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2
3 **A Functional Framework for Improved Management of**
4 **Western North American Aspen (*Populus tremuloides* Michx.)**
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26

27 **ABSTRACT**

28

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

46

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

48 **INTRODUCTION**

49

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

61 By the very nature of its continental distribution, aspen has adapted to broad ranges of
62 environmental gradients, such as topographic position, annual precipitation, growing season length, soil
63 type and depth, maritime or continental climate pattern, disturbance types, and plant associates. Though
64 early American foresters were skeptical of the existence of diverging aspen communities (Baker, 1918,
65 1925), others pointed out prominent examples of apparently long-term “pure” aspen forests in the
66 southern Rocky Mountains (Fetherolf, 1917; Sampson, 1916; Weigle and Frothingham, 1911). In
67 Canada, the debate over the existence of a stable type was moot given huge expanses of parkland with
68 nearly pure stands of aspen (Bird, 1930; Moss, 1932). Still, professional guidance on management of
69 aspen forests has widely favored the successional model of moving from aspen to conifer. This may be
70 attributed, in part, to a 20th century bias for managing toward productive—predominantly
71 softwood—timber values to the detriment of many aspen communities (Johnstone, 1982; Haig, 1959;
72 Wagar and Myers, 1958). For example, Weigle and Frothingham (1911, p.5) stated, “the dense thickets

73 of root sprouts or suckers which aspens ordinarily produce immediately after logging may choke out and
74 for many years prevent the seeding in of other species. When this happens the presence of aspens
75 becomes a distinct menace instead of a help to the establishment of more desirable trees.”

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

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

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

107

108 **ASPEN COMMUNITY TRAITS**

109

110 **KEY DIFFERENCES IN ASPEN COMMUNITIES**

111

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

120 Baker's (1918, 1925) early aspen work struggled with the notion of whether to distinguish two
121 basic forms of aspen existing in the central Rocky Mountains. Since that time, we have progressed
122 substantially. Mueggler (1988) implicitly recognized seral and stable "cover types," but went much

123 further in detailing 59 vegetative “community types” within his aspen classification scheme. While this
124 approach has utility at the stand-level, it does not facilitate wider application due to its dependence on
125 taxonomic descriptions of plant communities. More importantly, however, is the fact that composition-
126 based classifications largely neglect ecological function, as well as related process-based applications
127 across larger geographic reaches. Taking a silvicultural approach, Shepperd (1990) distinguished
128 between stable aspen types of different ages and regeneration patterns in Wyoming and Colorado.
129 Functional typing of aspen as suggested here incorporates both compositional and structural differences,
130 plus inclusion of system processes specific to physiographic, climatic, and geographic situations, as well
131 as anthropogenic alterations.

132 Still, questions linger as to basic ecological differences for why some stands remain relatively
133 pure and others follow an aspen-conifer successional path. Specifically, why don't stable aspen stands
134 succumb to conifer invasion on certain landscapes? Early research (Baker 1918; 1925) suggested that
135 large disturbances on the Colorado Plateau in the late 19th century had favored pure aspen stands, but
136 given a long enough disturbance-free period conifers would seed in, presuming long-term succession, and
137 establish seral stands. Clearly, this has not happened across large swaths of this landscape in the
138 intervening century (Langenheim, 1962; Harniss and Harper, 1982; Rogers et al., 2010). The same is true
139 for the Canadian parkland. Even on smaller landscapes framed by aspect, slope, edaphic, and
140 microclimatic features (i.e. putative functional subtypes described herein), we witness long-term
141 persistence of pure aspen stands even in the presence of conifer seed sources (e.g., Kulakowski et al.,
142 2004; Kurzel et al., 2007; Strand et al., 2009). Rainfall, evapotranspiration, and soil moisture may play
143 key roles, as stable stands are often on drier sites, though systematic testing of this theory has not taken
144 place. Perhaps repeated short-interval or high-severity disturbance events could maintain stable
145 communities, effectively eliminating conifer establishment (i.e., Romme et al., 2001; Shinneman et al.,
146 2013)? While this scenario may exist, adequate evidence is not yet available to firmly establish a “semi-
147 persistent” aspen type (Shinneman et al., 2013). Additionally, multiple studies have indicated advanced

148 stand ages (80-120 years and more)—well within the time needed for conifer establishment—of stable
149 aspen types (Harniss and Harper, 1982; Shepperd, 1990; Cumming, et al., 2000; Smith and Smith, 2005;
150 Rogers et al., 2010). Efforts to use soil types and genetic differences to explain this key division of
151 functional aspen ecology are in progress, though conclusive results are unavailable at this time.

