

Spatial Pattern and Population Dynamics of *Populus tremuloides* in a Saskatchewan Aspen Grove

O. W. ARCHIBOLD and M. R. WILSON

Department of Geography, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0

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The spatial pattern of nine 5-yr age-classes of trees in a grove of Trembling Aspen (*Populus tremuloides*) was studied by applying nearest-neighbor analysis to a transect, 10 × 60 m. Three marked differences of pattern were noted in the transect: random spacing of trunks in the peripheral part of the transect, more regular spacing in the transition zone, and a return to nearly random spacing at the core. From the literature on aspen ecology these results are interpreted as localized differences in age structure and density within a single clonal population, with cycles of replacement that are of shortest duration at the periphery of the grove where moisture stress is most frequent and severe.

Key Words: aspen groves, spatial pattern, nearest-neighbor analysis, age-classes, transect.

Previous studies of the geographical distribution of Trembling Aspen (*Populus tremuloides*) have been conducted either as broad ecological surveys (Bird 1961; Maini 1960; Maini and Cayford 1968) or as historical accounts in which change in the range of the species has been documented with respect to land settlement (Watt 1960). More detailed surveys have been of the forest inventory type with any information on stand characteristics and local distribution patterns obscured in generalized growth and yield data (Kirby et al. 1957; Steneker 1976), although extensive work has been carried out on delineating the boundaries of individual aspen clones (Barnes 1966). Techniques of pattern analysis such as those developed by Greig-Smith (1957) and Kershaw (1957) have typically been applied to herbaceous vegetation, although mean square/block size analysis of this type has been applied by Shinn (1971) to an old-growth cedar-hemlock stand. The study by Whitney and van Groenewoud (1964) of the rate at which fungal infection thinned a White Spruce stand is exceptional in that a map of the stand is given, but no quantitative assessment of the resulting patterns was made. Analysis of spatial pattern is limited by the fact that the general problem of pattern analysis in plants has proved to be awkward biologically as well as mathematically (Pielou 1969, p. 122).

Trembling Aspen grows in a wide range of plains and montane environments across

northern North America but is best represented in the "Aspen Grove Section" of the Boreal Forest Region (Rowe 1972), the southern margin of which is fragmented with the trees occurring as groves interspersed with grass prairie and cropland. Throughout this region groves of aspen are most often found on land too sandy or stoney to be broken even for improved pasture. The site selected for study is within an area of fixed sand dunes about 30 km SW of Saskatoon, Saskatchewan (52° 2½'N, 106° 51'W); the study transect extended from a level area that had been cleared for haying down a slope of about 4° to an elongated, infrequently flooded depression. The length of time that the selected aspen grove has gone without disturbance is not known, but the age of the oldest trees, about 50 yr in 1977, and the time when prairie fires were effectively suppressed, about 1919 (Raby 1966), provide upper and lower estimates.

This study describes the distribution pattern of individual trees in a prairie aspen grove and postulates some processes through which such patterns could have developed.

Methods

Preliminary inspection of aspen groves on dune sands in central Saskatchewan showed large older trees predominating in or near swales, or around the margins of willow-filled depressions that are close to the water table. A single-clone portion of one grove was identified by means of crown notch evidence (Barnes 1966,

p. 445). A transect 10 m wide was surveyed across the margin of the grove through the depression at its center and a series of survey stations was set up from which to plot the position of each tree by bearing and distance.

Measurements were made of trunk diameters at 1.2 m aboveground level (dbh) for each tree in the mapped transect. Thirty trees, selected as a representative though not strictly random sample of trunk diameters, were cored at the same height in order to produce a graph of dbh against ring-count age (Figure 1). The annual rings of aspen, like those of many other hardwoods, are not easily distinguished and many methods have been proposed to solve this problem (Maini and Coupland 1964). A very simple method and one which served well in this research was to dip the air-dry cores into hot black coffee for about 1 min. Air was expelled from the porous wood and the rings were clearly visible while they remained wet. Dead trees were included in the mapping and their dbh measured, a distinction being made between dead trees still standing and stumps with rotting trunks beside them. To evaluate the spatial pattern of trees, we divided the transect into six quadrats of 10×10 m and applied nearest-neighbor analysis (Clark and Evans 1954) to the mapped distributions. The significance of the nearest-neighbor index (R) was tested using the z -score technique of King (1969).

