Journal of Ecology 1993, **81**, 533–542

Genet dynamics of the clonal plant *Rubus saxatilis*

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Summary

1 Populations of *Rubus saxatilis* were investigated between 1988 and 1991 in a study area (*c.* 2.5 km^2) in central Sweden. Different phases in the life cycle were studied: flowering, pollination, fruit-set, fruit-removal and seedling recruitment. Identification of genets was made by use of RAPD (random amplified polymorphic DNA). Information concerning these life-cycle phases were then used to infer processes in the population dynamics of *R. saxatilis*.

2 A path analysis suggested a strong effect of fruit-set on total patch fruit production. Fruit-set varied between 6.6% and 8.3% (yearly averages) and was influenced by distance to nearest flowering conspecific patch. Isolated patches tended to have a low fruit-set. Size of patches was of minor importance for fruit-set and fruit-production, whereas intrapatch ramet density influenced fruit production positively via an effect on the proportion of ramets that flowered.

3 A pollination experiment confirmed that *R. saxatilis* is self-incompatible. Within-patch pollinations indicated that isolated patches comprise single genets (or incompatibility types). Between-patch pollination indicated that fruit-set may be pollen limited, at least some years. Deficiency of compatible pollen (or 'partners') is the most likely mechanism behind the distance-effect on fruit production found in the path analysis.

4 A bagging experiment suggested that *c.* 50% of the fruits (drupelets) were removed by animals. No relationship was found between fruit removal rate and either fruit production of patches or distance to neighbour patch.

5 Seedlings of *R. saxatilis* were carefully searched for during four years in three different localities 'coniferous forest', 'deciduous forest' (DF) and 'mixed semi-open woodland' (MSOF). Seedlings were found only during one year and in one locality (MSOF). Ramets from carefully mapped 20-m × 30-m plots in localities DF and MSOF (one plot per site) were sampled for genet identification with RAPD analysis. In DF, 20 ramets were found to belong to 10 different genets. In MSOF, 24 ramets belonged to eight different genets. In addition, a sample of three ramets from an isolated road-side patch indicated that it consisted of one genet.

6 The dynamics of the genet population of *R. saxatilis* in the study area was interpreted by a source–sink concept. Source populations represent local clusters of genets with high fruit production which enhances further local recruitment in source populations and provide the surrounding sink areas with propagules. Sink populations represent low-density populations comprising isolated genets suffering from partner-limited fruit production. These isolated genets may be loci for future colonization. The source–sink structure implies an apparent positive genet density effect on recruitment, but to what extent this effect is due to variation in the local 'quality' of sites or is a real density effect, remains unresolved.

Keywords: clone identification, demography, pollen limitation, population regulation, recruitment

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Introduction

The existence of density dependent processes in plant population dynamics is well documented (Antonovics & Levin 1980; Watkinson 1986; Crawley 1990). Even if density-independent factors may set limits to population size, density dependence is essential for population regulation in a strict sense, i.e. the extent to which variation in population growth rate is causally related to the number of

individuals inhabiting a certain area. Originally borrowed from animal ecology (Nicholson 1933; Andrewartha & Birch 1954), the theories of population regulation are based on an unproblematic concept of individuals. In contrast to most animals, plants are hierarchically organized (White 1979, 1984) and this organization is most obvious in clonal plants (Eriksson & Jerling 1990). A genet, i.e. the developmental product of a single zygote, is an inclusive unit comprised of functional units, ramets, which are potentially independent physiologically. In some clonal plants further organizational levels, e.g. 'clonal fragments' (Angevine & Handel 1986), might be recognized. In addition to the inherently abstract nature of density (which is an averaging of interindividual interactions and may be less relevant to sessile organisms; cf. Pacala 1989) one must thus recognize several hierarchical levels of density in clonal organisms. Despite a considerable recent interest in the particular features of clonal plants, or clonal organisms in general (Jackson, Buss & Cook 1985; Watkinson & White 1986; van Groenendael & de Kroon 1990), most studies of dynamics and regulation of populations of clonal plants have focused on the ramet level (Harper 1977, 1978; Hutchings 1979; Pitelka 1984; Cook 1985; Crawley 1990). The rationale for this 'ramet centred view' may be either methodological (genets are difficult to identify in the field) or conceptual (related to the problem with units of selection; Tuomi & Vuorisalo 1989a,b). There are, however, several obvious reasons for an interest in the population dynamics of genets. Primarily, genetic variation in clonal populations is dependent on the size and structure of genet populations. Because genetic variation is necessary for natural selection to operate, whatever is the unit of phenotypic selection (Endler 1986; Tuomi & Vuorisalo 1989a,b), the regulation and dynamics of genet populations become important issues. Furthermore, in most clonal plant species sexually produced seeds are the only diaspores capable of long-distance dispersal, and seeds are the common means for initiating new populations. It follows that the recruitment rate of genets becomes an important factor for clonal species distribution and abundance.

