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A Functional Framework for Improved Management of Western North American Aspen (*Populus tremuloides* Michx.)

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ABSTRACT

Quaking or trembling aspen (*Populus tremuloides* Michx.) forests occur in highly diverse settings across North America. However, management of distinct communities has long relied on a single aspen-to-conifer successional model. We examine a variety of aspen dominated stand types in the western portion of its range as ecological systems; avoiding an exclusive focus on seral dynamics or single species management. We build a case for a large-scale functional aspen typology based on existing literature. Aspen functional types are defined as aspen communities that differ markedly in their physical and biological processes. The framework presented here describes two "functional types" and seven embedded "subtypes": Seral (boreal, montane), Stable (parkland, Colorado Plateau, elevation and aspect limited, terrain isolated), and a Crossover Seral-Stable subtype (riparian). The assessment hinges on a matrix comparing proposed functional types across a suite of environmental characteristics. Differences among functional groups based on physiological and climatic conditions, stand structures and dynamics, and disturbance types and periodicity are described herein. We further examine management implications and challenges, such as human alterations, ungulate herbivory, and climate futures, that impact the functionality of these aspen systems. The functional framework lends itself well to stewardship and research that seeks to understand and emulate ecological processes rather than combat them. We see advantages of applying this approach to other widespread forest communities that engender diverse functional adaptations.

KEYWORDS: *forests, climate, landscape, classification, biodiversity, adaptive management*

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.), the most widespread tree species in North America, is found in most ecological regions of the continent (Preston, 1976). It follows that a species of such wide ecological amplitude should exhibit a range of adaptive features to sustain itself in settings from moist mixed forests of the East, to pure Rocky Mountain stands, to seral boreal forests. While the distribution of aspen is well known, there has been little effort to distinguish aspen forests by their ecological function for management purposes. F.S. Baker proclaimed that aspen possessed an "essential uniformity…throughout its wide range" and that "there is always a successional tendency working in aspen stands" (Baker, 1925, p.2). These sentiments largely persist, where much of current management relies on grouping all aspen into a seral response model set apart only by regional variations in "climax" conifer species. We believe this approach is inappropriate for widely varying situations spanning aspen's vast western range.

By the very nature of its continental distribution, aspen has adapted to broad ranges of environmental gradients, such as topographic position, annual precipitation, growing season length, soil type and depth, maritime or continental climate pattern, disturbance types, and plant associates. Though early American foresters were skeptical of the existence of diverging aspen communities (Baker, 1918, 1925), others pointed out prominent examples of apparently long-term "pure" aspen forests in the southern Rocky Mountains (Fetherolf, 1917; Sampson, 1916; Weigle and Frothingham, 1911). In Canada, the debate over the existence of a stable type was moot given huge expanses of parkland with nearly pure stands of aspen (Bird, 1930; Moss, 1932). Still, professional guidance on management of aspen forests has widely favored the successional model of moving from aspen to conifer. This may be attributed, in part, to a 20th century bias for managing toward productive—predominantly softwood—timber values to the detriment of many aspen communities (Johnstone, 1982; Haig, 1959; Wagar and Myers, 1958). For example, Weigle and Frothingham (1911, p.5) stated, "the dense thickets of root sprouts or suckers which aspens ordinarily produce immediately after logging may choke out and for many years prevent the seeding in of other species. When this happens the presence of aspens becomes a distinct menace instead of a help to the establishment of more desirable trees."

As we view the present range of aspen in western North America there appear to be distinct biogeographic aspen types, though we know of no formal delineation of these forests. To address this situation, we developed an aspen classification based on ecological function. We define "aspen functional types" as *broad aspen communities that differ markedly in their physical and biological processes and interactions* (i.e., functions). Such communities would be expected to respond differently to management actions. While others have relied on floristic composition to classify aspen (addressed in detail by Shepperd et al., 2006; p.35-38), we believe a functional approach is more intuitive and less botanically technical and, thus, favors practical application. This system draws on the concepts of *plant functional types* (Semenova and van der Maarel, 2000; Ustin and Gamon, 2010), as well as key recent works in the aspen literature (Kurzel et al., 2007; Kashian et al*.,* 2007; Shepperd et al., 2006; Shepperd, 1990).

We explicitly define *stable* as stands remaining dominated by aspen cover through several ecological rotations of the stand—with little or no invasion by conifers—and *seral* as stands following a successional pathway where aspen dominates early on and is slowly replaced by conifers within an ecological rotation of the forest. (Ecological rotation, or the *average* lifespan of mature canopy trees in a stand, may vary considerably over our study area, therefore we are hesitant to specify even a range of years.) Note this primary division focuses on tree composition; thus, "stable" in no way implies a lack of dynamic stand processes. In stable stands tree composition remains constant, though there is regular mortality and regeneration among individuals and small groups of aspen stems. This definition of stable is consistent with earlier descriptions that simply stated, "...a system is stable if it persists despite perturbations." (Connell and Slatyer, 1977, p.1120). Thus, stable stands remain in aspen cover after small and large disturbance, while seral aspen stands are temporarily dominated by an aspen and may attain alternate vegetative states over time.

We narrowed our scope to western North America because of the large availability of literature, distinct physiographic diversity, and broad professional and public interest in aspen regionally. The objective of this paper is to initiate a discussion of western aspen types based on a critical review of environmental characteristics, including key processes, described in the existing literature. To explore these topics in-depth and apply them to aspen forests in the West this article will (1) review key differences in aspen-dominated communities and whether a functional typing approach is warranted; (2) present a classification framework via a matrix of functional aspen communities and environmental variables; (3) provide aspen functional type descriptions; and 4) discuss practical challenges and management implications of this scheme.

ASPEN COMMUNITY TRAITS

KEY DIFFERENCES IN ASPEN COMMUNITIES

Recent reports indicate a range of environmental factors affecting aspen forests in different geographic settings (Bailey et al., 2007; Logan et al., 2007; Rogers et al., 2010; Wolken et al., 2009; Worrall et al., 2008).   However, interaction with forest managers across the range of western aspen, as well as some published works, seem to favor a seral type bias and one-size-fits-all management approaches. For example, recent work examined the modeled effects of climate warming on future aspen stands throughout the western U.S. (Rehfeldt et al., 2009). These authors apply a seral aspen habit to the entire region, thereby ignoring vital differences in processes and compositions that will likely dominate broad-scale aspen futures.

Baker's (1918, 1925) early aspen work struggled with the notion of whether to distinguish two basic forms of aspen existing in the central Rocky Mountains. Since that time, we have progressed substantially. Mueggler (1988) implicitly recognized seral and stable "cover types," but went much further in detailing 59 vegetative "community types" within his aspen classification scheme. While this approach has utility at the stand-level, it does not facilitate wider application due to its dependence on taxononic descriptions of plant communities. More importantly, however, is the fact that composition-based classifications largely neglect ecological function, as well as related process-based applications across larger geographic reaches. Taking a silvicultural approach, Shepperd (1990) distinguished between stable aspen types of different ages and regeneration patterns in Wyoming and Colorado. Functional typing of aspen as suggested here incorporates both compositional and structural differences, plus inclusion of system processes specific to physiographic, climatic, and geographic situations, as well as anthropogenic alterations.

Still, questions linger as to basic ecological differences for why some stands remain relatively pure and others follow an aspen-conifer successional path. Specifically, why don't stable aspen stands succumb to conifer invasion on certain landscapes? Early research (Baker 1918; 1925) suggested that large disturbances on the Colorado Plateau in the late 19th century had favored pure aspen stands, but given a long enough disturbance-free period conifers would seed in, presuming long-term succession, and establish seral stands. Clearly, this has not happened across large swaths of this landscape in the intervening century (Langenheim, 1962; Harniss and Harper, 1982; Rogers et al., 2010). The same is true for the Canadian parkland. Even on smaller landscapes framed by aspect, slope, edaphic, and microclimatic features (i.e. putative functional subtypes described herein), we witness long-term persistence of pure aspen stands even in the presence of conifer seed sources (e.g., Kulakowski et al., 2004; Kurzel et al., 2007; Strand et al., 2009). Rainfall, evapotranspiration, and soil moisture may play key roles, as stable stands are often on drier sites, though systematic testing of this theory has not taken place. Perhaps repeated short-interval or high-severity disturbance events could maintain stable communities, effectively eliminating conifer establishment (i.e., Romme et al., 2001; Shinneman et al., 2013)? While this scenario may exist, adequate evidence is not yet available to firmly establish a "semi-persistent" aspen type (Shinnemen et al., 2013). Additionally, multiple studies have indicated advanced stand ages (80-120 years and more)—well within the time needed for conifer establishment—of stable aspen types (Harniss and Harper, 1982; Shepperd, 1990; Cumming, et al., 2000; Smith and Smith, 2005; Rogers et al., 2010). Efforts to use soil types and genetic differences to explain this key division of functional aspen ecology are in progress, though conclusive results are unavailable at this time.

