

STAND DEVELOPMENT OF TREMBLING ASPEN IN CANAAN VALLEY, WEST VIRGINIA

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Abstract.—In wetlands of Canaan Valley, West Virginia, trembling aspen occurs as a disjunct population well south of its primary natural range. Based on sample data from 15 stands, we found that aspen occurs as nearly monospecific stands or clones. Eight stands had median ages between 30 and 40 yrs, and we suggest that stand initiation was related to changes in land use after the 1950s. Nine stands were in the stem exclusion stage of development, with mortality concentrated in smaller aspen stems. Five stands showed evidence of overstory mortality and expansion at the stand boundary, based on a comparison of ages of the largest and smallest trees along a distance gradient from stand center to edge. We suggest that the lack of stronger evidence of stand expansion can be attributed to competition from adjacent plant communities, and the presence of unfavorable soil and/or hydrologic conditions necessary for successful aspen ramet emergence and survival.

INTRODUCTION

Trembling aspen (*Populus tremuloides* Michx.) is the most widely distributed native tree species in North America (Perala 1990). The species grows singly and in multi-stemmed clones, and often depends on fire for establishment. During the past 50 years, a major land management controversy has developed in North America over the extent to which altered fire regimes, increasing ungulate populations, and climate change have or have not resulted in declines in aspen abundance, vigor, or regeneration (Hessl 2002, Kaye and others 2003, Kashian and others 2007). In western settings, researchers have emphasized the need to apply appropriate spatial and temporal scales to assess aspen condition (Turner and others 2003, Kashian and others 2007). In West Virginia, a disjunct population of trembling aspen occurs approximately 100 km south of its primary range (Perala 1990) in the 30-km² wetland areas of Canaan Valley. Although trembling aspen occurs elsewhere in the state, climatic conditions in Canaan Valley closely resemble boreal conditions to the north, and aspen assumes a clonal growth form that is readily observable.

In its primary range, aspen has high commercial value. In Canaan Valley, wildlife, biodiversity, and aesthetic values are more important. Aspen stands provide habitat for several plant species of concern, including *Viburnum lentago* (state rank S2, “rare and imperiled,” West Virginia Natural Heritage Program 1995), *Equisetum sylvaticum* (S1, “extremely rare and critical imperiled”) and *Polemonium vanbruntiae* (S2). Aspen stands are also an important food source for beaver (*Castor canadensis*), and habitat for a wide variety of breeding birds and other wildlife needing young forests, particularly woodcock (*Scolopas minor*) (Kletzly 1976). Canaan Valley has historically contained the best habitat and highest woodcock populations in the state (Webb and Samuel 1982, Steketee 2000), and the area is an important migration staging area for the species (U.S. Fish and Wildlife Service 1990). Habitat loss is thought to be a primary factor contributing to woodcock population declines in the state (Bruggink 1997) and elsewhere.

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OBJECTIVES

Because of wildlife and biodiversity concerns, wildlife managers are interested in sustainable management and thus the population dynamics of these disjunct aspen stands. The purpose of this study was to evaluate the composition and structure of trembling aspen stands in Canaan Valley National Wildlife Refuge (CVNWR) in Tucker County, WV. Specifically, we assessed tree diameter and age structures and distributions, patterns of stand initiation, stem mortality, and species replacement. As part of a final objective, we determined whether the CVNWR aspen stands tend to expand or whether they are relatively static in size.

STUDY AREA AND METHODS

Canaan Valley is an elongated, eroded valley in Tucker County, WV, in the Allegheny Mountain Section of the Appalachian Plateau Physiographic Province (Fennerman 1939). The diverse assemblage of bogs, fens, wet meadows, and swamps in the valley totals nearly 3,000 ha (Fortney and Rentch 2003).

Aspen occurs on poorly drained, mottled, silt or clay loams, underlain by clay or clay loams, including those of the Blago (Typic Umbraquults), Brinkerton (Typic Fragiaqualfs), and Lickdale (Haplaquepts) series (Fortney 1975, Nat. Resour. Conserv. Serv. 1995). Organic soils are largely absent, and hydric soil indicators include depleted matrix and redox depressions (Byers and others 2007).

