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Demography and modelling of clonal fragments in the pseudoannual plant *Trientalis europaea* L.

Jesús Piqueras[1] & Leoš Klimeš[2]
[1] *Department of Botany, Stockholm University, S-106 91 Stockholm, Sweden;* [2] *Academy of Sciences of the Czech Republic, Institute of Botany, Section of Plant Ecology, Dukelská 145, 379 82 Třeboň, Czech Republic*

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Abstract

The clonal growth pattern and demography of clonal fragments (aggregation of ramets derived from a common parent ramet) in the pseudoannual plant *Trientalis europaea* were studied in field conditions from 1991 to 1993. During this period the population of clonal fragments declined, with a half-life of 7.4 years. Number and size of the clonal progeny and stolon length were positively related to the size of the mother ramet. Survival rates of ramets and tubers increased with size. The rate of clonal growth was low: after three years, about 70% of the clonal fragments had only one ramet. This suggests that the pseudoannual growth habit in *T. europaea* is more important as mechanism of perennation than of ramet multiplication.

Field data were used in a simulation model of architecture and population dynamics of clonal fragments. About 10% of the clonal fragments survived to the end of the simulation (15 years) and the mean survival was 4.7 years. The model predicted a positive correlation between persistence of the clonal fragment and number of ramets produced. Sensitivity analysis showed that the production of a daughter ramet of at least the same size as the parent ramet was the most important pathway for the survival and the number of ramets of the clonal fragment, whereas the production of secondary ramets had a very small effect. This confirms the interpretation of the pseudoannual life-cycle as a mechanism of ramet replacement in this species. Sensitivity analysis also revealed that changes in survival probabilities of the smallest ramets had the largest impact on clonal fragment dynamics. This reflects the important role of the smallest size class of ramets as a source of new vegetative propagules, maintaining a hierarchy in the size structure of the population.

Introduction

In clonal plants, at least two levels of organisation may be recognised: genets and ramets. The genet is the product of a single zygote which consists of one to several physiologically dependent or independent units, the ramets (Schmid 1990). A consequence of this organization is that a genet can achieve a life-span of hundreds or even thousands years (Cook 1985; Watkinson & White 1985). However, in most clonal plants, especially in those in which ramets split up into physically independent parts, ramets are the fundamental units that live, reproduce and die. Thus, the ramet level may be considered as the primary level of the demographic process (Eriksson & Jerling 1990).

Ramets of different species of clonal plants show a great variation in life-span; from only one growing season as in the forest herb *Medeola virginiana* (Cook 1985) to more than 100 years for aerial shoots of *Populus tremuloides* (Barnes 1966). The pattern of physiological integration among ramets in a genet is crucial for the understanding of the dynamics of ramets and their response to environmental changes (Pitelka and Ashmun 1985). Connections between ramets may be functional for decades in some species, while in others the physical contacts decay in a few months, after the production of daughter ramets. For clonal plants in which the connections between ramets are broken at the end of the growing season, e.g. *Potentilla anserina* or *Fragaria vesca*, the ‘splitting behaviour’ is a characteristic part of their ontogeny (Eriksson & Jerling 1990). In other clonal plants, it is the age of the ramets which is ontogenetically determined; for instance in the understory rhizomatous species *Clintonia borealis*, *Maianthemum bifolium* and *Cypripedium calceolus* where the individual ramets live only for one year though the underground connections persist for many years (Pitelka & Ashmun 1985; D'Hertefeldt & Jónsdóttir 1994; Kull 1995).

In clonal plants with pseudoannual growth habit such as *Trientalis europaea* and *Glaux maritima* (Warming 1918; Jerling 1988a), individual ramets live for only one season. Before they die back in autumn, they produce one or more overwintering vegetative propagules which give rise to new ramets in the following spring. Since connections between the mother ramet and the overwintering propagules also decay in autumn, the future ramets become physiologically independent immediately after their formation. This growth form is found in several members of the Primulaceae, but also in other families such as the Lamiaceae, the Solanaceae, the Onagraceae, the Asteraceae, the Ranunculaceae and the Liliaceae (Warming 1918; Kawano et al. 1987). The term pseudoannual has also been used in a wider sense by Pitelka and Ashmun (1985) to characterise every clonal plants possessing annual ramets, including those with long-lived connections. In this paper, however, the concept of pseudoannuals is in accordance with Warming's interpretation and assumes that both ramet life-span and clone integration are limited to one growing season.

The pseudoannual growth habit has important implications for the population structure and spatial distribution of ramets. Since all ramets observed in a particular year have emerged from propagules produced the year before, there is no age structure in the ramet population and, consequently, no overlapping generations. Vegetative growth in pseudoannual plants results in an unusual form of ramet mobility: as the mother plant dies back at the end of the growing season and resources are reallocated to newly produced structures, the plant changes its growth site from year to year. In *Glaux maritima*, for instance, the magnitude of such displacement can be considerable and results in an extensive lateral spread of the clone (Jerling 1988a, b). Another example is provided by *Trientalis borealis*, a forest herb which, despite its small size (ca. 8–15 cm), can move over one meter from the location of the previous year (Cain et al. 1991).

Presumably as a consequence of these 'extremely mobile' ramets in pseudoannuals and because most of them are geophytes or hydrophytes (Warming 1918; Sculthorpe 1967), very little is known about their population biology. To date, only two long-term demographic studies have been published on the pseudoannuals *Glaux maritima* and *Ranunculus lingua* (Jerling 1988a; Johansson 1993). These studies identified biotic and abiotic factors regulating the population dynamics of these two species, but were limited in that the fate of the ramets was not individually followed in successive years. Thus, although overall trends in ramet number, density or ramet performance were determined, the underlying patterns of mortality remained unknown.

In this paper, we investigated the patterns of clonal growth, mobility and survival of clonal fragments of the pseudoannual plant *Trientalis europaea*. These patterns were assessed in two different ways. First, morphological and demographic studies were conducted in the field, in which the fate of individual ramets was followed in successive years. Second, a stochastic simulation modelwas developed which combine clonal architecture and population dynamics, calibrated with our field data. The modelling approach has previously been applied to other species of clonal plants such as *Medeola virginiana* (Cain & Cook 1988), *Lycopodium annotinum* (Callaghan et al. 1990), *Solidago altissima* (Cain 1990; Cain et al. 1991), *Rumex alpinus* (Klimeš 1992), *Trifolium repens* (Cain et al. 1995), *Anemone nemorosa* (Cowie et al. 1995), *Asarum europaeum* (Kisljuk et al. 1996). Most of these studies have highlighted aspects of growth form, space exploitation and architecture of the studied species (but see Callaghan et al. 1990). In the present study, however, modelling emphasized populational aspects of the pseudoannual life-cycle. Particularly, the effect of changes in clonal behaviour, ramet size and survival on the performance of clonal fragment were investigated with a sensitivity analysis performed in the model. Different aspects of the foraging behaviour in *T. europaea*, also addressed with our simulation model, are presented in a forthcoming paper (J. Piqueras, L. Klimeš & P. Redbo-Torstensson, unpublished manuscript).

