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SPATIAL DYNAMICS OF A PRIMARY SUCCESSION: NUCLEATION

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INTRODUCTION

Changes in spatial pattern during the course of succession have attracted considerable interest in recent years. Such changes are of interest not only for their own sake, but because they may throw light on mechanisms of successional change. Greig-Smith (1964) summarized the currently accepted hypothesis of successional variations in pattern. He suggested that the variations are determined by the establishment and growth of clumps (often clones) of persistent species. As these clumps enlarge, and eventually coalesce, the scale of pattern will increase, not necessarily smoothly, to a maximum at climax; on the other hand, the intensity of pattern will decline as the range of scale of contagion increases with age. Work by Whitford (1949), Greig-Smith (1952), Margalef (1958), Kershaw (1958), Pielou (1966) and Brereton (1971) supports this view.

Williams *et al.* (1969) have examined the question of whether succession is a gradual or stagewise process, i.e. does the rate of change of composition of the vegetation fluctuate? In a secondary succession in a Queensland rain forest they found a change from predominantly temporal to predominantly spatial variation after 6 years. If successional stages exist they are likely to influence variations in spatial pattern: patterns may differ from stage to stage but the pattern at times of transition may also differ from that within stages. Shafi & Yarranton (1973) have demonstrated stages of differing heterogeneity during a post-fire succession in the boreal forest. Their discovery that a stage may be succeeded by another of greater homogeneity implies that the scale of pattern may decrease during at least part of a succession. Anderson (1967) has also noted a decrease in the scale of pattern early in a succession. Morrison & Yarranton (1973) showed that heterogeneity is greatest during a sand dune succession at the transition between stages. Webb, Tracey & Williams (1972) raise the question of whether patches of vegetation occurring in a succession represent different stages of maturity; both Morrison & Yarranton and Shafi & Yarranton (1973) suggest that transitions from stage to stage take place heterogeneously on the ground so that this is indeed the case. If this is admitted as at least a possibility, it establishes the connection between the mechanism of succession and variations in spatial pattern.

On the basis of this reasoning it was decided that detailed examination of the pattern of vegetation on the ground before, during and after a stage-to-stage transition in a succession might not only clarify the sequence of spatial pattern but also help to elucidate the mechanism of succession itself. The sand dune succession at Grand Bend, Ontario, previously described by Morrison (1973), was selected for such a study.

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THE GRAND BEND SUCCESSION

The Grand Bend sand dune system is located in Pinery Park, Lambton County, Ontario, at 43° 15′ N, 81° 50′ W. It is underlain by limestones of the Hamiltonian formation. Sand is provided for dune formation by currents flowing south along the eastern shore of Lake Huron. The prevailing westerlies blow exposed sand towards the beach and over the past 5000 years or so have given rise to a 3-km series of sand dunes. Most of the dunes are 6–10 m in height but one reaches 30 m. The dunes nearest the beach, generally not more than 1200 years old, have occasionally been breached by the wind and substantial blow-outs have occurred. In the last 20 years excessively heavy recreational use has greatly increased the frequency of blow-outs. At present the leading edges of the youngest dunes are being eroded by wave action because of unprecedentedly high lake levels.

Hough (1958), Chapman & Putnam (1966), Lewis (1969) and Prest (1970) have described the glacial history of the region. The estimates of sand dune age used in this paper are based on radiocarbon dates for ancient shore lines of Lake Huron given by Lewis (1969). The ages, which range from 100 to 4800 years, were obtained by topographic levelling of the water-borne deposits beneath each dune and interpolation between Lewis's levels. Morrison (1973) provides detailed information about soil development. Details of the climate of the area are given by Brown, McKay & Chapman (1968).

Phytogeographers assign the area to the Niagara section of the deciduous forest region of Canada (Halliday 1937; Rowe 1959), and it lies just within the northern boundary of the 'Carolinian' zone of Fox & Soper (1955). The Carolinian affiliation implies a link with more southerly floristic elements. The diversity, richness and evenness of the vegetation show an initial rapid increase as succession begins, but their increases become asymptotic after 1000 years or so (Morrison & Yarranton 1973). The asymptotic value of the diversity is comparable with Monk's (1967) values for mature forest at this latitude. Superficially the succession appears to proceed from an open grassland, dominated by *Calamovilfa longifolia* and *Andropogon scoparius* with scattered *Juniperus communis* and *J. virginiana*, to a more or less closed oak–pine forest. Taxonomic nomenclature in this paper follows Gleason (1968).