A presumption advanced by Cryer and Murray (1992), that soil types may be used to differentiate between aspen, mixed, and conifer types, holds that the soils themselves are relatively stable over time, when in fact host trees and dependent flora contribute to fluctuating soil components. It is likely that multiple environmental characteristics, such as those described herein (see Table 2) and others, contribute to functional distinctions and will help enlighten our quest for better answers to this long-standing debate. By describing key differences in a systematic way, we hope to provide direction for future lines of inquiry for deciphering stable and seral aspen.

SUPPORT FOR FUNCTIONAL TYPES

Variation in stand composition does not necessitate distinct ecological function. Subtle or sweeping differences in dominant vegetation suggest altered interactions within the biotic community, however. To distinguish proposed subtypes, we present common tree associates only as an initial means of comparison (Table 1). Other than the great range of aspen associates overall, we draw attention to the apparent greater tree species diversity in the seral systems (i.e., montane, elevation/aspect limited, Colorado plateau, terrain isolated). Highly distinct arboreal floras are evident between the remaining types. We attribute these major compositional differences primarily to soil moisture retention and physiographic factors, sometimes augmented by land use changes, leading to differences in disturbance types.

As direct causes for functional distinctions, examination of environmental characteristics form the basis of support for aspen functional types (Table 2). Broadly speaking, functional types occur in contiguous stands widely varying by size, from boreal aspen at tens of thousands of hectares to small one hectare groves isolated by terrain, elevation, edaphic, or hydrological conditions. The dominant regeneration pattern has a large bearing on vertical architecture of a stand. While this is certainly influenced by frequency and intensity of disturbance, there is an apparent distinction between regeneration patterns in seral and stable types. Seral aspen more commonly responds to stand replacing events which lead to synchronous regeneration, whereas stable types follow continuous or episodic regeneration patterns (Kurzel, et al., 2007; Shepperd, 1990).

Major biotic and abiotic processes are also presented here as a means of discerning functional subtypes (Table 2). Relatively drier sites, from landscapes to regions, appear to favor stable aspen communities. As topography influences numerous processes (e.g., rainfall, evaporation, soil type and depth, disturbance type and extent, and runoff) we note a range of distinct landscapes by subtypes. Generally, there is less variation in precipitation where topography is more uniform. The wide range of annual moisture may be somewhat tempered by considering “usable moisture,” where deep snow in mountainous terrain will incrementally lose water as seasons change via melting, runoff, and high evaporation rates. Related to this, ecohydrology (i.e., plant, soil, and water relations) and rooting depth affect aboveground aspen growth. These two factors are somewhat-to-highly variable across types and seem largely dependent on local soils and topography. Thus, it follows that terrain isolated aspen occur in settings so variable that subterranean water storage and use cannot be easily characterized for all situations.

Perhaps the widest and most thoroughly documented variation between subtypes exists under the heading “Dominant disturbance frequency or type” (Table 2). These distinctions are related to many environmental and compositional factors. For example, associations with the disturbance-dependent lodgepole (*Pinus contorta var. latifolia* Engelm.) and jack pine (*P. banksiana* Lamb.) will be distinct from aspen subtypes where disturbance-resilient species govern (e.g., aspen itself or other hardwoods). In general, disturbances in seral stands occur at larger scales and higher intensities than those in stable types, although mixed-severity fires may result in mosaics of small-patch seral and semi-persistent aspen (Shinneman et al., 2013). Stand size alone may have sweeping effects regarding disturbance size and spread. Even at the functional subtype level, there are clear differences where stand size, terrain, water relations, other species, and adjacent communities impart synergistic effects which result in widely varying dominant disturbances. For example, a small, stable aspen community may collaterally burn in a high wind scenario where the adjacent stand is composed of fire-prone conifers (Shinneman et al., 2013).

While we find sound support for distinct aspen types (see shading, Table 2), we caution against using the functional subtype descriptions presented here in an exclusive manner. There are common exceptions within the broad classes we have developed. For example, mature boreal stands may appear stable in nature and there are many instances of seral communities throughout the Colorado Plateau. Appropriate discretion is warranted for local and regional adjustments to the following functional types. Since this work intends to provide a starting point in the discussion of aspen functional types, we expect future refinements within western aspen environs and potential expansion to the eastern distribution of aspen forests.

FRAMEWORK ASPEN FUNCTIONAL TYPES

Critical examination of aspen functional types is based on systematic characterization of environmental variables (Table 2). Functional types should be applied at regional scales and include multiple ecological factors, whereas compositionally based community typing systems pertain to smaller geographic areas. A more detailed discussion of vegetative classification schemes for aspen is presented elsewhere (Shepperd et al., 2006, p.36-38).

For our purposes, functional types include only those areas where aspen dominates or has the potential to dominate the forest canopy over wide areas and for one or more ecological rotations. We examine the framework of proposed aspen types presented in Fig. 1 for marked differences among the following key environmental variables: tree associates, topography, stand size, annual precipitation, ecohydrology, rooting depth, regeneration type, and dominant disturbance. Logically, the major delineation in this scheme occurs between stable and seral types. From a process perspective, aspen generally responds to conifer-driven changes in seral landscapes, while in stable settings aspen itself is the driver of process and change. This central division is similar to Connell and Slatyer's (1977) dichotomy between successional and stable communities. Aspen subtypes describe variations in functionality within the types. Geographic depictions of subtype areas in western North America are shown in Fig 2. Note that there are sizable areas of aspen’s total range—particularly in the East and North—where aspen occurs, but does not commonly dominate canopy coverage. Eastern boreal forests and the Great Lakes aspen are beyond the scope of this discussion, though we speculate that a sub-boreal functional division merits further consideration (Fig. 2). We focus explicitly on aspen west of the 100th Meridian; a coarse demarcation of the moist East from the arid West. Rocky Mountain aspen subtypes (montane, elevation or aspect limited, terrain isolated) are further differentiated at landscape scales (Fig. 3). Riparian aspen may be characterized as either stable or seral, often depending on surrounding upland situations.

ASPEN FUNCTIONAL TYPES

SERAL ASPEN

Aspen in seral systems reacts to processes initiated, most often, by the presence and condition of conifers. After stand replacing disturbance, for example, aspen responds via rapid root sprouting that is eventually overtopped by shade-tolerant species. Aspen dominance in seral settings may last up to several decades or even a century, depending on setting and development of competing species, but also on the vitality of post-disturbance aspen, physiographic and climate conditions, and subsequent human impacts. Cohort species in seral aspen range from xeric junipers (*Juniperus spp.*), to mesic spruces (*Picea spp.*), to montane and boreal pines (e.g., *Pinus contorta, P. banksiana, P. albicaulis*, *P. longaeva*; Table 1**)**.

The following seral aspen subtypes are mostly predicated on governing *processes* of these systems, some of which are closely allied with vegetative communities. Key differences are highlighted by functional subtypes via the environmental characteristics matrix (Table 2).

Boreal (western Canada)

Aspen has its largest continuous expanse in the western North American continent in the mixedwood zone of the boreal forest region of Manitoba, Saskatchewan, Alberta, northeastern British Columbia, south-central Northwest Territories, and Alaska (Rowe, 1972; Walter and Breckle, 1991). Depending on successional stage and stand history, the stand composition can range from pure aspen to structured and intimate mixtures of aspen and conifers widely varying in proportions. The variation of the aspen and conifer component in the mixedwood zone can be seen as the transitional zone to the conifer dominated boreal forest to the north (Rowe 1972; Larsen 1980; McCune and Allen 1985) and the aspen parkland to the south (transition between the prairie grasslands and the boreal biome). With increasing elevation in the mountainous regions within its boreal distribution, aspen are replaced by coniferous forests of the boreal and montane cordillera.