The available information on genet dynamics in clonal plants is scanty and partly anecdotal. Apart from a few notable exceptions (e.g. DeSteven 1989), most information is confined to either occurrence of seedlings (Bierzychudek 1982a; Eriksson 1989) or inferences from static descriptions of spatial structure of adult genets (e.g. Oinonen 1967a,b). Genets have often been viewed as developing patches with a spatial structure that changes through time (Watt 1945; Cook 1985; Angevine & Handel 1986; Hughes, Fahey & Bormann 1988; Maddox *et al.* 1989; Chambers 1991), a view congruent with the 'pattern and process' theory of plant community dynamics (Watt 1947). The population dynamics of genets would thus operate at large spatial and temporal scales, as a kind of higher level patch dynamics (Eriksson 1989). In the present study a series of field experiments and observations concerning pollination, fruit production, fruit removal and seedling recruitment, combined with genet identification by RAPD (Random amplified polymorphic DNA, Williams *et al.* 1990), were used to investigate density dependent processes in the genet dynamics of the clonal plant *Rubus saxatilis* L. (Rosaceae). The main objective was to examine the hypothesis that intergenet distances (genet 'density') affects fruit production and recruitment of new genets to the population. A number of factors hypothesized to affect fruit set and fruit production were investigated. Structural aspects of patches, such as patch size, density of ramets, and behavioural variation among ramets, for instance the proportion of flowering ramets, may reflect resource availability experienced by patches. Moreover, because *R. saxatilis* was suspected to be self-incompatible, patch structure and interpatch distances may affect pollination within and among patches and thereby fruit set. Previous studies have indicated a possibility of positive genet density effects on seed production in clonal plants, presumably due to pollen deficiency or partner limitation (Tammisola 1982; Bierzychudek 1982b; Handel 1985; Barrett & Helenurm 1987; Worthen & Stiles 1988; Laverty & Plowright 1988; Widén & Widén 1990). However, an increased seed production may not affect local population growth rate if recruitment is limited by factors other than seed availability (Aspinwall & Christian 1992). Therefore, a demonstration of positive density effects should also include recruitment of genets.

Material and methods

STUDY SPECIES

Rubus saxatilis is distributed over the temperate parts of Eurasia. It occurs in semi-open woodlands, but also in more shaded forests, as well as in open habitats such as road-sides. *R. saxatilis* possesses a capacity for extensive clonal propagation. A ramet consists of a perennial subterranean stem and one, occasionally two, annual above-ground stems. The annual stem is either procumbent or erect. Procumbent stems may root at the apex, or if branched, at several apices. The apex rooting behaviour is similar to other *Rubus* species (Heslop-Harrison 1959). Above-ground tissue withers each year and a successfully rooted shoot (apical meristem) develops next year into a new, physiologically independent ramet. The length of procumbent stems ranges from 0.3 to 2.8 m (1.3 ± 0.6 m, mean $\pm$ SD; $n = 30$). The stems usually develop one to three daughter ramets, but a considerable proportion of procumbent stems

fail to produce any daughter ramets at all (O. Eriksson, unpublished data).

Erect stems may be either flowering or vegetative. Because inflorescences are only developed on erect stems, the behavioural variation among ramets is simple; they are either procumbent, erect-flowering or erect-vegetative. The number of flowers per flowering ramet ranges from 2 to 14 (5.6 ± 2.1, $n = 100$). *R. saxatilis* is probably self-incompatible as is the closely related species *Rubus arcticus* (Tammisola & Ryynänen 1970). Bumble-bees (*Bombus* spp.) are the only pollinators that have been observed on flowers of *R. saxatilis*. A flower may produce one to six red fleshy drupelets containing one seed each (cf. Eriksson & Ehrlén 1991). These fruits are dispersed by vertebrates, e.g. thrushes (*Turdus* spp.) and badgers *Meles meles*. Germinability of seeds under laboratory conditions is high (over 90%) using the technique described by Nybom (1980). Preliminary investigations in the study area indicate that *R. saxatilis* does not develop a permanent seed bank (O. Eriksson & A. Telenius, unpublished data). Seedlings are very rarely observed in the field. The scarcity of seedlings is probably a common pattern in clonal *Rubus* species. The predominance of vegetative propagation in species of this genus is well documented (Abrahamson 1975; Kirby 1980; Taylor 1980; Whitney 1986; Nybom 1987; Nybom & Schaal 1990; Tappeiner *et al.* 1991).

