MODELS OF CLONAL GROWTH IN SOLIDAGO ALTISSIMA

MICHAEL L. CAIN*

Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, U.S.A.

SUMMARY

(1) Patterns of clonal growth are described for the old-field perennial Solidago altissima in three fields located in the Finger Lakes region of New York. S. altissima shows considerable variation within fields for branching angles, rhizome lengths and numbers of daughter rhizomes. There also was variation between fields for rhizome lengths.

(2) Statistical analyses for autocorrelation over time suggest that S. altissima rhizome lengths and branching angles are independent of each other, and of previous branching angles and rhizome lengths. The modal direction for S. altissima clonal growth was 0°.

(3) Because clonal growth is highly variable, deterministic models should not be used to describe the spread of S. altissima clones. Instead, the process of clonal growth is consistent with stochastic simulation models and random-walk models: the critical assumption of these models, that branching angles and rhizome lengths are not correlated over time, appears to be satisfied by this clonal plant. This study represents the first application of random-walk models to the vegetative spread of a clonal plant species.

(4) There was no statistical difference between observed ramet displacements from a point of origin and displacements expected in a correlated random walk. This result allowed an exact formula to be used to make quantitative predictions about the expansion of S. altissima clones.

(5) Random-walk models can be approximated by diffusion models when time is large. Therefore, an estimate was developed of the effective rate of diffusion, i.e. the diffusivity that would be observed if long-term data were gathered on the expansion of S. altissima clones. This approach yielded an effective diffusion constant estimate of 322 cm² year⁻¹ for S. altissima clones.

(6) Field data and computer simulations were used to compare the accuracy of the (effective) diffusion constant estimate developed here to the estimate obtained by standard regression techniques. If only short-term data are available, the correlated random-walk estimate is more accurate than the standard regression estimate. If long-term data are available, the two approaches yield similar results.

INTRODUCTION

Patterns of vegetative spread influence many important aspects of the biology of rhizomatous and stoloniferous clonal plants. Clones with relatively long rhizome lengths and a strong tendency to continue in their previous direction of growth will spread rapidly through their horizontal substrate, forming a nearly linear chain of widely spaced daughter ramets. At another extreme, species with comparatively short rhizome lengths and little directionality will form roughly circular clones that expand slowly. Such differences in the shape of clones can affect the likelihood of outbreeding (Cook 1983), the rate of expansion into new habitat (Lovett Doust 1981; Angevine & Handel 1986), the probability that near-neighbour interactions are interspecific, intraspecific or intraclonal (Lovett Doust 1981; Maddox et al. 1989), and the efficiency of substrate exploration (Hutchings & Bradbury 1986). The degree to which clonal growth patterns alter in response to environmental stimuli also may influence a plant’s ability to utilize favourable conditions and avoid unfavourable conditions (McIntyre 1967; Ginzo & Lovell 1973; Gray 1985; Salzman 1985; Slade & Hutchings 1987).

* Present address: Department of Biology, Washington University, St Louis, MS 63130, U.S.A.
To link vegetative spread to these and other factors requires both careful description and detailed analyses of the process of clonal growth. For many clonal plant species, however, these tasks can be quite difficult: the data may be difficult to collect, and observed patterns of vegetative growth can be so erratic that they deny simple categorization. Descriptive statistics (Angevine & Handel 1986; Cook 1988), deterministic (Bell 1976; Waller & Steingraeber 1985) and stochastic (Cain & Cook 1988) simulation models have been used to describe clonal growth patterns. In addition, the growth patterns of many rhizomatous clonal plants have been interpreted as adaptive (Bell 1974; Smith & Palmer 1976; Bell & Tomlinson 1980).

Detailed simulation models of clonal growth patterns can be used to predict rates of clonal expression and to construct population dynamic models. Because such models are usually based on species-specific growth rules, however, it can be difficult to generalize their results or to make comparisons between species. In addition, because the vegetative spread of clonal plants is usually viewed as a growth process, the models developed to date are models of clonal growth per se. However, the spread of clonal plants can also be considered as a movement process (Slade & Hutchings 1987): the locations of ramets over time can be thought of as the positions of a genet as its moves across its horizontal substrate. Viewed as a movement process, the spread of clonal plants can be described with models used by animal ecologists, such as stochastic simulation models (Jones 1977; Jones et al., 1980), diffusion models (Okubo 1980; Kareiva 1982) and random-walk models (Kareiva & Shigesada 1983).

There is a well-developed mathematical theory associated with random-walk and diffusion models (Okubo 1980). Results from this theory can be used to predict rates of clonal expansion and to perform standardized comparisons of clonal growth patterns between species. Random-walk models are discrete-time models and are therefore well suited to describe the discrete locations of ramets over time. On a long time scale, a random walk can be approximated by simple diffusion (Okubo 1980); thus, if a random-walk model can be used to quantify short-term clonal growth patterns, a diffusion model can be used to quantify long-term rates of clonal expansion.

In this paper, field data on the old-field perennial *Solidago altissima* were used to test a variety of clonal growth models, including random-walk models, a new way to analyse the vegetative spread of clonal plants.

