+
<i>Inocybe squamata</i> Lge	MT	+			B	?
<i>Inocybe sindonia</i> (Fr.) P. Karst	MT	+			B	–
<i>Inocybe whitei</i> (B & Br) Sacc. v. <i>whitei</i>	MT	+	+	+	BCT	–
PAXILLACEAE						
<i>Paxillus vernalis</i> Watling	MT, ID	+	+	+	BCT	+
BOLETACEAE						
<i>Chalciporus piperatus</i> (Bull.:Fr.) Singer	MT, ID		+	+	CT	+
<i>Leccinum aurantiacum</i> (Bull:St.Amans) SF Gray	MT, ID	+	+	+	BCT	+
<i>Leccinum holopus</i> (Rostk.) Watl.	ID				?	?
<i>Leccinum insigne</i> Smith, Thiers & Watling	MT, ID	+	+	+	BCT	+
<i>Phylloporus rhodoxanthus</i> (Schw.) Bres.	MT	+			B	?
<i>Xerocomus spadiceus</i> Fr.	MT	+			B	+
THELEPHORACEAE						
<i>Thelephora terrestris</i> Fr.	MT, ID	+			B	+

^a(+) fungus grew on MMN, (–) fungus showed no growth on MMN, (?) fungus was not tested on MMN. MMN is Melin-Norkrans media (Molina and Palmer 1982).



Figure 2—Ectomycorrhizal fungi associated with aspen. Row 1: *Amanita muscaria*, *Amanita pantherina*, *Laccaria proxima*. Row 2: *Lactarius controversus*, *Russula aeruginea*, *Cortinarius trivialis*. Row 3: *Cortinarius subbulaustinus*, *Inocybe squamata*, *Inocybe lacera*. Row 4: *Leccinum insigne*, *Boletus piperatus*, *Paxillus vernalis*.

Table 4—General condition of aspen seedlings inoculated with mycorrhizal fungi after 3 months. Native fungi were isolated from aspen stands in Idaho and Montana. Nonnative fungi are from VPI culture collection and origins are unknown.

	Seedling mortality	Leaf color general condition	Mycorrhizal	Average biomass as % of control
	Percent		Percent	Percent
Control	0	Green	0	100
Native fungi				
<i>Amanita muscaria</i>	0	Green	15	400
<i>Amanita pantherina</i>	0	Green	11	250
<i>Boletus piperatus</i>	10	Green with black tips	0	430
<i>Inocybe lacera</i>	100	Most black	1	100
<i>Paxillus vernalis</i>	0	Red/yellow/green/black	12	300
<i>Tricholoma sculpturatum</i>	0	Green	1	430
Nonnative fungi				
<i>Cenococcum graniforme</i>	20	Yellow-green, black tips	5	275
<i>Piloderma croceum</i>	10	Yellow-green, black tips	1	300
<i>Pisolithus tinctorius</i>	20	Dark green, black tips	86	350

Pisolithus tinctorius were a healthy looking dark green. Mycorrhizae were slow to form with the first two, but the root systems of aspen inoculated with *P. tinctorius* (PT) were heavily colonized by the fungus in a short period of time (table 4).

Aspen biomass, stem diameter, height, number of root tips

All of the inoculated aspen seedlings (except those with *I. lacera*) showed a significant increase in total plant biomass over uninoculated controls (figure 3a). In most cases, the increase in average biomass was substantial, and as a percent of the controls the biomass was 430% for *Tricholoma scalpturatum* and *Boletus piperatus*, 400% for *Amanita muscaria*, 350% for *Pisolithus tinctorius*, 300% for *Paxillus vernalis* and *Piloderma croceum*, 275% for *Cenococcum graniforme*, and 250% for *Amanita pantherina*. The biomass of aspen inoculated with *Inocybe lacera* was not significantly different from the control, and plants were in poor condition.

Stem diameter in aspen seedlings increased significantly with the addition of all the mycorrhizal fungi, except *I. lacera* (figure 3d). While the average height of aspen seedlings was increased by inoculation with some fungi, this was only marginally significant for others (figure 3b). Inoculation also affected leaf shape, size, and number differentially, with a general increase of surface area, but the details are not reported here. The average number of root tips doubled with inoculation for most fungi, even those with *Boletus piperatus* that did not form mycorrhizae (figure 3c). *Inocybe lacera* eventually killed the seedlings. The average number of root tips after inoculation with *Pisolithus tinctorius*, *Cenococcum graniforme*, and *Tricholoma scalpturatum* was generally four times that of the control (figure 3c).