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

159

160

161 SUPPORT FOR FUNCTIONAL TYPES

162

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

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

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

193 Perhaps the widest and most thoroughly documented variation between subtypes exists under the
194 heading “Dominant disturbance frequency or type” (Table 2). These distinctions are related to many
195 environmental and compositional factors. For example, associations with the disturbance-dependent
196 lodgepole (*Pinus contorta* var. *latifolia* Engelm.) and jack pine (*P. banksiana* Lamb.) will be distinct

197 from aspen subtypes where disturbance-resilient species govern (e.g., aspen itself or other hardwoods). In
198 general, disturbances in seral stands occur at larger scales and higher intensities than those in stable types,
199 although mixed-severity fires may result in mosaics of small-patch seral and semi-persistent aspen
200 (Shinneman et al., 2013). Stand size alone may have sweeping effects regarding disturbance size and
201 spread. Even at the functional subtype level, there are clear differences where stand size, terrain, water
202 relations, other species, and adjacent communities impart synergistic effects which result in widely
203 varying dominant disturbances. For example, a small, stable aspen community may collaterally burn in a
204 high wind scenario where the adjacent stand is composed of fire-prone conifers (Shinneman et al., 2013).

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

213

214 **FRAMEWORK ASPEN FUNCTIONAL TYPES**

215

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

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

238

239 **ASPEN FUNCTIONAL TYPES**

240

241 **SERAL ASPEN**

242

243 Aspen in seral systems reacts to processes initiated, most often, by the presence and condition of
244 conifers. After stand replacing disturbance, for example, aspen responds via rapid root sprouting that is
245 eventually overtopped by shade-tolerant species. Aspen dominance in seral settings may last up to several

246 decades or even a century, depending on setting and development of competing species, but also on the
247 vitality of post-disturbance aspen, physiographic and climate conditions, and subsequent human impacts.
248 Cohort species in seral aspen range from xeric junipers (*Juniperus spp.*), to mesic spruces (*Picea spp.*), to
249 montane and boreal pines (e.g., *Pinus contorta*, *P. banksiana*, *P. albicaulis*, *P. longaeva*; Table 1).

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

253

254 *Boreal (western Canada)*

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

265 Tree species dominance and distribution patterns in boreal mixedwood forests are mostly driven
266 by the frequency and scale of the disturbance. Where disturbances occur at higher frequencies (e.g., < 80
267 years) and at larger spatial scales, the establishment and maintenance of early successional forest
268 communities dominated by aspen and white birch (*Betula papyrifera* Marsh.) are favored. Natural and
269 anthropogenic disturbances include fire, insect outbreaks, windthrow, and forest harvesting. Under high
270 disturbance frequency, pure aspen stands can be self-perpetuating, especially in the absence of significant

271 nearby conifer seed sources (Peters et al., 2005). Increased harvesting throughout the boreal forest region
272 has resulted in a shift from conifer to hardwood-dominated stands, particularly in the boreal mixedwood
273 region where the vegetative regeneration of aspen can be prolific (Peterson and Peterson, 1992; Frey et
274 al., 2003). As these aspen stands mature, multi aged stand structures may develop. The formation of these
275 multi aged aspen stands can be the result of gap dynamics, drought, or insect outbreaks that have
276 weakened or killed portions of the mature canopy and initiated advanced vegetative regeneration under
277 the canopy (Cumming et al., 2000).

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

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

294 The boreal mixedwood region contributes significantly to the fiber supply of North America and
295 the volume of aspen harvested in Canada has experienced a significant increase over the last 25 years. As

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

309

310 *Montane*

311

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

320 region. At finer scales, even more "aspen types" may be delineated (Kashian et al., 2007; Kurzel et al.,
321 2007).