The value of R is found by defining a sample area, measuring the mean distance from each point (in this case, tree trunk) to its nearest neighbor, then dividing by the mean distance to be expected from a corresponding number of points randomly distributed over the same area. Mean random distance is calculated as the reciprocal of twice the square root of points per unit area, or $\frac{1}{2\sqrt{N/A}}$. R approaches 0 for completely clustered points, is 1.0 for a random distribution, and reaches 2.15 for a perfectly uniform pattern. The z -score for R is a two-tailed test in which the difference between observed and random mean distances is divided by the standard error of the random mean distance (King 1969, p. 100). It provides a probability of chance occurrence for a given R value; no test of the significance of differences between R values exists.

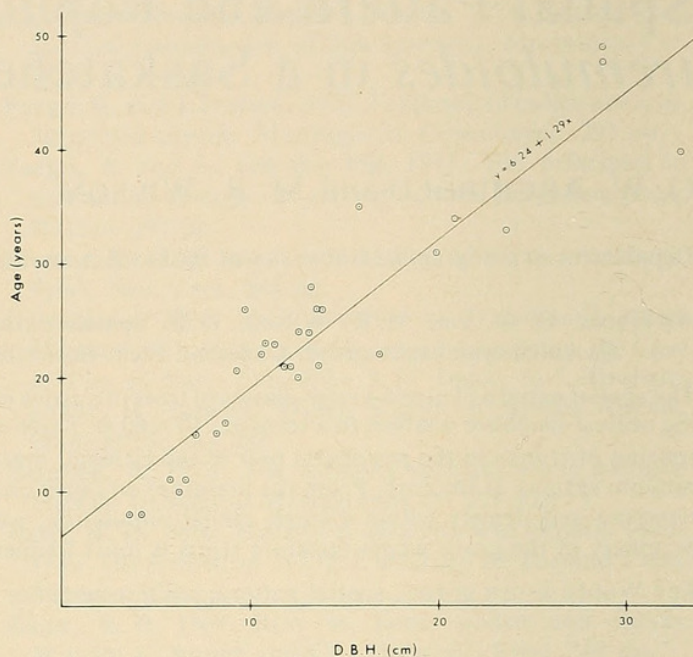


FIGURE 1. Relationship between diameter at breast height (dbh, measured at 1.2 m) and age of Trembling Aspen trees ($y = 6.24 + 1.29x$).

Results

Because of the absence of clear break points in the age distribution of the sample an arbitrary 5-yr division was used to derive the age-class data presented in Figure 2. Three zones can be distinguished: periphery (0 to 10 m), transition (10 to 40 m), and core (40 to 60 m). The periphery of the grove represents a zone of active reproduction characterized by an abundance of young trees less than 10 yr old. No trees older than 30 yr were found here and only one dead tree was present. Within the transitional zone the number of young trees steadily declined with only four young individuals found in the 30- to 40-m quadrat. Older trees increased in number, but none were older than 35 to 39 yr. Dead trees and stumps are common in this zone, particularly in the 20- to 30-m quadrat. Within the core zone of the grove only five older trees were encountered with all other individuals in the youngest age class.

Analysis of spatial patterns in the transect is based on Figure 3, which shows the distribution of the trees, with associated data presented in Table 1. The density measurements depend somewhat on the choice of quadrat boundaries but the general pattern is not obscured. Density is greatest at the periphery of the grove (0.53 individuals/m²), decreases to 0.17 individuals/m² in the fourth quadrat, and rises slightly