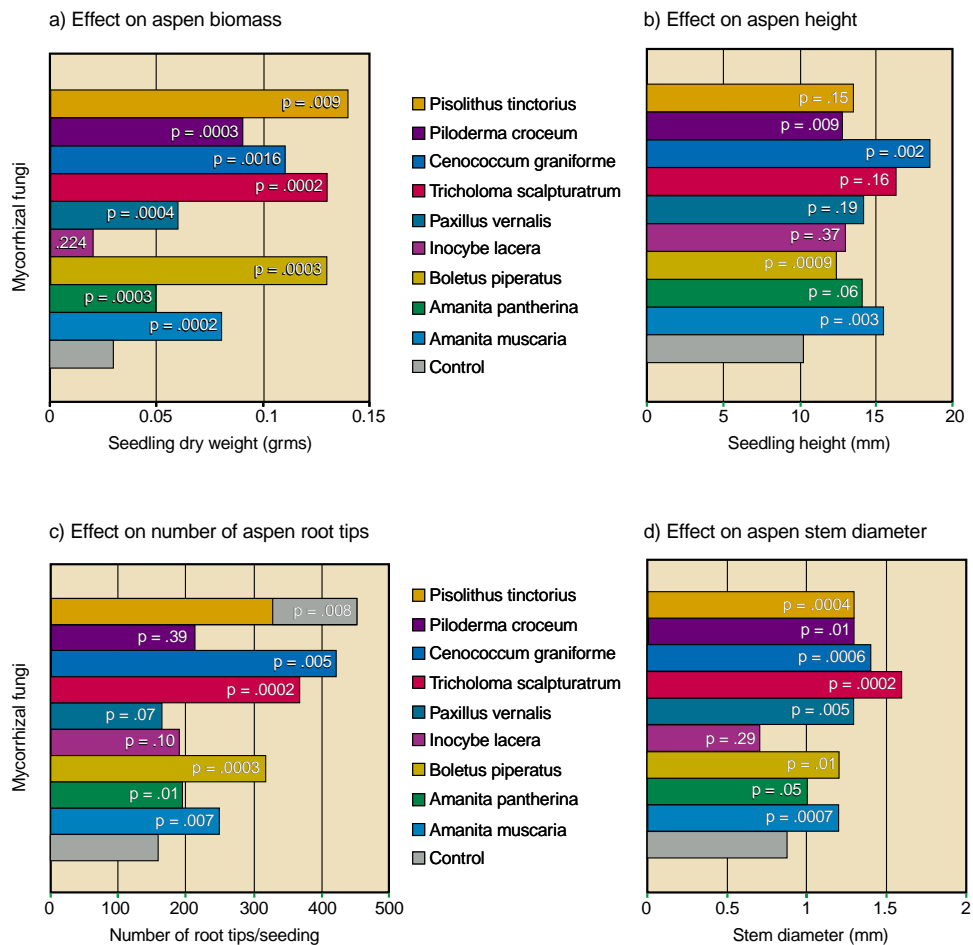


Figure 3—Effect of ectomycorrhizal fungi on early seedling growth of aspen. First three fungi are nonnatives, followed by six native species occurring with aspen in Montana and Idaho. A p-value of less than 0.05 is considered significantly different from the control.

Discussion

Mycorrhizal Associates of Aspen

Quaking aspen is now known to be associated with over 54 species of ectomycorrhizal fungi in the north-central Rocky Mountains and more species of fungi are yet to be identified, particularly in the *Russulaceae*. Aspen's ability to form a mutualistic association with such a diverse array of fungi could help account for its wide geographic range and its ability to proliferate in many different habitats (Cripps and Miller 1993). All of the mycorrhizal fungi are Basidiomycetes and members of the Agaricales (gilled mushrooms), except *Thelephora terrestris* (Aphyllophorales). Many of the same species have been reported with aspen in Canada and their mycorrhizae synthesized in the lab (Godbout and Fortin 1985). In that study, aspen formed mycorrhizae with several species of *Scleroderma*, which is of interest because of its use as a commercial inoculum (but not recorded for our study). Aspen did not form mycorrhizae with *Rhizopogon*, also used as a commercial inoculum, which occurs naturally with conifers. Sister species *Populus tremula* L. in Europe is mycorrhizal with the same fungal genera, and often with the same or related species (Anselmi et al. 1990; Heslin and Douglas 1986; Pirazzi et al. 1989). Many groups of mycorrhizal fungi found in conifer forests are absent from the aspen stands of Montana and Idaho. Mycorrhizal members of whole families such as the Sclerodermataceae, Hydnaceae, Clavariaceae, Cantharellaceae, Hygrophoraceae, Corticiaceae, and hypogeous (subterranean) Ascomycota and Basidiomycota, i.e., the truffle-like fungi, were not recorded in Rocky Mountain aspen forests. Conversely, many of the mycorrhizal fungi found in aspen forests are infrequent or absent from conifer forests.