Morrison & Yarranton (1974) have analysed the vegetational changes in detail and found a number of stages. The first dune, probably about 100 years of age, is somewhat different from those immediately following it, being characterized by *Populus balsamifera*, *Prunus pumila*, *Ammophila breviligulata* and *Salix glaucophylloides* which occur rarely elsewhere in the dune system. The vegetation on the remaining dunes was classified into two types, in the form of species groups of non-exclusive membership, by the method of Yarranton *et al.* (1972). Membership of the groups is as follows: I (colonizing group): *Andropogon scoparius*, *A. gerardi*, *Carex* sp., *Calamovilfa longifolia*, *Poa compressa*, *Stipa spartea*, *Artemisia caudata*, *Arctostaphylos uva-ursi*, *Juniperus communis*, *J. virginiana*, *Smilacina stellata*, *Symphoricarpos racemosus*, and *Quercus prinoides*; II (persisting group): *Rhus aromatica*, *R. radicans*, *Carex lanuginosa*, *Pteridium aquilinum*, *Fragaria virginiana*, *Rubus flagellaris*, *Ceanothus americana*, *C. ovatus*, *Vitis argentea*, *Quercus alba*, *Q. rubra*, *Q. velutina*, *Festuca ovina*, *Prunus serotina*, *P. virginiana*, *Amelanchier stolonifera*, *Symphoricarpos racemosus*, *Pedicularis canadensis*, *Lonicera dioica*, *Gaultheria procumbens*, *Comandra richardsiana*, and *Diervilla lonicera*. *Symphoricarpos racemosus* belongs to both groups. Group I dominates the vegetation on dunes of up to 1600 years of age and Group II dominates it on dunes more than 2900 years old. These two stages represent the 'grassland' and 'oak–pine forest' referred to above. Between these times is a transitional period which may help to elucidate the mechanism of succession and clarify the sequence of changes in spatial pattern during succession. This paper examines it in detail.

METHODS

During the transitional period Group II (persistent) species become established and increase in abundance as Group I (colonizing) species decline. The results of Morrison & Yarranton (1974) suggest that the replacement of Group I by Group II does not occur uniformly over the area and that some sites become covered by predominantly Group II vegetation earlier than others; at any given point the transition from Group I to Group II occurs rapidly relative to the length of the transitional period as a whole. To observe this phenomenon in detail it was decided to examine an area of the dune system covering the appropriate range of age by means of a grid of contiguous samples. Because of the effects of human activity in the park this proved impossible and two separate, laterally displaced grids were selected: one included dunes of estimated ages 800 and 1100 years, and measured 28 m wide (parallel to beach) and 70 m deep (perpendicular to the beach); the other included dunes of 1600 and 1900 years of age and measured 28 m wide by 56 m deep.

The sampled area was divided into 2 × 2 m squares and in each area an estimate of the percentage cover of each species present was agreed on by the two observers; where a 2 × 2 m plot appeared to be floristically heterogeneous it was subdivided into 1 × 1 m squares and these were sampled separately. The plot on the younger dunes was sampled in September 1971, and that on the slightly older ones in June 1972. Records for species belonging to Group I and Group II respectively were summed for each sample; *Symphoricarpos racemosus* was included in both totals.

It quickly became apparent that the deductions made by Morrison & Yarranton (1974) were substantially correct and that the appearance and growth of Group II vegetation is strongly heterogeneous. For reasons that will become evident later a transect was laid through a developing patch of this persistent vegetation. The length of the transect was 17 m and the height and species of all plants within 0·5 m of the transect line were recorded. Morrison (1973) has found evidence of heterogeneity in the soil profile contemporaneously with the vegetational heterogeneity at Grand Bend. For this reason a trench of at least 1 m depth was dug along the transect line and the soil profile recorded at 10 cm intervals.