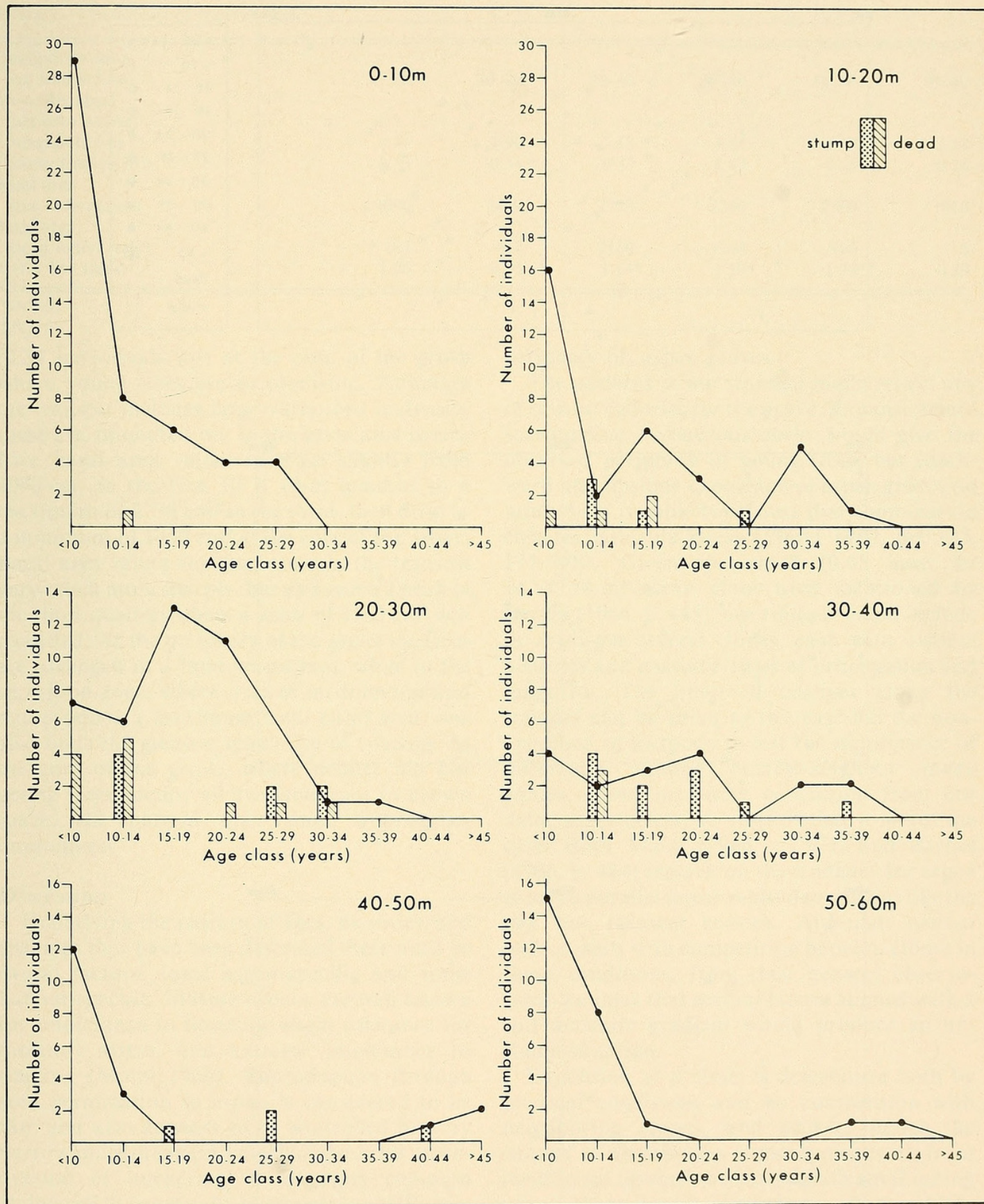


FIGURE 2. Age-class distributions for Trembling Aspen trees in each 10-m quadrat of the transect.