**METHODS**

*Study organism and field sites*

*Solidago altissima* L. (Asteraceae), the tall goldenrod, is a common perennial found throughout south-eastern Canada, eastern and midwestern United States. In central New York, the location of this study, most ramets emerge in March–April from the apical tips of underground rhizomes, and increase in height until August, at which time flower heads begin to form. The apical tips of some rhizomes emerge the previous season, but the leaves of such rhizomes do not expand until spring (i.e. there are no overwintering rosettes). Rhizome growth is sympodial, Rhizomes usually are initiated at the base of the stem (in June) and they continue to grow throughout autumn, reaching a final length of 0.5–60.0 cm. The above-ground portion of ramets die over winter, and their daughter rhizomes remain dormant until the following spring (Bradbury & Hofstra 1976). Ramets are not produced at the same node in successive years, so genet survival depends upon the new
ramets that emerge in the spring from overwintering rhizomes. ('Ramet' is defined here to indicate an above-ground shoot with its associated below-ground vertical stem and roots. For *S. altissima*, it also would be reasonable to define a ramet as a rhizome-root-shoot complex, where the rhizome connects parent ramets to daughter shoots. This definition was not used as it leads to semantic difficulties that can only be avoided with frequent alternation of 'ramet' and 'shoot'.) Although above-ground shoots die after one season, roots and rhizome connections persist for up to 5-6 years. This process creates clonal fragments (sets of interconnected ramets and old shoot stubs with the potential to function as a physiological unit) and, within a given clonal fragment, allows the location of ramets in previous years to be determined. For detailed information about the demography and biology of *S. altissima*, see Werner, Bradbury & Gross (1980), Bradbury (1981) and Cain (1989a).

Old-field populations of *S. altissima* were studied at three sites in the Finger Lakes region of central New York: Jacksonville, Hamilton Reserve and Lydell, all located near Ithaca, NY (42°25'N, 76°30'W). These fields differed in age, successional stage and history of use. Hamilton Reserve, used as a soil dump until 1965, was almost a monoculture of *S. altissima*, broken only by patches of other clonal species (e.g. *Bromus inermis, Apocynum medium, S. graminifolia, S. gigantea*; nomenclature follows Fernald 1950) and a few scattered invading shrubs (*Lonicera tatarica, Viburnum dentatum, Rosa multiflora*). The site at Jacksonville, used as a corn field until c. 1980, was dominated by *S. altissima*, but also had a number of other herbaceous species (including *Fragaria virginiana, Aster sagittifolius, S. graminifolia, Hieracium aurantiacum, H. pratense*), considerable cover of the shrub *Lonicera tatarica* (an estimated 15% of the field), as well as a few scattered young trees (*Robinia pseudoacacia, Rhus typhina, Betula populifolia*). Lydell, an old field abandoned before 1960 (agricultural history unknown), was dominated by scattered invading trees (*Fraxinus americana, Ulmus americana, Rhamnus cathartica*) and shrubs (*Cornus racemosa, Viburnum dentatum, Lonicera tatarica*). Herbaceous old-field perennials were located in patches among the trees and shrubs, and included *S. rugosa, S. altissima, Phleum pratense, Anthoxanthum odoratum, Satureja vulgaris* and *Achillea millefolium*.

The three fields also differed in *S. altissima* genotypic diversity: large, pure (single-genotype) stands predominated at Hamilton Reserve (R. B. Root and G. D. Maddox, unpublished electrophoretic and morphological data), whereas clones intermingled at Lydell and Jacksonville (Maddox *et al.* 1989). The variation between sites in genotypic diversity may have resulted from the fields' different histories of use. In this paper, differences in genotypic diversity between sites were ignored and no attempt was made to determine the genetic identity of clonal fragments.

In late November and early December 1985, ten circular plots (each c. 0.25 m²) were located randomly and excavated to a depth of 15-20 cm in each of the three field sites. The plot size diameter was chosen to be equal to the longest previously observed *S. altissima* rhizome length (personal observation). For each of these thirty plots, all soil and ground cover was carefully removed in the laboratory, allowing determination of ramet connections via underground rhizomes. At the three field sites studied, the above-ground method of determining ramet connections described by Hartnett & Bazzaz (1985) was not reliable (regardless of ramet density) due to the fact that sets of interconnected ramets frequently crossed each other; this was true even in Jacksonville, a field abandoned from corn only 4-6 years previously. Plot number, clonal fragment number, parental ramet identity, rhizome initiation point, rhizome length, and branching angle were recorded for
all ramets, old shoot stubs, and current rhizomes (the latter having been produced in the summer and autumn of 1985).

To record branching angles and rhizome lengths, the vegetative spread of *Solidago altissima* was approximated as a series of linear displacements (Fig. 1). This approximation was reasonable because actual rhizome lengths (total displacements) differed little from the linear distance (net displacement) between a rhizome tip and its point of origin: the mean ratio of total to net displacement was 1-05 at Jacksonville (*n* = 185), 1-05 at Lydell (*n* = 148), and 1-03 at Hamilton Reserve (*n* = 196). Branching angles between successive locations of ramets were measured relative to the previous direction of growth (Fig. 1), with zero degrees defined as straight ahead.

Numbers of daughter rhizomes, rhizome lengths and branching angles have a critical impact on the size and shape of clones in rhizomatous plant species. These variables are referred to collectively as ‘clonal growth parameters’, where parameter is used in the sense of a physical property whose values determine the behaviour or characteristics of something.

The data collected in 1985 provided information on clonal growth parameter variation and on the process of clonal growth over time. Digging plots out of the ground, however,
cut rhizome connections and thereby biased the samples against containing long time series (4–5 years) and long rhizome lengths. This presented no difficulty for much of the data analysis. For estimation of diffusion rates and for comparison of observed to predicted displacements, however, it was necessary to sample without such a bias. To do this, in August 1987 sixty-two ramets were chosen at random within a large patch of *S. altissima* at Lydell. For each of the selected ramets, all rhizomes connected to the initial ramet were carefully dissected from the substrate *in situ* (thus preventing the breakage of rhizome connections that occurs when plots are dug out of the ground). All variables measured in 1985 except current rhizome numbers were recorded for each of the sixty-two clonal fragments uncovered in this fashion. In addition, the net displacement of each ramet and old shoot stub was measured from its point of origin, defined as the location of the oldest shoot stub in each chain of connected ramets.