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

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

343

344 STABLE ASPEN

345

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

350 A prime distinction of the stable aspen type is its incremental stand replacement, typified by
351 “gap-phase” stand dynamics (Kashian et al., 2007; Kurznel et al., 2007; Mueggler, 1985; Rogers et al.,
352 2010). In contrast to large scale stand replacing disturbance, small scale disturbances such as individual
353 tree or small group mortality characterize the stable aspen type. Canopy successors are often already
354 present as mid story ramets and are able to quickly take advantage of available light, nutrients, and water
355 (Table 2). Stable types are often uneven, or multi aged, aspen communities (Better and Woods, 1981).
356 Aspen basal area is not expected to change markedly in stable stands over time; whereas a steady
357 decrease in aspen basal area occurs in seral stands while overall volume increases (Harniss and Harper,
358 1982; Smith and Smith, 2005).

359

360 *Aspen Parklands*

361

362 The aspen parkland is an ecotonal region in western Canada between boreal forest to the north
363 and grassland to the south where the dominant tree species is aspen. It extends from the Peace Region of
364 northern British Columbia and Alberta, through Saskatchewan and Manitoba, and ends in northern
365 Minnesota (Figure 2). The general vegetation pattern is a mosaic of discrete stands of aspen, shrublands,
366 and grasslands, which also represent successional stages with shrubs first colonizing grasslands and then
367 aspen colonizing shrublands (Bird, 1930). Isolated upland areas further south in the grassland, such as the
368 Cypress Hills in Saskatchewan and Alberta, also support aspen parkland. Prior to agricultural settlement,
369 aspen cover on the landscape was typically less than 30% with most of the landscape dominated by

370 grassland (Archibold and Wilson, 1980). The ability of aspen to survive in this environment has been
371 linked to its clonal integration (Peltzer, 2002), an extensive system of very fine roots which are more
372 similar to grass root systems than to boreal aspen trees (Pinno et al., 2010), and the ability of aspen to
373 alter belowground resources to benefit itself relative to the surrounding grasslands (Kleb and Wilson,
374 1999).

375 Currently, the dominant land use in the aspen parkland is agriculture with cropland and rangeland
376 covering most of the land area, leaving aspen located in scattered patches, typically in areas less suitable
377 for agriculture (Acton et al., 1998). Climate change and ecosystem predictions for the aspen parkland
378 predict a retreat north for aspen in the coming decades, resulting in a loss of aspen from much of the
379 current parkland area (Sauchyn et al., 2009). However, actual aspen coverage has expanded southwards
380 since settlement due to the elimination of bison (*Bison bison*) and fire (Campbell et al., 1994; Hansen,
381 1949), both of which controlled aspen expansion on the landscape. Estimates for Saskatchewan indicate
382 that aspen have expanded south by approximately 100 km since settlement (Archibold and Wilson, 1980).

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

390 Fire was historically the major disturbance in the parkland with fire frequency estimates of 10-25
391 years (Brown and Sieg, 1999; Weir and Johnson, 1998), but fire has now been virtually eliminated from
392 the landscape. Other important disturbance agents in parkland stands include herbivores and weather
393 events. For example, in expanding clones, browsing of suckers by rabbits (*Sylvilagus* spp.; Bird, 1930),
394 white-tailed deer (*Odocoileus virginianus* Raf.; B. Pinno, personal observation), and historically browsing

395 by bison (*Bison bison* L.; Campbell et al., 1994) can reduce the growth of more than 90% of the stems in
396 years of locally high herbivore abundance. Cattle grazing can also prevent aspen canopy development
397 following fire (Bailey et al., 1990), while insect defoliation (Hogg et al., 2005) severely reduces aspen
398 growth in localized areas. In terms of weather events, hail and drought are both important disturbances in
399 the aspen parkland. For example, after a severe hailstorm in southern Saskatchewan, Peltzer and Wilson
400 (2006) found that 36% of the mature aspen stems had been killed. Also, drought events significantly
401 reduce aspen growth for up to 4 years after the drought ends (Hogg et al., 2005), and the combination of
402 drought and insect defoliation has been linked to aspen dieback in the area (Hogg et al., 2002).