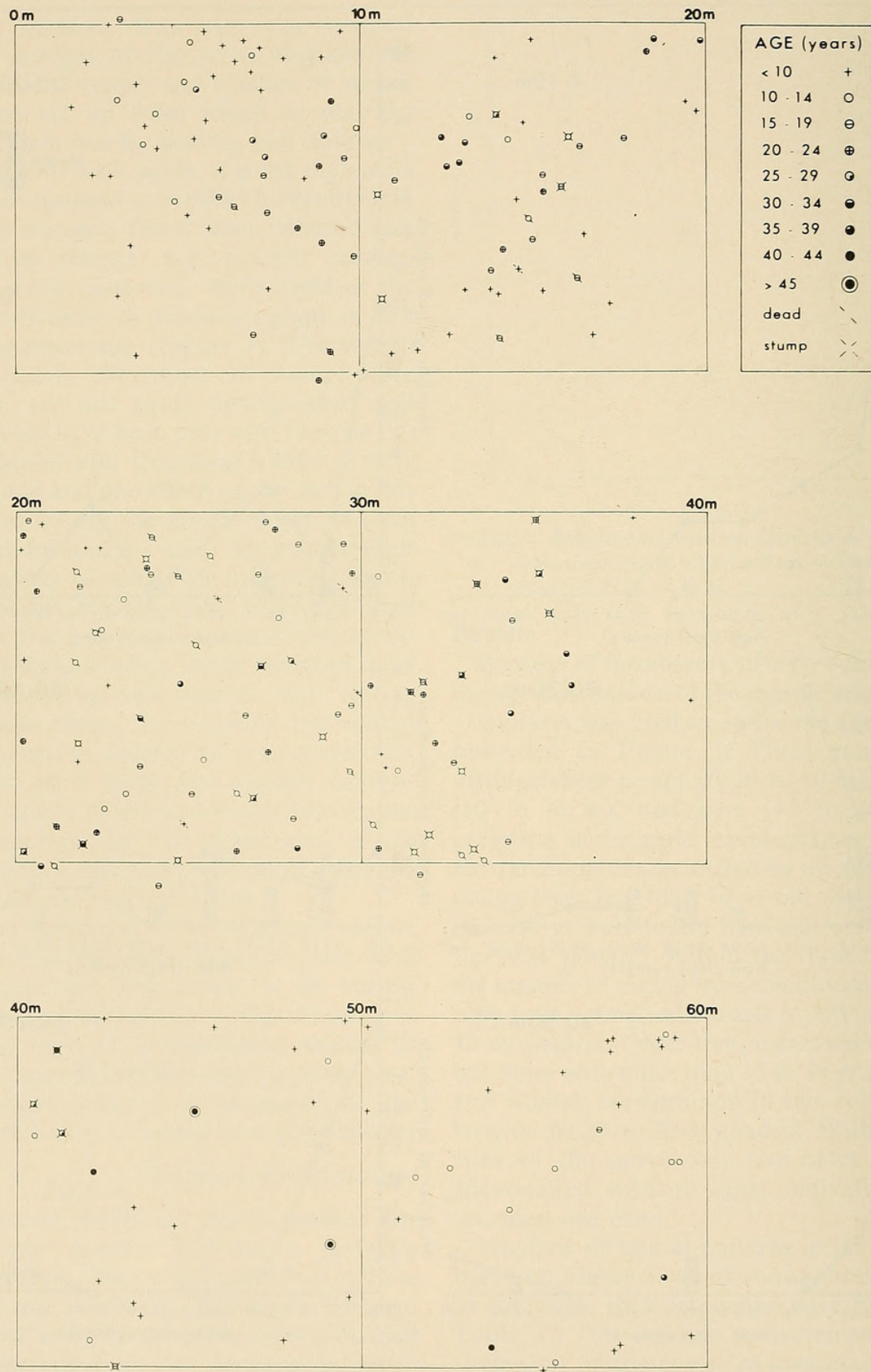


FIGURE 3. Spatial pattern of Trembling Aspen trees in the transect.

TABLE 1 — Summary of transect data

Quadrat position on transect (m)	0-10	10-20	20-30	30-40	40-50	50-60
Mean distance between nearest neighbors (m)	1.71	1.90	2.18	3.65	3.67	2.13
Density (indivs/m ²)	0.53	0.34	0.37	0.17	0.18	0.24
Basal area live indivs (cm ²)	2090	2400	2730	2240	2560	1410
Basal area dead indivs (cm ²)	184	467	2160	1240	960	0
R (for live trees)	1.06	0.95	1.14*	1.29*	1.33**	0.89

* $P < 0.05$.** $P < 0.01$.

(0.24 individuals/m²) at the core of the grove where young trees are recolonizing. Although the transect includes large variations in density these are smoothed out in the basal area totals. Live basal area values increase slightly from 2090 cm² in the first 10 × 10-m quadrat to a maximum of 2730 cm² in the third, then drop to a minimum of 1410 cm² at the core of the grove. Basal area values for dead trees in the transect vary much more sharply, but also reach a peak in the third quadrat where a value of 2160 cm² was recorded. At the periphery of the grove the trees are arranged in a random pattern, while in the transition zone, where trees of medium age and size produce a maximum total basal area, one also finds the greatest regularity of spacing. At the core of the grove, where neither old nor young trees occupy all available root or crown space, the pattern once more approaches randomness.

Discussion

Underlying the pattern of ages, densities, and spacings that have been described there must be causal factors, some aspen-specific and some habitat-specific. Mature aspens are well known for intolerance to flooding, slight tolerance for moisture stress, and extreme intolerance to shading (Maini 1960). Reproduction through seed germination in aspen is considered to be rare and also appears to be controlled by very narrow moisture requirements; vegetative reproduction or 'suckering' is far more common giving rise to genetically identical clones (Barnes 1966, p. 441). For abundant and vigorous suckering, strong light and heat must reach the forest floor so that conditions most favorable to suckering are found in openings in, or on the

periphery of, aspen groves.

The patterns in our transect might reflect any of several histories for the grove. Expansion into surrounding herbaceous cover would give the observed periphery of young trees, but southward and upslope expansion of aspen groves on sandy soils is unlikely because that combination elevates moisture stress (Maini 1960, pp. 175, 177-178). Given the small (0.05 acre, or 14 × 14 m) mean clone area mentioned by Barnes (1966, p. 445), our transect could include or cross-cut several clones, each with distinct histories and characteristics of propagation and longevity. The observed changes along the transect can be fitted to this case but the non-existence of methods to test the significance of differences among nearest-neighbor index values allows no direct conclusion from our data; nevertheless we suspect that it is not the case. Both Maini (1960, p. 171) and Barnes (1966, p. 444) remark on the tendency for aspen roots to parallel linear moist depressions like the one our transect crosses. Although neither author deals with competition between clones in these conditions, from their general observations we infer that several clones aligned with a soil moisture gradient would produce an unstable situation.

