Plant Ecology **141:** 117–127, 1999.

Modelling the morphological response to nutrient availability in the clonal plant *Trientalis europaea* L.

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Key words: Nitrogen, Pseudoannual, Spatially explicit simulation model, Tuber

Abstract

The morphological responses to changes in environmental quality shown by many clonal plants have been interpreted as an expression of foraging behaviour, as they allow the ramets to become concentrated in more favourable microhabitats. The morphological response to increased nutrient availability in the pseudoannual plant *Trientalis europaea* was studied in a field experiment. The response was largely size-dependent and consistent with enhanced clonal growth. Fertilized ramets produced more tubers and a larger main tuber. In contrast, stolon length was not affected by the treatment. A spatially explicit simulation model calibrated with data from the field experiment examined the population dynamics of *T. europaea* ramets in a spatially hetereogeneous, temporally constant, environment. The model showed that *T. europaea* was effective at concentrating its ramets in favourable patches, but this process was strongly influenced by patch size. The analysis of this response at the clone level showed that ramet aggregation was mainly due to the enhanced performance of clones located initially in the favourable patches, or clones that located a favourable patch by chance. In these clones, the simultaneous increase of ramet size and survival accelerated the production of ramets. The temporal and spatial scale at which the aggregation of ramets in favourable patches was manifested suggests that the effectiveness of the morphological response in *T. europaea* is favoured by a high spatio-temporal predictability in the environment. Overall, the model emphasized the important role of population dynamics in understanding the nature of the foraging response.

Introduction

Rhizomes and stolons give clonal plants the capacity of spatial mobility. One of the potential benefits of mobility in clonal plants is that ramets can exploit a spatially heterogeneous environment. This was suggested by Warming (1918), who wrote: 'The biological advantages of the underground runners consist in furthering the migration of the individual to richer soil, occupation of new space with more food, increasing the number of aerial shoots, and reproduction of the species, and thus also the prospect of victory in the struggle against competing forms'. However, the more elaborated view of clonal spreading as a method of foraging is relatively recent (Bell 1984; Eriksson 1986; Slade & Hutchings 1987a, b; Hutchings & Slade 1988; Sutherland & Stillman 1988; Oborny 1991; Lopez et al. 1994). According to this idea, foraging in plants is accomplished by morphological plasticity, i.e. plastic responses of the growth of individual ramets to the immediate environment that allow them to locate and use favourable patches in a selective manner or to avoid unfavourable patches (Cain 1994; Hutchings & de Kroon 1994; de Kroon & Hutchings 1995). For example, ramets may respond to favourable growing conditions by changing their morphology, i.e. elongating/shortening their spacers, changing their numbers, or both. Ramet accumulation in favourable patches results either from 'active' response, by decreasing spacer lengths, or from 'passive' response, by increasing branching intensity (Slade & Hutchings 1987a, b; de Kroon & Knops 1990). Such patterns of clonal growth would confer an adaptive benefit since they

improve utilisation of available, patchily distributed resources (de Kroon & Schieving 1990; Hutchings & de Kroon 1994).

Many studies have documented morphological responses in clonal plants that agree with this concept of foraging for resources (Slade & Hutchings 1987a, b; Carlsson & Callaghan 1990; Hutchings & de Kroon 1994; de Kroon & Hutchings 1995; Dong & Pierdominici 1995; Dong et al. 1996). However, strikingly few studies have examined experimentally whether these responses are associated with an effective foraging behaviour, i.e., ramets are selectively located in favourable patches (but see Eriksson 1986; Evans & Cain 1995). As demonstrated for the clonal herb *Glechoma hederacea*, a plant can display a foraging response in 'static experiments' (i.e. performed in pots where ramets are treated with different levels of resources), but may be inefficient at placing their ramets in the resource-rich patches of a heterogeneous environment (Birch & Hutchings 1994), or only exhibit an effective morphological response at large patch scales (Wijesinghe & Hutchings 1996, 1997). An important limitation of greenhouse experiments is, however, that only clonal plant species possessing several generations of ramets per season or a continuous clonal growth under greenhouse conditions (e.g., *Glechoma hederacea*, *Hydrocotyle bonaerensis* or *Potentilla anserina*) can be tested in a reasonable period of time.