The average freeze-free period in Canaan Valley is 90 days (Beverage 1967), and frost may occur during any month. Mean January and July temperatures are -3.5 °C and 18.7 °C, respectively. Mean annual precipitation is 127.2 cm (Natl. Climate Data Center 2003). A distinguishing climatic feature of Canaan Valley is a frost pocket effect: the drainage of cold, nocturnal air downslope into concave land formations, depressing temperatures on the valley floor.

One notable feature of aspen in Canaan Valley is that the species is more abundant now than in the prelogging environment. Accounts of prelogging vegetation (e.g., Brooks 1911, Clarkson 1993) suggest that the primary vegetative cover on the valley floor was a mixed spruce-hemlock swamp forest with an understory of *Rhododendron maximum* L. During the railroad logging era of 1886-1924, forests were clearcut and slash and exposed soils were subject to extreme drying. As a result, much of the valley burned repeatedly from ignitions from logging operations. Following burning, the plant environment became more favorable to aspen, primarily by the exposure of mineral soil, critical for aspen germination (Barnes 1966, Perala 1990), and the reduction of seed source of red spruce and other woody competitors.

Trembling aspen stands were identified from 1997 National Aerial Photography Program imagery (Fortney and Rentch 2003). Using ArcView 3.2 (Environmental Systems Research Inc., Redlands, CA), we identified aspen stands based on the vegetation signatures of the 1997 imagery and ground truthing activities. This shape file was then overlaid on an orthorectified 1945 U.S. Department of Agriculture black and white panchromatic print and modified based on vegetation signatures. From forest cover classification, we estimated descriptive statistics in the valley for the two time periods. Because the distribution of aspen polygon size was heavily skewed toward smaller stands (skewness = 8.7 and 6.0 for 1945 and 1997 data, respectively), we used median as the measure of central tendency.

We then selected 14 stands in the field that were representative of a broad range of age and size classes from several different areas of the valley. In each stand, a 20 x 25 m permanent plot was established in the center. Additional data from one 400 m² sample plot were provided by WV Division of Natural Resources. In each plot, we conducted a 100 percent tally for saplings (diameter at breast height [d.b.h.] <2.5 cm, height >1 m) and live and standing dead trees (d.b.h. ≥2.5 cm).