Tree species dominance and distribution patterns in boreal mixedwood forests are mostly driven by the frequency and scale of the disturbance. Where disturbances occur at higher frequencies (e.g., < 80 years) and at larger spatial scales, the establishment and maintenance of early successional forest communities dominated by aspen and white birch (*Betula papyrifera* Marsh.) are favored. Natural and anthropogenic disturbances include fire, insect outbreaks, windthrow, and forest harvesting. Under high disturbance frequency, pure aspen stands can be self-perpetuating, especially in the absence of significant nearby conifer seed sources (Peters et al., 2005). Increased harvesting throughout the boreal forest region has resulted in a shift from conifer to hardwood-dominated stands, particularly in the boreal mixedwood region where the vegetative regeneration of aspen can be prolific (Peterson and Peterson, 1992; Frey et al., 2003). As these aspen stands mature, multi aged stand structures may develop. The formation of these multi aged aspen stands can be the result of gap dynamics, drought, or insect outbreaks that have weakened or killed portions of the mature canopy and initiated advanced vegetative regeneration under the canopy (Cumming et al., 2000).

Boreal mixedwoods are considered the most diverse boreal forests in terms of tree species in North America, with stands typically consisting of canopy mixtures of aspen and white spruce (*Picea glauca* (Moench) Voss), along with other tree species such as balsam poplar (*Populus balsamifera* L.), balsam fir (*Abies balsamea* (L.) Mill), black spruce (*Picea mariana* (Mill.) B.S.P.), white birch and jack pine in the East and lodgepole pine in the West (Chen and Popadiouk, 2002; Brassard and Chen, 2006). Advance regeneration of white spruce under an aspen canopy is a consistent feature of the region.

Geographically, aspen appears to be quite variable in the timing of bud flush (Li et al., 2010). There is, however, little information on clonal size and distributions of genotype of aspen in the boreal forest, particularly since morphological features such as bark color and phenological features such as time of flush appear to be weakly correlated with clonal identity (Peterson and Peterson, 1992). However, work in Quebec (Jelínková et al., 2009; Namroud et al., 2005) and Alberta (Snedden, unpublished data) indicates that aspen clones are relatively small in size (< 1ha)—which may be a result of the higher disturbance frequency, but could also be related to the relatively short time these forests had to develop since the last glacial retreat. Factors influencing aspen mortality and breakup of boreal aspen stands are not well understood (Frey et al., 2004); however, it appears that longevity of aspen in the absence of fire is related to growing conditions with the longer lived aspen occurring on better quality sites.

The boreal mixedwood region contributes significantly to the fiber supply of North America and the volume of aspen harvested in Canada has experienced a significant increase over the last 25 years. As a result of the increased harvest, management issues of aspen have also been increasing steadily in order to secure future wood supplies. Aspen in these forests provides a significant economic benefit as a source of oriented strand board, pulp, and paper. This has forced a significant shift in thinking, away from seeing aspen only as a competitor to the more valuable conifers and towards viewing aspen as a valuable tree in its own right. As a result, research on boreal aspen ecology and management has increased significantly over the last decades (Zasada et al., 2001). Aspen stands normally regenerate well after clearfelling; however, aspen suckering can be negatively affected by a combination of factors related to site conditions, disturbance, and plant competition (Frey et al., 2003; Navratil and Bella 1990). Clonal variability, hormonal status, and root carbohydrate reserves were found to play a significant role in sucker initiation and early growth (Frey et al., 2003). In the boreal region the establishment of aspen from seed is much less studied and considered rare. However, more recent work indicates that aspen establishment occurs from seed in the boreal, but is much more noticeable at the fringes of its distribution where aspen seedlings can be more easily distinguished from sucker regeneration (Landhäusser et al., 2010).

Montane

Seral aspen communities are found along the entire length of the Rocky Mountains, at mid- to upper-elevations from north-central Mexico to central British Columbia and Alberta (Fig. 2). The total span of North American montane aspen is from approximately 23 N° in Mexico to 56 N° latitude in Canada. Lower elevations in particular in the southern regions are often too dry to support aspen and, though it can be found at treeline in some locales, coniferous species more commonly define the upper boundary of tree establishment. Though it appears that montane seral aspen is the dominant type within the Rocky Mountain region (Kashian et al., 2007; Mueggler, 1989; Rogers, 2002), both the *Terrain Isolated* and *Elevation and aspect limited* functional type of aspen stands can be found in the montane region. At finer scales, even more "aspen types" may be delineated (Kashian et al., 2007; Kurzel et al., 2007).

Key characteristics of montane seral aspen (similar to boreal) are regeneration instigated via stand replacing disturbance, even-age (or nearly so) aspen cohorts, primarily vegetative reproduction by root suckering, and eventual overtopping by shade-tolerant conifers. Seral communities of the Rocky Mountains are where much of the 20th century decline in aspen coverage has been documented (Bartos and Campbell, 1998; Gallant et al., 2003; Strand et al., 2009). Occurrence of new clones originating from seeds now appear to be more common than previously thought (Kay, 1993; Romme et al., 1997; Mock et al., 2008; Landhäusser et al., 2010), which, though not likely the dominant reproductive mode in seral aspen, may lead us to rethink long-term ecological development of the species on these landscapes (Long and Mock, 2012).

Human influences, including historic forest management practices, have had great influence in montane seral aspen (e.g., Kashian et al., 2007; Kulakowski et al., 2004; Rogers et al., 2007). Both fire ignitions in the 19th century and fire suppression in the 20th century have had uneven impacts on seral aspen communities at a variety of montane locales. For example, large wildfires developed almost annually in the Sierra Nevada range after the settlement era where sheep herders set fire to forests and rangelands upon exiting the mountains in autumn (Rogers et al., 2007). This type of intensive resource use was common during this period and probably led directly to the establishment of many contemporary aspen stands. After establishment, however, these seral aspen stands slowly developed toward conifer-dominated forests over the next century where relatively wet conditions prevailed, aided by concurrent fire suppression efforts (Rogers et al., 2007; 2011). Though this generalization may be evident for many montane areas, aspen expansions also occurred in adjacent forest communities during the same period (Kulakowski et al., 2004).

STABLE ASPEN

Stable aspen communities are those that remain in aspen dominance for extended periods (i.e., greater than the time required for conifers to gain dominance in seral stands; ≥ 80-120 years). While Mueggler (1988) believed that “community types” were relatively permanent (i.e., >300 years), this does not preclude eventual colonization by conifers over longer periods.

A prime distinction of the stable aspen type is its incremental stand replacement, typified by “gap-phase” stand dynamics (Kashian et al., 2007; Kurzel et al., 2007; Mueggler, 1985; Rogers et al., 2010). In contrast to large scale stand replacing disturbance, small scale disturbances such as individual tree or small group mortality characterize the stable aspen type. Canopy successors are often already present as mid story ramets and are able to quickly take advantage of available light, nutrients, and water (Table 2). Stable types are often uneven, or multi aged, aspen communities (Betters and Woods, 1981). Aspen basal area is not expected to change markedly in stable stands over time; whereas a steady decrease in aspen basal area occurs in seral stands while overall volume increases (Harniss and Harper, 1982; Smith and Smith, 2005).

Aspen Parklands

The aspen parkland is an ecotonal region in western Canada between boreal forest to the north and grassland to the south where the dominant tree species is aspen. It extends from the Peace Region of northern British Columbia and Alberta, through Saskatchewan and Manitoba, and ends in northern Minnesota (Figure 2). The general vegetation pattern is a mosaic of discrete stands of aspen, shrublands, and grasslands, which also represent successional stages with shrubs first colonizing grasslands and then aspen colonizing shrublands (Bird, 1930). Isolated upland areas further south in the grassland, such as the Cypress Hills in Saskatchewan and Alberta, also support aspen parkland. Prior to agricultural settlement, aspen cover on the landscape was typically less than 30% with most of the landscape dominated by grassland (Archibold and Wilson, 1980). The ability of aspen to survive in this environment has been linked to its clonal integration (Peltzer, 2002), an extensive system of very fine roots which are more similar to grass root systems than to boreal aspen trees (Pinno et al., 2010), and the ability of aspen to alter belowground resources to benefit itself relative to the surrounding grasslands (Kleb and Wilson, 1999).

Currently, the dominant land use in the aspen parkland is agriculture with cropland and rangeland covering most of the land area, leaving aspen located in scattered patches, typically in areas less suitable for agriculture (Acton et al., 1998). Climate change and ecosystem predictions for the aspen parkland predict a retreat north for aspen in the coming decades, resulting in a loss of aspen from much of the current parkland area (Sauchyn et al., 2009). However, actual aspen coverage has expanded southwards since settlement due to the elimination of bison (*Bison bison*) and fire (Campbell et al*.,* 1994; Hansen, 1949), both of which controlled aspen expansion on the landscape. Estimates for Saskatchewan indicate that aspen have expanded south by approximately 100 km since settlement (Archibold and Wilson, 1980).

