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USE OF NON-AREA ANALYTIC DATA TO DETERMINE SPECIES DISPERSION

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This report suggests a technique for assessing dispersion in plant populations by analyzing data from non-area analytic samples. Models for random and non-random dispersion are presented along with an analysis of dispersion in some natural plant populations and a discussion of some dispersion mechanisms in these populations.

THE METHOD

With any non-area analytic sample method in which a constant number of individuals is sampled at a given point, the number of points (P) containing 0, 1, 2, 3, 4, . . . n individuals of a species which is dispersed at random is a probability function

$$P_{o-n} = \frac{n!}{r!(n-r)!} q^{n-r} p^r$$

where n is the total number of individuals per point, r is the number of individuals of a given species per point, p is the mean density of a given species, and q is $1 - p$.

Given two individuals per point, as in the random pairs method of Cottam and Curtis (1949) or the order method of Morisita (1954),

$$\begin{aligned} P_0 &= q^2 \\ P_1 &= 2pq \\ P_2 &= p^2 \end{aligned}$$

Given three individuals per point, as in the order method of Morisita,

$$\begin{aligned} P_0 &= q^3 \\ P_1 &= 3pq^2 \\ P_2 &= 3p^2q \\ P_3 &= p^3 \end{aligned}$$

Given four individuals per point, as in the quarter (quadrant) method of Cottam, Curtis, and Hale (1953) and Morisita (1954) or the order method of Morisita,

$$\begin{aligned} P_0 &= q^4 \\ P_1 &= 4pq^3 \\ P_2 &= 6p^2q^2 \\ P_3 &= 4p^3q \\ P_4 &= p^4 \end{aligned}$$

For non-area analytic techniques which utilize more than four individuals per point, as does the order method of Morisita, appropriate distributions can be easily calculated. The order method of Morisita (1954) is based on formulae for determining the distance from a random

point to the first, second, third, . . . n th closest individuals in a random population. Morisita's paper was published in the first volume of a recently established journal and its importance merits reprinting in a scientific journal of wide circulation.

Since most non-area analytic samples at present are made with either the quarter method or the order method with four individuals per point, an examination will be made of dispersion at this level.

Dispersion models

Dispersion models for per cent densities of 0, 25, 50, 75 and 100, are given in Table I for a non-area analytic sample with four individuals per point. Random dispersions were calculated from the probability function given above. The regular dispersion models are for maximum regularity and assume individuals of all species are dispersed in the same regular pattern. The contagious dispersion models are for maximum contagion and assume that individuals occur in tight clumps of two, three, four, or more individuals so that a sample point will pick up all clump members before sampling a non-clump member. A sample point in the order method will pick up all members of a nearby clump, whereas a sample point in the quarter method may pick up only one or two clump members, unless it occurs in the center of a clump. For this reason the order method is more sensitive in detecting contagious dispersion, while the quarter method is more sensitive to regular dispersion. Since contagious dispersion is much more prevalent than regular dispersion it could be expected that the order method is a more accurate technique for estimating dispersion than is the quarter method. It is obvious that neither the regular nor contagious models outlined above are likely to occur in nature. These models represent extreme patterns which are theoretically possible.

The pattern of observed values of numbers of individuals per point in relation to the random model indicates whether dispersion tends toward regularity or contagion. If the observed values are successively lower, higher, and lower than the expected random values, the species is regularly dispersed. If the observed values

TABLE I. Dispersion models, class distribution in per cent

Individuals/ pt.	$p^1 = .00$	$p = .25$	$p = .50$	$p = .75$	$p = 1.00$
Regular					
0.....	100	0	0	0	0
1.....	0	100	0	0	0
2.....	0	0	100	0	0
3.....	0	0	0	100	0
4.....	0	0	0	0	100
Random					
0.....	100	31.6	6.2	0.4	0
1.....	0	42.2	25.0	4.7	0
2.....	0	21.1	37.5	21.1	0
3.....	0	4.7	25.0	42.2	0
4.....	0	0.4	6.2	31.6	100
Contagious two individuals/clump					
0.....	100	50	0	—	—
1.....	0	0	0	—	—
2.....	0	50	100	—	—
3.....	0	0	0	—	—
4.....	0	0	0	—	—
Contagious three individuals/clump					
0.....	100	66	33	0	—
1.....	0	1	0	0	—
2.....	0	0	1	0	—
3.....	0	33	66	100	—
4.....	0	0	0	0	—
Contagious four or more individuals/clump					
0.....	100	75	50	25	0
1.....	0	0	0	0	0
2.....	0	0	0	0	0
3.....	0	0	0	0	0
4.....	0	25	50	75	100