The Cortinariaceae are a dominant group in terms of species richness, but many of the dark-spored species do not grow well in culture and are not useful for growth studies. *Inocybe* species are particularly diverse with aspen (Cripps 1997), as are *Cortinarius* species. Perhaps the most characteristic fungi of aspen stands are the *Leccinum* species (rough-stemmed boletes), which often fruit in abundance in mid-summer after significant amounts of rain.

Almost one-third (30%) of the mycorrhizal fungi occurred on all three diverse soil types examined, including (1) a nutrient-poor sandy soil, (2) a fertile gravelly loam/glacial till, and (3) a deep silty loess. Interestingly, these fungi appear to be those most closely allied with aspen. For example, the following fungi are almost strictly with aspen (or birch) and are extremely rare in conifer forests and possibly absent altogether: *Lactarius controversus* (Fr.)Fr.; *Russula aeruginea* Lindbl.:Fr.; *Cortinarius trivialis* Lge.; *Cortinarius subbalaustinus* R. Hry.; *Hebeloma insigne* Smith, Evenson, and Mitchell; *Hebeloma populinum* Romagn.; *Paxillus vernalis* Watling; *Leccinum aurantiacum* (Bull:St.Amans) SF Gray; and *Leccinum insigne* Smith, Thiers & Watling. This close alliance, regardless of soil type, appears more characteristic of older aspen stands with sufficient organic matter and nutrient availability. *Amanita* species are the exception, occurring also in conifer woods, and could possibly be "crossover" species in successional processes.

Over one-third (37%) of the mycorrhizal fungi were found only on the acidic, sandy, nutrient-poor soil of the Butte-Anaconda site, where smelters have impacted the area, and high concentrations of copper, lead, and zinc are present. This subset of aspen's mycorrhizal flora prefers or tolerates these conditions. Many of these species are rather nonspecific in regard to host plant, and are considered "early colonizers" occurring with many species of young trees.

Thelephora terrestris Fr., *Laccaria laccata* Peck, *Laccaria proxima* (Boud.) Pat, *Hebeloma mesophaeum* (Fr.) Quel., and *Inocybe lacera* (Fr.:Fr) Kummer have all been observed on smelter sites, in coal spoils, and with many species of young trees in open habitats. These same fungi have been observed with aspen on smelter sites in Kellogg, Idaho, and Trail British, British Columbia (Cripps 1996). Since aspen is often the pioneering species in smelter-impacted areas of Montana and Idaho, these fungi have a potential value for use in reclamation. In contrast, many species of ectomycorrhizal fungi are inhibited by low pH and high metal content in soils (Harris and Jurgensen 1977; Hung and Trappe 1983; McCreight and Schroeder 1982). Other mycorrhizal species are believed to ameliorate effects of heavy metals in plants (Hartley et al. 1997).

For birch, the succession of mycorrhizal fungi on a tree is predictable, with early stage fungi colonizing young seedlings, followed by the prevalence of late stage fungi with older trees (Last et al. 1987). The succession of mycorrhizal fungi on aspen in the study area appears to start with the early colonizers listed above, which are eventually replaced by fungi more restricted to aspen. Given aspen's clonal nature, microhabitat could play more of a role in species distribution. Early colonizers often occurred in young aspen stands or with young roots on the edge of older clones. Late colonizing fungi preferred the interior of aspen stands with a relatively well-developed soil and understory. It should be kept in mind, however, that fungal sporocarps are not necessarily indicative of the predominance of a fungus in the soil and on the plant roots.

Screening native mycorrhizal fungi as inoculum for aspen

Only a limited number of mycorrhizal fungi were examined for their effect on aspen seedlings because many of the species do not grow or grow well in culture. Others with a high potential for use as mycorrhizal inoculum such as *Hebeloma*, *Laccaria*, *Thelephora*, and some *Tricholomas* are yet to be tested. Although mycorrhizal fungi enhanced the growth of young aspen, sometimes remarkably so, with a two- to four-fold increase in biomass, this is not necessarily indicative of enhanced establishment and survival of aspen seedlings under natural conditions. Field and pot experiments need to follow this in vitro study to evaluate inoculated aspen as outplantings and in greenhouse conditions. Anselmi et al. (1990) did report a significant increase in aspen volume with fungal inoculation of most species in pot cultures. In our study, stem diameter and height increased with inoculation of about half of the fungal species. How growth parameters translate into increased fitness of aspen is another question.