RESULTS

The total covers of Group I (colonizing) and Group II (persistent) species in the sampled plots are indicated by isopleths and shading in the right-hand and centre sections of Fig. 1. The top of the figure represents the western edge of the sampled plots and runs parallel to the beach. It is immediately apparent that there is an increase in the cover of Group II species and a decrease in the cover of Group I species as succession proceeds. The contagious distribution of the persistent species is marked in the younger sampled plot, but between 1600 and 1900 years the scale of contagion caused by clump size becomes very large as the patches of these species coalesce. The behaviour of the colonizing species is the exact opposite; they decline in abundance, showing smaller-scale clump-size pattern as the patches of the persistent species merge. It is also evident

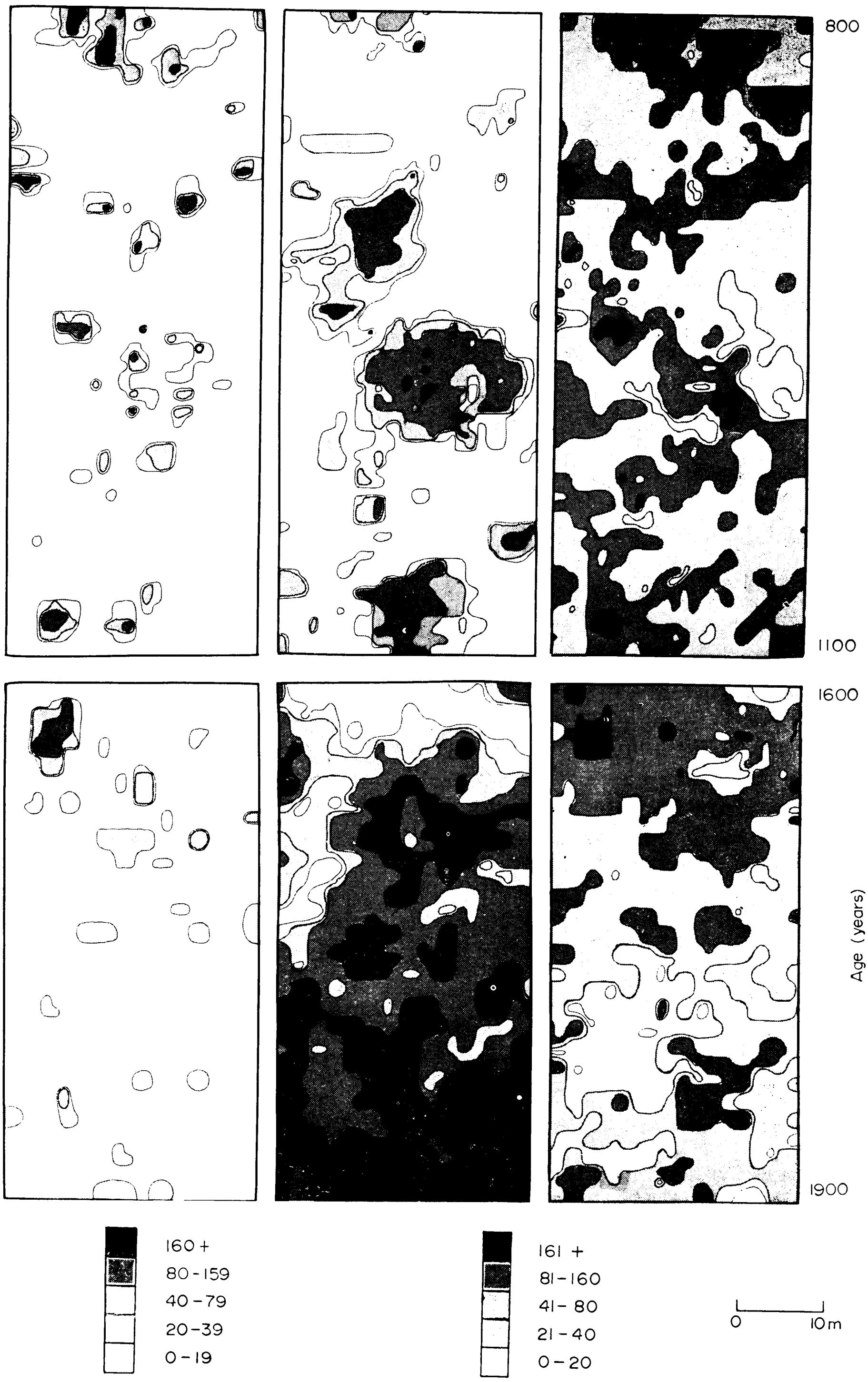

FIG. 1. Total cover of colonizing species (right), persistent species (centre) and *Juniperus virginiana* (left) on dunes at Grand Bend. Estimated surface ages are given on the right; the percentages of cover for the left, and centre and right panels are indicated in the keys.