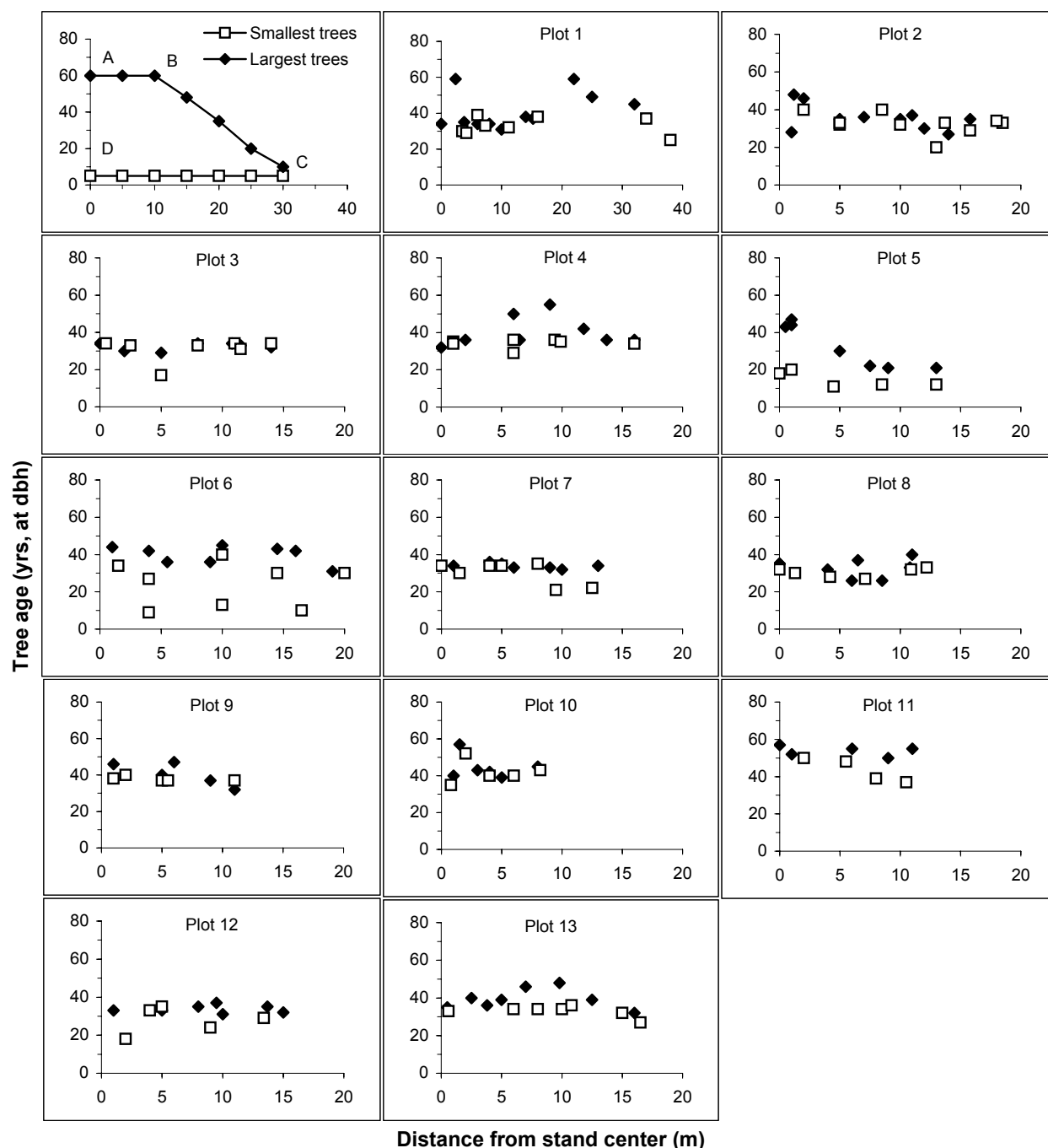


Figure 1.—Scattergrams of trembling aspen age at d.b.h. (yrs) and distance (m) from stand center along two distance gradients, Canaan Valley National Wildlife Refuge, Tucker County, WV. Large trees are diamonds, small trees are squares. Theoretical model, based on Leak and Graber (1976), is shown in first panel.

We adapted a method proposed by Leak and Graber (1974) that uses age structure to determine rate of stand expansion. They proposed that a change in stand boundary should be reflected in the relationship between maximum and minimum stem age over a distance gradient from the center of a stand to its edge (Leak and Graber 1974, Solomon and Leak 1994). When a stand first initiates, line AB of Figure 1 represents the theoretical model of age distribution of the largest trees. Advanced regeneration within the stand is represented by line DC, and recruitment at the stand edge and boundary advance is represented by line BC.

Using this technique, we established two random transects from the stand center to the outer edge, and we took increment cores or cross-sections (at breast height, 1.7 m) from both the largest and smallest aspen stems at regular intervals (i.e., every 3-5 m, depending on stand size and transect length) to the outer edge. Mean transect length from center to edge was 15.0 m (± 1.4). Age data were collected for 189 trees but not collected for plots 14 and 15. We prepared and cross-dated samples using standard dendrochronological techniques, and measured annual rings under a dissecting microscope to the nearest 0.001 mm. Tree-ring dating was validated using the program COFECHA (Holmes 1983). Aspen age distributions refer to minimum time since stand initiation, not true clonal age, which is very difficult to determine (Kashian and others 2007). In addition, tree ages do not include an estimate of the number of years required to reach breast height.

RESULTS

Valley-wide Trends 1945-2000

Landscape-level statistics for 1945 and 1997 were of the same order of magnitude for median stand size, total area, and total number of stands (Table 1). Results for the two time periods differed primarily in maximum stand size. In 1945, the largest stand was 0.85 ha, while in 1997 the largest stand was 9.8 ha, and

three areas were >5 ha in size. Estimates of median stand size are slightly larger than values in the literature cited for eastern aspen (e.g., Kemperman and Barnes 1976, Peterson and Squiers 1995), which we attribute to the difficulty of using GIS to identify and map very small stands of only a few trees.