Methods

The study species

Trientalis europaea L. (Primulaceae) is an understory herb widely distributed in boreal woodlands of the northern hemisphere. From September to May the plant persists as a tuber that lies below the litter layer of the forest (Figure 1). At the end of May the stem begins to elongate, bringing the leaves and the flower buds formed the previous autumn. Flowering occurs between May and June and, usually, one flower is produced per shoot. In July underground stolons are initiated from the tuber and continue to develop until the middle of August. Then, they cease growing apically and begin to form a tuber by thickening their apices. During August the daughter tuber continues to enlarge, reaching its maximum size at the beginning of September. At this time the mother plant manifests a rapid senescence. By the end of September most of the leaves have fallen and the stolons connecting the tuber of the mother plant with the new formed daughter tubers have decayed. Seed set is low (Hiirsalmii 1969; Kovanda 1995). Seedling recruitment is extremely rare in established populations and occurs only under very favourable moisture conditions combined with disturbances on the forest ground (Hiirsalmi 1969, Grivlova & Vahrameeva 1990, Eriksson & Ehrlén 1992).

Demographic study: a population of clonal fragments

The demography and clonal spreading of *T. europaea* were studied from 1991 to 1993 in a mesic spruce forest about 45 km SSW of Stockholm, Sweden. The dominating tree species were *Picea abies* and *Pinus sylvestris* and the field layer mainly consisted of *Vaccinium myrtillus*, *V. vitis-idaea*, *Maianthemum bifolium* and *Linnaea borealis*.

In June 1991, 23 permanent plots (200 × 200 cm in size) were spaced at distances between 2 to 10 m, to cover the variation in light conditions and vegetation in the forest. In each plot eight points were placed in a regular pattern and the nearest ramet of *T. europaea* to each point within a radius of 20 cm, were chosen. A total of 118 ramets were selected and their positions mapped. In September, stolons were followed by careful digging and the position and size of the tuber of the mother ramet and daughter tubers were recorded. Stolons and tubers, which grow superficially, appeared not to be affected by the digging. Survival was recorded for the ramets (i.e., the aerial shoots) and the daughter tubers. A ramet was considered to have survived the growing season if it had produced at least one daughter tuber. Tubers surviving the winter, i.e. those that had developed a new ramet in the following spring, were recorded in June 1992. The same procedure was repeated for all descendant ramets until the last census in September 1993. In this study, we refer to the aggregation of ramets descending from a common mother ramet as a clonal fragment (cf., Angevine & Handel 1986).

Additionally, 93 ramets were randomly selected in the proximity of the permanent plots in 1992. In June, the sum of the area of all leaves on a ramet were recorded (the area of a single leaf was assessed as the product of leaf length and leaf breadth). In September, these ramets were carefully excavated and brought into the laboratory. The lengths of the tuber of the mother ramet, stolons and their respective daughter tubers were recorded. The length of the tuber of the mother ramet showed a good correlation with the total leaf area ($r = 0.72$, $p < 0.001$, $N = 90$). Since tuber length allowed a direct comparison between the sizes of the mother ramet and the next generations of ramets in the excavated plants, this measure was used for ramet size throughout the study.

The growth rules of the simulation model

For the simulation we used a stochastic, spatial (two-dimensional) and nonstationary (Waller & Steingraeber 1985) model (programme CLONE, see for details Klimeš 1992). In the model, the clonal growth and architecture of a single *T. europaea* ramet was simulated from field estimates of tuber production, stolon lengths, branching angles and survival probabilities. The morphological study of the 93 excavated plants provided the relationships between the size of the mother ramet and the number and size of daughter tubers. These, expressed as frequencies, were used to construct a matrix of clonal growth probabilities (Table 1). Tuber lengths were classified into four size classes (size 1: ≤3 mm; size 2: 4–6 mm; size 3: 7–9 mm and size 4: > 9 mm) and a maximum number of three tubers per ramet were considered. Less than 4% of the ramets produced more than three tubers (see results). For these ramets, only the three largest tubers were considered. Similarly, a matrix of probabilities was created for the distribution of number and lengths of the stolons in relation with the size of the mother plant (Table 1). In this case the lengths of stolons were assigned to five classes (length 30: ≤60 mm; length

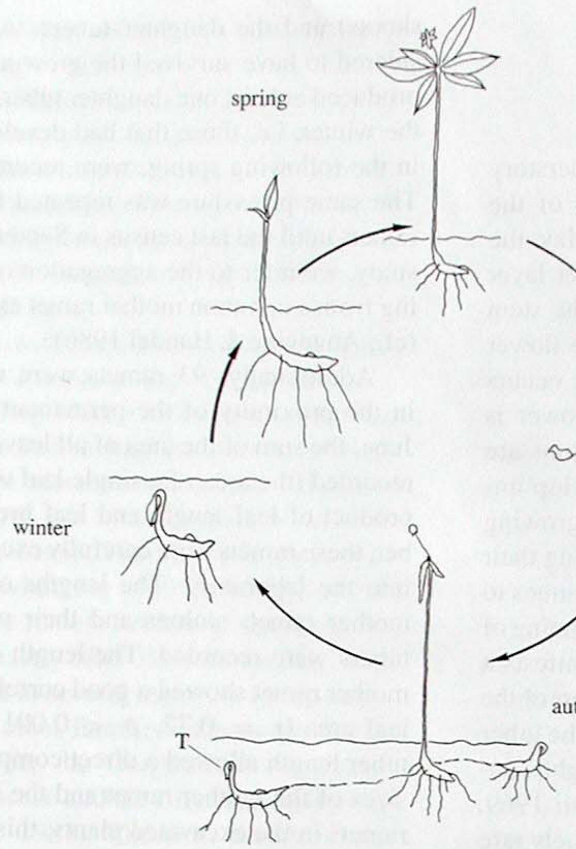

Figure 1. The pseudoannual life-cycle of *Trientalis europaea*. MR: mother ramet. TMR: tuber of the mother ramet. ST: underground stolon. T: daughter tuber.

90: 61–120 mm; length 150: 121–180 mm; length 210: 181–240 mm and length 270: >240 mm). When several stolons and tubers were produced, the first, second and third stolons, ordered in decreasing size, were assigned to the first, second and third daughter tubers, respectively (see results for explanation).

The demography and mapping of the 118 ramets in the permanent plots provided the data for the initial size class distribution, the survival probabilities and the frequency distribution of the branching angle (Figure 2). This was calculated by drawing the positions of the ramets and measuring the angle formed between the displacements in 1991 and 1993 (Figure 2). For the model, the size class distribution of ramets in 1992 was utilised. The survival for each size class was calculated as the probability of surviving the winter in 1992 and the subsequent growing season (Table 1).