that the colonizing species maintain an overall cover and very large-scale pattern until well after the initiation of the persistent patches. Young patches of Group II species appear to be associated with the densest cover of Group I species.

It became apparent during collection of the data that individuals of *Juniperus virginiana*, a member of Group I, are associated with the initiation of patches of Group II species. The youngest dunes on which scrub patches are found are 400 years old. On these and the 800-year-old dunes the patches consist almost exclusively of *J. virginiana* individuals; each patch includes plants ranging from seedlings to mature individuals, which frequently reach 8 m in height. These large individuals are very hard to core, but appear to be more than 100 years old. It appears that the *J. virginiana* patches are self-sustaining. Occasional dead stumps were found in the patches, but none was scarred; this suggests that burning was not a factor in renewal of the patches. On progressively older dunes more species appear in the scrub patches; on the 1100-year-old and older dunes oak hybrids dominate the patches and *J. virginiana* becomes subordinate to them. The left-hand part of Fig. 1 shows the cover of *J. virginiana* in the two sampled plots. Its association with Group II patches can be seen to be pronounced on the 800-year-old dune, but to decline on the 1100-year-old dune and to disappear as Group II species become dominant.

Fig. 2 shows a transect through a developing patch of persistent species; the patch sampled is the one that appears in the bottom centre of the upper plot in Fig. 1. The transect line runs from south-east (bottom left in Fig. 2) to north-west. A basic physiognomic difference between the colonizing and persistent vegetation is exemplified by the presence of the hybrid *Quercus rubra* × *velutina* in the centre of the persistent patch. The persistent vegetation is essentially oak–pine forest, whereas the colonizing vegetation is essentially open grassland with a few scattered bushes. Some individuals of *Q. prinoides* in the colonizing vegetation reach as much as 6 m in height; none of the very large individuals of this species or of *Juniperus virginiana* appears in the transect, so that the physiognomic difference between the vegetation types is slightly exaggerated in Fig. 2. However, the dense growth of bushes such as *Prunus virginiana*, *Amelanchier stolonifera*, *Shepherdia canadensis*, *Symphoricarpos racemosus* and *Rhus aromatica* is typical of these patches. The presence of *Juniperus virginiana*, already commented on, is also evident as is that of its congener *J. communis*.

Grasses and other subordinate plants are not shown in Fig. 2. Common species in the transect outside the clump are *Arctostaphylos uva-ursi*, *Artemisia caudata*, *Calamovilfa longifolia*, *Stipa spartea*, *Andropogon scoparius*, *A. gerardi*, *Sorghastrum nutans*, *Poa compressa* and *Liatris aspera*. These species are much less frequent within the clump, with the exception of *Poa compressa* which is more frequent. *Carex* sp. is another member of Group I that is more abundant in the persistent patches. *C. lanuginosa* is found mostly around the edge of the canopy of the oak tree and grows as dense tussocks; in later parts of the succession it is found as isolated stems that are widely distributed.

A relationship between the development of the soil profile and the growth of patches of persistent vegetation is indicated by Fig. 2. The development of a humus layer is confined to the persistent patch and the depth of soil layers is much deeper there than elsewhere. Morrison (1973) has analysed soil from many pits taken in and between patches of persistent vegetation on the sampled dunes; Table 1 lists analytical results from six of his pits on the 1100-year-old dune. All analyses were carried out on air-dried samples and the choice of analytical methods was influenced by the high carbonate content of the sand. Soil moisture capacity was determined by the difference between the 0·33-bar percentage (wet limit) and 15-bar percentage (dry limit) of oven-dried soil weight (Webber & Tell