¹ p = relative density.

are successively higher, lower, and higher than the expected random values, the species is contagious. The models in Table I demonstrate these relationships. At a density of 25%, for example, the pattern of regular values of 0, 100, 0, 0, 0 in relation to the random pattern of 31.6, 42.2, 21.2, 4.7, and 0.4 shows successively a lower value, a higher value, and three subsequent lower values. A contagious dispersion at the same density with two individuals per clump with values of 50, 0, 50, 0, 0 shows a pattern of higher, lower, higher, lower, and lower in relation to the random model. The number of higher or lower values is not pertinent; the pattern of the values of relatively high magnitude should be the deciding criterion.

At very high or very low relative density, the difference between random and non-random dispersion in the above models approaches zero, and no estimate of dispersion is possible. At relative densities of 0 or 100, the regular, random, and contagious dispersion models are identical (Table I). The suggested method does not directly measure pattern of areal dispersion but only indicates dispersion relative to that of other species. Since there is a tendency for the stems of all plant species to be randomly distributed as a whole (demonstrated by Curtis and McIntosh 1950 for forest trees; and G. J. Struik, personal communication, for forest herbs), there should be close agreement between relative dispersion as indicated by the present method and actual spatial dispersion.

Test of significance

The Chi-square test can be used to determine the cor-

respondence between the expected and the observed distribution. For this test, since the sample mean (*i.e.*, density) is a parameter of the binomial distribution, the degrees of freedom equal $n-2$. The recommendations of Cochran (1954) for strengthening the Chi-square test have been followed. Cochran notes that a rule requiring each expected class to be greater than five results in loss of power, especially when the significant difference between the expected and observed distribution may occur in the tails (or extremes) of the distribution. By grouping to bring each expected class value to five or more, the difference between the distributions is obscured and there is a large loss of power. For tests with unimodal distributions, as the Poisson or the binomial distribution in the present study, Cochran recommends grouping so that the minimum expectation at each tail is at least 1.0. In the present study both tails were grouped to at least 1.0 or higher, depending on which grouping gave the lower Chi-square probability. Exact Chi-square probabilities were determined from an enlargement of the Chi-square chart in Bliss (1944) which was kindly supplied by Dr. Bliss.

Application to field samples

The dispersion method was applied to forest surveys made in Minnesota, British Columbia and Ontario, and to the "Maple Forest" and "Northern Hardwood Forest" maps from Wisconsin (Curtis 1956).

The Curtis maps were sampled by the order method of Morisita (1954) with four trees per point and a random grid location of sample points. The Curtis maps are stylized representations of actual forest populations (J. T. Curtis, personal communication).

Stands 1 to 4 were surveyed in the Cedar Creek Natural History Area, Bethel, Minnesota, using the quarter (quadrant) method of Cottam, Curtis and Hale (1953) and Morisita (1954). Sample points were located at random distances along a predesignated line of walk ("random walk"). These stands have a tree complement which is intermediate between the southern and northern hardwood forests of Wisconsin as outlined by Curtis (1959). Description of upland forest vegetation in the area is contained in Bray (1960).

Stands 5, 6, 8, 19, and 20 were surveyed in Itasca State Park, Itasca, Minnesota, using the quarter method and a "random walk" location of points, except in stand 8 in which sample points were located at random on a grid. Stands 5, 6, and 8 are northern conifer-hardwood forest and range from late pioneer to late intermediate stages of development. Stands 19 and 20 are boreal forest and represent two of the typical developmental patterns for this forest. In stand 19, *Pinus banksiana* is being replaced by *Picea glauca* and *Abies balsamea*, and in stand 13 these species are replacing *Populus tremuloides*.

Stand 9 is located on the grounds of the former botanical garden of the University of Toronto in the Don Valley, Toronto, Ontario. It was surveyed with the quarter method, and sample points were located at random on a grid. This stand is an *Acer saccharum*, *Fagus grandifolia*, *Tsuga canadensis* forest and has been protected from disturbance for many years.