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

412

413 *Colorado Plateau highlands and mesas*

414

415 Early foresters noted the occurrence of large, nearly homogenous, tracts of aspen “groves” in
416 southern Utah and western Colorado (Baker, 1925; Fetherolf, 1917; Sampson, 1916). The greater
417 Colorado Plateau ecoregion—taking in large portions of the aforementioned sections of Colorado and
418 Utah, plus northern Arizona and northwest New Mexico—is home to extensive deserts, canyons, and high
419 elevation mesas (Bailey, 1995). The arid climate of surrounding landscapes makes the elevated plateaus

420 appear relatively moist by comparison. Aspen occurs almost exclusively between 2,300 - 3,500 m
421 elevation. Above 2,500 m, annual precipitation is 500 - 900 mm, while rainfall across the adjacent valley
422 bottoms is less than 300 mm (McNab and Avers, 1994). Though montane seral aspen environments are
423 common throughout this region, and coniferous forest types dominate much of the higher elevations,
424 stable aspen communities host some of the most productive and largest stands of aspen in the contiguous
425 United States (Baker, 1925; Barnes, 1975; Langenheim, 1962). The pure aspen “Pando Clone,”
426 measuring some 44 hectares and potentially the largest living organism on earth, is found in south-central
427 Utah’s Fishlake National Forest (DeWoody et al., 2008; Grant, 1993). The Colorado Plateau is thought to
428 support such vigorous aspen clones and forests because of regular summer “monsoon” flow from the
429 south and relatively minor deviations in topography across expansive mesa tops (Rogers et al., 2010;
430 Smith and Smith, 2005). Understory growth has widely been converted from lush forb communities to
431 grasses and shrubs as a result of intense livestock use over a century or more (Bowns and Bagley, 1986).

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

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

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

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

466

467 *Elevation or aspect limited*

468

469 In many montane regions of the western range of aspen, stable aspen forests may be found
470 adjacent to seral communities and are mainly differentiated by their topographical aspect. Long-term
471 dominance by aspen on these sites, as with other stable types, is likely associated with moisture and soil
472 conditions that could restrict conifer encroachment (Cryer and Murray, 1992). Particularly in the central
473 and southern Rocky Mountains, stable aspen often occur at mid-elevations on south and southwest facing
474 slopes where evaporative demands limit the moisture needed for conifer establishment (Langenheim,
475 1962; Rogers and Ryel, 2008; Strand et al., 2009). However, with changes in elevation and latitude, pure
476 stands may be found on a range of exposures. In western Colorado, lower elevation (2,590 – 2,895 m)
477 aspen remained relatively stable on east slopes, though the author does not provide an explanatory
478 mechanism (Langenheim, 1962). Front Range stable aspen are also commonly east facing and low
479 elevation (Kashian et al., 2007; Zeigenfuss et al., 2008). Near alpine treeline in Colorado’s San Juan
480 Mountains, Elliot and Baker (2004) describe aspen favoring south facing slopes where adjacent conifer
481 stands were present on the same and other aspects. Finally, Sankey (2008) describes pure aspen stands
482 along a grassland-forest ecotone (~2,100 m) on predominantly northern slopes in southwestern Montana.
483 While these elevation and aspect stable stands are common in the southern and central Rocky Mountains,
484 we were unable to find documentation of such occurrences further north into Canada. The authors
485 speculate that predominantly soil moisture, but also soil temperature and growing season length, likely
486 play a role in limiting the occurrence of elevation and aspect limited stands in the northern Rocky
487 Mountains, though more investigation is warranted.

488 While the general pattern of stable stand structure holds for the elevation and aspect subtype,
489 *proximity to conifers* increases the chance of periodic stand replacing disturbance, particularly on the
490 fringes of pure groves (Shinneman, et al., 2013). While previous work has pointed out aspen’s relative
491 inability to burn in many situations (Fechner and Barrows, 1976), it must be clear that even “surface fire
492 may be stand replacing” as minimal scorching can lead to high mortality in stable aspen (Baker, 2009, p.
493 181). Other catastrophic die offs, such as drought or old-age induced insect and disease complexes which

494 decimate overstory, may lead to periodic near stand replacement (Rogers et al., 2010; Worrall et al., 2008;
495 Kurzel et al., 2007). These incidences may originate within portions of stands weakened by minor fire
496 scorching related to proximity of more fire prone conifer stands. As the length of time increases after
497 stand replacing events, there will be a tendency to revert to stable communities of multi layered
498 appearance over a period of decades. In sum, elevation and aspect controlled aspen communities are most
499 likely to show a range of stand structures reflective of disturbance patterns: even-aged, mixed-age, and
500 mosaics of both may be common where relatively pure stands abut conifer and aspen-mixed-conifer
501 forests.