An alternative approach to study the effectiveness of the morphological response in clonal plants can be made by simulation models in which clonal growth is determined by environment-dependent rules. Most of the models simulating growth of clonal plants in heterogeneous environments to date have been general models (Ford 1987; Sutherland & Stillman 1988; de Kroon & Schieving 1990; Oborny 1994a, b). They examined the growth rules of the foraging response to provide general predictions applicable to a wide range of species . However, to our knowledge, only Cain et al. (1996) have developed spatially explicit simulation models of plant foraging based on empirical data. Besides their realism (they are developed from realistic responses), specific, spatially explicit models allow evaluation of the effects of a broad range of patterns of spatial resource heterogeneity on the foraging response.

The present paper has two parts. In the first, we investigated in a field experiment the morphological response to increased nutrient availability in *Trientalis europaea*, a forest clonal herb characterized by a pseudoannual growth habit. In the second part, we analysed the effectiveness of the response of *T. europaea* with a stochastic, spatially explicit simulation model calibrated with data from the above mentioned field experiment. Throughout this paper we consider a morphological response as 'effective' if it results in an accumulation of ramets in the favourable patches. Three specific questions were adressed via the simulation model: (i) Does *T. europaea* exhibit an effective morphological response when resources are patchily distributed? (ii) How is the morphological response affected by the cover and patch size of the favourable environment? (iii) How does the morphological response affect the dynamics and size structure of *T. europaea* populations?

Materials and methods

The study species

Trientalis europaea L. (Primulaceae) is a clonal understory herb widely distributed in boreal woodlands of the northern hemisphere. The species is characterised by a pseudoannual life-cycle (*sensu* Warming, 1918). 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 tuber sprouts and produces a stem bearing the leaves and flower buds formed in the previous autumn. In July underground stolons are initiated from the mother tuber and continue to elongate until the middle of August; they then cease growing and form a new tuber by thickening at the apex. Typically, only one tuber is produced per stolon and the longest stolon almost invariably bears the largest tuber (hereafter referred to the main daughter tuber, Figure 1). Tuber production is rather low; in natural populations about 60% of ramets (i.e. the aerial shoots) produce a single tuber that replaces the ramet of the current year (Piqueras & Klimeš 1998). During August the tuber continues to enlarge and reaches its maximum size at the beginning of September. At this time the mother plant senesces rapidly and, by the end of September, the stolons connecting the mother plant's tuber with the newly formed daughter tubers have decayed. Seedling recruitment is extremely rare in established populations and it seems to occur only under very favourable moisture conditions combined with disturbances of the forest floor (Hiirsalmi 1969, Grivlova & Vahrameeva 1990, Eriksson & Ehrlén 1992).

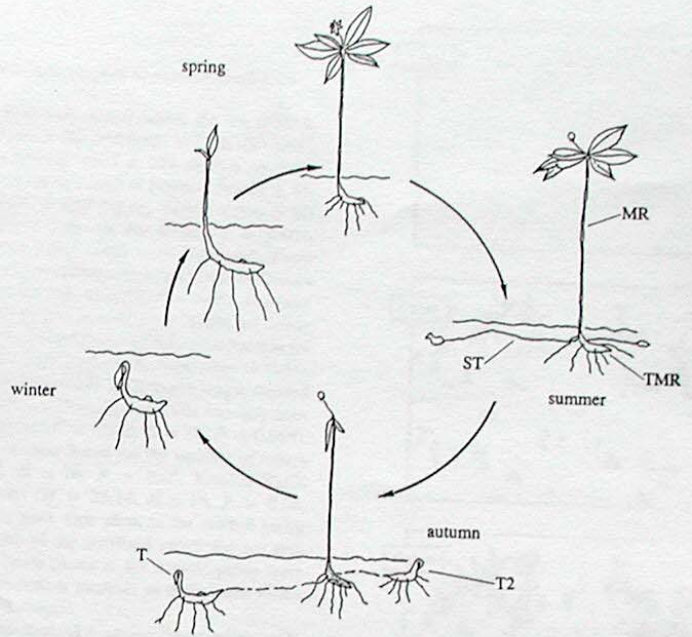

Figure 1. The pseudoannual life-cycle of *Trientalis europaea*. MR: Mother ramet. TMR: Tuber of the mother ramet. ST: Underground stolon. T: Main daughter tuber. T2: Secondary daughter tuber. Note that the mother ramet dies back in autumn (shaded).