Stands 7, 10, and 11 were surveyed with the order method and a random walk location of points in the University of Toronto Forest, Dorset Ranger School, near Dorset, Ontario. Stand 7 is a 39-year-old *Populus grandidentata* and *P. tremuloides* forest on the site of a former field. Stand 10 is a mesic forest which was burned about 100 years ago and is presently dominated

by *Fagus grandifolia* and *Acer saccharum*. Stand 11 is an old field which has been abandoned for about 20 years and is presently in the initial stages of tree invasion. In utilizing the order method to sample understory plants (herbs and shrubs) in stands 7, 10, and 11, an individual was defined as any stem and its appendages, a procedure which Dix (1961) found satisfactory in surveying prairie vegetation in North Dakota with the quarter method.

Stands 12 through 16 are northern hardwood forests located in Ontario along Lake Superior between Sault Ste. Marie and the Minnesota border. They represent a northward extension of hardwood forest into a predominantly boreal forest area. Of the more terminal hardwood tree species, only *Acer saccharum* and *Betula lutea* occur in the area. These stands were sampled by the order method with a random walk location of points.

Stands 17 and 18, in Mt. Revelstoke National Park, Revelstoke, British Columbia, were surveyed by the order method with a random walk location of points. Stand 17 is a river bottom forest (elev. 1,800 ft.) in which the pioneer *Populus trichocarpa* is being replaced by *Thuja plicata* and *Picea glauca*. Stand 18 is a lower slope forest at an elevation of 1,970 ft which has originated following an extensive fire. Fire scarred remnants of the original *Thuja plicata-Tsuga heterophylla* forest are still visible. Stand 18 is dominated by *Populus tremuloides* which is being rapidly replaced by *Thuja plicata* and *Tsuga heterophylla*.

All of the above stands were homogeneous as determined by a Chi-square test for uniform distribution of the dominant species among sub-areas. In stands 1, 2, and 3 samples from similar and proximate stands were combined to form a composite stand, if a Chi-square test among their sub-areas demonstrated homogeneity.

I wish to thank Miss A. L. Archer for data from the Cedar Creek Forest Natural History Area sampled with the financial support of the Louis W. and Maud Hill Family Foundation and Mr. J. E. Purchase for data from the Lake Superior forests sampled with the financial support of the Quetico Foundation of Canada. Nomenclature follows Gleason (1952) except for the three western tree species, *Populus trichocarpa* T. & G., *Thuja plicata* D. Don and *Tsuga heterophylla* (Raf.) Sarg.

RESULTS

Examples of random and non-random dispersion for low, medium and high density species are shown in Table II. In this table, the expected number of points containing 0, 1, 2, 3, or 4 individuals is the product of the probability function (P) and the total number of points in the sample. *Populus tremuloides*, for example, had a relative density (p) of 0.256 and the following probability function: P₀ = .306, P₁ = .420, P₂ = .216, P₃ = .050, and P₄ = .004. These values when multiplied by the number of points in the sample (in this case 40) give the expected values shown for *Populus tremuloides* in Table II.

The two regular dispersions illustrate the pattern of lower, higher and lower observed values in relation to the expected values for a random dispersion and the three contagious dispersions illustrate the reverse pattern of higher, lower, and higher values in relation to the expected values.

Map populations

Table III lists the dispersion and attendant probability for four species in the Northern Hardwoods map and