502

503 *Terrain isolated*

504

505 Stable aspen communities isolated by terrain or substrate are often limited in extent. These stands
506 include aspen in snowpocket (Fig. 3b), krummholz, lithic, prairie pothole, and avalanche track situations.
507 Sometimes small aspen stands are simply surrounded by large non-forest communities (e.g., montane
508 meadow or sagebrush dominated cover), not fitting neatly into the categories above. These physiographic
509 locations often display stunted aspen growth forms suggesting water, substrate, or disturbance limitations
510 that impede conifer invasion. Terrain isolated aspen may occur throughout the western range of the
511 species, particularly where variations in topography encourage subterranean moisture accumulation.
512 Occasionally, this subtype may be slowly infiltrated by conifers (D. Bartos, pers. comm.). Shepperd et al.
513 (2006) describe snowpocket aspen stands as those found in topographic depressions where snow
514 accumulates and is slow to melt. Krummholz occurs where exposed aspen stands are subjected to
515 persistent winds which severely limit twig growth via scouring and desiccation. Both snowpocket and
516 krummholz aspen are often isolated by surrounding alpine grassland or shrub cover. This situation
517 buffers potential impacts from fire or other stand-replacing disturbances, as well as limiting potential
518 invasion by seed-dispersed conifers. Likewise, lava flows and other rock outcrops where stable aspen

519 grow will repel wildfire, inhibit dense conifer establishment, and reduce access by large herbivores
520 (DeRose and Long, 2010).

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

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

532

533 CROSSOVER SERAL OR STABLE ASPEN

534

535 *Riparian*

536

537 Riparian aspen constitutes a crossover subtype; more commonly occurring as a seral type than a
538 stable type, but exhibiting a distinct ecological function related to the influence of water propinquity. For
539 example, these communities may be less susceptible to fire, but historically were greatly influenced by
540 beaver (*Castor canadensis* Kuhl) foraging (Johnston and Naiman, 1990) and in some regions, stream-
541 altering human intrusions, such as gold mining, water channelizing, and dam building (Rogers et al.,
542 2007). These stands—whether isolated “forest stringers” (Fig. 3b) surrounded by non-forest lands or
543 within a larger forest matrix—are found adjacent to ephemeral or permanent streams water sources.

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

561

562 CHALLENGES AND MANAGEMENT IMPLICATIONS

563

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

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

573

574 THREATS TO FUNCTIONAL TYPES

575

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

584 Past land uses and evolving management practices have significantly impacted aspen forests
585 across subtypes. For instance, resource extraction in the late 1800s, such as livestock grazing and
586 logging, was often followed by intentional burning, initiating contemporary aspen forests in many locales
587 during that era (Kaye 2011; Rogers et al., 2007, 2011; Kulakowski et al., 2004). These impacts apply to
588 seral more so than stable aspen, due to the lesser desirability of the stable aspen as a timber commodity
589 and the limited flammability of pure aspen types. Since then, moist 20th-century climates, management for
590 conifers, and fire suppression negatively affected aspen (Rogers et al., 2011). In general, timber harvest
591 in the West utilized vast expanses of conifer cover, relative to hardwoods, where stands were accessible.
592 Aspen was relegated to the status of a “weed species” in many areas. Similarly, aspen “rangelands” were
593 overused in earlier times and now even relatively low levels of grazing may reduce successful

594 regeneration, as well as reduce biodiversity in the understory. In sum, these types of activities, in
595 combination with sometimes misguided management responses, have the potential to severely alter
596 existing functional types by decreasing their resilience. For example, relatively low elevation stable
597 aspen in warming and drying climate patterns which is also subjected to continuous browsing will
598 eventually undergo type conversion to a non-aspen state.

599 Wildlife management, often related to boosting game populations, also may alter functional aspen
600 types. Large herbivore manipulations can potentially derail well-meaning aspen silvicultural practices.
601 Browsing ungulates—both wild and domestic—are inhibiting stand renewal via repeated aspen sprout
602 consumption at many locales (DeByle, 1985; DeRose and Long, 2010; Rogers et al., 2010; Zeigenfuss et
603 al., 2008). This phenomenon seems particularly acute where North American elk (*Cervus elaphus*) are
604 thought to be beyond HRV levels because of introduced populations (e.g., Bailey et al., 2007; Stritar et
605 al., 2010) or lack of predation to cull numbers in preserves that do not allow hunting (Beschta and Ripple,
606 2009). Moose (*Alces alces*), elk, or deer (*Odocoileus* spp.), as well as several smaller mammals, may also
607 damage mature trees by debarking portions of boles by chewing or rubbing, which may lead to stand-
608 level infections by a range of lethal pathogens (DeByle, 1985; Hinds and Krebill, 1975). Finally, human-
609 induced depletion of another herbivore, the beaver (*Castor canadensis*), has had negative impacts on
610 hydrology, habitat, and biodiversity in riparian aspen systems (Beier and Barrett, 1987; Hall, 1960). For
611 example, forage “switching” by beaver to willow (*Salix* spp.), where aspen are exhausted, is tied to
612 cascading effects of carnivore influences on elk populations and their patterns of herbivory (Smith and
613 Tyers, 2008). The combined effects of both overuse (ungulates) and underuse (beaver) by herbivores
614 may have widespread effects on successional and functional pathways.