The fertilization experiment

The fertilization experiment was carried out in a mesic spruce forest about 45 km SSW of Stockholm, Sweden. The dominating tree species were *Picea abies* and *Pinus sylvestris*, whereas the field layer consisted mainly of *Vaccinium myrtillus*, *V. vitis-idaea*, *Maianthemum bifolium* and *Linnaea borealis*. In June 1992, seventeen 200 × 200 cm plots were established along a transect, spaced at distances of about five metres. In each plot, between six to eight regularly distributed points were marked. Then, the nearest ramet of *Trientalis europaea* to each point was chosen and alternately assigned to a control or a fertilized group. In the fertilized group, the ramets ($N = 56$) were watered within a radius of 10 cm around the stem with 0.2 l of nutrient solution (0.46 g l^{-1} N, 0.07 g l^{-1} P, 0.33 g l^{-1} K, Superba S, manufactured by Hydro Agri AB, Sweden), every week from the first week in June to the first week of August (total: 14.89 g N m^{-2}, 2.29 g P m^{-2} and 10.88 g K m^{-2}). The ramets in the control group ($N = 57$) were watered on the same occasions with 0.2 l of tap water.

In June, leaf area (sum of the area of all leaves) and the number of flowers of all ramets were recorded. The area of individual leaves was assessed as the product of leaf length and leaf breadth. On 3 and 4 September all ramets with their corresponding stolons and tubers were carefully excavated and brought into the laboratory. Underground parts were washed and the number and length of the stolons and tubers recorded. Roots were removed and ramets were separated into stem, basal tuber, stolons and daughter tubers. All these parts were dried at 70 °C for 72 h and weighed.

Statistical analysis

A two-way ANOVA with treatment as fixed effect and plot as random effect was used to detect plot effects and interactions between plot and treatment in the quantitative characteristics of clonal growth (total daughter tuber mass, main daughter tuber mass, total stolon mass and total stolon length). Lengths and weights were log-transformed and normality of these variables was checked with a Kolmogorov-Smirnov test in the ANOVA. Nonparametric tests were used for those variables in which normality was not achieved after transformation (number of flowers and tubers). In *T. europaea*, as in many clonal plants, allocation to stolons and rhizomes is a function of plant size (Hartnett 1990; Dong & Pierdominici 1995; Verburg et al. 1996; Piqueras & Klimeš 1998). Therefore, to detect a significant treatment effect of nutrient supply in addition to size, effects on tuber daughter mass, stolon mass and stolon length were tested in an analysis of covariance. We first constructed a model for fertilized and control plants that assumes that the variables (Y) tuber mass, stolon mass and stolon length are a function of ramet mass (x) according to the expression $\log Y = \log_e b + m \log_e(x)$. Then, differences in the parameters of the regression lines for fertilized and control ramets were tested by ANCOVA (SYSTAT, Wilkinson et al. 1992). A significant effect of the treatment is indicated by a difference in the slopes (m) and/or intercept values (b). Ramet size, expressed as the mass of the basal tuber and the stem, was used as a covariate. Since no significant variation between plots was found, nor interactions between plots and treatment (see Results), these analyses were made on the pooled data.

The simulation model

We used a stochastic spatially explicit model which simulates clonal growth and population dynamics of established ramets of *Trientalis europaea* in a heterogeneous environment. The model was calibrated for number and size of daughter ramets, and stolon length from the fertilization experiment. In the simulation model, we used the length of the tuber of the mother ramet and the length of the daughter tubers as a measure of ramet size. This procedure allowed the results of the experiment to be directly related to data of ramet size distribution, size-specific survival probabilities and branching angles from a demographic study carried out in 1992 at the same locality (for more details of the simulation model and demographical data see Piqueras & Klimeš 1998).