Simulations and sensitivity analysis

The clonal growth of a single *T. europaea* ramet was simulated in annual time steps. A probabilistic event, such as selection of ramet size, branching or survival, happened if a randomly generated number between 0 and 1, was lower than the probability of that event (see Table 1 for probability values). After selection of the initial ramet, the number of daughter tubers was determined from the sum of probabilities for the main, second and third daughter tuber in the corresponding column. For instance, for a mother ramet of size 2, the associated probabilities were 0.793 (0.083 + 0.480 + 0.230), 0.167 (0.146 + 0.021) and 0.040 (0.020 + 0.020) for the production of one, two or three daughter tubers respectively (thus, if the randomly generated number is larger than 0.167, only one daughter tuber was produced). Then, the size of the tuber of a particular order (main, second or third) was determined in accordance with the subset of probabilities of its order, adjusted to sum up 1.00 prior to their use. Following the same example, the probabilities for the different sizes of the main daughter tuber were: 0.104 (0.083:[0.083 + 0.480 + 0.230]) for size 1, 0.605 for size 2, and 0.290 for size 3. Finally, the size-specific survival probabilities decided which ramets entered in a new period. Except for the first step (election of the initial ramet), this process was repeated in every simulation period until the death of the clonal

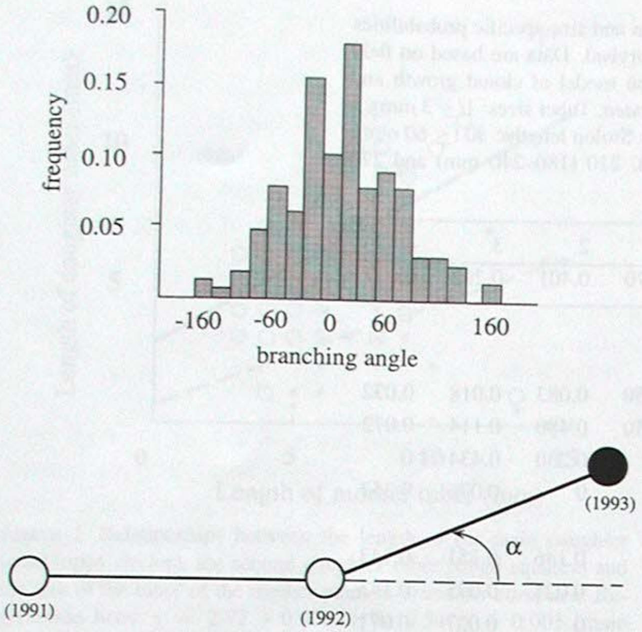

Figure 2. Distribution of branching angles in clonal fragments of *Trientalis europaea*. The branching angle (α) was measured as the deviation from the previous direction of growth (dotted line in the clone diagram), calculated from the positions of the ramets in 1991, 1992, and 1993. Branching angles range from −180 ° to 180 °. Deviations to the left were measures as negative angles, while right hand deviations were positive. 0 ° was considered as straight ahead.

fragment or a maximum of 15 iterations (years). At the end, a list of the output variables and a graphical representation of the clonal fragment were displayed. The output variables considered were survival of the clonal fragment (in years), the number of ramets per clonal fragment in the last generation and the distance reached by the clonal fragment. In this study, in order to obtain a basic knowledge of clonal fragment behaviour, we simulated the clonal growth of 2000 initial ramets. Simulations were not performed simultaneously since interactions between ramets and density effects were not incorporated in the model. An important assumption of the simulation model was that the values of clonal growth, stolon lengths, branching angle and survival probabilities operating in subsequent years are independent

A sensitivity analysis was performed in order to assess how clonal fragments responded to changes in the clonal growth probabilities and the survival values used in the model. The aim of this analysis is similar to the sensitivity analysis in transition matrix models (Caswell 1989). However, instead of assessing the effect of changes on the rate of population growth, our sensitivity analysis directly allows the evaluation of changes on the individual performance of the clonal fragment (i.e., life-span and number of ramets). Also, in contrast to transition matrix models, our sensitiviy analysis used simulations with gradual changes in the input values, instead of an analytical solution. For the clonal growth matrix, each value was changed, one at a time, from 0 to 1 in steps of 0.05. All other values for a particular size of mother ramet were adjusted, keeping proportions among the values constant, so that the sum of clonal growth probabilities within a size class equalled to 1. Each change was run for 100 initial ramets and the average of the output variables was obtained. The relationship between the changes in the value of clonal growth and the output variable was then calculated using linear regression analysis. The direction (positive or negative) and magnitude of the change in the output variable, as a consequence of changes in the value of clonal growth, was indicated by the regression coefficient (significant at $p < 0.05$, $N = 11$). Similarly, the survival probabilities were changed, one size class at a time, from 0 to 1 in steps of 0.1. 300 simulations were run for each combination of input variables. The output variables examined in the sensitivity analysis, both for changes in the clonal growth matrix and survival probabilities, were survival of the clonal fragment and number of ramets. For the second variable, only clonal fragments surviving the whole simulation (15 years) were considered.

Results

Clonal growth and clonal fragment dynamics

The study of the excavated ramets revealed a modest vegetative propagation in *T. europaea*. Of 93 ramets, 59.1% produced one tuber, 26.8% two, 5.3% three and 3.2% produced more than three tubers. Five plants (5.3%) did not produced any tubers. Each plant produced, on average, 1.52 tubers (SD = 0.86, $N = 88$). Typically, only one tuber was produced per stolon. When a ramet produced several stolons and tubers, the longest stolon bore the largest tuber (hereafter referred to as the main stolon and the main tuber) whereas secondary tubers grew from shorter stolons (Table 2). The size of the mother ramet was positively correlated with the number of produced tubers ($r = 0.49$, $p < 0.001$, $N = 88$), the size of the tubers (Figure 3) and the sum of the rhizome lengths ($r = 0.54$, $p < 0.001$, $N = 88$). On average, the main tuber was of similar size as the tuber of the mother ramet (Tab. 2).

Summer survival of ramets (i.e. the probability of producing at least one tuber) was very high (approach-

Table 1. Table 1. Initial size distribution and size-specific probabilities of clonal growth, stolon length, and survival. Data are based on field observations and used in the simulation model of clonal growth and population dynamics of *Trientalis europaea*. Tuber sizes: 1(≤ 3 mm), 2 (4–6 mm), 3 (7–9 mm) and 4 (>9 mm). Stolon lengths: 30 (≤ 60 mm), 90 (60–120 mm), 150 (120–180 mm), 210 (180–240 mm) and 270 (> 240 mm).