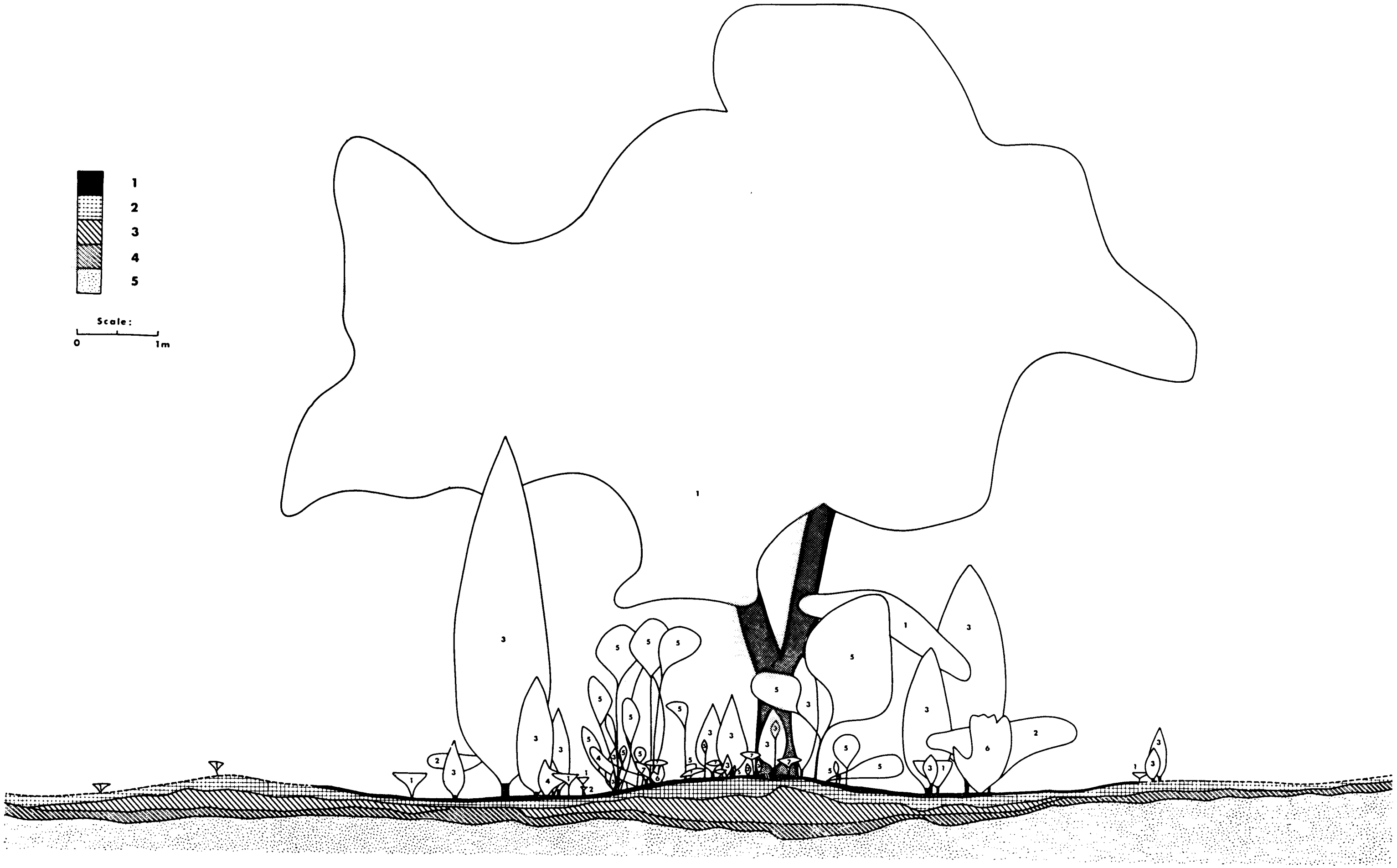

FIG. 2. Transect through a patch of persistent vegetation on the 1100-year-old dune at Grand Bend. Key to species: (1) *Quercus rubra* × *velutina*; (2) *Q. prinoides*; (3) *Juniperus virginiana*; (4) *J. communis*; (5) *Prunus virginiana*; (6) *Shepherdia canadensis*; (7) *Symphoricarpos racemosus*. Key to soil layers: (1) humus layer, black; (2) grey black layer; (3) dark brown-black layer; (4) brown to reddish-brown layer; (5) parent material, blown sand.