In a simulation a ramet of *T. europaea* was placed at random in a grid of square patches distributed regularly on a background. Patches were defined as nutrient-rich. The cover of the patches used represented 10%, 25%, 50% and 70% of the total field area and was obtained by adjusting the size and density of patches. The edges of the patches were 15, 30, 45, 60, 120 or 330 cm long. The clone, i.e. the aggregation of ramets derived from the initial ramet, grew according to the growth rules prevailing in the location, i.e. if a ramet was in a favourable patch, its clonal progeny and stolon lengths were calculated from data from fertilized plants in the experiment. Conversely, if a ramet was not in a patch its clonal performance was determined by data from control plants. Except for branching angle, all growth rules and survival probabilities were size dependent. Branching angle and survival probabilities were not affected by the environment quality. Also, an important assumption of the simulation model was that the values of branching probabilities, stolon lengths, branching angle and survival probabilities operating in subsequent years were independent.

The growth of 1000 clones was simulated during 25 years for each combination of patch cover and patch size. Some combinations were not tested because they could not be simulated practicably (e.g., too small patches in high percent cover or *vice versa*). The effectiveness of the morphological response of *T. europaea* was analysed at two different levels, clones and ramets. As *T. europaea* exhibits pseudoannual growth habit, the results presented in this study are based on the current generation of ramets present in each year.

In some cases, plants respond differently to patchy environments than to homogeneous environments (Evans & Cain 1995). Since the design of the fertilization experiment could not detect the possible impact of environmental heterogeneity on clonal behaviour, i.e., ramets grew under conditions that were either homogeneously good (fertilized) or homogeneously bad (control), the simulation model was based on the assumption that responses to environmental gradients did not occur in *T. europaea*.

Results

The morphological response to nutrient availability

Fertilized ramets and control ramets did not differ in leaf area (mean ± SD fertilized: 1523 ± 294 mm^2, mean ± SD control: 1507 ± 225 mm^2, $t = 0.16$, $P > 0.05$ two sided t-test) or biomass (mean ± SD fertilized: 21.51 ± 4.57 mg dry weight, mean ± SD control: 21.65 ± 3.62 mg dry weight, $t = 0.001$, $P > 0.05$ two sided t-test) when harvested. There were no significant differences in leaf area or biomass among plots (ANOVA, df = 16, $P > 0.05$). Two-way ANOVA analysis did not reveal any significant differences between plots or plot × treatment interaction for the total tuber mass, mass of the main tuber or stolon mass (df = 16, $P > 0.05$). Total stolon length showed differences between plots, however this was only marginally significant ($F = 1.736$, df = 16, $P = 0.058$). No plot effects were found for the number of tubers ($H = 16.68$, df = 16, $P > 0.05$, Kruskal-Wallis test) and flowers ($H = 23.14$, df = 16, $P > 0.05$, Kruskal-Wallis test). One plant in the control group and three plants of the fertilized group did not produce tubers. Three plants in the control group were excluded from further analysis as their main tubers were severely damaged.

T. europaea showed a strong linear relationship between the mass of the mother ramet and mass of daughter tubers (Table 1). ANCOVA showed that fertilization increased the mass of the main daughter tuber and the total tuber mass. Test for homogeneity of slopes showed no difference in slope between fertilized and control plants, indicating that the significant effect in ANCOVA is due to the difference in b-values (Table 1). The effect of fertilization was also expressed as an increment in tuber length in the subsequent ramet generation; thus, fertilized plants produced a main daughter tuber that was significantly larger than the tuber of the mother ramet (mean ± SD main daughter tuber: 7.43 ± 2.35 mm, mean ± SD tuber mother plant: 6.19 ± 2.32 mm, $t = 4.79$, $N = 53$, $P < 0.001$ paired sample t-test). In contrast, no significant differences were found between the length of the main daughter tuber and the tuber of the mother plant in the control group (mean ± SD main daughter tuber: 6.72 ± 2.58 mm, mean ± SD tuber mother plant: 6.48 ± 2.38 mm, $t = 0.42$, $N = 53$, $P > 0.05$, Paired sample t-test).