The natural forest cover for the parkland is a pure aspen type. The climate is too dry for the natural regeneration of conifers (Hogg and Schwarz, 1997) and other deciduous tree species are usually restricted to riparian areas. Within aspen groves, there is generally an overstory age gradient decreasing outward from the center of the stand (Archibold, 1999) reflecting the ongoing expansion of clones into the surrounding grasslands. Juvenile suckering is also common in older aspen stands as the canopy thins (Newsome and Dix, 1968). The result is multi layered and multi aged stands equipped to swiftly respond to disturbances resulting in overstory mortality.

Fire was historically the major disturbance in the parkland with fire frequency estimates of 10-25 years (Brown and Sieg, 1999; Weir and Johnson, 1998), but fire has now been virtually eliminated from the landscape. Other important disturbance agents in parkland stands include herbivores and weather events. For example, in expanding clones, browsing of suckers by rabbits (*Sylvilagus* spp.; Bird, 1930), white-tailed deer (*Odocoileus virginianus* Raf.; B. Pinno, personal observation), and historically browsing by bison (*Bison bison* L.; Campbell et al., 1994) can reduce the growth of more than 90% of the stems in years of locally high herbivore abundance. Cattle grazing can also prevent aspen canopy development following fire (Bailey et al., 1990), while insect defoliation (Hogg et al., 2005) severely reduces aspen growth in localized areas. In terms of weather events, hail and drought are both important disturbances in the aspen parkland. For example, after a severe hailstorm in southern Saskatchewan, Peltzer and Wilson (2006) found that 36% of the mature aspen stems had been killed. Also, drought events significantly reduce aspen growth for up to 4 years after the drought ends (Hogg et al., 2005), and the combination of drought and insect defoliation has been linked to aspen dieback in the area (Hogg et al., 2002).

Given the relatively small size of the trees, there has been little historic economic use for aspen timber in this region, aside from localized firewood harvesting. For example, average height of mature aspen stands range from only 11–15 m tall in the parkland (Archibold, 1999; Hogg and Hurdle, 1995). Given the lack of economic interest in the timber, much of the previous research on natural vegetation in the aspen parkland has focused on rangeland and ecological functions. For example, much research has been done on the economic benefits to rangelands of eliminating aspen (Bailey et al., 1990; Bailey and Anderson, 1980), the importance of aspen groves for wildlife habitat (Iverson et al., 1967; Johns 1993), and differences in ecological processes among vegetation types (Kleb and Wilson, 1999; Köchy and Wilson, 1997).

Colorado Plateau highlands and mesas

Early foresters noted the occurrence of large, nearly homogenous, tracts of aspen “groves” in southern Utah and western Colorado (Baker, 1925; Fetherolf, 1917; Sampson, 1916). The greater Colorado Plateau ecoregion—taking in large portions of the aforementioned sections of Colorado and Utah, plus northern Arizona and northwest New Mexico—is home to extensive deserts, canyons, and high elevation mesas (Bailey, 1995). The arid climate of surrounding landscapes makes the elevated plateaus appear relatively moist by comparison. Aspen occurs almost exclusively between 2,300 - 3,500 m elevation. Above 2,500 m, annual precipitation is 500 - 900 mm, while rainfall across the adjacent valley bottoms is less than 300 mm (McNab and Avers, 1994). Though montane seral aspen environments are common throughout this region, and coniferous forest types dominate much of the higher elevations, stable aspen communities host some of the most productive and largest stands of aspen in the contiguous United States (Baker, 1925; Barnes, 1975; Langenheim, 1962). The pure aspen "Pando Clone," measuring some 44 hectares and potentially the largest living organism on earth, is found in south-central Utah's Fishlake National Forest (DeWoody et al., 2008; Grant, 1993). The Colorado Plateau is thought to support such vigorous aspen clones and forests because of regular summer "monsoon" flow from the south and relatively minor deviations in topography across expansive mesa tops (Rogers et al., 2010; Smith and Smith, 2005). Understory growth has widely been converted from lush forb communities to grasses and shrubs as a result of intense livestock use over a century or more (Bowns and Bagley, 1986).

A distinguishing feature of stable aspen communities, particularly on the Colorado Plateau, is a multi layer stand profile (Kurzel et al., 2007; Mueggler, 1985; Rogers et al., 2010). Three or more distinct layers—regeneration (understory), recruitment (lower- to mid-story), and mature (overstory)—exist within intact stable stands. However, occurrences of single-storied aspen are quite common in contemporary settings (Shepperd, 1990; Kurzel et al., 2007; Rogers et al., 2010). So called "see through" (ability to view sky light from outside a stand through the opposite side) aspen forests of this region illustrate instances of reduced structural diversity likely resulting from past ungulate herbivory. Various metrics of regeneration and recruitment success, such as counts, volume, or condition of immature stems, plus subjective assessments of stand structure (i.e., number of distinct aspen layers) may be used to quantify stand health.

Kurzel et al. (2007) distinguish between four types of aspen recruitment related largely to different disturbance modes. Continuous and gap-phase regeneration characterize low-level scales of disturbance (i.e., none to individual trees) most common in large, stable communities of the Colorado

Plateau (Kurzel et al., 2007; Rogers et al., 2010). Catastrophic events, such as stand-replacing fire, are infrequent in this stable type, although late season curing of understory vegetation is conducive to ground fires which may severely scorch and kill mature aspen (Jones and DeByle, 1985; Romme et al., 2001). Moderate-size patches of disease infestations, likely related to clonal susceptibility at the sub-stand scale, provide a good example of episodic canopy mortality. Disease infestations affect larger diameter, older, aspen stems at a higher rate, thus allowing regrowth from surviving *in situ* mid and under story regeneration (Hinds, 1985). This pattern, in combination with predominant continuous and gap-phase disturbance and regeneration types, favors the multilayer stand structure of stable aspen.

Plant associations of Colorado Plateau stable aspen suggest a unique composition. Generally, drier site understory species than those of adjacent seral forests or aspen types further north prevail (Mueggler, 1985). Within this subtype, there are distinctions between lower elevation (2,590 m; understory shrub dominated) associates and higher elevation (3,200 m; lacking shrubs) forests (Mueggler and Bartos, 1977). Moreover, anthropogenic influences may be contributing not only to species conversions, but to transfers of biomass and related water storage capacity within the forests' vertical profile. Mueggler (1985) refers to a "grazing disclimax" wherein wholesale conversion toward a few browsing tolerant species, such as *Poa pretensis* L., *Rudbeckia spp., Taraxcum officinale* Weber ex Wiggers, and *Wyethia spp.*, contributes to further drying, soil exposure, and erosion loss. In extreme instances, ecohydrologic conversions—translocation of major water retention in a plant community from one structural layer to another—have transformed forb-dominated, multi layer aspen stands to "park like" mature trees only, exhibiting no canopy replacement layers and prolific low water retention grasses and shrubs.

Elevation or aspect limited

In many montane regions of the western range of aspen, stable aspen forests may be found adjacent to seral communities and are mainly differentiated by their topographical aspect. Long-term dominance by aspen on these sites, as with other stable types, is likely associated with moisture and soil conditions that could restrict conifer encroachment (Cryer and Murray, 1992). Particularly in the central and southern Rocky Mountains, stable aspen often occur at mid-elevations on south and southwest facing slopes where evaporative demands limit the moisture needed for conifer establishment (Langenheim, 1962; Rogers and Ryel, 2008; Strand et al., 2009). However, with changes in elevation and latitude, pure stands may be found on a range of exposures. In western Colorado, lower elevation (2,590 – 2,895 m) aspen remained relatively stable on east slopes, though the author does not provide an explanatory mechanism (Langenheim, 1962). Front Range stable aspen are also commonly east facing and low elevation (Kashian et al., 2007; Zeigenfuss et al., 2008). Near alpine treeline in Colorado's San Juan Mountains, Elliot and Baker (2004) describe aspen favoring south facing slopes where adjacent conifer stands were present on the same and other aspects. Finally, Sankey (2008) describes pure aspen stands along a grassland-forest ecotone (~2,100 m) on predominantly northern slopes in southwestern Montana. While these elevation and aspect stable stands are common in the southern and central Rocky Mountains, we were unable to find documentation of such occurrences further north into Canada. The authors speculate that predominantly soil moisture, but also soil temperature and growing season length, likely play a role in limiting the occurrence of elevation and aspect limited stands in the northern Rocky Mountains, though more investigation is warranted.