Table 1. *Soil profiles and analyses of samples from six sites at Grand Bend*

Site	Layer limits (cm)		pH	Fe (ppm)	Na (ppm)	Mn (ppm)	K (ppm)	Org. C (%)	Moisture capacity*
1	0–5	Humus	7·7	11·3	6·1	40·0	79·5	16·27	6·55
	5–8	Grey-black	7·9	22·3	6·6	21·2	21·8	12·77	1·06
	8–24	Dark to red brown	7·9	16·2	6·7	11·6	14·4	6·26	1·23
	24–35	Light red brown	8·0	24·4	5·9	5·2	8·2	2·37	0·74
	35–52	Dark brown	8·0	23·0	6·6	8·5	6·7	2·89	1·28
	52+	Parent material	7·9	55·7	6·4	1·5	4·2	0·28	0·29
2	0–5	Humus	7·5	29·3	6·2	56·7	41·1	25·54	3·32
	5–10	Grey-black	7·8	65·9	6·2	22·2	11·0	5·19	1·09
	10–34	Brown	7·7	30·2	6·3	9·3	7·4	1·80	0·61
	34+	Parent material	7·7	56·7	6·1	2·3	4·8	0·40	0·51
3	0–4	Humus	7·4	14·0	6·5	55·7	212·0	16·76	26·15
	4–10	Dark brown	7·6	29·4	8·6	25·5	34·4	7·64	1·12
	10–30	Brown red	7·7	18·2	7·2	13·2	10·0	3·83	1·57
	30+	Parent material	7·8	47·0	7·8	2·2	3·0	0·50	0·80
4	0–3	Humus	7·3	12·1	10·0	45·3	157·0	56·66	6·14
	4–12	Grey-black	7·8	34·0	7·0	19·8	28·8	8·98	1·82
	12–20	Dark brown to red	7·7	22·1	7·3	6·5	12·0	4·31	1·38
	20+	Parent material	8·0	49·6	6·8	2·0	4·2	0·48	0·13
5	0–13	Dark brown	7·9	25·0	6·0	11·7	13·7	8·78	0·85
	13–23	Dark reddish brown	7·8	56·8	6·7	4·7	7·0	4·71	0·85
	23+	Parent material	7·9	49·3	5·6	1·7	2·7	0·72	0·39
6	0–10	Dark brown	7·6	9·5	5·0	11·4	13·3	9·00	1·49
	10–15	Reddish brown	7·6	22·2	7·0	5·0	7·0	4·79	1·36
	15+	Parent material	7·9	46·4	6·0	2·0	3·8	0·44	0·63

* See text, p. 421.

1966). Soil pH was determined by a glass electrode in soil paste, and organic carbon by the Walkley–Black method. Available sodium, potassium and manganese were determined by atomic absorption analysis of 1:10 soil to N ammonium acetate (pH 7) extracts; available iron, combined ferrous and ferric, was determined by atomic absorption analysis of 1:5 soil to N ammonium acetate (pH 3) extracts.

The first two profiles are from beneath patches of persistent vegetation and the last two from typical 'open' colonizing vegetation; samples from sites 3 and 4 are from beneath clumps of *Juniperus virginiana*. Six other pits were sampled on this dune, yielding results intermediate between the extremes of Table 1. Differences in profile development, leaching and nutrient levels under the two vegetation types are apparent. The humus accumulation under *J. virginiana* and its high concentrations of potassium and manganese are also evident (Table 1). Results from the other pits sampled on the dune suggest that more of the variation in profile under colonizing vegetation is attributable to the plant cover: the depth of perceivable soil layers is greater under old tussocks of *Andropogon scoparius* than elsewhere.