FIELD OBSERVATIONS

The field study was performed between 1987 and 1991 at Tullgarn, 45 km south-southwest of Stockholm, Sweden. The study area covers about 2.5 km^2 and includes semi-open to dense deciduous and coniferous forests, and open meadows and pastures. In 1987 the distribution of *R. saxatilis* in the study area was mapped, and 25 patches, distributed over the whole area, were used for subsequent studies. In these patches the total fruit production was recorded during 1988 to 1991. Fruit-set (defined as proportion of flowers developing fruit) was estimated in 1990 and 1991. In 1990 and 1991 patch size (m^2), within-patch ramet density, and distance to nearest flowering *R. saxatilis* patch were measured. In 1991 the proportion of ramets that was flowering, procumbent and vegetative, respectively, was recorded in all patches.

To estimate natural seedling recruitment, seedlings were searched for in a standardized way from 1988 to 1991. In three localities in the study area, 'coniferous forest', 'deciduous forest' (DF), and 'mixed semi-open forest' (MSOF), *c.* 20 m^2 (in each locality) were carefully investigated for seedlings. In addition, occurrence of seedling recruitment has been under observation in the whole study area during 1987 to 1991.

At two sites, DF and MSOF, *R. saxatilis* occurs abundantly and the ground is, particularly at MSOF, more or less covered with *R. saxatilis*. Outside these two sites, *R. saxatilis* occurs in clearly delimited, approximately circular patches, sparsely distributed over the study area, particularly in coniferous woodland and along road sides.

DF is located in a deciduous forest dominated by oak (*Quercus robur* L.) birch (*Betula pendula* Roth.), hazel (*Corylus avellana* L.) and ash (*Fraxinus excelsior* L.). At MSOF, a sparse canopy consists of birch, and scattered spruce (*Picea abies* (L.) Karst.) and hazel. The surrounding coniferous woodland comprises pine (*Pinus sylvestris* L.) and spruce. The field layer is dominated by *Vaccinium myrtillus* L.

PATH ANALYSIS

The data set gathered for the 25 patches was subjected to a path analysis (Sokal & Rohlf 1981; Kingsolver & Schemske 1991). This analysis is suitable as an aid to identify and estimate the strength of causal mechanisms affecting some selected population variable. The method is based on an a-priori model, the path diagram, constructed by the investigator. This model describes causal relationships between predictor variables and criterion variables, as well as correlations between any of these variables. After defining the path diagram, correlation coefficients and standardized partial regression coefficients are used to estimate the relationships among the variables in the model. In a path diagram, a one-headed arrow depicts a hypothesized causal relationship. The path coefficient indicates the strength of this relationship. Two-headed arrows depict correlated variables, i.e. noncausal relationships. The unexplained variation in the path model is estimated from the path coefficients of residual variables denoted U_i.

In this study, path diagrams were constructed from preliminary correlation and regression analyses (most of which are not reported here). All proportions were arcsine transformed, and 'distance to neighbour patch', 'patch size', and 'within-patch ramet density' were log-transformed. For the 25 patches, patch size varied between 2 and 380 m^2, ramet density within patches varied between 3 and 106 m^{-2}, and proportion of flowering ramets varied between 0% and 45%. The distance to nearest flowering neighbour patch ranged from 8 to 250 m.

POLLINATION EXPERIMENTS

A study of whether distinct patches comprised one or several genets was performed by use of artificial pollination. If *R. saxatilis* is self-incompatible (which was tested in the experiment), a combination of among-patch and within-patch pollinations would

reveal the diversity of incompatibility types in patches, which is assumed to reflect the distribution of genets. Twelve patches (six in 1990 and six in 1991) were subjected to pollination treatments. All these patches were distinctly delimited, and were considered to be representative for *R. saxatilis* patches as they occur outside the areas (DF and MSOF) where *R. saxatilis* is most abundant. Within each patch, 30 inflorescences, on different ramets, were bagged before flowers had opened. After a few days (or a week in some cases) the bags were removed and 10 inflorescences received pollen from another patch (at least 50 m away), 10 inflorescences received pollen from flowers within the same patch, and 10 inflorescences were self-pollinated. In each inflorescence, three flowers were treated. Immediately after pollination, the bags were again placed on the inflorescences. The fruit-set was recorded later during the summer. Unfortunately, meaningful results were only obtained from seven patches. In 1990 two patches were destroyed, and in 1991 a period of heavy rain spoiled the experiment in three patches.