615 Current science strongly suggests that human-induced warming of the planet is occurring (IPCC,
616 2007). However, commensurate understanding of climate change on particular vegetative types is in its
617 investigatory infancy. Even so, we are already seeing potential alterations of functional types. For
618 example, exotic species, such as gypsy moth (*Lymantria dispar*), are projected to spread upslope from

619 urban areas into aspen, the most prominent hardwood in Rocky Mountain forests (Logan et al., 2007).
620 From a broader perspective, Rehfeldt et al. (2009) foresee current instances of drought-induced “sudden
621 aspen decline” (Worrall et al., 2008) as harbingers of aspen’s altitudinal retreat up slope in the coming
622 century. While this first approximation of climate effects on aspen lacks explicit accounting of different
623 functional types, as well as potential for increased disturbance providing additional aspen habitat, this
624 work does provide a launching point for refined efforts. Further caution is required, moreover, in
625 balancing the effects of climate change with human actions (Kaye, 2011). As an example of these
626 interactions, aspen expansion in the parklands appears to be driven largely by anthropogenic practices. In
627 spite of the changing climate which predicts aspen moving north, aspen has moved south (in some areas
628 by ~100 km) due to fire suppression, irrigation of croplands, elimination of bison, and recent disturbance
629 (Archibald, 1999; Campbell et al., 1994; Peltzer and Wilson, 2006). Overall, future work must weigh the
630 benefits of continental-scale climate modeling with application of type-specific aspen variability, such as
631 the functional system advocated here.

632

633 MANAGEMENT IMPLICATIONS

634

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

642 We foresee further application of functional classifications toward improved land stewardship for
643 other widespread forest systems that are adaptive to edaphic, ecological, climate, and human-altered

644 variance across landscape- to continental-scales. Examples of forest types potentially conducive to
645 functional classification include ponderosa (*P. ponderosa*), lodgepole pine (*P. contorta*), and Douglas-fir
646 (*Pseudotsuga menziesii*) in North America and European aspen (*Populus tremula*), European spruce
647 (*Picea abies*), and Scots pine (*P. sylvestris*) across Eurasia. Individual species growing under manifestly
648 distinct conditions (e.g., boreal and montane; continental and maritime) likely exhibit key functional
649 differences that may benefit from a similar treatment.

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

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

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

671
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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.

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984 Table 1

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

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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]

1 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.

1 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

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1 Table 3 (continued)
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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 stream 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.
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FIGURE CAPTIONS