What may not be obvious from our results is that each mycobiont affected the morphology of aspen in a recognizable manner for the given conditions. For example, inoculation with *Cenococcum* produced tall, pale seedlings with long, narrow leaves and long petioles. Aspen inoculated with *Tricholoma* had leaves that were two times as wide and long as the control, and plants in general were a deep rich green. Whether morphological changes produced by mycorrhizal fungi translate into form differences in older trees is not known but is an intriguing idea. The fact that various mycorrhizal fungi differ in their effect on aspen suggests that the physiology of each union is unique and that each fungus plays a particular role in the ecology of a host plant. For example, *Cenococcum* is known to tolerate drought conditions that inhibit other mycorrhizal fungi, and this fungus could be a crucial survival link in conditions of water stress. One could speculate that the diversity of fungi belowground in aspen stands enhances aspen's ability to survive a variety of conditions.

The percentage of mycorrhizal roots was not directly correlated with increases in aspen biomass, stem diameter, and height. The biomass of aspen increased substantially with addition of some fungi, but in most cases only a low percentage of roots were colonized in the given time period. This could be a result of high efficiency nutrient transfer through a small number of individual mycorrhizae or due to pre-mycorrhizal effects such as release of IAA. *Boletus piperatus* doubled the number of roots and increased the biomass of aspen seedlings without forming mycorrhizae, again suggesting a pre-mycorrhizal event such as hormone production by the fungus. *Pisolithus tinctorius* (PT) formed mycorrhizae quickly and extensively, covering the roots system in a few weeks and producing dark green healthy plants. PT is sold as a commercial inoculant, but is not native in Montana and Idaho and has failed in field trials in Oregon (Castellano and Trappe 1991). Inoculation with *Inocybe lacera* killed all the aspen seedlings, which could be due to an associated yeast or the high nutrient conditions that might increase its pathogenicity. *Inocybe lacera* typically occurs in sandy, nutrient-poor soil. The morphology of each type of mycorrhiza is unique and recognizable for each fungal species (Cripps and Miller 1995; Cripps 1997).

Nursery conditions can preclude or slow fungal colonization, since fertilizers are usually antagonistic to mycorrhizal formation. Mycorrhizae were slow to form in our study, and methods to speed up the process are necessary for commercial production. Some of the mycorrhizal inoculum tested produced aspen with discolored leaves, spotted black, red, and yellow. This is not a desirable quality for commercial plants, unless outplanting success can be proven to outweigh undesirable cosmetic problems. Another possibility is selecting a proper soil inoculum that could circumvent these problems (Helm and Carling 1990).

Native ectomycorrhizal fungi that are likely candidates for use in reforestation and reclamation with aspen are: *Paxillus vernalis*, *Tricholoma scalpturatum*, *Cenococcum graniforme* Fr., and some yet to be tested (*Laccaria* spp., *Hebeloma mesophaem*, *H. populinum*, and *Thelephora terrestris*). Care must also be taken in the nursery because *Pisolithus tinctorius* (Pers.) Coker & Couch and *Thelephora terrestris* have been known to adversely affect young plants, and proper timing for inoculation may be essential. It is also advantageous to know the soil type for outplantings. *Hebeloma* species are more likely to associate with young aspen under high fertility conditions such as lawns. Other fungi such as *Thelephora*, *Paxillus*, and *Cenococcum* may be more useful in heavy metal soils of low fertility.

Summary

Each aspen stand hosts a diverse community of mycorrhizal fungi as determined by soil type, age of the aspen stand, geographic region, and other edaphic and historical factors. Young aspen in pioneering situations, such as post-fire and smelter sites and previously unforested land, depend on “early stage” mycorrhizal fungi such as *Inocybe*, *Laccaria*, *Hebeloma*, *Thelephora*, and *Paxillus* for establishment and health. Their occurrence on the Butte-Anaconda smelter site also suggests a tolerance for heavy metals in some strains. Many of these “weedy” species of fungi also occur with young conifers. These are the fungi most likely to be of use in mined-land reclamation, and our results suggest they increase aspen biomass, height, and stem diameter in vitro. Further tests of outplantings are necessary to determine whether these mycorrhizal fungi

enhance establishment of aspen on actual mine sites. In older aspen stands, “late stage” mycorrhizal fungi make up a large part of the mycoflora, and these are species more closely allied with aspen than other tree species.

Soil type and other factors can affect the “succession” of mycorrhizal fungi. The impacts of various management strategies such as clear-cutting and fire on the mycorrhizal communities of aspen are not known. However, this should be given consideration, since management practices could apply selective pressures that promote certain species of mycorrhizal fungi, possibly to the exclusion of others, with long-term unintended consequences.