While the general pattern of stable stand structure holds for the elevation and aspect subtype, *proximity to conifers* increases the chance of periodic stand replacing disturbance, particularly on the fringes of pure groves (Shinneman, et al., 2013). While previous work has pointed out aspen's relative inability to burn in many situations (Fechner and Barrows, 1976), it must be clear that even "surface fire may be stand replacing" as minimal scorching can lead to high mortality in stable aspen (Baker, 2009, p. 181). Other catastrophic die offs, such as drought or old-age induced insect and disease complexes which decimate overstory, may lead to periodic near stand replacement (Rogers et al., 2010; Worrall et al., 2008; Kurzel et al., 2007). These incidences may originate within portions of stands weakened by minor fire scorching related to proximity of more fire prone conifer stands. As the length of time increases after stand replacing events, there will be a tendency to revert to stable communities of multi layered appearance over a period of decades. In sum, elevation and aspect controlled aspen communities are most likely to show a range of stand structures reflective of disturbance patterns: even-aged, mixed-age, and mosaics of both may be common where relatively pure stands abut conifer and aspen-mixed-conifer forests.

Terrain isolated

Stable aspen communities isolated by terrain or substrate are often limited in extent. These stands include aspen in snowpocket (Fig. 3b), krummholz, lithic, prairie pothole, and avalanche track situations. Sometimes small aspen stands are simply surrounded by large non-forest communities (e.g., montane meadow or sagebrush dominated cover), not fitting neatly into the categories above. These physiographic locations often display stunted aspen growth forms suggesting water, substrate, or disturbance limitations that impede conifer invasion. Terrain isolated aspen may occur throughout the western range of the species, particularly where variations in topography encourage subterranean moisture accumulation. Occasionally, this subtype may be slowly infiltrated by conifers (D. Bartos, pers. comm.). Shepperd et al. (2006) describe snowpocket aspen stands as those found in topographic depressions where snow accumulates and is slow to melt. Krummholz occurs where exposed aspen stands are subjected to persistent winds which severely limit twig growth via scouring and desiccation. Both snowpocket and krummholz aspen are often isolated by surrounding alpine grassland or shrub cover. This situation buffers potential impacts from fire or other stand-replacing disturbances, as well as limiting potential invasion by seed-dispersed conifers. Likewise, lava flows and other rock outcrops where stable aspen grow will repel wildfire, inhibit dense conifer establishment, and reduce access by large herbivores (DeRose and Long, 2010).

Avalanche tracks are narrow strips of vegetation running parallel to the slope direction. As their name implies, existing plant communities are maintained by regular snow avalanches. While conifers can and do persist, most often in broken form, the greater pliability of aspen stems (along with a variety of shrubs) affords greater resilience under such conditions. While the limiting disturbance is obviously recurring avalanches, the capacity of these linear features to deter fire spread across forested slopes has been noted by others (Fechner and Barrows, 1976).

Though terrain isolated aspen stands tend to be small, their isolation may make them quite valuable at the landscape-level from a biodiversity standpoint. Dense and gnarled aspen stems may also serve to limit access by domestic livestock, a further protection to understory plants and aspen regeneration. However, the limited size of terrain isolated stands may also increase their vulnerability when or if browsing herbivores do gain access.

CROSSOVER SERAL OR STABLE ASPEN

Riparian

Riparian aspen constitutes a crossover subtype; more commonly occurring as a seral type than a stable type, but exhibiting a distinct ecological function related to the influence of water propinquity. For example, these communities may be less susceptible to fire, but historically were greatly influenced by beaver (*Castor canadensis* Kuhl) foraging (Johnston and Naiman, 1990) and in some regions, stream-altering human intrusions, such as gold mining, water channelizing, and dam building (Rogers et al., 2007). These stands —whether isolated “forest stringers” (Fig. 3b) surrounded by non-forest lands or within a larger forest matrix—are found adjacent to ephemeral or permanent streams water sources.

Proximity to wetlands, for both seral and stable aspen variations, poses unique functional considerations. We expect to see even greater biodiversity where aspen, already a diversity oasis within many arid landscapes, is associated with water. Many wildlife species require at least daily visits to lakes or streams where they may also use aspen and understory communities as browse, cover, or bedding grounds. Researchers in Yellowstone National Park have described a complex system of vegetation dynamics associated with ungulate cover, prey visibility, and protection from roving predators (Ripple et al., 2001). Where visibility for elk is low, such as streamside thickets or riverine draws, there is a purported rebound of aspen communities since reintroduction of wolves (*Canis lupus* L.). In the absence of predators, however, high populations of either wild or domestic ungulates may curtail successful streamside regeneration via browsing or trampling of young sprouts. On the other hand, a plentiful water supply logically engenders relatively resilient aspen communities (compared to drier uplands) in the face of drought, fire, and animal impacts. While stable communities, in general, are more resistant to wildfire, both seral and stable aspen in riparian settings are even more so. Water sharing within clones may also allow nutrients gathered at relatively rich riparian sites to be "shared" with ramets at a distance from the moist corridor (Hansen and Dickson, 1979), thus promoting fringe expansion into relatively dry habitat. Except where overuse has transformed understory communities, wetland plant associates are among the most lush and diverse of any aspen types (Mueggler, 1988).

CHALLENGES AND MANAGEMENT IMPLICATIONS

Our examination of aspen functional types (Tables 1 and 2) underscores a need for appropriate, targeted, aspen management practices. Nonetheless, management of these forests has become dominated by the idea that aspen stands function similarly everywhere. Concerted efforts to summarize the state of the science (DeByle and Winoker, 1985; Peterson and Peterson, 1992), though valuable technical resources, are erroneously interpreted in many settings as the final word on aspen silviculture.

These views tend to entrench oversimplification of aspen functional ecology and management. In fact, we are witnessing a vibrant evolution of applied research in long-term cover change, plant-animal relations, disturbance interactions, molecular ecology, and climate modeling which generally support high functional variability across aspen's western range (e.g., Rogers et al., 2013).

THREATS TO FUNCTIONAL TYPES

Inappropriate management, wildlife herbivory, and climate warming threaten functional type resilience. Aspen forests, like other communities, may be gauged by the concept of Historical Range of Variability (HRV; Keane et al., 2009; Landres et al., 1999). HRV is a measure of whether a natural system maintains its basic structure, function, and composition within a range of historically documented variation. Ecologically based parameters may be gleaned from HRV approaches to guide management decisions. A generalized approach to such an effort is presented here based on aspen functional subtypes (Table 3). Where the previous sections have outlined functional type ecology, we now turn to broad impacts that may force aspen types outside their HRV.

Past land uses and evolving management practices have significantly impacted aspen forests across subtypes. For instance, resource extraction in the late 1800s, such as livestock grazing and logging, was often followed by intentional burning, initiating contemporary aspen forests in many locales during that era (Kaye 2011; Rogers et al., 2007, 2011; Kulakowski et al., 2004). These impacts apply to seral more so than stable aspen, due to the lesser desirability of the stable aspen as a timber commodity and the limited flammability of pure aspen types. Since then, moist 20th-century climates, management for conifers, and fire suppression negatively affected aspen (Rogers et al., 2011). In general, timber harvest in the West utilized vast expanses of conifer cover, relative to hardwoods, where stands were accessible. Aspen was relegated to the status of a "weed species" in many areas. Similarly, aspen "rangelands" were overused in earlier times and now even relatively low levels of grazing may reduce successful regeneration, as well as reduce biodiversity in the understory. In sum, these types of activities, in combination with sometimes misguided management responses, have the potential to severely alter existing functional types by decreasing their resilience. For example, relatively low elevation stable aspen in warming and drying climate patterns which is also subjected to continuous browsing will eventually undergo type conversion to a non-aspen state.

Wildlife management, often related to boosting game populations, also may alter functional aspen types. Large herbivore manipulations can potentially derail well-meaning aspen silvicultural practices. Browsing ungulates—both wild and domestic—are inhibiting stand renewal via repeated aspen sprout consumption at many locales (DeByle, 1985; DeRose and Long, 2010; Rogers et al., 2010; Zeigenfuss et al., 2008). This phenomenon seems particularly acute where North American elk (*Cervus elaphus*) are thought to be beyond HRV levels because of introduced populations (e.g., Bailey et al., 2007; Stritar et al., 2010) or lack of predation to cull numbers in preserves that do not allow hunting (Beschta and Ripple, 2009). Moose (*Alces alces*), elk, or deer (*Odocoileus* spp.), as well as several smaller mammals, may also damage mature trees by debarking portions of boles by chewing or rubbing, which may lead to stand-level infections by a range of lethal pathogens (DeByle, 1985; Hinds and Krebill, 1975). Finally, human-induced depletion of another herbivore, the beaver (*Castor canadensis*), has had negative impacts on hydrology, habitat, and biodiversity in riparian aspen systems (Beier and Barrett, 1987; Hall, 1960). For example, forage "switching" by beaver to willow (*Salix* spp.), where aspen are exhausted, is tied to cascading effects of carnivore influences on elk populations and their patterns of herbivory (Smith and Tyers, 2008). The combined effects of both overuse (ungulates) and underuse (beaver) by herbivores may have widespread effects on successional and functional pathways.