Unfortunately, even after the 1985 data sets were corrected for the fact that some rhizomes were cut off in the sampling process (see below), rhizome lengths for the 1985 and 1987 data sets were not directly comparable. In 1985, plots were dug out of the ground and data were collected for all clonal fragments contained in the plot. Thus, the 1985 data sets included data from small *S. altissima* ramets that put out very short rhizomes and persisted (far below the canopy) from year to year. No such ramets were included in the 1987 data set: the above-ground portion of most small ramets is dead by August (Cain 1989a), and so were unlikely to have been selected by the random sampling method used in August 1987.

**Data analysis**

Mean values, measures of variation (standard or angular deviations), and frequency distributions were determined for rhizome lengths, branching angles and rhizome numbers in each of the three field sites. Branching angles were analysed with statistical methods designed for use with angular data. It is necessary to use such techniques because standard statistical methods do not account for the fact that angles wrap upon themselves (for example, 0°, 360° and 720° are all the same angle). Branching angle mean vectors (directions and lengths) and angular deviations were calculated as in Batschelet (1981). The length of the branching angle mean vector is a measure of how tightly angles are clustered, and ranges from zero (no mean vector) to one (all angles in the same direction). Chi-square contingency tables were used to compare frequency distributions between field sites for the 1985 data. Because some rhizome lengths were right-censored (i.e. the observed lengths for rhizomes that were cut represented minimum lengths, not actual lengths), survival analysis log-rank tests (Lee 1980; Pyke & Thompson 1986) were also used to compare rhizome-length frequency distributions.

Several different methods were used to analyse the process of *Solidago altissima* clonal growth. Spearman rank correlation tests for associations across years between branching angles and between rhizome lengths were performed. Cross correlations between angles and rhizome lengths also were computed within and across years, as were parametric and non-parametric survival analysis tests for association among rhizome lengths (LIFEREG and LIFETEST procedures, SAS Institute Inc. 1985). In addition, the dependence of current branching angles upon previous branching angles was analysed with three-way and two-way χ²-tests for independence. Independence among rhizome lengths across years also was tested by comparing observed and predicted numbers of runs (of signs of the first difference; see Edgington 1961) with a χ² goodness-of-fit test, where the predicted
numbers of runs were determined from calculations based on the assumption that rhizome lengths were independent across years.

The discrete locations of *S. altissima* ramets over time were modelled as a correlated random walk. Correlated random walks are discrete movement processes in which the direction and distance travelled can be represented as independent, random draws from frequency distributions of branching angles and rhizome lengths (Kareiva & Shigesada 1983). In such a situation, branching angles and rhizome lengths are not correlated with each other, or with previous branching angles or rhizome lengths. The distribution of branching angles determines the degree of correlation that a current rhizome has with the previous direction of growth (e.g. if the distribution of angles were tightly clustered around zero degrees, or straight ahead, there would be a strong tendency for daughter rhizomes to continue growing in the same direction as their parent). It is this correlation in directionality that the phrase 'correlated random walk' refers to. For the special case in which all branching angles are equally likely (i.e. branching angles are uniformly distributed), a correlated random walk reduces to a simple random walk with no correlation in directionality.

Statistical methods developed in Cain (1989b) and McCulloch & Cain (1989) were used to compare observed ramet displacements from a point of origin to correlated random-walk predicted displacements. The statistical tests used branching angle and rhizome-length frequency distributions as the basis for comparing observed net displacements (or net squared displacements) to correlated random-walk predicted displacements. The tests were move-by-move statistical tests. The null hypothesis that observed displacements did not differ from correlated random-walk expected displacements was not rejected if observed data fell within the appropriate confidence interval on each of the *n* moves for which data were collected (Cain 1989b). The statistical methods in Cain (1989b) and McCulloch & Cain (1989) were also used to compare observed ramet displacements to displacements predicted in a simple random walk.

In addition, observed displacements were compared to those predicted by a simple diffusion model. To do this, the diffusion constant was estimated as described in Okubo (1980) and Kareiva (1982). A $\chi^2$ goodness-of-fit test then was used to compare the observed distribution of net displacements to that predicted by a diffusion model (parameterized by the estimated diffusion constant). Finally, the net squared displacement expected in a correlated random walk (Kareiva & Shigesada 1983) was used to develop a new estimate of (effective) ramet diffusion rates. Diffusion rates are usually estimated by a regression of variance in position vs. time (Okubo 1980). Field data and computer simulations were used to compare these two techniques for estimating diffusion rates.

**RESULTS**

*Growth parameter variation*

Clonal fragment maps suggest that there is considerable variation for *S. altissima* clonal growth parameters (Fig. 2). Frequency distributions of branching angles, rhizome lengths and numbers of daughter rhizomes (Fig. 3) also revealed large amounts of morphological variation, as do standard deviations (or angular deviations in the case of branching angles) for rhizome lengths, branching angles, and numbers of daughter rhizomes (Table 1). In addition, coefficients of variation in rhizome lengths and numbers of daughter rhizomes varied from 47% to 97%, again demonstrating considerable natural
Fig. 2. Maps of three *Solidago altissima* clonal fragments (a–c) from the 0.25-m² plots sampled in 1985: (△) current ramet locations; (▲) locations of ramets in previous years (the number of years before present is indicated next to each open triangle); solid lines connecting triangles represent underground rhizomes.

variation. The rhizome-length standard deviations and coefficients of variation were not corrected for censoring, and therefore underestimate the variation in the 1985 samples. Coefficients of variation were not computed for branching angles because the usual arithmetic mean and standard deviation are not appropriate for the analysis of angular data with large amounts of variation (Batschelet 1981). The mode and mean direction of *S. altissima* branching angles was zero degrees.