Size of the mother ramet		1	2	3	4
Initial distribution		0.270	0.401	0.292	0.037
Clonal growth matrix					
Size of the main daughter tuber	1	0.250	0.083	0.018	0.072
	2	0.750	0.480	0.114	0.072
	3	0	0.230	0.434	0
	4	0	0	0.076	0.357
Size of the second daughter tuber	1	0	0.146	0.151	0.143
	2	0	0.021	0.095	0.143
	3	0	0	0.057	0.071
	4	0	0	0	0
Size of the third daughter tuber	1	0	0.020	0.037	0.071
	2	0	0.020	0.018	0.071
	3	0	0	0	0
	4	0	0	0	0
Stolon length matrix					
Main stolon	30	0.600	0.500	0.200	0.091
	90	0.400	0.240	0.320	0.182
	150	0	0.019	0.100	0.182
	210	0	0	0.040	0
	270	0	0.019	0.020	0.091
Second stolon	30	0	0.148	0.240	0.182
	90	0	0.019	0.020	0.090
	150	0	0.019	0.020	0
Third stolon	30	0	0.036	0.040	0.182
Survival probabilities		0.122	0.708	0.927	0.973

Table 2. Clonal growth and lateral spreading of *Trientalis europaea*. Length (Mean ± SD) in millimeters of tubers and respective stolons produced by a mother ramet. Differences between tubers and stolons of different order in the same mother ramet were tested with Wilcoxon signed ranks test. For each column, the data sharing the same letter are not significantly different at $p = 0.05$.

Order	Stolon length (mm)	Tuber length (mm)	N
Mother ramet		6.6 ± 2.2^{a}	85
Main	78.1 ± 69.3^{a}	6.6 ± 2.4^{a}	88
Second	45.2 ± 37.7^{b}	3.6 ± 2.1^{b}	30
Third	15.5 ± 8.6^{c}	2.7 ± 1.7^{b}	7

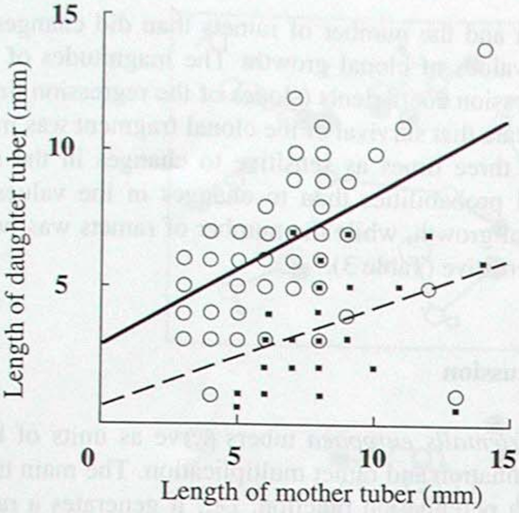

Figure 3. Relationships between the length of the main daughter tuber (open circles), the second daughter tuber (filled squares) and the size of the tuber of the mother plant in *Trientalis europaea*. Regressions lines: $y = 2.77 + 0.67x$, $r = 0.54$ $p < 0.001$ (main daughter tuber); $y = 0.372 + 0.56x$, $r = 0.29$ $p = 0.035$ (second daughter tuber).

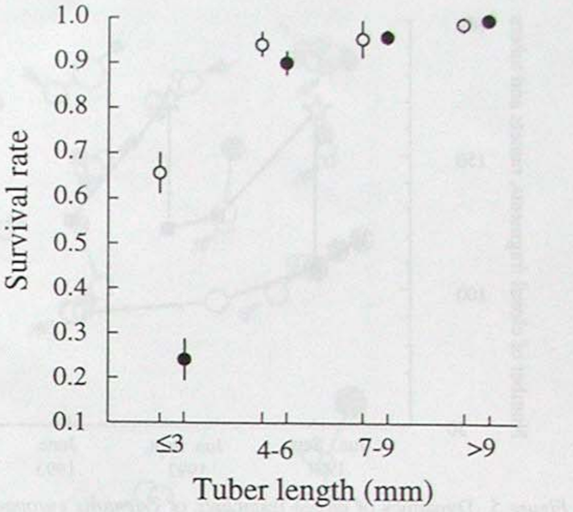

Figure 4. Survival in *Trientalis europaea* in relation to tuber length. Summer survival of ramets, i.e. probability of producing at least one daughter tuber (open circles, means of 1991–1993) and winter survival of tubers (filled circles, means of 1991–1992). Vertical bars represent ± Standard Error.

ing 100%), even for the smallest ramets (Figure 4). Winter survival of the smallest tubers was low but increased swiftly with tuber size (Figure 4). From June 1991 to June 1993, the number of clonal fragments decreased from 118 to 90 (Figure 5). Thus, assuming an exponential decay, the half-life of this population of clonal fragments is 7.4 years (calculated from $t\ln 2/(\ln a-\ln b)$ where a is the initial number of clonal fragments and b is the number of clonal fragments still alive after t years). In June 1993, the mean number of ramets per clonal fragment, was 1.36 ($SD = 0.66$, $N = 90$).

The longest stolon observed during the study was 93 cm. However, the annual mean value of the longest stolon, was 17.2 cm ($SD = 14.9$, $N = 74$) in 1991 and 7.10 cm ($SD = 4.9$, $N = 74$) in 1992. The net displacement, calculated as the distance between the position in 1991 and 1993, was 20.7 cm ($SD = 11.7$, $N = 74$). The mean branching angle of stolons was 20 ° relative to the direction of the previous year (Figure 2).

Simulations

The spatial arrangement of ramets of simulated clonal fragments showed a considerable variation. Although a common pattern corresponded to plants growing away from the initial position (cf., 'guerrilla' growth form, Lovett Doust 1981), more intricate paths also occurred (Figure 6). Population dynamics and and ramet size structure of simulated clonal fragmets showed a good agreement with the observed in the field (Figures 7A, B). An age class distribution of the simulated clonal fragments showed that more than 36% of them did not survive the first year (Figure 7C). Assuming an exponential decline, the half-life of this population of clonal fragments was 4.5 years. The mean life-span of the clonal fragments was 4.7 years. Still, 10% of the clonal fragments reached the maximum age of 15 years, suggesting their potential for even longer life-spans (Figure 7). The average number of ramets per clonal fragment increased with age (Figure 7), ranging from 1.1 ($SD = 0.341$, $N = 1277$) for those surviving the first year, to 1.93 ($SD = 1.24$, $N = 197$) for 15-year-old clonal fragments. For these clonal fragments, the net displacement from the initial position was 102 cm. ($SD = 41.4$, $N = 102$).