DISCUSSION

Nucleation

The most conspicuous feature of the Grand Bend succession is the change from the colonizing stage to the persistent stage. This change begins with the establishment of seedlings of persistent species (Group II) under large individuals of *Juniperus virginiana* which are common in the colonizing stage. Conditions beneath these plants are distinguished by less extreme microclimate that is found in the surrounding vegetation and by the accumulation of litter and the formation of humus from the juniper needles. This marks the first appearance of a humus layer in the successional process. Juniper humus differs from that of most other conifers being of the mull type (Daubenmire 1959); the results in Table 1 illustrate the high levels of nutrients there, especially of potassium and manganese.

It appears likely that the changes in environmental conditions brought about by *J. virginiana* are crucial to the establishment of the persistent species. The reaction of *J. virginiana* on the environment leading to its eventual replacement accords with the classical theory of succession. *Carex* sp., *Poa compressa*, and *Smilacina stellata* are the commonest colonizing species beneath *Juniperus virginiana*; *Symphoricarpos racemosus*, *Prunus virginiana*, *Amelanchier stolonifera*, *Rhus aromatica* and hybrid oaks are the earliest persistent species to appear there. *Juniperus virginiana* behaves as a centre of establishment and a nucleus for the subsequent growth of patches of persistent species. This suggests an analogy with the phenomenon of nucleation encountered in the physical sciences, for example in the growth of hailstones. The use of the term 'nucleation' follows from this.

As succession proceeds the oak seedlings that established in the nuclei mature and grow into trees; they come to play a dominant role in the existence and further development of the patches; the junipers become subordinate to the oaks and their association with the persistent patches disappears as the patches become too dense for their establishment and (eventually) survival. Olmstead (1937) has described a similar nucleation process in succession on Connecticut sand plains. He found that oak species were the principal determinants of the development of patches of forest type vegetation. He also demonstrated that the oaks germinated from the acorn caches of squirrels; acorns not buried in this way did not germinate successfully.

Many acorn caches did not give rise to mature trees, but Olmstead does not suggest what determines successful development. There is evidence that many oak trees in persistent patches at Grand Bend could arise from chipmunk caches; as in Olmstead's (1937) work the evidence comes from the frequent juxtaposition of several individuals that have evidently germinated from the same cache. Most chipmunk holes are found in areas where a humus layer is present; as it is under *J. virginiana* that a humus layer first appears acorns are more likely to be buried there than elsewhere in the colonizing stage. The appearance of oak seedlings under junipers could be the result of this method of dispersal or could be attributed to the possibly more congenial conditions for germination there. Olmstead (1937) reports *J. virginiana* in oak-dominated patches of vegetation but does not suggest that it precedes the oaks.

The evidence presented here appears to support the hypothesis that both *J. virginiana* and *Quercus rubra* × *velutina* exert a strong influence on successional development at Grand Bend, in particular the nucleation process, and on the life of the species associated with them. Their role in the vegetation apparently qualifies them for the epithet 'edifikators' introduced by Sukatschew (1925) and discussed by Goodall (1966). The relatively clear distinction between the two successional stages and the mechanism of the change from one to the other tends to support the organismal concept of vegetation as developed by Clements (1916), modified by Tansley (1935), and recently supported by Harper (1967), rather than the individualistic view that is attributed to Gleason (1926).

Is nucleation a common successional mechanism, or is the present example an isolated one? Olmstead's (1937) work, mentioned above, provides evidence of it in another sand dune succession, and there is evidence for its existence in at least one other type of succession. Cooper (1931), Viereck (1966) and Reiners, Worley & Lawrence (1971) allude with varying directness to such a pattern of development in succession following the retreat of Alaskan glaciers. For example, Viereck (1966) states that: 'As shrub clumps enlarge, meadow areas become confined to narrow corridors between clumps.' Reiners *et al.* (1971) also note the savannah-like appearance of the vegetation as tree cover is lost in the succession from closed forest to muskeg, presumably as muskeg patches coalesce.

Nucleation may or may not occur in secondary successions. There is plenty of evidence of heterogeneity in secondary successions (Williams *et al.* 1969), and differences between the patches may be determined by environmental variation or by successional maturity (Webb, Tracey & Williams 1972; Shafi & Yarranton 1973). However, there is no direct evidence of changes in the size of the observed patches. Indirect evidence that the process might occur comes from observations of increasing scales of pattern of individual species (Whitford 1949; Greig-Smith 1952). General mechanisms of successional change are harder to investigate in secondary successions because of the pronounced pattern usually superimposed by the initial heterogeneity of both environment and vegetation surviving the disturbance that initiates the succession.