Inspection of Table 1 suggests that there is variation between sites for rhizome lengths sampled in 1985. Linear constraints show that mean rhizome lengths were significantly shorter at Hamilton Reserve than at Lydell and Jacksonville (a posteriori t-test, $t = 9.8$, $P < 0.0001$). In addition, a $\chi^2$ contingency analysis indicated that rhizome-length frequency distributions differed between fields ($\chi^2_{14} = 96$, $P < 0.0001$), as did a log-rank test ($\chi^2 = 115$, $P < 0.001$) that corrected for right-censoring (Lee 1980). As discussed in the methods section, rhizome lengths for the Lydell 1985 and 1987 data sets are not directly comparable because of differences in the sampling procedures in the two years. Frequency distributions for branching angles ($\chi^2_{16} = 10$, $P = 0.87$) and rhizome numbers ($\chi^2_{10} = 9.3$, $P = 0.50$) did not differ between fields.
Fig. 3. Frequency distributions of *Solidago altissima* (a) branching angles, (b) rhizome lengths (cm) and (c) number of daughter rhizomes sampled in 1985 from (J) Jacksonville, (L) Lydell and (H) Hamilton Reserve. Because rhizome numbers were sampled in winter 1985 (before their spring emergence), these distributions (c) represent the number of potential daughter ramets. Values on the x-axis in (a) and (b) are class mid-points.
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome length (cm)</td>
<td>7.0 (8.4)</td>
<td>3.9 (4.0)</td>
<td>6.9 (7.8)</td>
<td>14.0</td>
</tr>
<tr>
<td>Mean</td>
<td>5.4</td>
<td>3.8</td>
<td>6.0</td>
<td>6.6</td>
</tr>
<tr>
<td>S.D.</td>
<td>77%</td>
<td>97%</td>
<td>87%</td>
<td>47%</td>
</tr>
<tr>
<td>n</td>
<td>235</td>
<td>401</td>
<td>315</td>
<td>220</td>
</tr>
<tr>
<td>Number of daughter rhizomes</td>
<td>2.4</td>
<td>2.7</td>
<td>2.8</td>
<td>—</td>
</tr>
<tr>
<td>S.D.</td>
<td>1.5</td>
<td>1.8</td>
<td>1.6</td>
<td>—</td>
</tr>
<tr>
<td>n</td>
<td>59</td>
<td>83</td>
<td>71</td>
<td>—</td>
</tr>
<tr>
<td>C.V.</td>
<td>63%</td>
<td>67%</td>
<td>57%</td>
<td>—</td>
</tr>
<tr>
<td>Branching angles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean vector direction</td>
<td>0°</td>
<td>5°</td>
<td>0°</td>
<td>0°</td>
</tr>
<tr>
<td>Mean vector length (cm)</td>
<td>0.54</td>
<td>0.55</td>
<td>0.57</td>
<td>0.73</td>
</tr>
<tr>
<td>Angular deviation</td>
<td>55°</td>
<td>54°</td>
<td>53°</td>
<td>42°</td>
</tr>
<tr>
<td>n</td>
<td>183</td>
<td>323</td>
<td>273</td>
<td>200</td>
</tr>
</tbody>
</table>

**Table 1.** Mean values and measures of variation for clonal growth parameters sampled at Jacksonville, Lydell and Hamilton Reserve in 1985 and 1987. The values for mean rhizome length in parentheses were right-censored (see text).

*Initiation of new rhizomes*

The most common point of rhizome initiation is at the base of the stem (Figs 1 and 2): 92% (876) of 951 sampled rhizomes began at this location. The remaining 8% of the sampled rhizomes were usually initiated at positions along the rhizome leading from the grandparent to the parent ramet (Fig. 4). Occasionally, new rhizomes were initiated at the base of the grandparent ramet (four of the 951 ramets).

The direction of growth for newly produced rhizomes tends to maintain (roughly) the direction of growth between the grandparent and parent ramets (Fig. 5a). The distribution of branching angles for newly initiated rhizomes is significantly different

![Fig. 4. Frequency distribution (summed over all sites) of the relative initiation points of new rhizomes in *Solidago altissima*, excluding those rhizomes initiated at the base of the stem (with a relative initiation point of zero). Relative initiation points equal \(d/L \times 100\), where \(L\) is the length (cm) of the rhizome connecting the grandparent–parent generation ramets, and \(d\) is the distance (cm) from the base of the parent generation ramet (measured along the grandparent–parent rhizome) to the point at which the new rhizome was initiated. Values on the x-axis are class midpoints.](image)
Clonal growth in Solidago altissima

Fig. 5. Frequency distributions (summed over all sites) of branching angles in Solidago altissima for (a) newly initiated rhizomes, (b) established ramets and (c) newly initiated rhizomes with length less than 1.5 cm. Values on the x-axis are class mid-points.