FRUIT REMOVAL

In 1990 an estimation of fruit removal was performed in 13 patches. Infructescences (n = 50, with a total of 220 drupelets) were bagged in control patches located in the vicinity of the untreated experimental patches. The number of fruits present in the untreated patches (1363 drupelets at the start of the observations) and in bagged infructescences in control patches were recorded at 10-day intervals from July 29 for 1 month onwards. The difference between proportions of fruit disappeared from untreated patches, and fruits dropped from the bagged infructescences, was used as a measure of fruit removal by dispersers.

GENET IDENTIFICATION

The investigation of genet distribution by RAPD was located at two sites, DF and MSOF. Because preliminary results from the 1990 pollination experiment (later confirmed in 1991) suggested that distinct patches, such as those inhabiting coniferous forest sites and road sides, were likely to consist of single genets, it was decided most 'cost-efficient' to sample only from sites DF and MSOF, where R. saxatilis is most abundant and, particularly at MSOF, the patch structure was less clear.

The sampling of ramets for genet identification was performed in early June 1991 when 20 ramets from DF and 25 ramets from MSOF were collected. In both sites, the ramets were sampled from a 20-m × 30-m plot, which had previously been carefully mapped to recognize patch distribution. The exact position of sampled ramets were chosen in relation to this patch distribution. In addition, three ramets were collected from an isolated road-side patch in the study area. Ramets were dug up and kept alive until their leaves were cleaned and homogenized in the laboratory. Total DNA was extracted by the method of Saghai-Maroof *et al.* (1984), as modified by Doyle & Doyle (1987). Amplification reactions of the DNA were the same as in Williams *et al.* (1990), except that the reactions were performed in volumes of 50 or 100 µl. The thermal cycler was programmed at 50 cycles of 1 min at 92°C, 1 min at 36°C, and 2 min at 72°C. Four informative primers (kit A, Operon) were used in the final analysis (Appendix). The amplified products were electrophoresed in 1.2% agarose gels and detected by staining in ethidium bromide. The gels were photographed, and the negatives were analysed for differences in fragment pattern.

A conservative interpretation of genet diversity was used. Ramets with identical banding patterns were considered to belong to the same genet. It is important to recognize that this implies that the true genet diversity may be under-estimated. Moreover, since all primers did not yield information for all ramets, some cases occurred where ramets A and B were interpreted as identical, but only B was identical to ramet C. Two different genets are implied, but the identity of ramet B could not be determined. In these cases, the most plausible interpretation was preferred, assuming that closely situated ramets are more likely to belong to the same genet than are distant ramets.

Results

PATTERNS OF FRUIT SET

The average total fruit production among the 25 patches of *R. saxatilis* varied about twofold between years (Table 1). Despite this variation, the rank order of patches with regard to their fruit production was very stable (Spearman rank correlation coefficients varied between 0.74 and 0.89 for the six pairwise combinations of years, all with $P < 0.001$). A considerable fraction of the flowers did not develop any fruit at all. Seven of the patches failed to produce fruit in all four years of observation.

The relationships between fruit-set and fruit production, and the factors hypothesized to influence these components of reproduction were analysed by

Table 1 Mean (±SE) fruit production per patch and fruit set (proportions of flowers developing fruit) in patches (n = 25) of *Rubus saxatilis* in a population in central Sweden

	Fruit production per patch	Fruit set
1988	55.1 ± 20.9	—
1989	87.0 ± 31.4	—
1990	70.0 ± 30.3	0.066 ± 0.021
1991	39.8 ± 15.6	0.083 ± 0.019

Table 2 Correlation matrix for variables related to fruit production in patches of *Rubus saxatilis* (n = 25) in a population in central Sweden during 1991. The variables are described in the text. Variables 2 and 6 were arcsine transformed, and variables 3, 4 and 5 were log-transformed. 1, Fruit production per patch; 2, fruit set; 3, patch size (area); 4, ramet density within patch; 5, distance to neighbour patch; 6, proportion of flowering ramets

	1	2	3	4	5
1					
2	0.586**				
3	0.437*	0.280			
4	0.543**	0.305	0.454*		
5	−0.365	−0.445*	−0.134	−0.332	
6	0.359	0.322	0.171	0.554**	−0.187

*P < 0.05, **P < 0.01.

use of a path model. The analyses were performed for the data sets gathered during 1990 and 1991 and gave essentially the same results. The data set for 1991 included one variable that was not estimated in 1990 (proportion of flowering ramets) and therefore the results for 1991 are presented. The basic correlation matrix (Table 2) and the path diagram (Fig. 1) suggest the following:

1 There is a strong positive effect of fruit set on total fruit production in patches.

2 Fruit set is influenced mainly by distance to nearest flowering neighbour patch. Isolated patches tend to have a reduced fruit set, and thereby a reduced fruit production.