There were no significant differences between fertilized and control plants in the mean weight of sec-

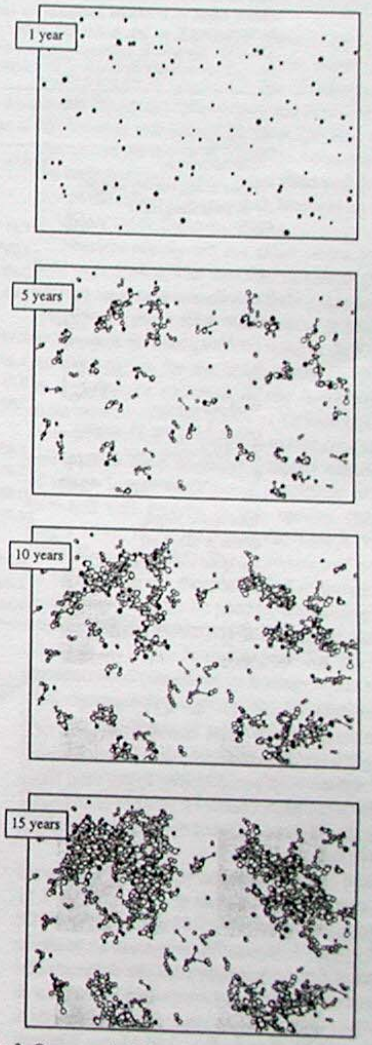

Figure 2. Computer simulation of clonal growth in *Trientalis europaea* with time. The growth of clones, derived from 100 ramets established in the first year, were simulated in a spatially heterogeneous environment. The grey squares represent nutrient rich patches (160 cm side) covering 50% of the total field area. Filled circles represent current living ramets. Open circles denote ramets produced in previous years (note that ramets in *T. europaea* are annual). Ramet sizes (tuber lengths) are represented by four different circle sizes (size 1 ≤ 3 mm, size 2: 3 < x ≤ 6 mm, size 3: 6 < x ≤ 9 mm and size 4 > 9 mm, not to scale in the figure). Stolons are represented by lines of five different lengths (L1 = 30 mm, L2 = 90 mm, L3 = 150 mm, L4 = 210 mm and L5 = 270 mm).

Table 1. Linear regression analysis between total daughter tuber mass, main daughter tuber mass, total stolon mass and total stolon length and the mass of the tuber of the mother ramet in *Trientalis europaea* for fertilized and control plants. Parameters in the model $\log Y = \log_e b + m \log_e$ (tuber of the mother ramet mass) were tested in ANCOVA. Significant differences in *b*-values denote a treatment effect. * slope (m) or intercept (b) different from zero at $P < 0.05$.

	Control ($N = 54$)	Fertilized ($N = 56$)	P
Total tuber mass	16.90 ± 3.86	24.16 ± 5.51	
(Mean ± SD, mg dry weight)			
Y = Total tuber mass			
m	1.31*	1.19*	0.346
b	−1.29*	−0.35	<0.001
r^2	0.67	0.80	
Main daughter tuber mass	14.91 ± 3.37	17.18 ± 3.39	
(Mean ± SD, mg dry weight)			
Y = Main daught. tub. mass m	1.24*	1.02*	0.082
b	−1.20*	−0.35	0.024
r^2	0.75	0.64	
Total stolon mass	7.07 ± 2.82	6.63 ± 2.76	
(Mean ± SD, mg dry weight)			
Y = Total stolon mass m	1.45*	1.12*	0.671
b	−2.96*	−1.91*	0.538
r^2	0.50	0.41	
Total stolon length	98.79 ± 22.32	111.00 ± 25.38	
(Mean ± SD, mm)			
Y = Total stolon length m	0.55*	0.67*	0.138
b	2.70	2.50	0.241
r^2	0.18	0.34	

ondary daughter tubers ($U = 437$, $P > 0.05$, Mann–Whitney U-test). Total stolon mass and total stolon length were also correlated with ramet biomass but the r^2 values were considerably lower than those obtained for tuber mass (Table 1). Neither stolon mass nor stolon length were affected by increased nutrient availability (Table 1).