Sensitivity analyses: clonal growth, survival and size

Ten out of 26 probability values of the clonal growth matrix had a significant effect on survival of the clonal fragment, all representing probability values associated with the main tuber (note the thick arrows in Figure 8A, B). Positive effects on survival of the clonal fragment were observed when the probabilities of producing a main tuber of the same size class as the tuber of the mother ramet (for size classes 2, 3, and 4), or larger (for size classes 2 and 3), were increased. In contrast, producing a main tuber of smaller size than

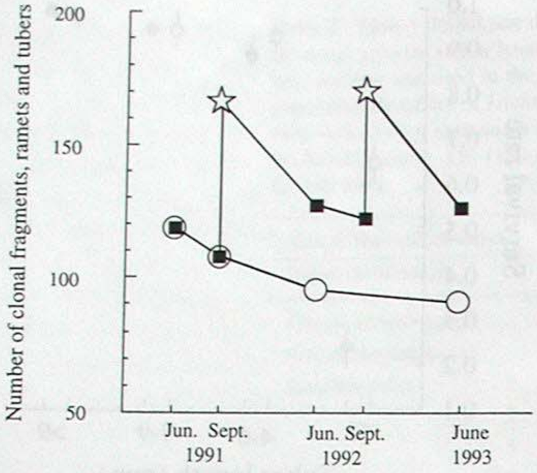

Figure 5. Dynamics of clonal fragments of *Trientalis europaea* in 1991–1993. Clonal fragments (open circles) are formed by annual ramets in June (squares),which produce overwintering tubers (stars) in September. Tubers surviving the winter arise the new generations of ramets of the clonal fragment in the following growing season. The number of clonal fragments is equal to the number of initial ramets in 1991. The values are the sum of all 23 plots.

the tuber of mother ramet or producing a main tuber belonging to the smallest size class had a negative effect on survival of the clonal fragment.

Changes in seven probability values of the clonal growth matrix, exclusively of plants in size classes 2 and 3, resulted in significant changes in the number of ramets per clonal fragment (Figures 8A, C). Producing a main tuber larger than the tuber of the mother ramet increased the number of ramets, whereas the production of a smaller tuber decreased the number of ramets (Figure 8C). Only in size class S3, variation in the probability values of the second tuber accounted for significant changes in the number of ramets. In general, either survival of the clonal fragment or the number of ramets were most sensitive to changes in the probability values of plants of size class 3, followed by size class 2.

The increased survival and number of ramets of the clonal fragments after increasing the survival probabilities differed between different size classes (Figure 9). Clonal fragment survival was more sensitive to changes in the probability values of the size classes 1 and 2 than to those of larger size classes (Figure 9A). The largest effect on the number of ramets was associated with survival changes in the smallest size class, whereas changes in survival probabilities of the largest class had no effect (Figure 9B).

Altogether, changes in the survival probabilities had a greater impact on survival of the clonal fragment and the number of ramets than did changes in the values of clonal growth. The magnitudes of the regression coefficients (slopes of the regression lines) indicate that survival of the clonal fragment was more than three times as sensitive to changes in the survival probabilities than to changes in the values of clonal growth, while the number of ramets was twice as sensitive (Table 3).

Discussion

In *Trientalis europaea* tubers serve as units of both perennation and ramet multiplication. The main tuber has a perennation function, i.e., it generates a ramet that replaces the mother ramet in the next year. Only if supplementary tubers are produced an increase in the ramet number can be achieved in the following year. In about 70% of the plants in the study population, tuber production only served for perennation. Such clonal growth can be regarded as modest compared with other pseudoannual plants (Jerling 1988b; Westley 1993; Johansson 1994; Verburg et al. 1996) but it is in agreement with the relatively low rate of clonal growth observed in other species of forest herbs, at least in relatively undisturbed stands (Anderson & Loucks 1973; Kawano & Nagai 1975; Barkham 1980, 1992; Pitelka et al. 1980, 1985; Bierzychudek 1982a,b; Eriksson 1988a; Nault & Gagnon 1993; Hara & Wakahara 1994; Kull 1995). Moreover, when the population dynamics of *T. europaea* is described in terms of a population of clonal fragments, the general picture of this species as a long-living perennial plant, becomes evident. During the 3 years of field study, the survivorship of established clonal fragments followed a linear survivorship curve characteristic of a perennial plant species with a low turnover in the population (Harper 1967; Sarukhán & Harper 1973). Nevertheless, intense population growth due to extensive clonal growth and has been noticed in *T. europaea*, generally associated with disturbances, such as tree falls fire (Hansen 1964; Hiirsalmi 1969), or eutrophication (Kellner & Redbo-Tortensson 1995). As in other woodland understory herbs, populations of *T. europaea* seem to be dependent on a certain regime of disturbance to persist in the forest (Pitelka et al. 1980). However, our study suggests that populations of *T. europaea* can remain many years under rather undisturbed conditions without risk for local extinction.

Both the number of tubers and their size were positively correlated with the size of the mother ramet

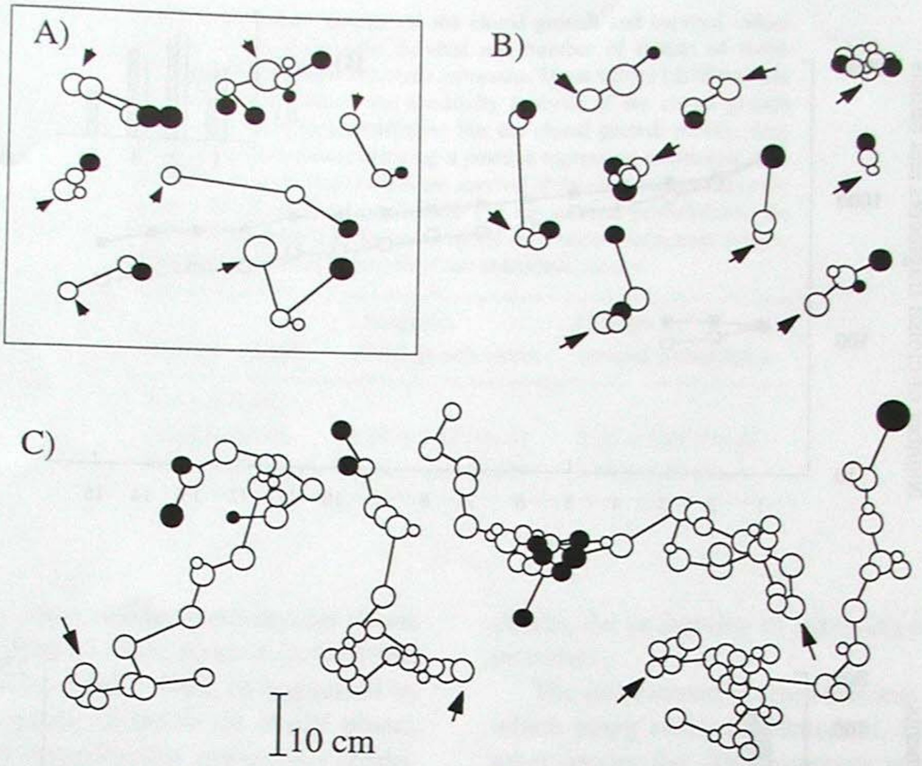

Figure 6. The spatial patterns of clonal fragments of *Trientalis europaea*. Three-years of growth of clonal fragments as mapped in the field (A). Three years (B) and 15 years (C) of growth of simulated clonal fragments with the model. Open circles represent ramets produced in the previous years. Filled circles denote the final number of ramets produced by each original ramet at the end of the demographic study (for A) or at the end of the simulation (for B and C). The arrows indicate the initial ramet. Ramet size is indicated by the different size of the circles. Ramet size and stolon length are not proportional in the drawing.