3 The size of patches has a weak positive effect on fruit set.

4 The intrapatch density of ramets has a positive effect on fruit production. According to the path model this effect acts partly via the proportion of flowering ramets. Dense patches tend to have a comparatively high proportion of flowering ramets, and thereby a high fruit production.

The path diagram below represents the best model found for the data set, in terms of explained variation of the dependent (criterion) variables fruit set and fruit production. The path model explains 25.4% of the variation in fruit set, and 58.4% of the variation in fruit production. The corresponding values for the 'best' multiple regression analyses were 14.7% and 41.8%, respectively.

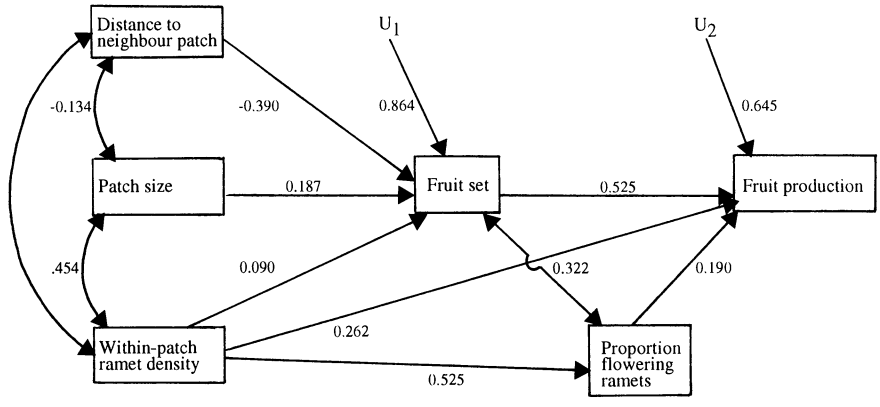

Fig. 1 Path diagram for determinants of fruit production in patches of *Rubus saxatilis* in central Sweden during 1991. One-headed arrows depict causal relationships, whereas two-headed arrows depict correlations. Variables are defined in the text. U_1 and U_2 denote residual variables that include unmeasured variables influencing fruit set and fruit production.

The key variable of the model is fruit set. Used as an independent variable it is the most important identified factor for explaining fruit production in patches, and viewed as a link in a causal chain it is the dependent variable upon which act structural aspects of the population of patches. The most important identified population variable for explaining fruit set was distance to nearest flowering neighbour patch. This suggests an interaction with pollinators, which was further investigated by pollination experiments.

POLLINATION AND FRUIT SET

The pollination experiments were performed during two years and in six different patches each year. As mentioned, only seven of the 12 patches yielded meaningful results (Table 3). The fruit set was generally lower in 1991 than in 1990, probably as a result of a rainy early summer in 1991. Despite this between-year variation, the results are straightforward. Self-pollination never results in fruit production. Pollination within patches yields almost the same result, with one exception: one single drupelet

Table 3 Results from pollination experiment performed in seven different patches of *Rubus saxatilis* in a population in central Sweden. 'Selfing' indicates that flowers only received pollen from flowers of the same treated ramet. 'Within-patch' indicates that flowers received pollen from ramets growing in the same patch as the treated ramet. 'Between-patch' indicates that flowers received pollen from patches situated at least 50 m apart from the treated patch. Fruit set was between patch, and N values represent the number of flowers

	No of infructescences with fruit			
	Selfing	Within patch	Between patch	Fruit set
1990				
Patch 1	0, n = 10	0, n = 9	7, n = 9	0.44, N = 27
Patch 2	0, n = 10	0, n = 10	9, n = 10	0.70, N = 30
Patch 3	0, n = 9	0, n = 9	8, n = 9	0.67, N = 27
Patch 4	0, n = 10	1, n = 10	1, n = 10	0.03, N = 30
1991				
Patch 5	0, n = 6	0, n = 7	2, n = 8	0.08, N = 24
Patch 6	0, n = 10	0, n = 8	2, n = 10	0.07, N = 30
Patch 7	0, n = 8	0, n = 9	1, n = 10	0.10, N = 30

in one patch in 1990. In contrast, between-patch pollination results in fruit development. In 1990 most inflorescences produced fruit, and the fruit set was high (0.44–0.70) in three patches, as compared to the observed average fruit set this year among the 25 'untreated' focal patches (0.066; Table 1). Even though these are not in a strict sense controls for the experiment, they indicate that pollen availability may have limited fruit set in some patches. In 1991, the resulting pattern concerning differences among treatments in the pollination experiment is similar to 1990 despite the generally lower fruit set, which in 1991 was close to the observed value among the 25 patches (0.083; Table 1).