Fertilized ramets produced significantly more tubers than control ramets (mean ± SD fertilized: 2.11 ± 0.25, mean ± SD control = 1.51 ± 0.22, $U = 2063$, df = 1, $P < 0.001$, Mann–Whitney test). In contrast, the number of flowers per ramet did not differ significantly between fertilized and control ramets (mean ± SD fertilized: 0.71 ± 0.17, mean ± SD control = 0.66 ± 0.14, $U = 1639$, df = 1, $P > 0.05$ Mann–Whitney U-test).

The simulations

A graphical display of the simulated clones of *T. europaea* is presented in Figure 2 and shows the accumulation of ramets in nutrient-rich patches with time. Initially, the proportion of the total number of ramets in nutrient-rich patches did not change, but after a lag of 4–5 years rapidly increased, achieving about 90% in 19–20 years (Figure 3A). However, the effectiveness of the morphological response was strongly influenced by the size of the nutrient-rich patch. The larger size patches resulted in the highest levels of ramet accumulation, whereas the response in the smallest patches was very little. The effect of patch size on the effectiveness of the morphological response was found at all four levels of patch cover studied (Figure 3B).

In order to limit the amount of information, the results of the influence of patch size on clone dynamics were based on simulations where the total patch area was held constant at 25% of the total field area.

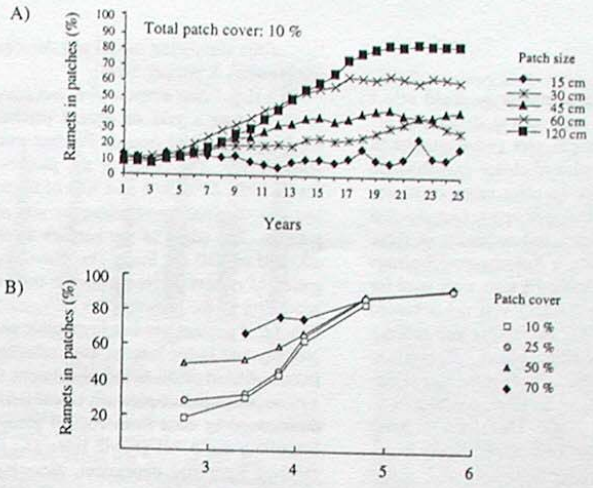

Figure 3. Effectiveness of the morphological response in *Trientalis europaea*. (A) Percentage of ramets situated in nutrient rich patches over time, at different patch sizes. 1000 clones were simulated for each patch size. The same level of resource was used for all patch sizes (10% of the total field area was covered by nutrient-rich patches). (B) Effect of patch size on the percentage of ramets situated in nutrient-rich patches at the end of a 25-year simulation with different level of resource (10%, 25%, 50% and 70% of the field was covered by nutrient-rich patches).

The results showed that for the same level of resource, the number of clones surviving 25 years increased very greatly with patch size (Figure 4A). However, two different types of clones were responsible for this increase: clones which stayed in a nutrient-rich patch throughout the simulation, and clones that began in the background and finished in a nutrient-rich patch (Figure 4A). The first category of clones increased substantially as patch size increased from 45 to 60 cm. In contrast, patch size did not affect the number of surviving clones that remained in the background and the number of clones that abandoned the nutrient-rich patches decreased with increasing patch size (Figure 4A). The number of ramets produced by a clone increased with increased patch size, but only in those clones that either located nutrient-rich patches or remained in them (Figure 4B). When all clones (surviving from 1 to 25 years) were considered, clone survival was always significantly greater in clones initially located in nutrient-rich patches than those in the background (Figure 4C). Furthermore, for those located in such patches, survival was affected by patch size ($F = 4.831$, df = 5, $P < 0.001$, ANOVA). A Tukey-test for pairwise comparisons revealed that clone survival in the three largest patch sizes differed significantly from the three smallest patch sizes ($P < 0.05$). Nevertheless, even if clones growing in nutrient-rich patches had their survival enhanced at larger patch sizes, the effect of patch size on the survival of the whole population of clones was less pronounced (Figure 4C).