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Aspen Ecosystems: Objectives for Sustaining Biodiversity

Robert B. Campbell, Jr.¹ and Dale L. Bartos²

Abstract—Recognizing the historical abundance of major vegetation cover types is the foundation for estimating the magnitude and significance of conversion from one cover type to another and the proportion of existing cover types that are in properly functioning condition. Techniques to determine desired conditions are discussed. Existing situations for the need to treat ecosystems where aspen (*Populus tremuloides* Michx.) occur are prioritized: highest—mixed-conifer with aspen but where conifers comprise greater than 50% of the canopy; high—aspen/sagebrush transition; and moderate—aspen dominated landscapes. Though aspen stands are evaluated, aspen landscapes are discussed in the context of aggregations of many stands. Within aspen dominated landscapes, five risk factors help determine the need for action: (1) conifer understory and overstory cover is greater than 25%; (2) aspen regeneration (5–15 feet tall) is less than 500 stems/acre; (3) aspen canopy cover is less than 40%; (4) dominant aspen trees are greater than 100 years old; and (5) sagebrush cover is greater than 10%. Management recommendations for treatments, as well as examples of successes and failures of efforts to restore aspen ecosystems, are summarized. Actions to restore aspen ecosystems must not be taken before excessive browsing by livestock and wildlife is addressed.

Introduction

Quaking aspen is the most widely distributed tree species in North America and as such has tremendous ecological amplitude. On a local scale, this ecological amplitude is manifested by the species' ability to occupy sites over great elevational ranges, differing aspects, and contrasting soils from deep mollisols to steep talus and scree slopes.

Aspen Clones

The clonal habit of quaking aspen adds to its uniqueness among tree species. It is possible for a clone with as many as 50,000 stems, all genetically identical, to occupy more than 200 acres and trace their common heritage to the germination of a single aspen seedling perhaps millennia ago (Barnes 1975; Kemperman and Barnes 1976). Such a clone has weathered the test of time on that site. Even the most decadent clones should be recognized as superior genotypes that have survived the process of natural selection and are most likely some of the best suited genetic material for that site.

Aspen clones exhibit high genetic diversity. Clones on similar sites may respond differently to treatments or environmental stresses. Such differences may be manifest in the number of suckers produced, browsing impacts, susceptibility to certain diseases, frost damage, and so on. Always keep the clonal concept in mind when comparing the responses of different aspen stands.

The preceding information gives insights about aspen, the species itself. However, for the remainder of this discussion, we shift the focus from a single tree species to the unique ecosystems that occur and are sustained when aspen

¹Fishlake National Forest, USDA Forest Service, Richfield, UT.

²Rocky Mountain Research Station, USDA Forest Service, Logan, UT.

dominates stands and provides a mosaic of compositionally and structurally diverse patches on the landscape. Aspen dominated landscapes are an aggregation of many aspen dominated stands and perhaps other stands where aspen remains a component of the canopy.

A Keystone Species

Wilson (1992) explained the concept of keystone species with the following passage:

In communities there are little players and big players, and the biggest players of all are the keystone species. As the name implies, the removal of a keystone species causes a substantial part of the community to change drastically.

He defined a keystone species as:

A species that affects the survival and abundance of many other species in the community in which it lives. Its removal or addition results in a relatively significant shift in the composition of the community and sometimes even in the physical structure of the environment.

Aspen is a keystone species. With the exception of riparian areas, aspen communities are considered the most biologically diverse ecosystems in the Intermountain West (Kay 1997). However, as aspen dominated landscapes convert to other cover types, tremendous biodiversity is lost (Bartos and Amacher 1998; Bartos and Campbell 1998a,b). These losses include not only vascular plants and vertebrate animals but also nonvascular and invertebrate organisms. Thus, measures taken to sustain aspen ecosystems will also meet coarse-filter objectives for sustaining biodiversity.

Properly Functioning Condition

In 1996, the Intermountain Region of the USDA Forest Service began a process that expanded the concept of proper functioning condition introduced by the Bureau of Land Management (Barrett et. al. 1993) and originally applied only to riparian communities. This new concept of properly functioning condition applied to the major upland vegetation cover types and provided an ecological basis for a rapid assessment of general conditions of sustainability on large landscapes. Properly functioning condition is defined with this statement (USDA Forest Service 1997):

Ecosystems at any temporal or spatial scale are in properly functioning condition when they are dynamic and resilient to perturbations to structure, composition, and processes of their biological or physical components.

That definition is often too technical to use with general audiences (e.g., school classes or public meetings). This alternate definition attempts to convey the same meaning:

Properly functioning condition exists when soil and water are conserved, and plants and animals can grow and reproduce and respond favorably to periodic disturbance.