It is conceivable that the nucleation process as described here is the 'ideal' case, i.e. it may be encountered only in homogeneous undisturbed environments. Elsewhere the departure from 'ideal' behaviour may depend on the scale and severity of heterogeneity and on the frequency and severity of disturbance.

Scales of pattern

Fig. 3 is a hypothetical representation of changes in the maximum clump sizes of colonizing and persistent species during the Grand Bend succession; the approximate scales were obtained from the plots in Fig. 1 and from crude field observations. It seems likely that if there were an additional stage in the succession, involving the replacement of Group II species, then the scale of their pattern would behave at the time of the replace-

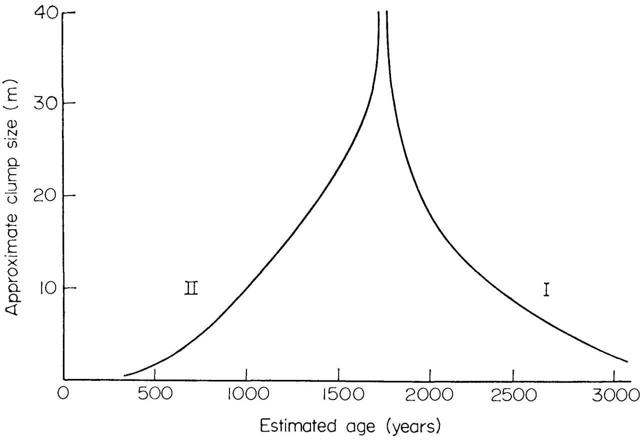

FIG. 3. Hypothetical maximum scales of pattern of Group II (persistent) and Group I (colonizing) species during the course of the Grand Bend succession.

ment as the scale of pattern of the colonizing species (Group I) behaves when they are eliminated. It is expected that the sequence of events at the transition described here would be repeated at each subsequent transition.

The change in scale of pattern of the persistent (Group II) species corresponds to Greig-Smith's (1952, 1964) general model of the change in species pattern during succession. The present results suggest that the clump sizes of a given group of species may first increase and then decrease during a succession provided more than one successional stage occurs. Brereton (1971) has reported such changes for species in a salt marsh succession. What is in fact suggested here is a cyclical version of Greig-Smith's model requiring its repetition for each successional stage. As he suggests, the scale of pattern of an increasing group increases, eventually to infinity as the developing patches coalesce; however, there is a further addition: as a second stage begins to replace the first the clump size of the species of the first stage will decrease in a reciprocal manner to the increase shown by those of the second stage, although not necessarily contemporaneously with it. In the present example the decrease in the early stage follows the increase in the late stage. The scale of pattern (*sensu* Greig-Smith) of the colonizing species may actually increase as they disappear because of an increase in the distance between clumps.

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SUMMARY

Two stages are recognized in the sand dune succession at Grand Bend: a colonizing stage characterized by open grassland with scattered *Juniperus virginiana* and *Quercus prinoides* bushes and a persistent stage taking the form of an oak–pine forest. The first stage lasts for 1600 years and the second begins at 2900 years; from 1600 to 2900 years there appears to be a transition. Persistent species first appear under *Juniperus virginiana* where a humus layer first accumulates and soil maturation proceeds rapidly; such sites act as nuclei for the subsequent growth of patches of persistent species which eventually coalesce at the onset of the persistent stage. As the individual oaks mature into trees they dominate the developing patches and the association of *J. virginiana* with the patches disappears. Species of the colonizing stage are eliminated between the growing patches of incipient oak forest.

The nucleation model suggests that Greig-Smith's suggested sequence of changes in spatial pattern during a succession is repeated during each stage of the process. The clump size of species of the invading stage will increase as they establish themselves and nucleation occurs and the rate of increase will become asymptotic to infinity as the patches coalesce; the clump size pattern of the disappearing species will be exactly the reverse as they suddenly cease to constitute the overall matrix of vegetation and become confined to gradually decreasing patches.

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