in *T. europaea*. Distinct size-dependent clonal growth is characteristic for several species of pseudoannuals (Jerling 1988b; Westley 1993; Verburg et al. 1996). However, in contrast to these species, *T. europaea* showed a rather rigid pattern of clonal growth. Thus, a mother ramet tends to produce a first daughter tuber of a similar size as its own. Only when the mother ramet has reached a certain critical size further stolons with smaller tubers are initiated. Such a 'conservative' pattern of clonal growth could be interpreted as a strategy to ensure the survival in the woodland, a relatively constant and predictable habitat, where size-dependent mortality is considered to be dominant (Begon et al. 1996). In such an environment, a *T. europaea* ramet would only invest in the production of supplementary ramets if its perennation is ensured by a sufficient size of the main tuber. This interpretation is further corroborated by the distinct pattern of size-dependent survival of ramets and tubers. Similar patterns of survivorship have been commonly observed in clonal forest plants (Bierzychudek 1982a, b; Pitelka et al. 1985; Eriksson 1988b; Barkham 1992; Nault & Gagnon 1993).

The capacity for lateral spread exhibited by *T. europaea* was noticeable, even compared with other species of forest clonal plants of considerably larger ramets (Antos & Zobel 1984). From the positive correlation between ramet size and stolon length, it can be inferred that the annual ramet displacement is determined to a great extent by ramet size; however, environmental factors as temperature, surrounding vegetation, soil structure and soil moisture can also affect the length of the stolons in this species (Hiirsalmi 1969; Kovanda 1995). Our results also suggest that, as a consequence of the ramet mobility imposed by the pseudoannual growth habit, the spatial structure of the ramet population is in continuous change and ramets may experience important variations in their microenvironment. Previous studies have demonstrated the significance of the mobility in clonal plants as a mechanism of escape from superior competitors in the surrounding plant community (Eriksson 1986) and resource acquisition by means of foraging responses (Sutherland & Stillman 1988; Hutchings & Mogie 1990; de Kroon & van Groenendael 1990; Hutchings & de Kroon 1994). Whether the explorative behaviour

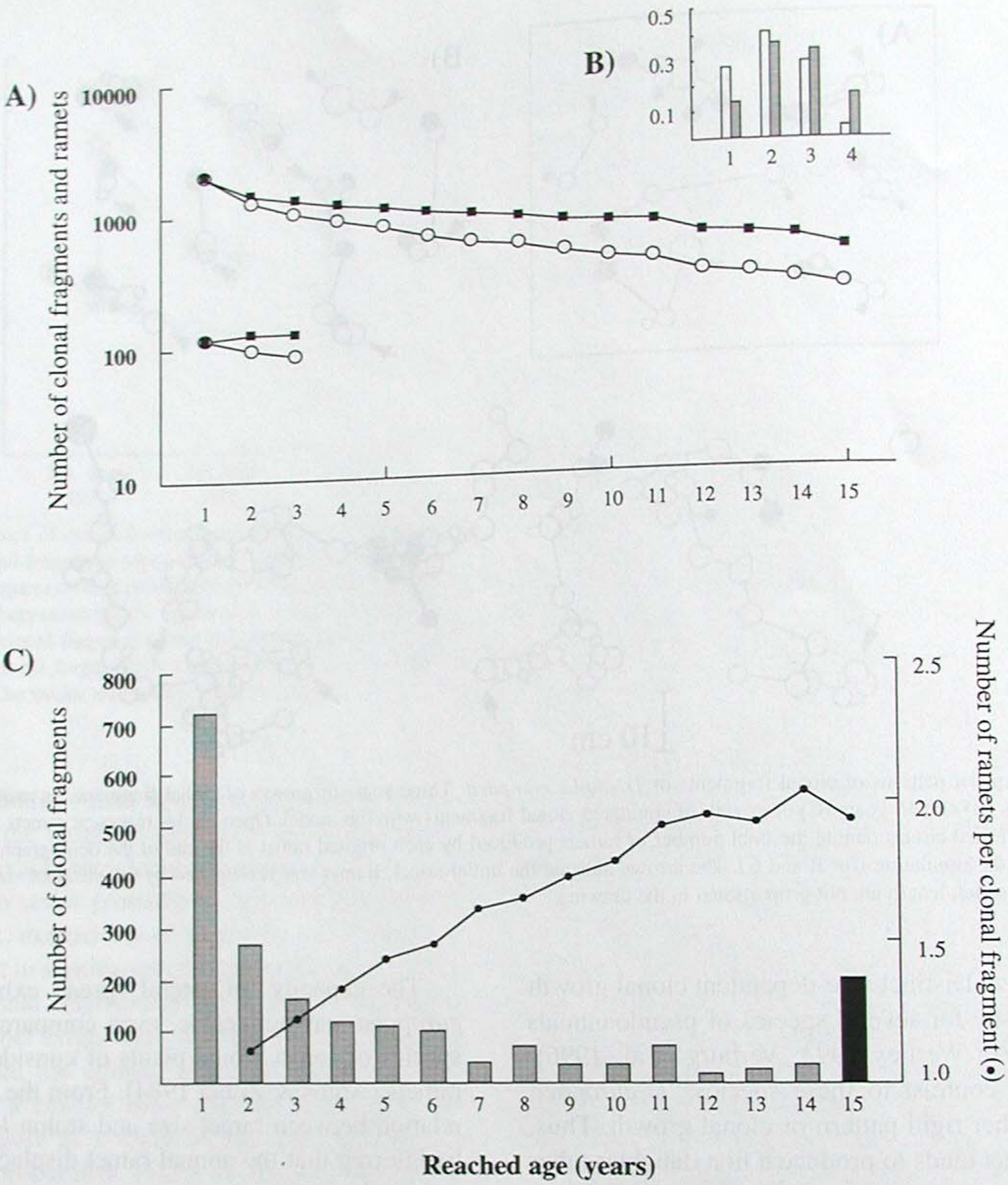

Figure 7. Dynamics of field and simulated clonal fragments of *Trientalis europaea*. (A) Number of clonal fragments (circles) and ramets (squares) over time in the field (3 years) and in computer simulations (15 years). Logarithmic scale. (B) Size class distribution of the ramet population in the field, in 1992 (open bars) and in the simulation, at the stable stage structure at 15 years (shaded bars). Bars indicate relative proportion. (C) Age class distribution of 2000 clonal fragments of *Trientalis europaea* simulated for 15 years of growth (bars), and the mean number of ramets produced by a clonal fragment (dots). The black bar at age 15 of the simulation ($N = 197$) denotes clonal growth with potentially longer life-span.

manifested by the ramets in *T. europaea* could be advantageous in colonisation of favourable patches has not been investigated. However, it has been observed that *T. europaea* belongs to the understory species which, by means of vegetative spreading, first reach areas of bare soil after disturbances (Hansen 1964; Hiirsalmi 1969; Piqueras, personal observation).