Current science strongly suggests that human-induced warming of the planet is occurring (IPCC, 2007). However, commensurate understanding of climate change on particular vegetative types is in its investigatory infancy. Even so, we are already seeing potential alterations of functional types. For example, exotic species, such as gypsy moth (*Lymantria dispar*), are projected to spread upslope from urban areas into aspen, the most prominent hardwood in Rocky Mountain forests (Logan et al., 2007). From a broader perspective, Rehfeldt et al. (2009) foresee current instances of drought-induced "sudden aspen decline" (Worrall et al., 2008) as harbingers of aspen's altitudinal retreat up slope in the coming century. While this first approximation of climate effects on aspen lacks explicit accounting of different functional types, as well as potential for increased disturbance providing additional aspen habitat, this work does provide a launching point for refined efforts. Further caution is required, moreover, in balancing the effects of climate change with human actions (Kaye, 2011). As an example of these interactions, aspen expansion in the parklands appears to be driven largely by anthropogenic practices. In spite of the changing climate which predicts aspen moving north, aspen has moved south (in some areas by ~100 km) due to fire suppression, irrigation of croplands, elimination of bison, and recent disturbance (Archibald, 1999; Campbell et al., 1994; Peltzer and Wilson, 2006). Overall, future work must weigh the benefits of continental-scale climate modeling with application of type-specific aspen variability, such as the functional system advocated here.

MANAGEMENT IMPLICATIONS

As the most widely distributed tree in North America, it is not surprising that aspen and associated species form multiple distinct types that have important compositional, structural, and functional differences. This review supports the concept of multiple functional types (Table 3) and management regimes which strongly suggest the need for targeted approaches (Table 4). We believe that differentiating aspen communities through this approach is useful to practitioners interested in addressing historic cover changes, anticipatory efforts related to climate warming, and general tactics for sustainable stewardship.

We foresee further application of functional classifications toward improved land stewardship for other widespread forest systems that are adaptive to edaphic, ecological, climate, and human-altered variance across landscape- to continental-scales. Examples of forest types potentially conducive to functional classification include ponderosa (*P. ponderosa*), lodgepole pine (*P. contorta*), and Douglas-fir (*Pseudotsuga menziesii*) in North America and European aspen (*Populus tremula*), European spruce (*Picea abies*), and Scots pine (*P. sylvestris*) across Eurasia. Individual species growing under manifestly distinct conditions (e.g., boreal and montane; continental and maritime) likely exhibit key functional differences that may benefit from a similar treatment.

Human impacts on aspen have occurred throughout its geographic range and likely predate European settlement. Increased disturbance and manipulations since Euro-American settlement has both enhanced and inhibited conditions for aspen communities (Rogers et al., 2007; 2011). For example, elevated incidents of fires during the settlement period likely changed stand structure and perhaps genetic diversity within aspen forests. Fires may also have increased the dominance of aspen within mixed aspen-conifer stands. In boreal and lower elevation montane aspen, 20th century fire suppression may have resulted in localized conifer dominance outside the range of natural variability. Fire suppression likely had little effect in landscape-level stable types (Parklands and Colorado Plateau), but may have affected stand-level aspect limited, terrain isolated, and riparian forests. Changes in stand structure due to ungulate herbivory have shifted biomass to fewer, but larger trees that likely will affect stand resilience in the face of increased drought, pathogens, insects, and human impacts.

The functional approach proposed here initiates usage of distinct aspen types based on environmental conditions, stand structure and dynamics, and interrelations with the greater biotic community at broad scales. Adoption of a focus on ecological process represents a departure from classification based predominantly on composition. Assuming an adaptive management approach and targeting resilience, functional aspen types have the advantage of being intuitive, integrative, flexible, and ecologically sound. This framework should be viewed as geographically hierarchical; managers should employ appropriate functional types as “starting points” for tailored prescriptions. Documentation of local variants of functional types will be an improvement over past one-size-fits-all aspen management.

Only through flexibly integrating functional and practical perspectives will we be able to appropriately manage aspen for full ecological and human services.

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TABLE CAPTIONS

Table 1 - Aspen Functional Type Associates. Major associates include those that may potentially overtop aspen or reach a predominance of stocking at some point during a given stand's history. Minor associates mostly do not dominate a site, and in the case of stable subtypes, rarely constitute more than 25 % of total stand canopy cover.

Table 2 - Environmental variation in aspen functional types. Boxes containing numbers convey the authors' confidence in the statements made (1 = strong information, plus citation; 2 = moderate confidence; extension of knowledge from other locales; 3 = low confidence; reasonable estimate). Shaded boxes denote significant differences in subtypes within types by environmental variables. Riparian aspen variables were shaded if they differed significantly from both seral and stable subtypes.

Table 3 - Aspen functional types and management considerations. Long-term considerations generally follow the concept of Historical Range of Variation (HRV; Landres et al., 1999; Keane et al., 2009). HRV and functional typing rely on restoration of ecological processes toward a goal of system resilience.

Table 1

Type/subtype	**Major Associates**	**Minor Associates**
SERAL		
Boreal	*Picea glauca; P. mariana; Pinus banksiana; P. contorta; Populus balsamifera*	*Betula papyrifera*
Montane	*Abies lasiocarpa; A. magnifica; Juniperus occidentalis; Picea engelmannii; Pinus contorta; P. jeffreyi; P. ponderosa; Pseudotsuga menziesii*	*Acer glabrum; A. grandidentatum; Abies concolor; A. grandis; Juniperus scopulorum; Larix occidentalis; Libocedrus decurrens; Quercus gambelii; Picea pungens; Pinus albicaulis; P. aristata; P. lambertiana; P. flexilis; Salix scouleriana*
STABLE		
Parklands		*Quercus macrocarpa; Picea glauca; Pinus banksiana; Populus balsamifera;*
Elevation/aspect limited		See Montane Major Associates
Colorado Plateau		*Abies concolor; A. lasiocarpa; Quercus gambelii; Picea engelmannii; Pinus aristata; P. ponderosa; Pseudotsuga menziesii*
Terrain isolated		See Montane Major Associates
SERAL-STABLE		
Riparian	*Abies magnifica; Picea engelmannii; P. pungens; Populus angustifolia;*	*Abies magnifica; Acer grandidentatum; Betula occidentalis; Picea engelmannii; P. pungens; Populus angustifolia;*

1 Table 2

Type and subtype	Topography, aspect	Stand size	Annual Precipitation*	Ecohydrology
SERAL				
Boreal	rolling to flat land	10-10,000s ha	317-479 mm	(2)annual top recharge; likely linked to water table in other areas precipitation less than potential evapotranspiration
Montane	highly variable slope/aspect	10-100s ha	379-1807 mm	(1) annual top recharge; limited lateral flow (Burke, 2009)
STABLE				
Parklands	flat, low slope interspersed with deep valleys and hilly uplands	1-100s ha	350-450 mm	(1) precipitation less than potential evapotranspiration, very low annual runoff (Hogg and Hurdle, 1995)
Elevation or aspect limited	mostly south facing, slopes moderate	1-10s ha	Presumed similar to Montane precipitation range, although these sites may have higher evapotranspiration rates (data not available at this scale)	(1) annual top recharge; limited lateral flow (LaMalfa & Ryel, 2008; Burke 2009)
Colorado Plateau	flat, modest slopes	10-100s ha	412-784 mm	(2) annual top recharge
Terrain isolated	(highly variable) concave snowpockets; isolated rocky slopes, moraines, or lava fields; avalanche shoots	1-10s ha	Presumed similar to Montane precipitation range (data not available at this scale)	(1) top recharge; subterranean reserve with high clay content (Robinson et al. 2008)
SERAL-STABLE				
Riparian	steep to low gradient; all aspects	1-10s ha	Presumed similar to Montane precipitation range (data not available at this scale). Available moisture augmented by hyporheic flow.	(2) top recharge; subsurface flow

* Source: WorldClimate, average rainfall (1900-1990): http://www.worldclimate.com/ [accessed 3/29/11]

Table 2 (continued)