Stand composition and structure

At minimum, aspen constituted 96 percent of the total basal area and 88 percent of the total sampled trees (Table 2). The only non-aspen overstory species present was red spruce (*Picea rubens* Sarg.), which occurred once in each of two plots. Understory tree species present but not abundant were hawthorne (*Crataegus* sp.) and serviceberry (*Amelanchier laevis* Wieg) and no aspen saplings were tallied in four plots (4, 10, 11, 14). Shrub cover averaged 26.5 percent (SE = 5.0 percent), primarily *Vaccinium myrtilloides* Du Roi and *Spiraea alba* Michaux. For all but two sample plots, the distribution of live and dead trees tended to approximate normality (Fig. 2), although positively skewed with a heavy right tail (Krasny and Johnson 1992). Based on age distributions, eight stands (plots 3, 7, 8, 9, 11, 12, 13) were in the stem exclusion stage (Oliver and Larson 1996) and the remaining stands were in understory reinitiation, indicated by the presence of younger cohort(s). Quadratic mean diameter (QMD) of standing snags in two URI stands (plots 5, 10) was >QMD of live stems; for these and two additional stands, the ratio of dead:live basal area >0.28, which met the criteria for the onset of stand breakup as proposed by Pothier and others (2004).

Median age for 10 stands was between 30 and 40 yr, with relatively tight age distributions around the median and a range of ≤ 8 yr between the 25th and 75th percentile, suggesting either that little mortality of the initial cohort had occurred, or that stand expansion was in its relatively early stages. Similarly, for 10 stands, the difference between the median age for large and small trees was ≤ 5 yr (Table 3).

Stand/Clone Expansion

For most stands (plots 2, 3, 6, 7, 8, 9, 11, 12, 13), the ages of smallest and largest trees along the distance gradient from center to edge were very similar, and no or only slight changes in stem age across the outer

Table 1.—Descriptive statistics for trembling aspen stands in Canaan Valley, Tucker County, WV, 1945-1997, from interpretation of aerial photographs.

Parameter	1945	1997
Median size (ha)	0.06	0.10
Minimum size (ha)	0.02	<0.01
Maximum size (ha)	0.85	9.83
Total area (ha)	43	61
Count	148	142

Table 2.—Density (TPH, trees/ha; BAH, basal area/ha, m²), and quadratic mean diameter (QMD, cm) for live and dead saplings (d.b.h. < 2.5 cm, height > 1 m) and trees (d.b.h. > 2.5 cm) from 15 trembling aspen stands, Canaan Valley National Wildlife Refuge, Tucker County, WV. Ratio is the ratio of dead BAH to live BAH. “Other” includes red spruce, hawthorns, and serviceberry.

Plot	Live aspen			Dead aspen			Ratio D/LBa	Other		
	TPH	BAH	QMD	TPH	BAH	QMD		TPH	BAH	QMD
1	1100	23.0	16.3	360	6.7	13.8	0.29	150	0.5	6.2
2	1680	26.0	14.0	280	2.6	10.8	0.10	-	-	-
3	1340	25.0	15.4	440	6.7	13.9	0.27	20	0.1	5.5
4	1500	26.1	14.9	500	3.8	10.0	0.15	-	-	-
5	4600	18.9	7.2	920	5.3	8.5	0.28	-	-	-
6	2200	21.8	11.2	1060	7.2	9.3	0.32	-	-	-
7	2400	30.0	12.6	600	4.7	10.0	0.16	-	-	-
8	2020	26.8	13.0	1040	4.6	7.5	0.17	-	-	-
9	2600	22.9	10.6	440	1.5	6.6	0.07	-	-	-
10	1020	28.2	18.8	360	11.3	20.0	0.40	120	0.3	5.2
11	1200	32.2	18.5	360	4.0	11.9	0.12	-	-	-
12	2700	15.9	8.7	500	1.8	6.8	0.11	20	0.1	5.6
13	1620	19.3	12.3	420	1.4	6.6	0.07	-	-	-
14	1020	5.6	8.3	na	na	na	na	20	0.1	5.6
15	1275	18.5	13.4	225	2.1	18.9	0.11	25	0.6	17