On the basis of these results we conclude that *R. saxatilis* is self-incompatible and that patches exhibit signs of being dominated by one single incompatibility type, presumably one genet. These results add to the distance-effect on fruit set found in the path analysis (Fig. 1). Genet density, which is approximated by an inverse of interpatch distance, has a positive effect on fruit production. As a corollary, at low genet population densities an increase in density is expected to cause enhanced reproductive success, in terms of fruit production.

FRUIT REMOVAL

To estimate whether fruit production affects removal of fruit by animals, the 'nondispersed' loss of fruits from infructescences must be estimated. This was made by a bagging experiment. The results (Fig. 2) indicated that about 50% of the fruit crop is eaten and removed by animals (The mean (± SE) difference in proportion of drupelets disappeared after 30 days, between bagged and unbagged infructescences was 0.49 ± 0.094 (n = 13 patches).) Most fruits were removed before 20 days after fruit maturation (Fig. 2a). This time interval was therefore chosen for estimating a variable 'fruit removal rate' in the 13 patches in which fruit depletion was observed. No significant relationships were found in regression analyses of fruit removal rate and, respectively, fruit production (P = 0.361), fruit set (P = 0.076) or distance to neighbour patch (P = 0.225). Thus, none of the observed variables seem to influence the rate of fruit removal.

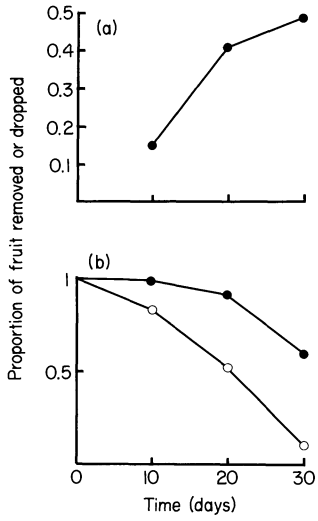

Fig. 2 Removal of fruits of *Rubus saxatilis* in a population in central Sweden. (a) Cumulative removal over the observation period (proportion of fruits lost from open infructescences – proportion fruits dropped in bagged infructescences). (b) Depletion curves. The upper curve (●) represents the fruit depletion in bagged infructescences (in all, 220 drupelets in 50 bags), and the lower curve (○) the depletion of fruits exposed to frugivors (in all, 1363 drupelets from 13 patches).

RECRUITMENT AND GENET POPULATION STRUCTURE

In general, very few seedlings of *R. saxatilis* were observed during the observation period 1988–91. Within the areas where seedlings were searched for carefully (three *c.* 20-m^2 plots at three localities), seedlings were observed only in one year (1991) and at one site (MSOF) (2.1 ± 2.6 seedlings m^{-2}, n = 20). In addition, a single seedling was observed in the coniferous forest locality.

The pollination experiment (Table 3) indicated that distinct patches comprise single genets (or at least incompatibility types). In contrast, the results of RAPD analysis for the two sites DF and MSOF revealed a considerable genet diversity (Fig. 3). In DF, 10 different genets (from 20 sampled ramets) were identified, and in MSOF, eight different genets (from 24 ramets) were identified. The basic data from these analyses is presented in the Appendix. In DF, there were six distinct patches of *R. saxatilis* within the 20-m × 30-m plot (Fig. 3a). In this plot no ramet occurred outside the patches delimited by the broken lines in Fig. 3(a). Except from the patch with the ditch, no one patch was found to comprise more than one genet. At the MSOF site, where the population is composed of a more diffuse patch structure and ramets occur even outside the identified 'patches' (Fig. 3b), all but one patch comprised more than one genet. In congruence with conclusions from the pollination experiment concerning distinct isolated patches, the RAPD results indicated that the isolated roadside patch comprised only one genet.

Because no effect of fruit production on fruit removal rate was found, the absolute number of both dispersed seeds and seeds deposited within patches is expected to increase with increasing fruit production. Accordingly, we expected to find a positive relationship between genet density, fruit production and seedling recruitment in local populations of *R. saxatilis*. Information on recruitment and genet population structure thus confirmed this expectation for MSOF but not for DF.