Type/subtype	Rooting depth	Regeneration type**	Dominant disturbance frequency or type
SERAL			
Boreal	(2) Soils exceed rooting depth; water table confined	(1) asexual; some sexual; spatially dynamic/fluid (Peterson & Peterson, 1992; Frey et al., 2003)	(1) Fire: stand-replacing disturbance moderate to high severity depending on conifer content with 50-200 year frequency depending on location (Stocks et al.2002; Flannigan et al. 2001).
Montane	(2) Bedrock confined	(2) dominant asexual; common spatially dynamic sexual (Mock et al., 2008; Zeigenfuss et al., 2008)	(1) Stand-replacing-mixed-severity fire; moderate-to-infrequent correlated to increased conifer cover (Kulakowski et al., 2004)
STABLE			
Parklands	(2) Soils exceed rooting depth; water table confined	(2) dominant asexual; some sexual	(1) historic disturbances were fire and bison (Archibold 1999; Campbell et al. 1994), now mainly stand replacing drought and insect outbreaks (Hogg et al. 2005)
Elevation or aspect limited	(1) bedrock confined (LaMalfa & Ryel, 2008)	(2) dominant asexual; common spatially dynamic sexual (Zeigenfuss et al., 2008)	(1) no dominant type (insect; disease), but surface fires from adjacent conifers possible; gap-to-stand-replacing (Baker, 2009)
Colorado Plateau	(2) Bedrock confined	(2) dominant asexual; common spatially dynamic sexual (Mock et al., 2008)	(1) no dominant type (insect/disease), low intensity, patchy (Rogers et al., 2010)
Terrain isolated	(3) Bedrock confined (snowpocket & lithic); variable	(3) assumed similar to other montane types; highly variable conditions (e.g., lithic substrates limit vegetative & protect sexual regeneration?)	(2) infrequent/ persistent drought and low intensity (insect; disease), gap-to-stand-replacing; avalanches (Fechner & Barrows, 1976)
SERAL-STABLE			
Riparian	(2) Bedrock confined; water table confined	(3) favors asexual; ample moisture, but limited seed bed for sexual regeneration	(1) flooding, beaver damage (Johnston & Naiman,1990); fire infrequent/ variable depending on available moisture and conifer presence

** Confidence levels are lower for reproductive type, even where citations are provided, due to the infancy of research in the realm of sexual reproduction in aspen at landscape/regional scales.

Table 3

Type and subtype	Stand structure target	Landscape dynamic target	Ecosystem services
SERAL			
Boreal	Successionally dynamic; structurally complex and multiple species	Dynamic mosaic; medium- to large-scale disturbance; succession driven (Johnson 1992; Lloyd et al., 2006)	Wildlife; biodiversity; carbon sequestration; water retention; wood harvest; livestock forage; aesthetics; recreation
Montane	Successionally dynamic: structurally complex and multiple species	Dynamic mosaic; medium- to large-scale disturbance/ succession driven	Wildlife; biodiversity; carbon sequestration; water retention; wood harvest; livestock forage; aesthetics/recreation
STABLE			
Parklands	Successionally stable; structurally complex; single species	Sedentary mosaic; dynamics between co-occurring aspen clones, marginal stand or clone die-offs, and non-forest cover types	Wildlife; biodiversity; carbon sequestration; water retention; wood harvest; livestock forage; aesthetics/recreation
Elevation or aspect limited	Successionally stable; structurally complex and single species; species mixing at stand margins	Mixed mosaic; abut adjacent aspect and upslope conifer, mixed conifer, and montane aspen types	Wildlife; biodiversity; carbon sequestration; water retention; livestock forage; aesthetics; recreation
Colorado Plateau	Successionally stable; structurally complex and single species	Sedentary mosaic; dynamics between co-occurring aspen clones, marginal stand or clone die-offs, and non-forest cover types	Wildlife; biodiversity; carbon sequestration; water retention; wood harvest; livestock forage; aesthetics; recreation
Terrain isolated	Successionally stable; structurally complex and single species	Sedentary mosaic; dynamics between co-occurring aspen clones, marginal stand or clone die-offs, and non-forest cover types	Wildlife; biodiversity; carbon sequestration; water retention; aesthetics; recreation
SERAL-STABLE			
Riparian	Mixed type; depending on seral-stable setting	Mixed mosaic; depending on seral-stable setting	Wildlife; biodiversity; carbon sequestration; water retention; aesthetics; recreation

Table 3 (continued)

Type/subtype	Short-term considerations	Long-term considerations
SERAL		
Boreal	Sustainable management of aspen resource. Maintaining and protecting root system after harvesting allowing for healthy and vigorous regeneration of harvested aspen stands (Frey et al., 2003)	Due to increased stresses such as drought and insect outbreaks aspen stands might deteriorate at the fringes of current boreal forest distribution (Hogg and Hurdle 1995; Frey et al 2004). Human developments such as agriculture and mineral extraction increasing in the region.
Montane	Disturbance processes and regeneration "health" are key. If past management has favored conifers, thinning or burning may assist in creating resources for aspen recruitment. Vegetation manipulation provides a sprouting response, but may be ineffectual where intense browsing is present (Shepperd et al., 2006)	Landscape-level processes vary widely. Multi-decadal periods without disturbance common. Metrics include a component of healthy aspen overstory and understory. New habitat related to climate change may be created at range and elevation margins (Landhäusser et al., 2010; Crimmins et al., 2011)
STABLE		
Parklands	Widespread aspen dieback (Frey et al. 2004) occurring across the landscape. At the stand level, monitor for successful regeneration following disturbance events.	As an ecotonal area, the parklands are expected to be most impacted by changing climatic conditions with grasslands expected to extend northwards (Hogg and Hurdle 1995). Human developments such as agriculture and mineral extraction have also left very little parkland in a "natural" state.
Elevation/ aspect limited	Restore structural diversity where absent. If lapses in recruitment are present, investigate and address potential causes. Vegetation manipulation to simulate gap/phase dynamics, not large-scale/high-severity disturbance.	Structural and genetic diversity aid resilience in the face of expected process alterations. Commercial uses often limited. South-facing aspect limited stands, particularly low elevation, may be vulnerable to climate shifts.
Colorado Plateau	Restore structural diversity where absent. If lapses in recruitment are present, investigate and address potential causes. Vegetation manipulation to simulate gap/phase dynamics, not large-scale/high-severity disturbance.	Structural and genetic diversity aid resilience in the face of expected process alterations. Anticipate greater vulnerability at range and lower elevation margins due to climate shifts.
Terrain isolated	Isolated sites have minimized functional disruptions. Monitor for successful regeneration. Unique conditions may protect from, or enhance, frequent disturbance. E.g., lithic/lava substrates may dissuade browsing (DeRose et al., 2010) or frequent avalanches limit tree growth and act as fire breaks (Fechner & Barrows, 1976).	Remoteness and lack of commercial uses limit need for active management. These forests are often naturally stressed, slow growing, and thus inherently resilient. Their greatest vulnerability may be due to climatic change at lower elevation margins.

SERAL-STABLE		
Riparian	Monitor for successful regeneration. Limit domestic browsing and other human uses to the extent possible to maximize ecosystem services (Newlon & Saab, 2011). These corridors, particularly where surrounded by non-forest, act as biodiversity oases.	Altered steam flow or community structure can have lasting effects on riparian aspen (Rogers et al., 2007). Restoration of processes, such as beaver use and occasional flooding, affect (+/-) long-term resiliency (Naiman et al., 1988). Stand replacing disturbances should be uncommon and thus should not drive restoration efforts.

FIGURE CAPTIONS

Figure 1: A framework for classifying aspen types and subtypes by ecological function in North America. Riparian aspen may occur as either seral or stable, often depending on surrounding forest conditions.

Figure 2: The map distinguishes between aspen's total distribution (gray) and areas of functional dominance. The 100th meridian delineates aspen's western range as defined by the authors. Functional types/subtypes include only those areas where aspen dominates, or has the potential to dominate, canopy coverage over wide areas and for (at least) multiple decades. Functional subtypes that occur at regional scales are shown here, while those occurring at landscape scales are depicting in Figure 3. A provisional "sub-boreal" aspen is mapped here, though it is unclear at this time whether an additional subtype is warranted.

Figure 3: Because of the highly dissected nature of mountainous terrain and vegetative communities, some widespread aspen subtypes are best illustrated at the landscape rather than regional scale (Figure 2). Figure 3a shows common alignment of seral and stable communities by aspect in the central Rocky Mountains. Figure 3b depicts additional subtypes that occur in isolated (i.e., surrounded by non-forest communities) situations.