Although the evaluation of ability of the present model to simulate clonal architecture and mobility of T. europaea is only visual and, therefore, subjective, comparisons between simulated clonal fragments and mapped clonal fragments in the field suggest a good agreement. The population dynamics of the simulated clonal fragments resembled the dynamics of those observed in the field. The number of ramets per clonal fragment in the simulations was low and only those clonal fragments which reached the age of 15 years had an average of two ramets. The progressive increase of ramets with the life-span of the clonal fragment resembles the clone dynamics of sev-

Table 3. Impact of changes in the clonal growth and survival values used in the model on the survival and number of ramets of simulated clonal fragments *Trientalis europaea*. Mean values (± SD) of the regression cofficients in the sensitivity analysis of the clonal growth matrix and survival probabilities. For the clonal growth matrix, only those probability values showing a positive regression coefficient (significant at $p<0.05$, N=11) with the survival of the clonal fragment or the number of ramets were considered. For the survival probabilities, the value was calculated as the mean of the regression coefficients (slopes of regression lines in Figure 9) of the individual classes.

Affected variable	Changes in clonal growth values	Changes in survival probabilities
Survival of the clonal fragment	1.10 ± 0.27 (N=5)	3.76 ± 2.07 (N=4)
Number of ramets	0.85 ± 0.66 (N=5)	1.59 ± 1.47 (N=4)

eral, slow-growing, rhizomatous forest species (Cook 1985; Angevine & Handel 1986; Antos & Zobel 1984; Kull 1995; Czarnecka 1996). Thus, as suggested by the model, two aspects of fitness in clonal plants, i.e. persistence and generation of new ramets (Eriksson & Jerling 1990) appear intimately connected in the pseudoannual life-cycle of *T. europaea*. However, quantitative predictions must be considered with caution, since the model assumes that the growth rules and demographic parameters do not vary from year to year, which is unlikely in natural populations. For instance, the difference between the half-life of simulated clonal fragments and clonal fragments in the field could be attributed to the utilisation in the model of the survival values in 1992. These values were, for the smallest size class, the lowest in the 3-year period.

The sensitivity analysis of the clonal growth matrix showed that perennation through the replacement ramet was more important than the production of supplementary ramets in determining the persistence and growth rate of a clonal fragment. This is in accordance with the results obtained from other clonal plants, such as *Lycopodium annotinum* and *Linnea borealis* (Callaghan et al. 1990; Eriksson 1988a). However, the response of survival of the clonal fragment and number of ramets to changes in the clonal growth matrix was not identical. While survival was positively affected just by maintaining a similar size as the mother plant, increments in size (transitions to larger size classes of the main tuber) were necessary to assess positive responses in the number of ramets. In this way, the sensitivity analysis further reinforced the significance of producing a first daughter ramet of at least equal size as the mother ramet. As long as this occurs, the probability of surviving in following years increases.

The most sensitive size class was the size class S3, which being relatively abundant, had a high rate of tuber production. This contrasts with the analysis of changes in the survival probabilities, where survival of the clonal fragment and the number of ramets were more sensitive to changes in the smallest size class. A possible explanation for this high sensitivity could be the role of the smallest size class as a source of new propagules for the clonal fragment, which is reflected in the cycle graph (Figure 8A) by the considerable number of arrows converging to this size class. In the dynamics of the clonal fragments of *T. europaea* , the majority of the secondary ramets produced belong to this category. Therefore, an increment in the survivorship of these ramets should have an enormous positive effect on survival of the clonal fragment and clonal growth. The importance of the small or young classes of ramets in determining the population growth rate has also been demonstrated in several demographic studies of clonal plants (Bierzychudek 1982a; McGraw & Antonovics 1983; Svensson & Callaghan 1988; I. Jónsdóttir 1989; G. Jónsdóttir 1993). In *T. europaea*, two possible advantages of the existence of a permanent pool of small ramets in the population could be hypothesised. Firstly, even though their present contribution to the actual clonal growth or survival is insignificant, an eventual increase in their survival may lead to a pulse in the population of clonal fragments. If this interpretation is correct, the production of small ramets could represent an opportunistic investment in a future expansion of the clonal fragments. Secondly, the production of small