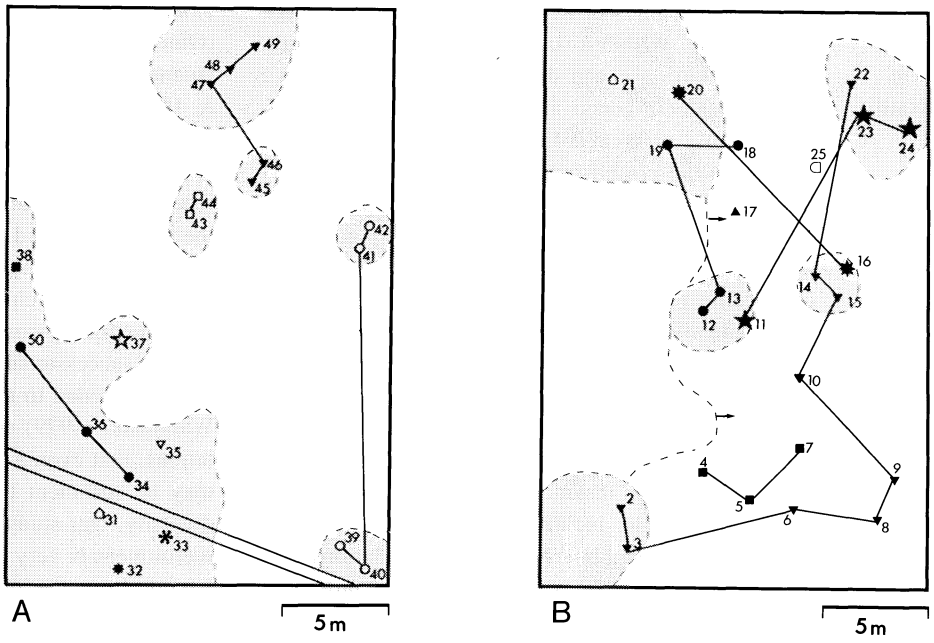

Fig. 3 Distribution of *Rubus saxatilis* genets within 20-m × 30-m plots at two localities in central Sweden, 'deciduous forest' (A) and 'mixed semi-open forest' (B), as revealed by RAPD-analysis. The dark areas delimited by broken lines indicate limits of patches identified in the field prior to sampling of the analysed ramets. In (A), no ramets were found outside patches, whereas in (B) the area marked by arrows was inhabited by ramets not occurring in discrete patches. Symbols mark the position of sampled ramets, which are numbered in accordance with the Appendix. Different symbols indicate different genets. A conservative interpretation of genet diversity was used. Ramets which were not found to differ in banding pattern (Appendix) were considered to belong to the same genet, and these ramets are connected by solid lines on the maps. The two lines in the lower left corner in (A) mark the position of a ditch.

Discussion

In this study we have performed a series of field observations and experiments, in combination with genet identification by a molecular technique (RAPD; Williams *et al.* 1990), on a clonal plant, *Rubus saxatilis*. The aim was to provide insight into processes that determine dynamics of genets of this species, particularly reproduction and recruitment. The long temporal scale over which genet dynamics operates in many clonal plants makes it difficult to perform cohort studies. The use of indirect methods and inferences from static population data are one available alternative approach to studies of genet dynamics. Such a methodology, however, is connected with some weaknesses against which the conclusions should be evaluated; namely that processes must be inferred from observations of pattern, that hypothesized causal factors such as intergenet distances and patch size, are not experimentally manipulated and that confounding correlated variables cannot be excluded.

With these weaknesses in mind, we provide evidence that suggests an apparent positive effect of genet population density on fruit production in *R. saxatilis*. Also, seedling recruitment occurred only at a site with high genet density and high fruit production. We cannot resolve to what extent the effect reflects a correlation with general habitat quality, obscuring possible negative competitive density effects among genets. The observation that genet diversity at the localities DF and MSOF was similar (or slightly higher at DF), but seedling recruitment occurred only at MSOF, implies that factors other than genet density must be invoked to explain recruitment patterns. However, we believe that it is justified to conclude that a positive, albeit probably weak, density effect is operating in the *R. saxatilis* population, mediated primarily by pollinator interactions. Isolated genets suffer from pollen deficiency. Accordingly, low intergenet distances promote fruit production and recruitment in *R. saxatilis*.