TABLE II. Examples of random and non-random dispersion

# Trees/pt.	REGULAR					
	<i>Acer saccharum</i> Stand 14		<i>Acer saccharum</i> Stand 16			
	p=47.5 Expected	α=<.04 Observed	p=88.3 Expected	α=<.002 Observed		
0.....	1.5	1	0.0		0	
1.....	5.5	4	0.2		0	
2.....	7.5	12	1.9		6	
3.....	4.5	2	9.7		12	
4.....	1.0	1	18.2		12	
# Trees/pt.	RANDOM					
	<i>Populus tremuloides</i> Stand 18		<i>Abies balsamea</i> Stand 19		<i>Acer saccharum</i> Stand 15	
	p=25.6 Expected	α=>.80 Observed	p=41.9 Expected	α=>.70 Observed	p=85.0 Expected	α=>.60 Observed
0.....	12.2	13	4.6	6	0.0	0
1.....	16.8	15	13.1	10	0.3	0
2.....	8.6	10	14.3	16	2.9	4
3.....	2.0	2	6.8	7	11.1	10
4.....	0.2	0	1.2	1	15.7	16
# Trees/pt.	CONTAGIOUS					
	<i>Tilia americana</i> Stand 4		<i>Abies balsamea</i> Stand 20		<i>Quercus ellipsoidalis</i> Stand 2	
	p=27.5 Expected	α=<.04 Observed	p=52.5 Expected	α=<.001 Observed	p=86.2 Expected	α=<.004 Observed
0.....	5.5	9	3.6	11	0.0	0
1.....	8.4	4	16.0	11	1.0	3
2.....	4.8	4	26.5	20	8.5	12
3.....	1.2	2	19.5	18	35.3	22
4.....	0.1	1	5.4	11	55.2	63

¹ p=percent density, α=probability.

TABLE III. Comparison of dispersion indexes, Curtis maps

	Non-area sample probability ¹	HOPKINS		CLARK-EVANS	
		Index value	Probability	Index value	Probability
Northern hardwood					
<i>Acer saccharum</i>	>.05	1.8	<.02	.89	<.03
<i>Populus grandidentata</i> ...	<.001	3.3	<.001	.69	<.001
<i>Tsuga canadensis</i>	<.003	15.4	<.001	.47	<.001
<i>Tilia americana</i>	<.001	86.1	<.001	.20	<.001
Maple forest					
<i>Acer saccharum</i>	>.05	1.5	<.05	.97	<.04
<i>Ulmus rubra</i>	<.05	10.0	<.001	.54	<.001
<i>Tilia americana</i>	<.001	11.7	<.001	.36	<.001

¹ Overlined probability values indicate a contagious dispersion.

three species in the Maple Forest map. The first column of the table gives the probability of the difference between the observed distribution and the expected binomial distribution. Overlined values show a contagious dispersion. Subsequent columns list the dispersion index and statistical significance of the methods of Hopkins (1954) and of Clark and Evans (1954). The results (first column of Table III) are in general agreement with the Hopkins and Clark-Evans indices and there may be, therefore, a correspondence between relative dispersion as measured by the present method and actual spatial dispersion. In the *Acer saccharum* dispersion on both

maps, the present method gives a probability of greater than .05 (less than .10), whereas the other two methods are slightly less than .05. For *Tsuga canadensis* and *Ulmus rubra* statistical probability by the present method is higher, although it still shows a significant departure from chance expectation.

The low probabilities of the Hopkins and Clark-Evans methods in the Curtis maps reflect a tendency for these methods to lack discrimination when applied to natural populations. If there is areal heterogeneity in a population, the distance from a random individual to its nearest neighbor will be smaller than from a random point to the closest individual (measured with Hopkins' index; predicted from parameter density in Clark-Evans' index). Since areal heterogeneity (variation in density over the population) is present to some degree in many plant populations, especially among non-dominant species, both indices tend to show this heterogeneity as contagious dispersion. Microsite differences insufficient to cause heterogeneity might result in two individuals of the same species occurring in slightly closer proximity than can be expected by chance, but would not result in clumps of larger numbers of individuals. This will again result in an estimate of contagious dispersion by the Hopkins and Clark-Evans methods which do not differentiate between clumps of two individuals and clumps with more than two individuals.

The wider spread of Chi-square probabilities of the present method for the populations of the Curtis maps may indicate the method is less affected by local lack of homogeneity since no square transformation which emphasizes larger distances of point to individual measurement is present, as in Hopkins' index. It may also reflect the sensitivity of the method to clumps of three, four, or more individuals, depending on the number of individuals sampled per point.

The method presented here is not intended as a substitute for a technique which estimates dispersion directly by area or non-area measurements, or by a combination of both (as in Pielou 1959 and Mountford 1961). It is recommended as a means of gaining initial insight into manner of dispersion by the use of non-area analytic data of a type which is being gathered by ecologists at present in large quantity. Further studies can examine the dispersion of a given species in greater detail, including a study of its manner of dissemination and regeneration and its position in successional development. Such study would be greatly benefited by the enumeration of models of contagious distributions based on biologic mechanisms, with specific field populations being checked against specific models.