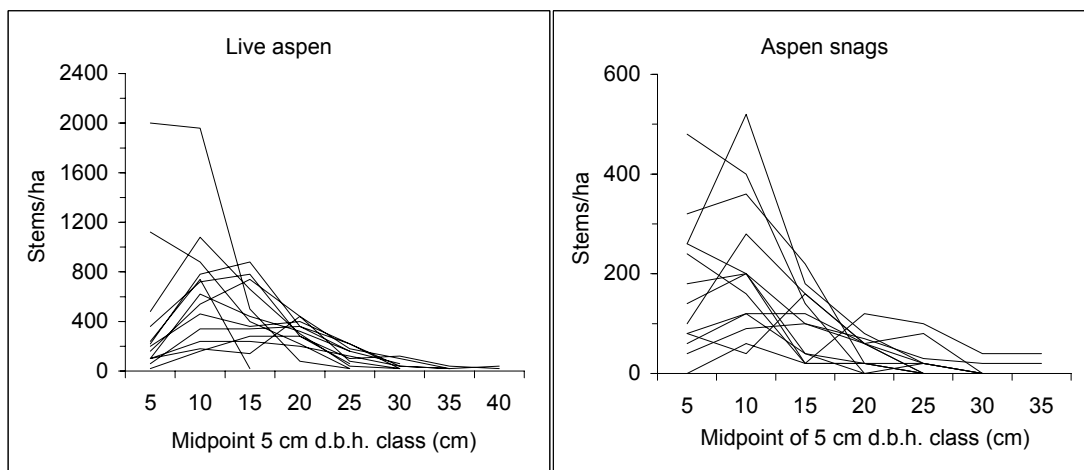


Figure 2.—D.b.h distribution (stems/ha) of live aspen and standing aspen snags (d.b.h. >2.5 cm) for 15 sample stands, Canaan Valley National Wildlife Refuge, Tucker County, WV.

stand boundaries were observed (Fig. 1). For the four remaining stands there was a general trend of decreasing stem age at the stand edge, although only stand 5 closely approximated the model of Figure 1.

Age distributions of several plots (1, 4, 5, 6) also suggest that scattered overstory mortality and replacement have occurred. In these plots, diameter differences reflect different times of establishment. For example, the oldest cored tree in plot 1 (Figure 1) occurred 22 m from stand center, and tree age declined from there to stand edge at 38 m. Toward the center of this plot, tree ages ranged from 31 to 59 yr. Based on the ages of the oldest and youngest trees, the earliest overstory stem mortality/replacement occurred between stand-ages of 20 and 30 yr.

Table 3.—Median tree ages for largest and smallest trees along transects from center to edge of stand, for 13 trembling aspen plots, Canaan Valley National Wildlife Refuge, Tucker County, WV.

	Median Age (yrs)	
	Largest trees	Smallest trees
Plot 1	37	32
Plot 2	35	33
Plot 3	33	33
Plot 4	36	35
Plot 5	30	12
Plot 6	42	28
Plot 7	34	34
Plot 8	34	na
Plot 9	40	37
Plot 10	42	40
Plot 11	55	44
Plot 12	33	29
Plot 13	39	34

DISCUSSION

Aspen stands in Canaan Valley have been a feature of the landscape since exploitative harvesting ceased during the late 1920s. Between 1945 and 1997, little change in the number of stands, total area, or median size was found. We suggest that the initiation of aspen in the study area was linked to land-use changes following harvest. Beginning in the early 1940s, many of the better drained lowland areas that are now aspen stands were converted into agricultural land. Large areas were sown in grass for pasture and hay, and hundreds of head of stock grazed. Tillable areas also were converted to row crops, including potatoes and cauliflower (Fortney 1993). Row-crop agriculture was largely abandoned in the 1950s, and the last of the grazing horses and cattle were removed during the 1960s (Michael 2002).

Stand median ages are synchronous with this chronology. Stands initiated between 30 and 55 yr ago, and we propose that the oldest stems of aspen were from seedlings that initiated after the forests were first harvested and burned. Younger trees may have been ramets of these pioneer seedling-origin trees—suckers that initiated after some type of disturbance or overstory mortality—and the youngest stems were probably second-generation ramets of the seedling-initiated stems.

Ages of the largest and smallest trees from center to edge were relatively uniform for more than two-thirds of the stands, indicating that all stems generated more or less simultaneously, and that stands were in the stem exclusion stage of development. Conversely, the remaining stands showed evidence of overstory mortality and the initiation of new stems from center to edge, as well as an advancing edge. The onset of overstory mortality and establishment within the stand and along its edge does not appear to be simply age-related, since there were few overall differences in median stand age between those that were stationary and those that were expanding. Peterson and Squiers (1995) noted that stand boundaries may be relatively fixed because of competition from adjacent plant communities. In Canaan Valley, the juxtaposition of some aspen stands with *Sphagnum* and *Polytrichum* bogs, shrub thickets, and sedge clones (*Carex* sp.) may provide conditions that resist encroachment by aspen suckers. Hogg and Lieffers (1991) found that vigorous competitors such as bluejoint grass (*Calamagrostis canadensis* Michx.) can significantly reduce

sucker growth. Fortney (1975) found aspen stands in Canaan Valley that were established in *Polytrichum* bogs, but these stands tended to be of low vigor, and short-lived due to nutrient shortages, competition, and cold-injury.