Expansion of a clone is determined both by physical conditions and by competition with neighboring clones, and suckers under the canopy of neighboring clones typically die from insufficient insolation unless significant thinning occurs through some disturbance (Barnes 1966, p. 445). The extreme annual variability of precipitation in the interiors of continental landmasses leads to frequent periods of water stress (Maini 1960, p. 170). Hence not only is

expansion into surrounding areas limited but significant thinning should allow expansion of favored clones to occur periodically. Where a gradient of moisture availability is steep enough to stress one clone more than another, the clone at the wetter end of the gradient can be expected to 'capture' the drier end through more vigorous suckering. It follows logically that clone-to-clone boundaries should radiate from moist depressions, but this requires confirmation by further study.

The profile of age composition along the transect is therefore interpreted as a series of growth cycles within a single clone, increasing in duration toward the core zone. Trees in the periphery (0 to 10 m) appear to have a shorter maximum life span than those nearer the core, although repeated sprouting keeps the zone well stocked with suckers. Through the transition zone (10 to 40 m) trees attain ages up to 40 yr, although the stand is nevertheless thinned by deaths of individuals of all ages. Periodic 'die-offs' are mentioned by Graham et al. (1963, p. 91), but it is not clear whether these are attributed to aspen-aspen competition, environment-aspen stress, or a combination of these. In the core zone (40 to 60 m) a few trees live to ages in excess of 45 yr; after these die the absence of middle-aged trees will give the false appearance of a grove expanding into the central depression.

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Literature Cited

- Barnes, B. V. 1966. The clonal growth habit of American aspens. *Ecology* 47: 439-447.
- Bird, R. D. 1961. Ecology of the aspen parkland of western Canada, in relation to land use. Canada Department of Agriculture Research Branch, Publication Number 1066.
- Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35: 445-453.
- Graham, S. A., R. P. Harrison, Jr., and C. E. Westell, Jr. 1963. Aspens, phoenix trees of the Great Lakes region. University of Michigan Press, Ann Arbor.
- Greig-Smith, P. 1957. Quantitative plant ecology. Butterworths, London.
- Kershaw, K. A. 1957. The use of cover and frequency in the detection of pattern in plant communities. *Ecology* 38: 291-299.
- King, L. J. 1969. Statistical analysis in geography. Prentice-Hall, Englewood Cliffs, New Jersey.
- Kirby, C. L., W. S. Bailey, and J. G. Gilmour. 1957. The growth and yield of aspen in Saskatchewan. Department of Natural Resources, Province of Saskatchewan, Forestry Branch, Technical Bulletin Number 3.
- Maini, J. S. 1960. Invasion of grassland by *Populus tremuloides*, in the northern Great Plains. Ph.D. thesis, University of Saskatchewan, Saskatoon.
- Maini, J. S. and J. H. Cayford. 1968. Growth and utilization of poplars in Canada. Canada Department of Forestry Rural Development, Forestry Branch Publication Number 1905.
- Maini, J. S. and R. T. Coupland. 1964. A simple technique for age determination in Trembling Aspen. *Forestry Chronicle* 40: 219-220.
- Pielou, E. C. 1969. An introduction to mathematical ecology. John Wiley and Sons Inc., New York.
- Raby, S. 1966. Prairie fires in the north-west. *Saskatchewan History* 19: 81-99.
- Rowe, J. S. 1972. Forest regions of Canada. Department of the Environment, Canada Forest Service, Publication Number 1300.
- Shinn, T. L. 1971. Patterns of regeneration in old-growth cedar-hemlock forest in coastal British Columbia. M.A. thesis, University of California, Berkeley.
- Steneker, G. A. 1976. Guide to the agricultural management of Trembling Aspen in the prairie provinces. Environment Canada, Canada Forest Service, Northern Forest Research Centre, Edmonton, Alberta, Information Report Number R-X-164.
- Watt, F. G. 1960. The natural vegetation of the southern great plains of Canada. *Geographical Bulletin* 14: 25-43.
- Whitney, R. D. and H. van Groenewoud. 1964. The rate of advance of stand-opening disease over a ten year period in White Spruce at Candle Lake, Saskatchewan. *Forestry Chronicle* 40: 308-312.

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