At the end of a 25-year simulation the mean size of the ramets in the nutrient-rich patches was significantly greater than in the background in all patch sizes except for the smallest one (Figure 4D). In the nutrient-rich patches, mean ramet size increased drastically from patch size 15 to patch size 30, but for larger patch sizes the increment in mean ramet size was only marginal (Figure 4D). However, when the whole population of ramets was examined, a progressive increase in mean ramet size with increasing patch size was found (Figure 4D).

Simulated clones located initially in good patches had a larger net displacement (i.e., distance between the initial ramet and the furthest living ramet at the end of a simulation) than clones in the background (Figure 5). Similarly to clone survival and number of ramets per clone, clone net displacement in the

Figure 4. Effect of patch size on the effectiveness of the morphological response in *Trientalis europaea*. (A) Number of simulated clones that reached the age of 25 years and (B) their ramet production (mean ± SE). Open bars: clones in the background (i.e., not in a patch); hatched bars: clones that abandoned the nutrient-rich patches; shaded bars: clones that located a nutrient-rich patch; solid bars: clones that remained in nutrient-rich patches. (C) Clone survival in years (mean ± SE). Open bars: clones initially located in the background; solid bars: clones initially located in the nutrient-rich patches; shaded bars: survival for the whole population of clones. Differences in survival between clones initiated in background and patches were tested with *t*-test. (D) Size of ramets (length of tubers, mean ± SE) in the background (open bars), patches (solid bars) and for the whole population for clones (shaded bars) simulated during 25 years. Differences in size between ramets situated in the background and patches were tested with *t*-test. All results are based on the simulation of 1000 clones for each patch size. The field area covered by nutrient-rich patches was held constant at 25%. Significance levels: ns (not significant) $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Figure 5. Figure 5. Effect of patch size on the net displacement (mean ± SE) of simulated clones of *Trientalis europaea* initiated in the background (open bars), or initiated in patches (solid bars). Shaded bars include only clones that achieved the same age (25 years) either in background or patches. Differences between clones initiated in the background and patches were tested with *t*-test. *** $P < 0.001$. The results are based on the simulation of 1000 clones for each patch size.

nutrient-rich patches increased greatly from patch size 45 to patch size 60. A Tukey-test for pairwise comparisons showed significant differences between the patch sizes 15 to 45 cm and the patch sizes 60 to 330 cm ($P < 0.05$). Since clone displacement is dependent on clone survival, this variable was analysed in clones of the same age, i.e., those that had survived 25 years. Also in this case there was a significant effect of patch size on clone displacement (Figure 5; $F = 14.960$, df $= 5$, $P < 0.001$, ANOVA).

Discussion

Experimental results

The results of the field experiment showed that enhanced nutrient supply had two important effects on the clonal growth of *T. europaea*. Firstly, it increased the number of daughter tubers and, secondly, it increased the individual mass of the daughter tubers. As indicated by the shape of the relationships (*m*- and *b*-values in the ANCOVA analysis), the effect of nutrient supply was significant, even when size-dependent effects were considered. Enhanced clonal growth conforms with the most consistent morphological responses shown by clonal species under conditions of higher resources supply (Sutherland & Stillman 1988; de Kroon & Hutchings 1995; Dong et al. 1996; Verburg et al. 1996). These results also conform with observations on two clonal plant species with a pseudoannual life cycle like *T. europaea*, namely potato (*Solanum tuberosum*) and Jerusalem artichoke (*Helianthus tuberosus*). In these species, it was found that increased nitrogen supply increased branching of the underground stolons, tuber yield and the individual size of the tubers (Gupta 1993; Maier et al. 1994; Joern & Vitosh 1995; Denoroy 1996).

Nutrient supply did not affect stolon length in our field experiment. The majority of clonal plant species studied to date have shown little response of stolon length to nutrient supply (Sutherland & Stillman 1990; de Kroon & Hutchings 1995; Dong & de Kroon 1994). An explanation for the insensitivity of stolon length in *T. europaea* observed in our fertilization experiment may be that the effect of various environmental factors overrides the response to resource supply. Several studies have revealed a highly plastic response of stolon length to different conditions of soil moisture and soil texture in this species (Matthews & Roger 1941; Hiirsalmi 1969; Grivlova & Vahrameeva 1990; Kovanda 1995). The importance of environmental variation in the morphological response to nutrient availability can also be seen by comparing our results with a recently published study on the same species (Dong et al. 1997). In that experiment, performed under controlled conditions in homogeneous soil, ramets of *T. europaea* responded quite differently despite the fact that the levels of nutrient added were comparable, i.e., they produced more, but smaller, tubers and shorter stolons under high nutrient supply. Nevertheless, genetic differences in the morphological response cannot be neglected.