Properly functioning condition is not a single state in time or space. Indeed, properly functioning condition includes a range of conditions and situations that allow for the full variation of composition (numbers and kinds of species) and structure (size and age classes) within the processes of functioning ecosystems for that specific cover type.

Properly functioning condition is intended to be a rapid assessment, a triage, to prioritize general conditions on large landscapes. Assessments were made at

multiple scales. Some assessments were made for the entire Intermountain Region. Then a more detailed assessment was made for the Utah High Plateaus and Mountains section in south-central Utah. The concept of properly functioning condition used in this paper ties to all of these assessments. The ideas presented in this paper are applicable, at a minimum, throughout the Intermountain West.

Historical Conditions

Baker (1925) wrote about aspen in the central Rocky Mountains and included a fire history case study from Ephraim Canyon on the Wasatch Plateau in central Utah:

...These results indicate that small, light fires occurred at intervals of 7 to 10 years in the same general region previous to the settlement of the country. After the logger and stockman invaded the mountains, there was a period of frequent and larger fires, after which fires became fewer and fewer, and now virtually none occur.

...Conifers are, of course, more resistant to fire when past the sapling stage, but once destroyed they seed in slowly. A 50-year fire rotation would probably keep conifers entirely out of all the aspen type, except on north slopes or in moist localities favorable to the rapid development of the coniferous trees, although aspen would flourish under such conditions.

But under present conditions, fire is not a factor to be reckoned with in forest management in the aspen zone.

Baker's description from 75 years ago is a valuable assessment from a trained forest examiner.

We assume that if aspen are present, even a single aspen, then the area has had an aspen cover type at some time during the past 200 to 400 years. The areas where aspen occur typically had fire return intervals of 20 to 60 years. Aspen are not considered capable of establishing true seedlings under a conifer canopy. True aspen seedlings in the Great Basin and central and southern Rocky Mountains would be extremely rare to nonexistent, but aspen do regenerate profusely following a fire. In these situations, the aspen cover type might be considered a fire induced disclimax rather than an early seral stage. Some feel that it is "normal succession" for aspen to be replaced by a conifer cover type. Based on Baker's (1925) observations and these assumptions, we affirm that it is not "normal" for conifers to completely replace the aspen cover type. However, historical aspen cover types are replaced by conifers or sagebrush with the absence of frequent fires and the presence of heavy browsing by livestock and wildlife.

Repeat photos or historical photos (Rogers et. al. 1984; Kay, in press), fire histories (Chappell et. al. 1997), and landscape assessments (Jackson et. al. 1998) combine to provide an indication of the abundance, historically, of the major cover types on the Fishlake National Forest.

Soils inventories can also be used to provide a better understanding of the historical cover types for certain landscapes. The Fishlake National Forest is fortunate to have the soils mapped and GIS layers created at a scale of 1:24,000 largely through the efforts of soil scientist Michael D. Smith. We displayed this information for the Monroe Mountain subsection and reported that the historical (during the past 200 to 400 years) abundance of the aspen cover type was nearly 71,000 acres (Bartos and Campbell 1998a). Of that amount, currently about 17,000 acres remain in the aspen cover type. Almost 42,000 acres is dominated by mixed-conifers [largely subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with some Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco)] scattered throughout. Also, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*

(Rydb.) Beetle) replaced the aspen cover type on nearly 12,000 acres. Fire history data, soils survey data, presence of old aspen logs in a sea of sagebrush, and abundance of heavily browsed aspen suckers at the sagebrush/aspen ecotones all indicate that fewer fires and heavier ungulate pressure contributed to this cover type conversion. Aspen decline occurs when landscapes with aspen are outside of properly functioning condition.

The desired condition should not be identical to the historical condition. Much has changed on these landscapes. Changes include new socioeconomic factors that preclude the landscapes from returning to presettlement conditions.

Social Assessments

We talk about properly functioning condition and desired conditions. Some might say, “Properly functioning condition, how pompous!” Others may question, “Properly functioning to whom? Desired to whom?” The answers to these questions are really social assessments. The techniques necessary to determine desired conditions are those that promote and encourage healthy interpersonal relations. Use of the following 4 C’s in the planning and management phases helps determine the desired condition for a landscape (Mrowka and Campbell 1997):

- Commitment: devote the time and resources to allow the process to occur and mature.
- Communication: talk and interact willingly and openly with each other.
- Collaborative sharing: promote intense and enthusiastic sharing of information.
- Cooperation: work together; walk the talk; make it happen!