($\chi^2 = 11, P < 0.05$) from the distribution of branching angles leading to established ramets: branching angles of established ramets more frequently continue in the previous direction of growth than do branching angles of newly initiated rhizomes (compare Fig. 5a and b). However, if newly initiated rhizomes are classified as ‘short’ ($\leq 1.5$ cm) and ‘long’ ($> 1.5$ cm), there is no significant difference between branching angle frequency distributions for long rhizomes and established ramets. This occurs because the distribution of branching angles for short new rhizomes is considerably flatter than the overall distribution of branching angles for newly initiated rhizomes (compare Fig. 5a and c); the physiological mechanism that causes the difference between the distributions of short and long rhizomes is not known. Rhizomes function as storage organs, and ramets initiated from short rhizomes have a lower chance of survival than ramets initiated from long rhizomes (Cain 1989a). Thus, the differences between Fig. 5(a) and (b) may be due in part to differential mortality among short and long rhizomes.

The process of clonal growth in S. altissima

Branching angles were not significantly correlated with those of the previous generation for any of the four S. altissima data sets examined (three data sets for 1985, one for 1987). The association of branching angles across generations also was tested with
three-way (year_i/year_{i+1}/year_{i+2}), and their component two-way, \( \chi^2 \) contingency tests for independence. The three-way contingency analyses were not significant in the 1985 or the 1987 samples (\( P > 0.05 \) for all four data sets), nor were any of the two-way analyses significant (\( P > 0.10 \) in all cases). The combined information from correlations among branching angles and \( \chi^2 \)-tests for independence suggested that directions of rhizome growth were not correlated over time.

Rhizome lengths were not significantly correlated with those of the previous generation for ten of the twelve (four data sets and three generations per data set) relationships tested. For the 1985 data sets, censored data points were excluded from the calculations. Excluding censored data points decreases the sample size and may introduce bias. The significance values of these twelve statistical tests were combined with a \( \chi^2 \) statistic: the result supported the null hypothesis of no correlation between rhizome lengths across generations (\( \chi^2_{34} = 34.8, \ P > 0.05 \)). In addition, \( \chi^2 \) goodness-of-fit tests indicated no statistical difference between the observed number of runs (of signs of the first difference in rhizome lengths across years) and the number of runs that would be expected if rhizome lengths were selected randomly (1985: \( \chi^2 = 6.6, \ P > 0.05 \); 1987: \( \chi^2 = 2.0, \ P > 0.50 \); overall: \( \chi^2 = 8.6, \ P > 0.25 \)). For these analyses, censored data (1985 only) were excluded if they could affect the sign of the first difference in rhizome lengths. The 1985 data sets were also analysed with parametric and non-parametric techniques that accounted for right-censoring (Lee 1980): parametric (Weibull log-likelihood test, \( \chi^2 = 0.53, \ P = 0.47 \)) and non-parametric (log-rank test, \( \chi^2 = 1.7, \ P = 0.19 \)) tests both indicated no association between rhizome lengths across generations. Thus, three types of statistical analyses suggested that rhizome lengths were not correlated over time.

Cross-correlations between angles and rhizome lengths were computed within and between generations. One of twenty correlations was significant between generations, exactly the number of significant correlations expected at the 0.05 level under a null hypothesis of no correlation. Three of twelve correlations were significant within generations. With the exception of a correlation of 1·0 for a low-sample-size test (\( n = 6 \)), these correlations, although significant, were low (\( r = 0.36 \) and 0·37). The three significant correlations were all positive in sign, which indicates that large rhizome lengths were associated with large branching angles. The 1985 data sets were sampled by digging plots out of the ground: because rhizomes initiated with a large branching angle tend to reverse the previous direction of growth, large branching angles increased the probability that a chain of connected ramets and old shoot stubs would remain within the 1985 sample plots. In contrast, rhizomes with small branching angles continue in the previous direction of growth, and would thus tend to migrate from the plots. This would decrease the chance that small rhizomes could be observed in association with large rhizome lengths in the 1985 data set; thus, the three significant correlations between large branching angles and large rhizome lengths may have been an artefact of a sampling bias introduced by right-censoring. In support of this claim, there were no significant cross-correlations within or between generations for the 1987 data set, which was sampled without a censoring bias.

**Random-walk models of clonal growth**

The placement of ramets in *S. altissima* is a discrete process, and results in the preceding section suggest that branching angles and rhizome lengths are not correlated with each other, nor with previous branching angles or rhizome lengths. Thus, *S. altissima* appears to meet both of the key assumptions of a correlated random walk. Therefore, statistical
methods developed in Cain (1989b) were used to compare the vegetative spread of *Solidago altissima* with displacements predicted by a correlated random walk. Such comparisons complement, but do not necessarily confirm, statistical tests for correlation over time; i.e. it is possible for these two approaches to give conflicting results (Cain 1989b).

The branching angle and rhizome-length frequency distributions for the (unbiased) 1987 data set (Fig. 6) were used to calculate correlated random-walk expected displacements. Expected net displacements were determined by stochastic simulation (see

![Diagram](image)

**Fig. 6.** Frequency distributions for (a) rhizome lengths and (b) branching angles of *Solidago altissima* sampled at Lydell in 1987. Values on the x-axis are class mid-points.

![Diagram](image)

**Fig. 7.** Relationship between (a) the net displacement and (b) the net squared displacement of *Solidago altissima* ramets and their year of growth. The solid line indicates the correlated random walk predicted values; (●) indicates the observed values. The vertical bars indicate the move-by-move 90% confidence intervals about the predicted values. Variances necessary for calculation of the confidence intervals were determined as in Cain (1989b) and McCulloch & Cain (1989).
Cain 1989b), and expected net squared displacements were calculated from eqn 1 in Kareiva & Shigesada (1983). Observed net displacements and net squared displacements from a point of origin did not differ significantly from the values predicted by a correlated random walk (Fig. 7). These results indicate that Kareiva & Shigesada's (1983) formula for the expected net squared displacement can be used to predict the rate of expansion of Solidago altissima clones. In contrast, for each of the three 1985 data sets, observed displacements were significantly different from correlated random-walk predicted displacements. This result may be due to the fact that the 1985 data were biased and therefore did not meet the assumptions of a correlated random walk.