Field populations

Central Minnesota stands are depicted in Table IV. *Quercus macrocarpa* and *Q. ellipsoidalis* are randomly dispersed in stand 1, a savanna which is still occasionally burned. Both these species sprout from the fire repressed root systems (grubs) of former trees or saplings with cessation of burning. In *Q. ellipsoidalis*, sprouts from either side of a grub may be separated by 0.3 m or more of soil. If trees develop from these sprouts, their trunks will be separated by soil and they will be tallied as distinct individuals, even though their root systems may be united. *Q. macrocarpa* also sprouts from grubs, but usually only a single sprout survives and adult *Q. macrocarpa* rarely have double trunks separated at the trunk base by soil. Both *Quercus* species are clumped in stand 2 and *Q. ellipsoidalis* is clumped in stand 3. Stands 2 and 3 are pioneer stands which have grown

TABLE IV. Per cent density and dispersion—Conifer-hardwood forest, central Minnesota¹

	STAND 1		STAND 2		STAND 3		STAND 4	
	Den.	Dis.	Den.	Dis.	Den.	Dis.	Den.	Dis.
<i>Quercus macrocarpa</i> ...	75.0	>.30	9.2	<.001	1.7	—	0.0	—
<i>Quercus ellipsoidalis</i> ...	25.0	>.30	86.2	<.004	34.6	<.001	18.7	>.15
<i>Pinus strobus</i> ...	0.0	—	0.0	—	17.1	>.70	0.0	—
<i>Quercus borealis</i> ...	0.0	—	0.0	—	18.7	>.07	10.0	>.90
<i>Acer rubrum</i> ...	0.0	—	0.0	—	18.1	>.30	7.5	—
<i>Tilia americana</i> ...	0.0	—	0.0	—	0.0	—	27.5	<.04

¹ Dispersion values in body of table are chi-square probability and if overlined indicate a contagious dispersion, if underlined, a regular dispersion.

from prairie containing grubs following settlement. It is possible that the contagion of *Q. macrocarpa* in stand 2 has been determined by that of *Q. ellipsoidalis*. In stand 4, a more advanced forest, *Q. ellipsoidalis* is again random, as it dies and is replaced by more mesic species. *Quercus ellipsoidalis* thus displays a pattern of random to contagious to random dispersion within one of the usual forest development sequences for the area. Whitford (1949) has noted similar patterns for herbaceous species along developmental gradients.

The other non-random species in the central Minnesota sample is *Tilia americana* which forms stump sprouts which grow to clumps of young stems, some of which may be separated at base by soil. Plate 9 in Curtis (1959) shows a circle of *Tilia* trunks formed by vegetative reproduction.

Of the contagious species in the conifer-hardwood forests of Table V, both *Populus tremuloides* and *Populus grandidentata* frequently spread by long underground runners which may grow up to 100 m from an adult tree. J. B. Falls (personal communication) dug up 2- to 3-year-old *Populus* seedlings near Penetang, Ontario, on the site of a forest stand which had been destroyed by fire. He found the seedling roots were interconnected and assumed they had originated from trees in a nearby forest or perhaps from surviving roots. There was evidence that these seedlings had not come from remnant roots since they formed a fringe of up to 100 m from the nearby forest but did not extend further into the burned area. In stand 7 it is possible that the two *Populus* species originated from underground invasion by runners following the agricultural abandonment of the field, although the age of the trees precluded finding these runners. Such an origin would produce patches of trees of the same species depending on the proximity of the parents. *Populus tremuloides* is also clumped in stand 8 where it occurs mainly in a small burned circular area 10 m in diameter which was caused by lightning striking a tall *Pinus strobus* and starting a ground fire which was apparently soon stopped by rain. *Populus* entered this burned area by runners which were still present when the stand was sampled.