Without consistent application of these key concepts, support for efforts to move these landscapes toward the desired condition within the range of properly functioning condition will not mature. And most landscapes with aspen present will not be sustained into the next century or even decades in some cases.

Characteristics of Aspen Stands in Properly Functioning Condition

Aspen stands in properly functioning condition will often have the following characteristics: multi-aged stems in the stand, adequate regeneration to perpetuate the stand, age classes mostly less than 100 years old, and good undergrowth beneath the canopy. Both compositional and structural diversity are important.

An argument could be made for any acre of land to be in properly functioning condition as long as that acre does not have compositional and structural characteristics similar to most of the surrounding area. Comparing and contrasting a smaller area (e.g., the stand) in the context of a larger landscape is critical to recognizing the diversity of a landscape in properly functioning condition. Landscapes (aggregations of stands) that are compositionally and structurally homogeneous are not in properly functioning condition.

Risk Factors for Stands With Aspen

We prioritized situations where actions are needed to sustain landscapes with aspen. The highest priority is the mixed-conifer/aspen cover type (particularly where subalpine fir dominates). High priority exists for the aspen/sagebrush transition. Also, action is needed on aspen dominated landscapes where the risk

factors are present (Bartos and Campbell 1998a). The five risk factors for aspen dominated stands are:

- conifer cover (understory and overstory) greater than 25%;
- aspen canopy cover less than 40%;
- dominant aspen trees greater than 100 years old;
- aspen regeneration less than 500 stems per acre (5 to 15 feet tall); and
- sagebrush cover greater than 10%.

Prioritized Key to Risk Factors for Landscapes With Aspen

The risk factors described above are considered in the prioritized key to risk factors associated with stands where aspen is present in the Intermountain West (table 1). We feel that the ecological underpinnings of this key have application to areas beyond the Intermountain West. However, we recognize that within the extensive range of quaking aspen distribution, there might be situations where this key is not applicable.

Three different categories of cover are referred to in this key. Canopy cover is the percent of the ground surface that is covered from directly overhead by the crowns of dominant and codominant trees. Overstory cover would be that cover that is provided by trees, including the subcanopy, that are greater than 5 feet tall. Understory cover is the percent of ground covered by individual plants that are less than 5 feet tall.

In the key, couplet 1 refers to relative cover; couplets 2 through 5 use absolute cover. Therefore, elements 1b and 2a are not inconsistent. In couplet 1, for example, even though total conifer canopy cover might be 60%, if total aspen canopy cover is 70%, then 1b is the appropriate choice. Also, for element 2a to be selected, the actual aspen canopy cover could be 35% while the conifer canopy cover might be 25%, but sagebrush would exceed 15% cover.

Clearly, situations that have the greatest risk and the highest priority are those where canopy cover from conifer species combined exceed the canopy coverage from aspen. These are mixed-conifer rather than aspen cover types.

Table 1—Key to the risk factors used to prioritize areas with aspen for restoration and conservation actions in the Intermountain West. Assumption: Aspen are present with a density of at least 20 mature trees per acre. Note: Couplet 1 refers to relative cover; couplets 2 to 5 use absolute cover.

1. a. Conifer species comprise at least half of the canopy cover.	Highest priority
b. Aspen comprises more than half of the total canopy cover.	2
2. a. Aspen canopy cover is less than 40%; <i>and</i> sagebrush, usually a dominant understory species, exceeds 15% cover.	High priority
b. Not as above.	3
3. a. Conifer cover (including overstory and understory) exceeds 25%.	Moderate to high priority
b. Conifer cover is less than 25%.	4
4. a. Aspen regeneration (5 to 15 feet tall) is less than 500 stems per acre.	Moderate priority
b. Aspen regeneration exceeds 500 stems per acre.	5
5. a. Any two of the following three risk factors are represented: 1—Aspen canopy cover is less than 40%. 2—Dominant aspen trees are greater than 100 years old. 3—Sagebrush cover exceeds 10%.	Low to moderate priority
b. Two of the three risk factors in 5a are not represented.	6
6. a. One of the three risk factors in 5a is represented.	Low priority
b. None of the risk factors above are represented.	Candidate for properly functioning condition

However, with proper treatments the aspen cover type can usually be restored and sustained. The literature is sparse with reference to stocking or the minimum number of mature aspen that are necessary to expect adequate regeneration of the aspen stand. Peterson and Peterson (1992) provided some guidelines applicable to Ontario and suggested stands need at least 16 parent aspen stems per acre to produce the minimal acceptable stocking and about 50 parent aspen stems per acre to fully stock a stand. Thus, for the key, we assume that at least 20 mature trees per acre are present. There might not be sufficient aspen roots to restock a stand if fewer than 20 trees per acre are on site. Also, areas with aspen canopies less than 40% and sagebrush greater than 15% have a high risk and high priority for aspen restoration treatments. As the risk factor key indicates, stands dominated by aspen have a lower risk and lower priority for treatments to sustain the aspen ecosystems. However, if some situations are not addressed, even these stands might not be sustained into the 22nd Century.