Whether or not observed ramet displacements differed from the displacements expected in a simple random walk was also tested. In a simple random walk, all directions of growth should be equally likely (i.e. branching angles should be uniformly distributed). This was clearly not the case for S. altissima (Fig. 6b); a \( \chi^2 \) goodness-of-fit test confirms this observation (\( \chi^2 = 282.6; P < 0.0001 \)). Nevertheless, it is of interest to determine whether the methods employed here can distinguish between the displacements expected in a simple vs. a correlated random walk. The expected squared displacement after \( n \) steps in a simple random walk is \( R_s^2 = n \cdot E[l^2] \), where \( E[l^2] \) is the expectation of the squared step length (Kareiva & Shigesada 1983). Observed squared displacements for S. altissima were significantly different from the simple random-walk expected displacements for all except the first year of growth (Fig. 8). The simple random-walk model is, therefore, not adequate to describe the spread of S. altissima clones.

**Diffusion models of clonal growth**

The spatial position of ramets that undergo simple diffusion (in two dimensions) should follow a bivariate normal distribution (with \( \mu_1 = \mu_2 = 0, \sigma_1^2 = \sigma_2^2 = \sigma^2 \), and \( \rho = 0 \)):

\[
F(a,b) = P(x \leq a, y \leq b) = \int_{-\infty}^{a} \int_{-\infty}^{b} \frac{1}{2\pi \sigma^2} e^{-\left(x^2 + y^2\right)/2\sigma^2} \, dx \, dy
\]

where \( \sigma^2 = E[X^2] = 2Dt \) (Okubo 1980), \( t \) is time (years), and \( D \) is the diffusion constant. To compare S. altissima net displacement data to the predictions of a simple diffusion model,
Clonal growth in Solidago altissima

eqn 1 was first transformed to polar coordinates and integrated over \( \theta \) to provide the expected distribution of the polar coordinate, \( r \) (\( r \) is the net displacement from the origin):

\[
F(R) = P[r \leq R] = \int_0^R \frac{1}{\sigma^2} e^{-r^2/2\sigma^2} r dr
\]

Integration of the right hand side of eqn 2 yields:

\[
F(R) = 1 - e^{-R^2/2\sigma^2} = 1 - e^{-R^2/4D_t}
\]

Equation 3 is a function of time (\( t \), in years) and is parameterized by the diffusion constant, \( D \). Under the assumption that ramets follow simple diffusion, the diffusion constant is estimated (by regression) from data on rates of clonal expansion (see below): when this is done for \( S. \) altissima, a diffusion constant estimate of \( D = 130 \text{ cm}^2 \text{ year}^{-1} \) is obtained. If this value for \( D \) is substituted into eqn 3, the expected distribution of \( S. \) altissima net displacements can be calculated for each year (\( t \)) for which sufficient data are available.

The calculations outlined above were performed, and then a \( \chi^2 \) goodness-of-fit test was used to compare the observed distribution of net displacements to that predicted by a diffusion model (i.e. by eqn 3). For all four years for which there was sufficient data, observed and expected distributions were significantly different (for each year, \( \chi^2 > 14, P < 0.01 \)). These results indicate that simple diffusion models should not be used to describe the short-term expansion of \( S. \) altissima clones. However, as described in the following section, diffusion models do provide a useful approximation to long-term rates of clonal expansion.

Estimation of long-term rates of ramet diffusion

For simple diffusion in a two-dimensional homogeneous environment, there is a linear relationship (Okubo 1980) between the expected squared displacement, \( E[R^2(t)] \), and time (\( t \)):

\[
E[R^2(t)] = 4Dt + C_0
\]

Here \( C_0 \) is the initial variance in position, and \( D \), the diffusion constant, is a measure of the long-term rate of spread in a population. This relationship holds for populations that undergo exponential growth, as well as for populations that remain constant in size (Okubo 1980). Similarly, in eqn 1 in Kareiva & Shigesada (1983), after a large number of moves the expected squared displacement (\( E[R^2] \)) in a correlated random walk increases linearly with the number of moves, \( n \). Because the mean squared displacement asymptotically grows linearly with \( n \) (i.e. time), for large values of \( n \) the correlated random-walk process can be approximated by simple diffusion. Indeed, solutions to the telegraph equation, the continuous-time analog of a correlated random walk, are indistinguishable from diffusion equation solutions when time is large (Okubo 1980). Thus, the asymptotic slope

\[
\frac{(E[l^2] + 2E[l])^2(c - c^2 - s^2))/((1 - c)^2 + s^2))}{4(E[l^2] + 2E[l])^2(c - c^2 - s^2))/((1 - c)^2 + s^2)}
\]

of a correlated random walk (calculated from eqn 1 in Kareiva & Shigesada 1983) and the slope (\( 4D \)) from eqn 4 may be equated to estimate an effective diffusion constant:

\[
D = \frac{1}{4}(E[l^2] + 2E[l])^2(c - c^2 - s^2)/(1 - c)^2 + s^2)
\]
In this estimate, the expected rhizome length \( E[l] \), the expected squared rhizome length \( E[l^2] \), and the expected cosine \( c \) and sine \( s \) of the branching angles are all calculated directly from empirical distributions of rhizome lengths or branching angles. This estimate is referred to as an ‘effective diffusion constant’ because eqn 5 is not derived from the assumption that simple diffusion occurs; rather, eqn 5 predicts the diffusivity that would be observed if long-term data were gathered on a population of individuals known to follow a correlated random-walk process. An interesting feature of this estimate is that it utilizes detailed observations of individual movements (microscale behaviours) to predict long-term, macroscopic consequences of vegetative spread in a clonal plant population. Also, note that the variance in rhizome lengths \( \sigma_l^2 \) provides a lower bound for the diffusion constant estimate:

\[
D = \frac{1}{4}E[l^2] + \frac{2E[l]^2(c-c^2-s^2)}{(1-c)^2+s^2} \geq \frac{1}{4}\sigma_l^2.
\]

Equation 6 holds because the inequality \( c^2 + s^2 \leq 1 \) (Kareiva & Shigesada 1983) implies (for \( c \neq 1 \)) that

\[
\frac{c-c^2-s^2}{(1-c)^2+s^2} \geq \frac{c-1}{(1-c)^2+1-c^2} = -\frac{1}{2}.
\]

When this relation is substituted into eqn 5, eqn 6 results.

Equation 5 was used to estimate the effective diffusion constant for the 1987 data set, resulting in an estimate of \( D = 322 \text{ cm}^2 \text{ year}^{-1} \). The 1985 data sets were not analysed in this way because rhizome lengths were right-censored.

Diffusion constants are usually estimated by a regression of observed squared displacements vs. time (Okubo 1980). This approach is based on the result shown in eqn 4, and it yields a diffusion constant estimate of \( D = m/4 \), where \( m \) is the slope obtained from the linear regression. When this standard technique was used to estimate the diffusion constant for \( S. altissima \) ramets, a value of \( D = 130 \text{ cm}^2 \text{ year}^{-1} \) was obtained (Fig. 9). This value is considerably smaller than the correlated random-walk estimate of 322 cm² year⁻¹. The regression line in Fig. 9 was constrained to pass through the origin because the variance in initial position \( (C_0) \) was zero [this variance was zero because the oldest shoot
stub in each clonal fragment was recorded as (0,0), and thus, eqn 4 reduces to $E[R^2(t)] = 4Dt$.

The difference between the correlated random walk and the regression estimates of $D$ can be explained in terms of the time scale of observation. The derivation of the regression estimate of the diffusion constant assumes that simple diffusion is followed. However, over the period for which field data were available (a maximum of 5–6 years, because of clone fragmentation), the location of ramet positions over time is consistent with a correlated random walk, but not with simple diffusion. Thus, the standard regression approach is an incorrect application of a procedure whose assumptions are violated by short-term *Solidago altissima* growth patterns. Furthermore, unlike simple diffusion, in a correlated random walk the relationship between $R^2_t$ and time is not linear initially. For *Solidago altissima*, the graph of expected squared displacements vs. time is noticeably concave upward for the first ten years (Fig. 10); thereafter it is approximately linear. As a consequence of this, the regression approach yields different estimates of $D$ depending when data are sampled: if data are sampled for years 1–5, a diffusion constant estimate of 148 cm$^2$ year$^{-1}$ is obtained, while if data are sampled for years 15–19 (with year 14 treated as the origin), a diffusion constant estimate of 321 cm$^2$ year$^{-1}$ is obtained (Fig. 10). If rhizome connections could have been followed for greater than ten years, it is predicted that the standard regression estimate of the diffusion constant would be close to 322 cm$^2$ year$^{-1}$. It was not possible to test this prediction with field data; therefore, computer simulations were used to study the influence that the time scale of observation had upon standard regression estimates of the diffusion constant.

To do this, a computer program that simulated the spread of *Solidago altissima* ramets as a correlated random walk was written. Modelling the spread of goldenrod clones in this way is justified by the results described in the preceding sections. In the simulations, each ramet formed only one daughter ramet. This assumption, while not true in the field, should not alter the average squared displacements of ramets obtained by simulation: because branching angles and rhizome lengths are selected randomly, the net squared displacement of paths that split (by forming more than one daughter ramet) still represent typical $R^2_t$ values. Averaging over many split paths, should then result in the same squared displacement as averaging over paths that do not split. (However, the variance in squared displacement obtained from these two approaches would not be the same.) This line of
reasoning was supported by the analysis of field data: there were no statistically significant differences in rhizome lengths, branching angles, and squared displacements between the split and the non-split paths. Therefore, because only average squared displacements are needed to determine the standard regression estimate of the diffusion constant, the program did not incorporate the complications that result from allowing ramets to produce more than one daughter ramet.

In each of forty runs of the program, the spatial position of fifty clones was followed for fifty generations. Two estimates of the diffusion constant (D) were calculated from these data. The first estimate (denoted D₃) was obtained by regressing simulated squared displacements vs. time for generations one to five only; this estimate corresponded to the field estimate of \( D = 130 \text{ cm}^2 \text{ year}^{-1} \), which was also calculated from five years of data. The second estimate (denoted D₉₀) was obtained by regressing simulated squared displacements vs. time for years 10–50. The first nine years of simulated data were excluded because the relationship between \( R^2 \) and time is not close to linear during this period. The D₉₀ estimate should be close to the correlated random-walk estimate of the diffusion constant (\( D = 322 \text{ cm}^2 \text{ year}^{-1} \)) because the time scale is sufficiently long that the assumptions behind the regression method of estimating the diffusion constant are valid.