The other contagious species in Table V is *Fagus grandifolia* which reproduces frequently by root sprouting. In many forests this method is the usual, if not exclusive, manner of reproduction (Ward 1956). In both stands 9 and 10 there was clumping of younger *Fagus* around the larger and older trees. In Stand 9 there were several clumps of *Fagus* which grew in rows of larger trees whose connecting roots had been partially exposed by erosion. Every "seedling" examined in

TABLE V. Percent density and dispersion—Conifer-hardwood forest, northern Minnesota and southern Ontario¹

	STAND 5		STAND 6		STAND 7		STAND 8		STAND 9		STAND 10	
	Den.	Dis.	Den.	Dis.	Den.	Dis.	Den.	Dis.	Den.	Dis.	Den.	Dis.
<i>Pinus banksiana</i>	48.7	> .90	40.0	> .85	0.0	—	0.0	—	0.0	—	0.0	—
<i>Pinus resinosa</i>	6.2	—	51.2	> .60	0.0	—	0.0	—	0.0	—	0.0	—
<i>Populus tremuloides</i>	15.0	> .10	7.5	—	27.5	< .001	13.1	< .03	0.0	—	0.0	—
<i>Populus grandidentata</i>	0.0	—	2.5	—	65.0	< .001	0.0	—	0.0	—	0.0	—
<i>Pinus strobus</i>	20.0	> .30	0.0	—	0.0	—	16.9	> .70	3.1	—	0.0	—
<i>Quercus borealis</i>	0.0	—	0.0	—	0.0	—	12.5	> .70	11.9	> .40	0.0	—
<i>Tsuga canadensis</i>	0.0	—	0.0	—	0.0	—	0.0	—	13.1	> .15	0.0	—
<i>Tilia americana</i>	0.0	—	0.0	—	0.0	—	10.0	> .08	3.2	—	0.0	—
<i>Fagus grandifolia</i>	0.0	—	0.0	—	0.0	—	0.0	—	13.1	< .003	61.2	< .006
<i>Acer saccharum</i>	0.0	—	0.0	—	0.0	—	34.4	> .70	38.1	> .20	31.9	> .08

¹ Values in body of table as in Table IV.TABLE VI. Percent density and dispersion—Conifer-hardwood forest, northern Ontario¹

	STAND 12		STAND 13		STAND 14		STAND 15		STAND 16	
	Den.	Dis.	Den.	Dis.	Den.	Dis.	Den.	Dis.	Den.	Dis.
<i>Populus tremuloides</i>	16.0	> .25	40.0	< .02	0.0	—	0.0	—	0.0	—
<i>Betula papyrifera</i>	39.0	< .03	0.0	—	0.0	—	0.0	—	0.8	—
<i>Betula lutea</i>	0.0	—	0.0	—	25.0	> .70	12.5	> .15	12.5	> .60
<i>Acer saccharum</i>	29.0	< .02	57.5	< .004	47.5	< .04	85.0	> .60	88.3	< .002

¹ Values in body of table as in Table IV.TABLE VII. Percent density and dispersion—Conifer forest, British Columbia and northern Minnesota¹

	STAND 17		STAND 18		STAND 19		STAND 20	
	Den.	Dis.	Den.	Dis.	Den.	Dis.	Den.	Dis.
<i>Populus trichocarpa</i>	18.7	> .15	0.0	—	0.0	—	0.0	—
<i>Populus tremuloides</i>	0.0	—	25.6	> .80	4.3	—	29.6	> .50
<i>Thuja plicata</i>	51.2	> .90	25.6	> .50	0.0	—	0.0	—
<i>Tsuga heterophylla</i>	0.0	—	30.0	> .10	0.0	—	0.0	—
<i>Pinus banksiana</i>	0.0	—	0.0	—	16.2	> .07	0.5	—
<i>Pinus resinosa</i>	0.0	—	0.0	—	10.6	< .006	0.7	—
<i>Picea glauca</i>	25.0	> .30	0.0	—	16.9	< .001	12.7	> .08
<i>Abies balsamea</i>	0.0	—	0.0	—	41.9	> .70	52.5	< .001

¹ Values in body of table as in Table IV.

stand 9 was found to be the sprout of a larger individual.

Tsuga canadensis may occur in clumps because it frequently reproduces on cut stumps or along down logs, as in the northern hardwood forest in Table III. In stand 9, however, *Tsuga* is reproducing on the mineral soil of cool slopes and is randomly dispersed.