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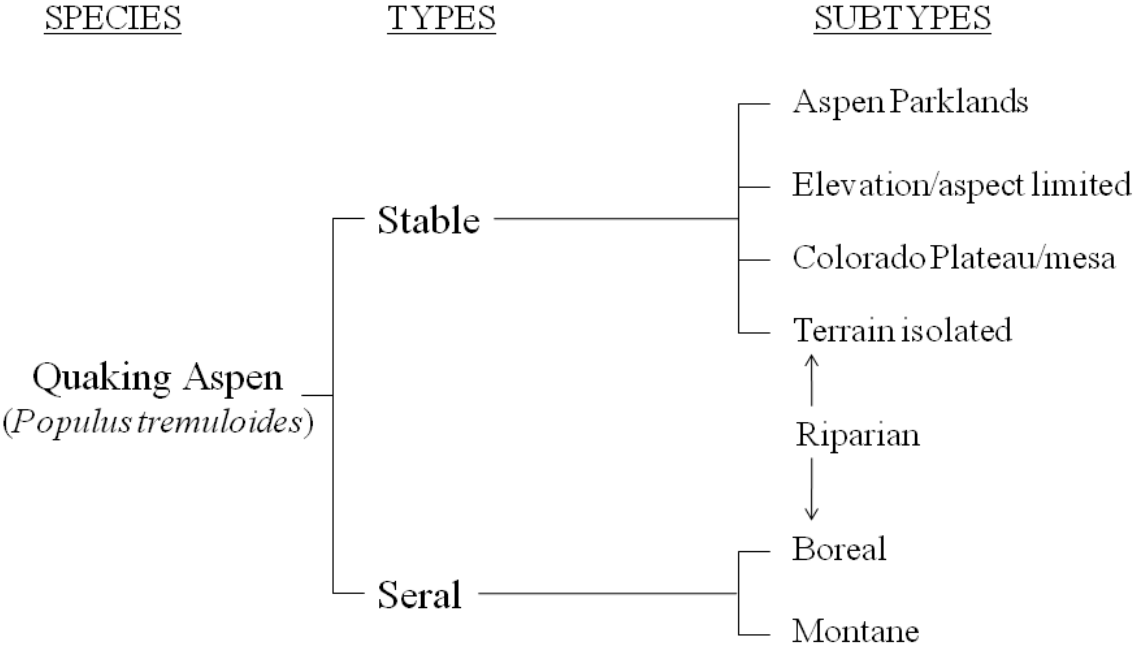
Figure 1: A framework for classifying aspen types and subtypes by ecological function in North America. Riparian aspen may occur as either seral or stable, often depending on surrounding forest conditions.

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.

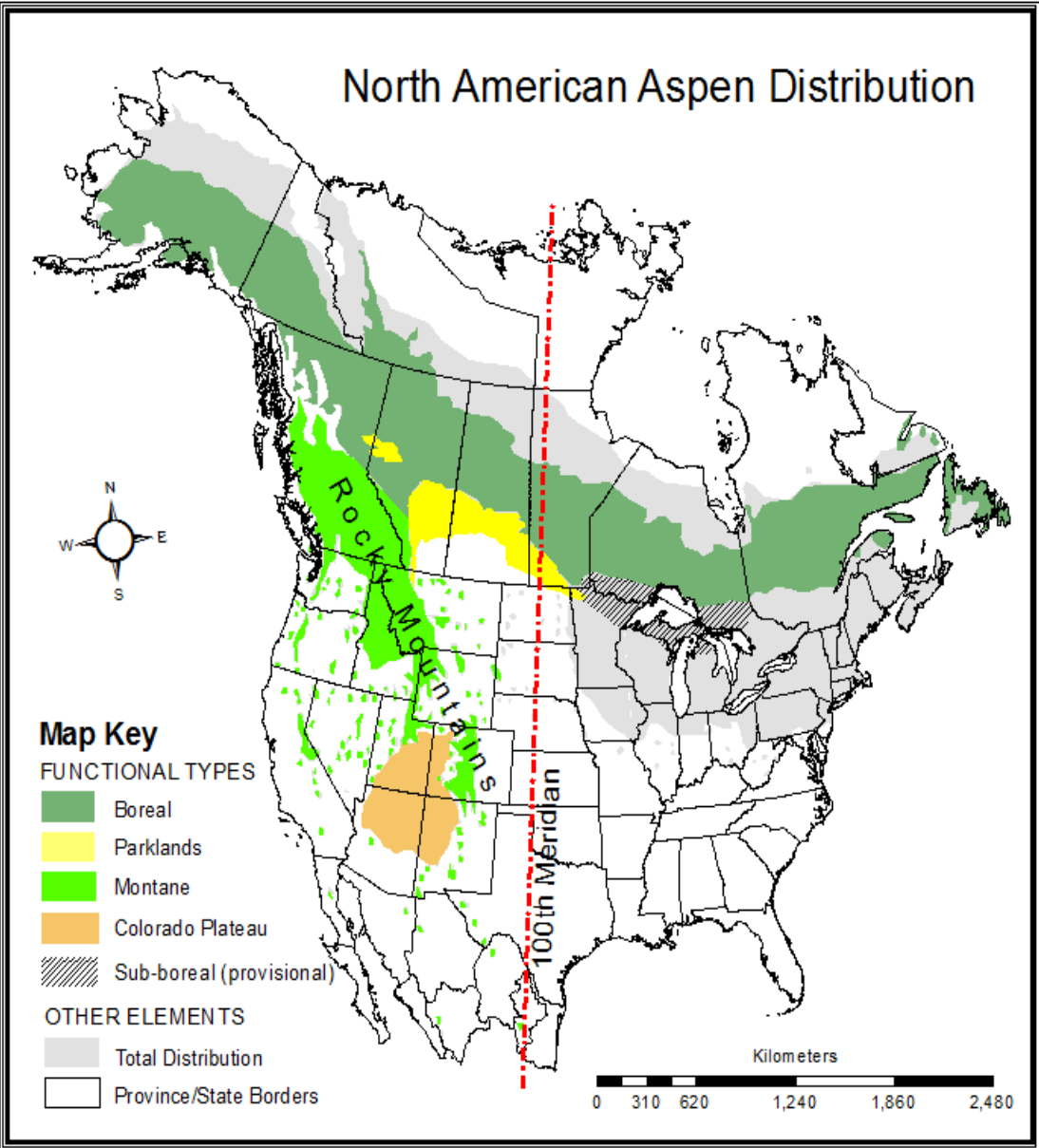
1 **Figure 1**
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Aspen Functional Types