The results indicated that the differences between the standard and the correlated random-walk estimators of the diffusion constant indeed can be accounted for by the time scale of observation. Summing over the forty runs yielded an average D₃ estimate of 148 cm² year⁻¹. The range of the D₃ estimates was 128–174 cm² year⁻¹, which included the value of 130 cm² year⁻¹ obtained in the field. The average D₉₀ estimate was 317 cm² year⁻¹, very close to the correlated random-walk predicted estimate of 322 cm² year⁻¹.

**DISCUSSION**

In describing patterns of vegetative spread in clonal plants, it is important to quantify the amount of morphological variation for clonal growth parameters. The data reported here indicate that *Solidago altissima* has considerable variation within fields for such growth parameters as branching angles, rhizome lengths and numbers of daughter rhizomes. There was also variation between fields for rhizome lengths.

Many clonal plant species are thought to have consistent, well-defined growth rules that confer advantages in substrate exploration and exploitation (Bell 1974; Smith & Palmer 1976; Bell & Tomlinson 1980); such plants are said to have an ‘adaptive architecture’. Although it is common to interpret the vegetative spread of clonal plants as adaptive, to date all models upon which such interpretations are based have been deterministic. For example, Smith & Palmer (1976) obtained a bimodal distribution of *Solidago canadensis* branching angles in which the most common direction of growth was a 60° deviation to the right or left of the previous direction of growth. Based on these data, Smith & Palmer (1976) constructed a deterministic model of *Solidago* clonal growth, in which clones spread through space along a hexagonal grid. Because ramets positioned on a hexagonal grid can be closely packed, *S. canadensis* was said to possess an adaptive architecture.

*S. altissima* and *S. canadensis* are closely related taxonomically and are very similar morphologically. However, rhizome lengths in *S. canadensis* are rarely longer than 5.0 cm
(Schmid et al. 1988; B. Schmid, personal communication). The mean rhizome length reported in Smith & Palmer (1976) was 7.5 cm and the rhizome-length standard deviation was large (8.0 cm, calculated from the standard error of the mean and the sample size). This implies that many rhizomes must have been considerably longer than 10.0 cm; thus, it is possible that Smith & Palmer worked with *S. altissima*, not *S. canadensis*.

The modal direction of growth observed in this study was 0°. In conjunction with the fact that *Solidago* clonal growth patterns are highly variable, this indicates that hexagonal and deterministic models should not be used to describe the spread of *S. altissima* clones. For many clonal plants, it may be possible to construct deterministic models of vegetative spread that position ramets in an adaptive fashion. Results from deterministic models should not, however, be used to argue that plants with considerable clonal growth variation possess an adaptive architecture. Many clonal plants exhibit large variation in characters that control vegetative spread (Cain & Cook 1988), and others, as described in the introduction, are highly responsive to environmental variation. It would therefore be both useful and interesting to construct models of the optimal spread of clonal plants that incorporate natural variation in clonal growth parameters.

Frequency distributions of clonal growth parameters document the range of behaviours exhibited and may suggest habitat- or genotype-dependent differences in clonal growth form, but they do not provide information on the details of the clonal growth process. It is also necessary to analyse the process by which growth parameters are ‘selected’ (over time) from such frequency distributions. The results reported here suggest that *Solidago altissima* branching angles and rhizome lengths are not correlated over time. This indicates that the vegetative spread of these plants can be represented as a series of independent, random draws from branching angle and rhizome length frequency distributions. Such a representation is, in essence, a stochastic simulation model. Thus, these results justify construction of a stochastic simulation model of *S. altissima* clonal growth, but, as described above, they do not support a deterministic models of vegetative spread.

This was the first study to apply random-walk models to the vegetative spread of a clonal plant species. There are several advantages associated with random-walk models: they are general models, they are readily comparable between species, and they can aid in the description and prediction of rates at which clonal plants gain space in natural communities. Such models, however, are not designed to produce realistic maps of the growth of individual genets over time; therefore, they cannot provide information on the spatial structure of plant communities. To do this would require development of stochastic simulation models that not only incorporate variation in branching angles and rhizome lengths, but also account for variation in the number and initiation point of daughter rhizomes.

The fact that the spread of a clonal plant can be modelled as a type of random walk does not imply that these plants respond randomly to their environment. For example, clonal plants might shorten their rhizome lengths upon encountering a high nutrient environment, yet still ‘select’ rhizome lengths from the resulting new distribution according to a correlated random-walk process. In such an example the plants are responsive to their environment, but the details of their growth can be represented as a (habitat-dependent) correlated random walk. In addition, because the response of such plants would cause them to remain in high nutrient patches, their growth form clearly would be adaptive, despite containing elements of ‘randomness’.
ACKNOWLEDGMENTS

I thank V. Andreasen, B. Bedford, M. Braner, N. Cappuccino, R. Cook, S. Levin, R. Root, D. Vam Vikites, J. White and P. Wimberger for discussions and/or for comments on an early version of this paper. I also thank V. Andreasen and C. McCulloch for statistical advice, and V. Andreasen, H. Damman, R. Rosenberg, H. Shimbo and Mo for help with field work. Finally, thanks to B. Berry for her help with the final revisions of this manuscript. This work was supported by the Cornell Plantations, by National Science Foundation grants to S. Pacala and J. Silander, and by a McIntyre-Stennis Project and a National Science Foundation grant to S. Levin.

REFERENCES


Clonal growth in Solidago altissima


(Received 15 April 1988; revision received 8 September 1989)