Figure 1

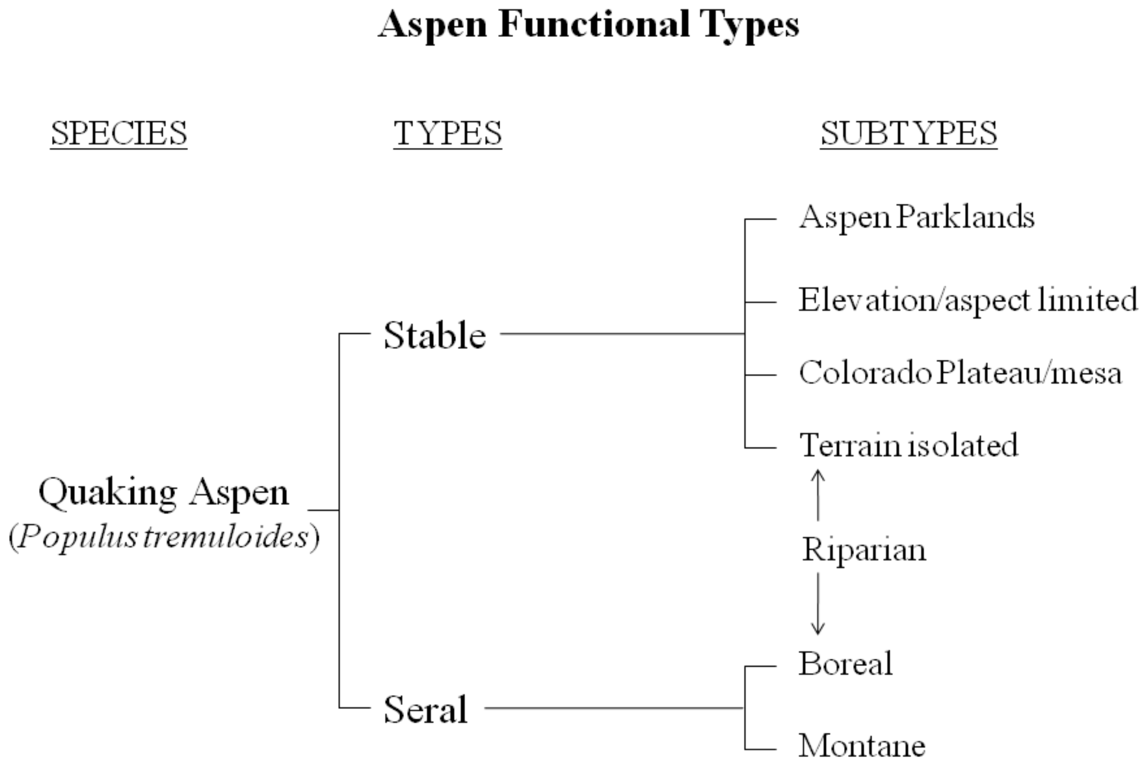

Aspen Functional Types
SPECIES
TYPES
SUBTYPES
Quaking Aspen
(Populus tremuloides)
Stable
Seral
Aspen Parklands
Elevation/aspect limited
Colorado Plateau/mesa
Terrain isolated
Riparian
Boreal
Montane

Figure 2

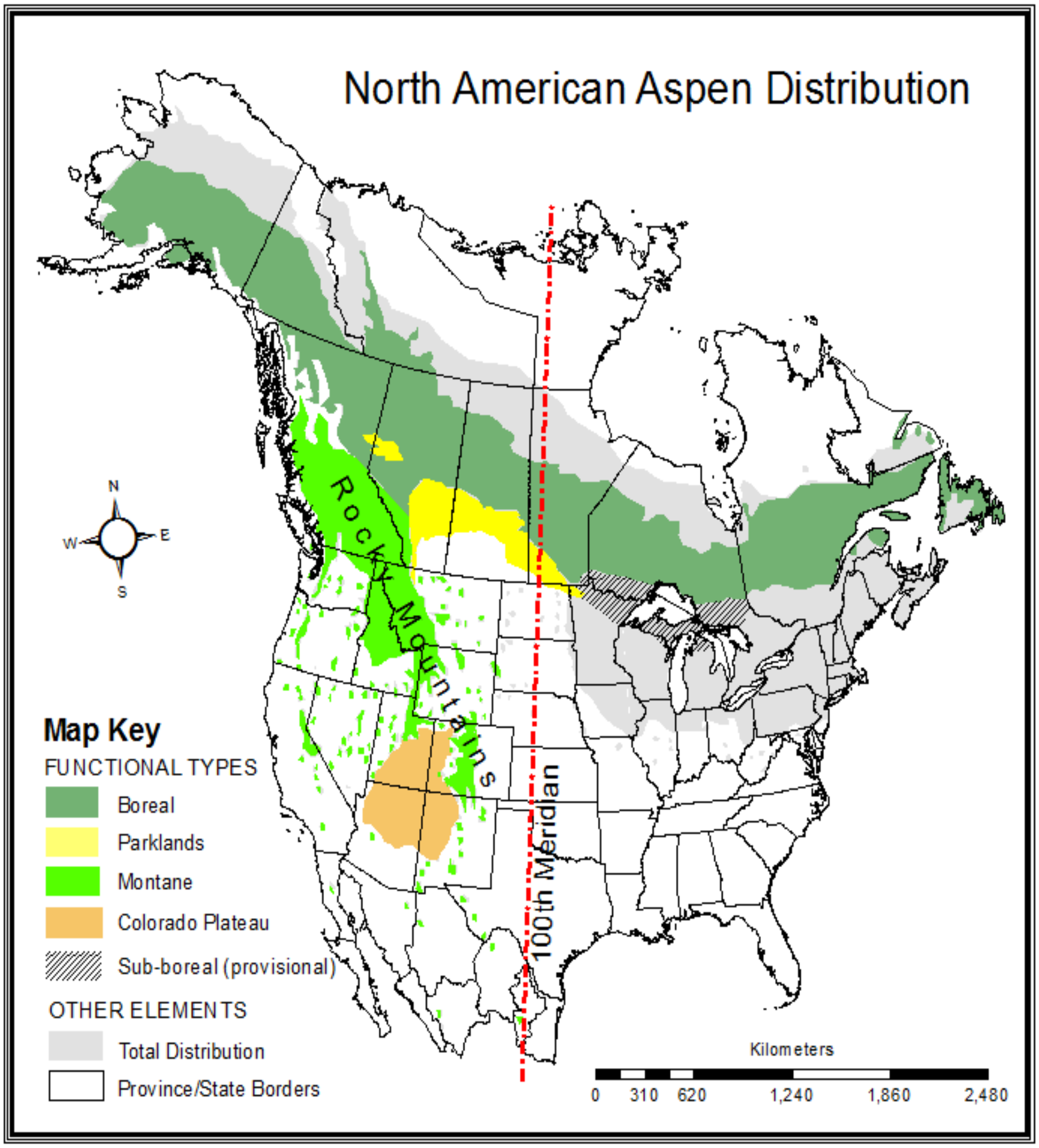
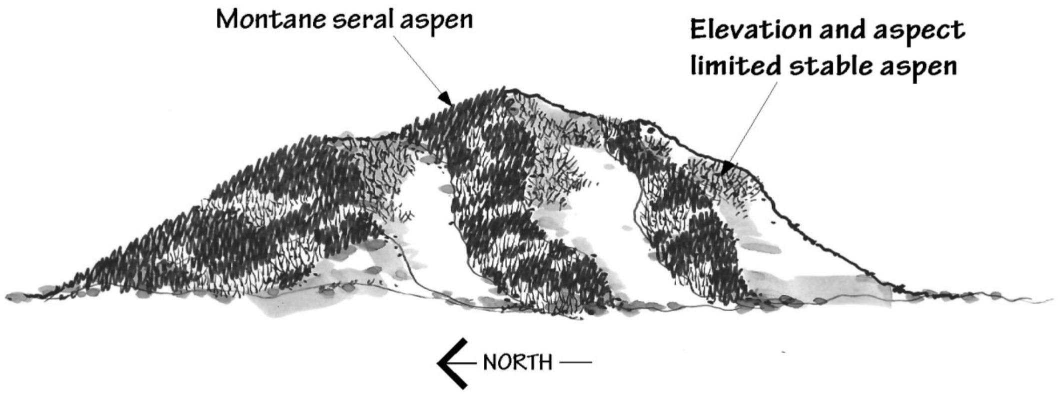

North American Aspen Distribution
Rocky Mountains
100th Meridian
N
E
S
W
Map Key
FUNCTIONAL TYPES
Boreal
Parklands
Montane
Colorado Plateau
Sub-boreal (provisional)
OTHER ELEMENTS
Total Distribution
Province/State Borders
Kilometers
0
310
620
1,240
1,860
2,480

Figure 3

3a



3b