In the conifer-hardwood forest of northern Ontario, *Betula papyrifera* is clumped in stand 12 and *Populus tremuloides* is clumped in stand 13 (Table VI). The contagion of *Populus* may depend on vegetative reproduction; no reason for the contagion of *Betula* is apparent. Both these species are more pioneer in forest development than *Acer saccharum*, and it is possible that the invading *Acer* is entering the stand in a contagious pattern which results in contagion for the original populations. In the remaining three stands the pioneer species have been replaced by *Betula lutea* and *Acer*

saccharum, and in two of these *Acer* is regularly dispersed. *Acer saccharum* is a shade-tolerant, terminal species with exclusive sexual reproduction (except very rarely from stump sprouts), characters which are likely to result in regular dispersion in older stands if the site is homogeneous.

In the western conifer stands, both of which originated following a catastrophe, all species are random (stands 17 and 18, Table VII). In stands 19 and 20 in northern Minnesota *Picea glauca* and *Abies balsamea* alternate in being random and highly contagious. The presence of *Pinus banksiana* and of charcoal in the soil indicates both these stands originated after fire. Neither *Picea glauca* nor *Abies balsamea* reproduces vegetatively, and the reason for their contagious dispersion is not apparent. The contagion of *Pinus resinosa* in stand 19 is also hard to interpret, since it reproduces exclusively by seed.

Of the 16 contagious dispersions in the tree populations, 10 occur in species which are capable of vegetative reproduction. Some of these species, like *Fagus grandifolia* and *Tilia americana*, regenerate almost solely by vegetative propagation, once the species has entered the stand. Other species, like *Populus grandidentata* and *P. tremuloides*, may either seed into a large burn area, as in stand 18, and be randomly distributed or may enter an old field or a gap in a mature forest by runners and be contagious. The remaining species (Tables IV, V, VI, and VII) including *Acer rubrum*, *Betula lutea*, *Pinus banksiana*, *Pinus strobus*, and *Quercus borealis* reproduce by seed, and their random dispersal can be expected.

The tree data indicate that pioneer stands which have recently originated from disturbance over large areas, like stands 5, 6, 17, and 18, tend to have populations of random species, since all tree invasion must be by seed. Pioneer stands which originate on old fields or small burns and in which roots are already present or adult trees are in the near vicinity, like stands 2, 3, 7, 12, and 13, tend to have contagious populations. Older and more advanced forests, like stands 4, 8, 9, 10, 14, 15, 16, 19, and 20, tend to have random, regular, or contagious populations depending on age, manner of reproduction, microsite differences, and other factors.

The sample of understory plants in stands 7, 10, and 11 (Table VIII) shows five of seven species to be contagious which is in agreement with studies which have noted the non-randomness of shrubs and especially herbs.

TABLE VIII. Percent density and dispersion—Understory plants, southern Ontario¹

	Stand number	Density	Dispersion
<i>Danthonia allenii-compressa</i>	11	36.2	<.005
<i>Hieracium aurantiacum</i>	11	25.6	>.07
<i>Pteridium aquilinum</i>	11	18.7	<.001
<i>Aster macrophyllus</i>	7	18.1	>.70
<i>Gaultheria procumbens</i>	7	13.1	<.003
<i>Acer pennsylvanicum</i>	10	40.0	<.001
<i>Maianthemum canadense</i>	10	19.4	<.05

¹ Values in body of table as in Table IV.

SUMMARY

A method to estimate spatial dispersion is proposed which does not require a separate sampling procedure, but which utilizes non-area analytic sampling techniques such as the quarter and order methods. The method is based on the observation that in a non-area analytic sample with a constant number of individuals per point, the distribution of numbers of individuals of a given species per point should follow a binomial distribution if the species is randomly dispersed. Models for extreme regular, random, and extreme contagious dispersions are presented, and the use of Chi-square as a significance test is discussed.

Two map populations and 20 natural forest stands were sampled by the quarter or order methods in which four trees were tallied per point. There was agreement between the relative dispersion results of the present method and actual spatial dispersion as measured by the Hopkins and Clark-Evans methods. Sixteen of 53 tree dispersions in the field survey were contagious and two were regular; five of seven understory species were contagious. Some mechanisms which may underlie these dispersions were discussed including manner of dissemination and regeneration, stage in forest development, recovery from disturbance, and microsite differences.

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