The presence of unfavorable soil conditions within and at the stand boundary also may discourage ramet emergence and/or survival, and may hasten overstory mortality. Aspen growth tends to be reduced on finely textured soils with hardpans that restrict rooting depth (Stoeckler 1960), and flooding or saturation after disturbance inhibits root suckering (Frey and others 2003). Even in cases of high soil moisture, low oxygen availability may inhibit water uptake and create conditions of moisture stress, leading to poor vigor, reduced growth, and mortality (Frey and others 2004). In Canaan Valley, soil and hydrologic complexity on the valley floor may limit growth and regeneration and provide unseen obstacles to clonal expansion.

Finally, due to the clonal nature of aspen, stem growth, mortality, and ramet emergence are all group phenomena (Frey and others 2004). Therefore, observed differences in stand development may be, in part, attributable to genetic variability among clones and across the Canaan Valley population. These effects may be distinct from restrictions on growth and regeneration imposed by environmental variability of soils, soil moisture, and composition of adjacent plant communities.

In contrast to stand development patterns in other regions, where trembling aspen is often replaced by more shade-tolerant species (Bates and others 1989, Perala 1990, Peterson and Squiers 1995), the species appears to replace itself in Canaan Valley. The virtual absence of red spruce regeneration in these stands may be an artifact of remoteness of seed source in the aftermath of logging and fires. However, there were other tree species such as yellow birch (*Betula alleghaniensis* Britt.), red maple (*Acer rubrum* L.), and eastern hemlock (*Tsuga canadensis* L. (Carr.)) that survived post-logging fires and were relatively abundant in upland areas, as well as in non-aspen swamp forests on the valley floor. Although these species are tolerant of shade and moist soils, and thus, a potential successor to aspen, they were not present in our study stands.

Based on tree age distribution at stand center, we estimate that initial aspen overstory mortality may occur at as early as 20 yr in this region. This is consistent with the observations of Krasny and Johnson (1992) that self-thinning (and stand development) occur very rapidly in clonal stands, but it is considerably less than estimates that the onset of stand breakup and decline occur at 45-80 yr in other regions (Fralish 1972, Shields and Bockheim 1981, Perala 1990, Kurz and others 2007). However, aspen in the study area is at the edge of its southernmost distribution; across the species' North American range, there is considerable variation of the timing of dieback (Frey and others 2003), which may be influenced by climate and mean annual temperature (Shields and Bockheim 1981).

Selection of large and small trees along the distance gradient assumes that larger trees are older. We expected a strong d.b.h.-age relationship for trembling aspen, given its shade intolerance (Perala 1990), yet the linear relationship between age and diameter was surprisingly weak (large trees, $R^2 = 0.24$, small trees, $R^2 = 0.37$). Also, Leak and Graber (1974) developed their technique to detect stand expansion to investigate boundary movements over much longer time, distance, and elevational gradients, in response to regional climate shifts and disturbance patterns. In this study, distance gradients were only 12-38 m in length, and the number of sample trees available in such a short distance was limited. Both factors may tend to reduce the resolution of the technique and its ability to detect changes in stand boundaries at the distance and time scales of the study. Finally, although it is not uncommon for multiple clones to form a single stand, we did not identify separate clones/stand in this study. In cases where study stands were

comprised of more than one clone, this would tend to distort the modeled age-size relationship from “center” to edge for expanding stands.

CONCLUSIONS

In Canaan Valley, the majority of aspen occurs in single-species stands that initiated between 1950 and 1970. Less than one-third of the stands appear to be expanding, and some of these are expanding at a very modest rate. The species composition and age distributions suggest that most stands have a component of stems that are older, than the median age as well as a component that is younger than the median age, which indicates that in addition to expansion at the edge, stand replacement—but not species change—is occurring at the stand center. Most stands do not appear to be expanding, limited either by competitive pressure from adjacent plant communities, unsuitable habitat, or genetics. Resource managers who wish to retain aspen for biological diversity and wildlife objectives should monitor stands for age and vigor. In addition to natural regeneration, they also may consider partial or complete overstory removal of older clones as an alternative way to stimulate ramet emergence and stand replacement.

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