Simulation study

Simulations showed that the morphological response of *T. europaea* allowed the accumulation of ramets in favourable patches, although patch size influenced the magnitude of the response. Examination of the morphological response at the clone level revealed that the process of aggregation was mainly due to the enhanced performance of clones that were already established in a nutrient-rich patch or, by chance, located a nutrient-rich patch. This supports earlier results in simulation models calibrated with empirical data (Cain et al. 1996) and is consistent with a passive growth response. However, in our model the enhanced performance of the clones was not only the result of greater ramet production in the nutrient-rich

patches, but also a consequence of higher survival and increased ramet size. Thus, the larger the patch size, the more prolonged the positive effects on clonal growth, which in turn amplified the effectiveness of the response. This interaction between ramet size, survival and clonal growth can explain a pronounced 'foraging response' despite the relatively small difference in ramet production between fertilized and control ramets observed in the field experiment (cf., Dong et al. 1997). There was, however, an effect of increased ramet size that may reduce the tendency of the clones to remain in the favourable patch. Although nutrient supply had no statistically significant effect on stolon length in the field experiment, the model predicted larger net displacement for clones moving in a nutrient-rich patch. However, even though clones in nutrient-rich patches moved longer distances with increasing patch size, the results of the simulations suggested that these displacements were not sufficient to 'escape' from the favourable environment. This could explain the marked increment in the number of ramets and clone survival observed between the patch sizes of 45 and 60 cm, especially noticeable for clones that initiated and ended their growth in the good patch (Figure 4A). Although we did not observe an optimal patch size in the 'foraging' of *T. europaea* as found in simulation models for other clonal plants (cf., Sutherland & Stillman 1988; Cain et al. 1996), the transition between these two patch sizes may represent an important threshold for the effectiveness of the morphological response in this species.

Another important aspect in our model concerns the time scale at which the effectiveness of the morphological response was observed in *T. europaea*. The simulations showed that *T. europaea* was able to concentrate ramets at a wide range of resource availability when patches were sufficiently large, but under the assumption that the spatial arrangement of patches remained unchanged for a prolonged time (Figure 3A). This suggests that in *T. europaea* the effectiveness of the response should be favoured either by a high temporal predictability (the environment does not change over time) or by a high spatial predictability (the environment is coarse-grained, cf., Oborny 1994a). Both assumptions are in accordance with the results obtained for clonal plants with a similar growth strategy as *T. europaea* studied in simulation models incorporating temporal heterogeneity by Oborny (1994a).

A critical question arising from the results of our model is to what extent the scale of spatial heterogeneity in resources used in the model corresponds with the pattern occurring in the soil of a forest. This is important since proposed adaptations of clonal growth patterns to heterogeneity may not be valid if patch size distribution and aggregation patterns present in the field differ markedly from those assumed in experiments or simulation models (Stuefer 1996). Despite the scarcity of information on soil resource heterogeneity, there is good evidence that patches with high nutrient concentration frequently occur in forests at the sizes that *T. europaea* tends to concentrate more its ramets (Lechowicz & Bell 1991; Kleb & Wilson 1997). This means that, at least, a prerequisite for an effective morphological response for this species may occur in its habitat.

Acknowledgements

We are grateful to M. Cain, O. Eriksson, S. Jensen, L. Jerling, C. Marshall and an anonymous reviewer for valuable comments and suggestions on a previous draft of the manuscript. The visits to the Czech Republic by the first author were financed by the exchange programme of The Royal Swedish Academy of Sciences and The Czech Academy of Sciences. LK was financially supported by the grant 206/95/0503 of the Grant Agency of the Czech Republic. JP and PR-T received financial support from the Swedish Environmental Protection Board.

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