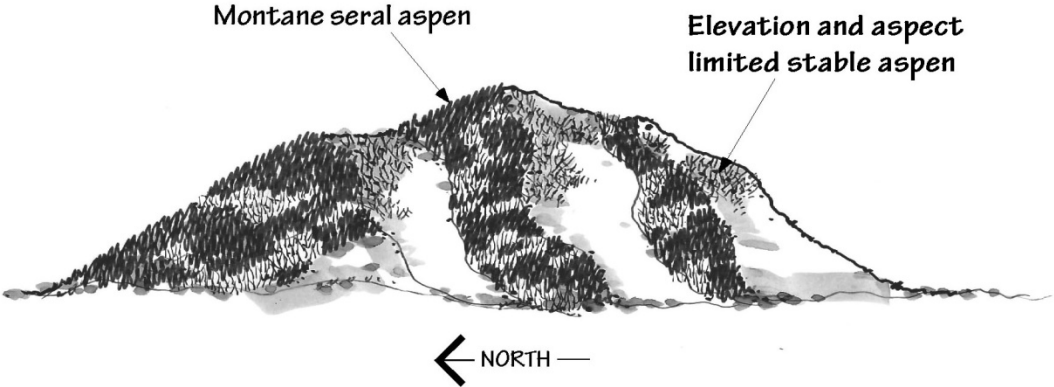
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1 Figure 2

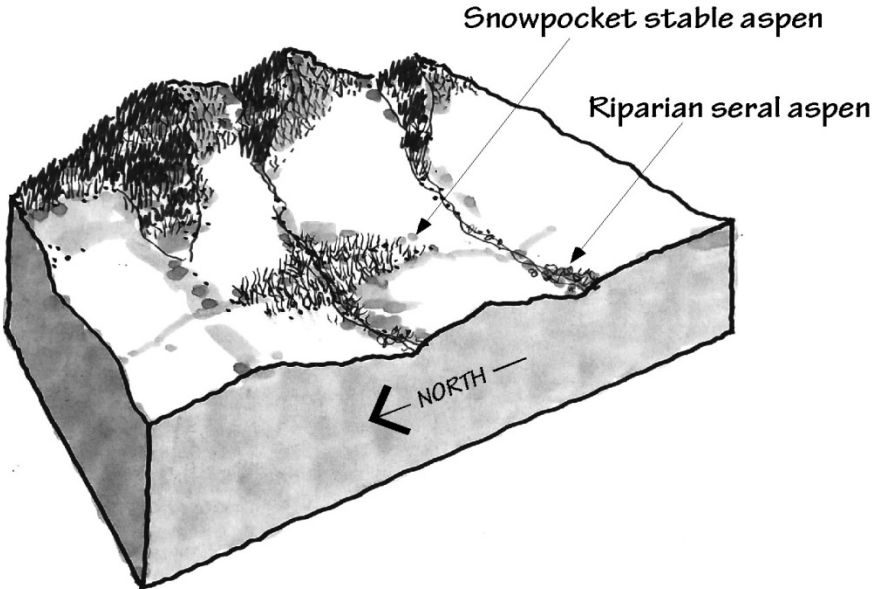


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1 **Figure 3**
2 3a



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4 3b



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