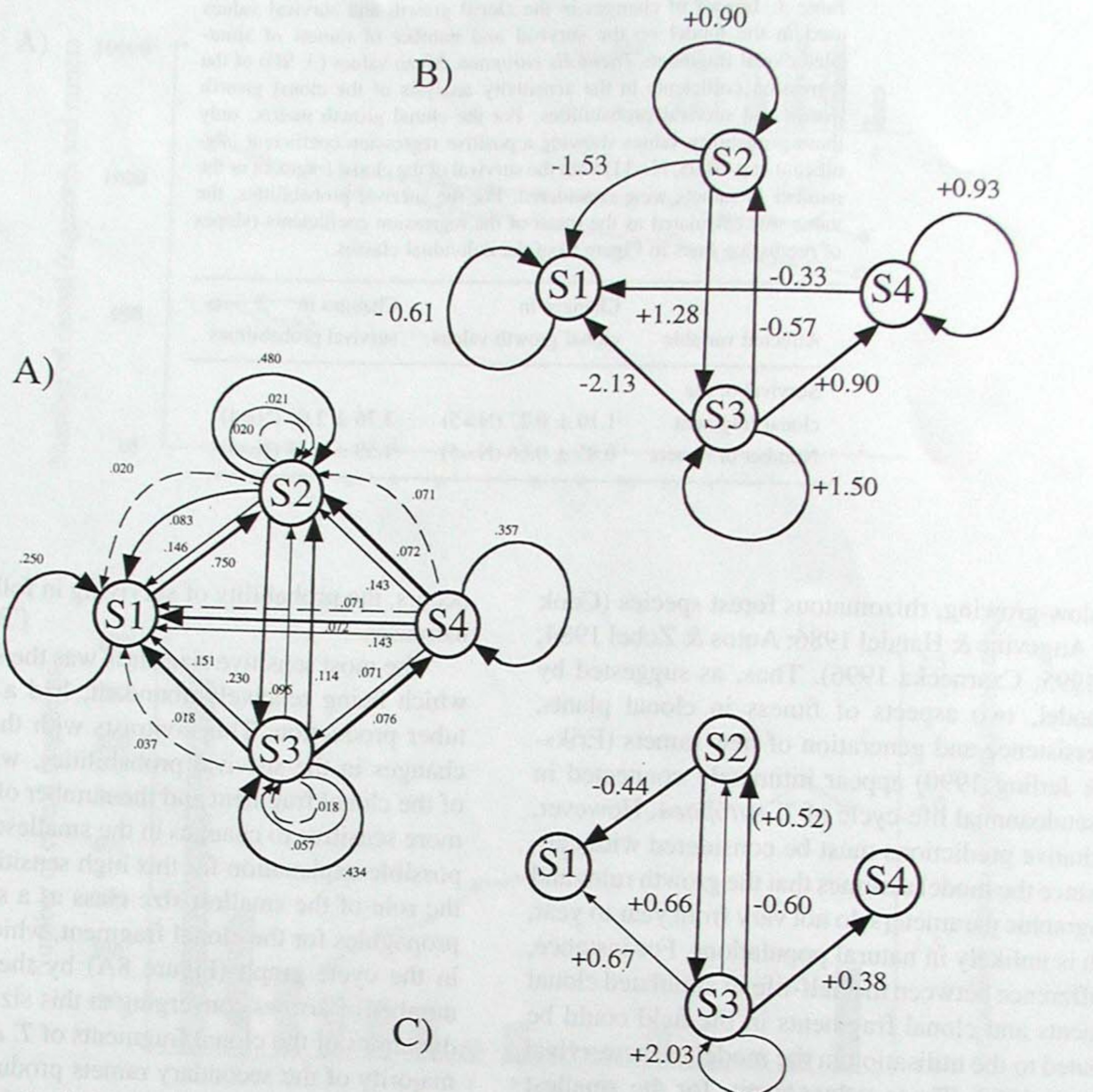

Figure 8. (A) Size-classified life cycle graph for *Trientalis europaea* based on the values of the clonal growth matrix (Table 1). Figures denote transition probabilities between a mother plant and the next generations of ramets through the production of a main daughter tuber (thick arrows), second daughter tuber (thin arrows) and third daughter tuber (discontinuous arrows). S1–S4 represent size classes calculated from the lengt of the tuber (S1 (≤ 3 mm), S2 (4–6 mm), S3 (7–9 mm) and S4 (> 9 mm). (B) Sensitivity analysis of the clonal growth matrix. Only significant transition probabilities for the survival of the clonal fragment are given. Figures denote regression coefficients significant at $p < 0.05$ ($N = 11$). (C) Sensitivity analysis of the clonal growth matrix. Only significant transition probabilities for the number of ramets produced by the clonal fragment are given. (+0.52) correspond to the thin arrow in the middle of the S3–S2 transition. Figures denote regression coefficients significant at $p<0.05$ ($N=11$).

ramets can be viewed as a mechanism of developing and maintaining a size hierarchy in the ramet population. This was found by Kawano et al. (1987) in the pseudoannuals woodland plants *Disporum sessile* and *D. smilacinum*. In these species the recruitment of vegetative offspring resulted in odd population structures possessing the highest number of intermediate size-classes. Eriksson & Jerling (1990) suggested that the occurrence of a size hierarchy in a population of ramets may lead to a stabilised population dynamics and reduced scramble competition. Also, a size hierarchy results in behavioural variation among ramets which has been hypothesized to increase fitness in clonal plants (Kingsolver 1986; Eriksson & Jerling 1990). Because seedling recruitment is very rare in established populations of *T. europaea* (Hiirsalmi 1969; Grivlova & Vahrameeva 1990), clonal growth should be the principal mechanism to ensure a permanent flow of small ramets into the population.

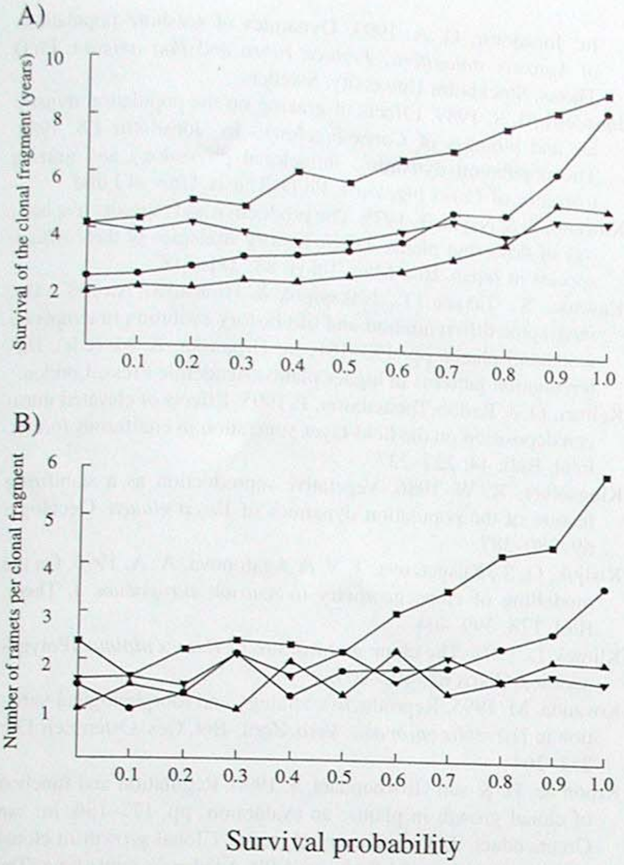

Figure 9. Sensitivity analysis of survival probabilities in the simulation of *Trientalis europaea*. Effect on the survival of the clonal fragment (A) and the number of ramets per clonal fragment (B) when the survival probabilities used in the simulation model were varied from 0 to 1, one size class at a time. Each point represents the mean value of 300 simulations. For the number of ramets, only those clones surviving at age 15 were considered. A) Slopes of the regression lines for clone survival: (■) size 1 $\beta = 5.2$ ($r = 0.98$, $p < 0.001$); (•) size 2 $\beta = 5.3$ ($r = 0.82$, $p < 0.001$); (▲) size 3 $\beta = 3.5$ ($r = 0.84$, $p < 0.001$); (▼) size 4 $\beta = 0.71$ ($r = 0.38$, $p = 0.04$). (B) Slopes of the regression lines. Slopes of the regression lines for the number of ramets: size 1 $\beta = 3.5$ ($r = 0.79$, $p < 0.001$), size 2 $\beta = 1.7$ (0.69, $p = 0.001$), size 3 $\beta = 1.0$ ($r = 0.44$, $p = 0.02$), size 4 $\beta = 0.1$ ($r = 0.02$, $p = 0.67$).

Finally, the sensitivity analysis revealed that clonal fragment survival and the number of ramets were more sensitive to changes in the survival probabilities than in the values of the clonal growth matrix. Our results seems to be in agreement with other studies in clonal plants (Bierzychudek 1982a; Eriksson 1988a, b; Svensson & Callaghan 1988; Callaghan et al. 1990; Nault & Gagnon 1993) which have demonstrated that survival is more important than clonal growth for determining the population growth. Moreover, even though the present model does not incorporate sexual reproduction, the behaviour of *T. europaea* suggests that, as in most of the iteroparous forest herbs (Silvertown et al. 1993), population growth depends heavily on the survival of established adult individuals.

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