Rules of Thumb to Identify Aspen Stands at Risk

1. If the profile of the aspen stand is rounded or sloping to the ground with foliage extending to the ground, the stand is probably not seriously at risk. If the white boles of mature trees can be seen from a distance, then the stand is most likely at risk. However, if the edge of a stand also marked the boundary of a clearcut, then the stand may not be at risk and young aspen will grow up in the clearcut to eventually mask the white boles at the edge of the stand.

2. Often we can observe aspen stands on distant ridges from the valley or other areas below the stand. Conditions are not right in the stand if sky can be seen between the canopy of the stand and the ground or understory in the stand.

3. Where aspen occurs at the sagebrush transition, if careful inspection of individual sagebrush plants adjacent to (within 25 to 100 feet) an aspen stand reveals young aspen suckers that have been hedged or browsed for several years and yet are still trying to grow, then the stand might be considered at risk of losing the aspen component. Hedging and browsing of the aspen regeneration is likely occurring also within the aspen stand to the point that most if not all of the regeneration is gone. These individual sagebrush plants become tiny exclosures that offer some protection to the aspen suckers. Such an observation confirms that the aspen stand is still capable of regeneration but not in the presence of heavy ungulate use.

Possible Actions or Treatments for Landscapes With Aspen

Several possible actions or treatments are available for managers to use in treating landscapes where aspen ecosystems are declining and not in properly functioning condition. These actions include:

- rest from use by domestic animals;
- use protection fencing to keep out wildlife and/or domestic animals;
- harvest (remove or cut and leave on site);
- burn (prescribed fires, wildland fire use, and/or wildfires);
- tip over mature trees (use bulldozers to chain or push over trees); and
- sever roots (use single-toothed ripper or similar equipment).

Detailed discussion of these treatments is beyond the scope of this paper. (For further information, see Bartos and Mueggler 1981, Bartos and Mueggler 1982, Bartos et. al. 1991; Kay and Bartos 2000; Mueggler and Bartos 1977; Shepperd 1993; Shepperd 1996.) However, characteristics of the clones, abundance of aspen in acres occupied, potential for utilization by ungulates, fuel

loading, available funding, and site conditions are all factors to consider when planning the types of actions used to implement a treatment.

Relief From Excessive Browsing Is Essential

Unwanted utilization of aspen suckers by livestock and wildlife in treated areas is a major reason why many actions fail to rejuvenate and sustain aspen stands. The following statement underscores this situation:

Heavy browsing of the suckers can deplete aspen root reserves, jeopardize successful regeneration, and threaten the very survival of the aspen stand. Coordinated and difficult decisions are needed before suckering will be successful. *Actions to induce suckering must not be initiated before relief from excessive browsing is obtained* [italics added] (USDA Forest Service 1994).

Examples of both successful aspen regeneration and failures following treatments (e.g., burns and harvests) in areas with aspen present are plentiful. Exclosures and fenceline contrasts provide ample evidence that success (or failure) is often keyed to the absence (or presence) of domestic and/or wild ungulates.

Recommendations

Recommendations for managing landscapes with aspen will require managers to be creative and use the 4 C's (commitment, communication, collaborative sharing, and cooperation) as they endeavor to restore and sustain aspen ecosystem in properly functioning condition. We challenge managers to be bold.

First, take action now! Do not let another decade or two slip by without substantial treatments on the landscape. Gullion (1985) gave a passionate plea for action:

Some sites that have lost aspen might still be stocked, had a regeneration program started 10 or 20 years ago. Due to their decadence now, it will be difficult to obtain quality regeneration of many stands today, and each year more stands will move into that category. In 30 years, it will be too late to rejuvenate many of the mature stands that are such an important part of Colorado's wildlife habitat and visual resources today.

Fifteen years have now passed since Gullion's call for action. Have sufficient acres been treated in the past 15 years to restore and sustain the diversity of composition and structure?

Second, make actions large. Where landscapes with aspen present are sufficiently large, treat 500 to 1,000+ acres at a time. These acres need not be contiguous but could be several smaller treatments in the same expanded project area. This will help to restore the structural mosaic to the landscape. Also, the larger areas treated will help disperse ungulate pressures, domestic and/or wild.

Third, take action often. Persistence over time is important. A program of successive actions will help to restore structural diversity to these landscapes.

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