The results are congruent with previous observations of among-patch density as one major determinant of fruit set in clonal plants (e.g. Tammisola 1982; Laverty & Plowright 1988; Worthen & Stiles 1988; but see Barrett & Thompson 1982; McCall & Primack 1987; Aspinwall & Christian 1992 for deviating results). Our results also support the arguments by Handel (1985) that clonal patch structure influences reproductive success. On a within-patch level, ramet density affected fruit production. This effect might result from pollinator attraction or differences in ramet size distributions among patches. The probability of a ramet flowering increases with increasing size and age (O. Eriksson, unpublished data). It may also reflect a correlation with an unmeasured variable, 'site quality', which influences both ramet density and reproduction.

Genet dynamics of *R. saxatilis* occurs on a large spatial scale. Within a scale of the size of the study area (2.5 km^2) we can define 'source populations', dense clusters of genets at favourable sites, and 'sink populations' in areas where occasional recruitment has led to the establishment of isolated genets, perhaps not capable of producing offspring to the extent necessary for maintaining a viable local population. Such source–sink relationships among large scale conspecific population systems have several important implications for niche utilization and population regulation (Pulliam 1988). Isolated genets of *R. saxatilis*, in the study area occurring mostly in coniferous forest and road sides, may be loci for colonization and extension of population distribution if conditions change, for instance due to clear felling of the forest, or due to incidental recruitment of other genets in their neighbourhood. Sink populations of a clonal plant such as *R. saxatilis* may thus provide a model of an exceptionally slow local colonization process of a clonal plant.

A comparison between the DF and MSOF sites gives some additional clues to large-scale dynamics of *R. saxatilis* genets. At the beginning of this century, these sites were used as grazed 'wooded pastures' (cf. Ryberg 1971). To a large extent this land-use has now disappeared and the areas are presently in different stages of succession, via a birch dominated intermediate stage to coniferous woodland. At the DF site, spruce has been felled, and this has resulted in the development of a dense canopy dominated by oak, birch, hazel and ash. In contrast, the canopy at MSOF is still relatively open. The *R. saxatilis* population at MSOF (dense, high fruit production and seedling recruitment) will probably deteriorate as the canopy closes, and develop into a stage similar to DF. Under such a closed canopy, the *R. saxatilis* population may comprise surviving genets from earlier stages, and genets established occasionaly and infrequently from seed produced at some other 'source site'.

As a tentative suggestion, the different sites may be viewed as representing a hypothesized temporal sequence. Initially, genets of *R. saxatilis* become established more or less randomly in different locations. If conditions are suitable, or become suitable during the life span of the colonizing genet, a 'source population' develops (such as the one at the MSOF site) and remains a source for further local and regional recruitment until the conditions deteriorate and *R. saxatilis* becomes suppressed, e.g. by a closed canopy (such as the DF site). On a large spatial scale the genet dynamics thereby consists of combined source and sink populations arranged in a slowly changing landscape mosaic.

Viewed as a spectrum of genet densities, the source–sink model also implies that a clonal plant species may exhibit intraspecific variation in genetic structure. Several studies, based both on morphological and genetic data, have indicated that patches of clonal plants often are inhabited by single genets (Oinonen 1967a; Anderson & Beare 1983; Huenneke 1985; Worthen & Stiles 1986; Murawski & Hamrick 1990). In many cases, though, clonal populations comprise a considerable genetic diversity (Ellstrand & Roose 1987; Aspinwall & Christian 1992). If a source–sink pattern occurs, however, the results obtained from a study of genetic structure on an arbitrary population of a clonal plant will be sensitive to the choice of study site. Comparative investigations incorporating several different habitats (or successional stages) inhabited by clonal species are needed to reveal such a variation. Soane & Watkinson (1979) suggested, from results of simulations, that even a low rate of seedling recruitment may be sufficient to maintain a high local genetic diversity. Our study confirms their results. Seedling recruitment is very seldom observed in *R. saxatilis*. Except from the mixed semi-open forest (MSOF) site in 1991 only occasional seedlings have been observed in the study area, and seedling recruitment has not been previously reported by other authors (cf. Eriksson 1989). It seems well founded to conclude that the rate of seedling recruitment in this species is indeed low. Despite this fact, there was a high genet diversity at both the DF and MSOF sites.

If genet density has a positive effect on recruitment rates of *R. saxatilis*, what sets limits to the genet population? How is the genet population regulated? It may seem self evident that further increase in genet population density must finally result in negative density effects. However, if the growth rate of the genet population is so slow that occurring large-scale 'disturbances' (defined as any exogenic agent killing an established genet), or habitat deterioration, effectively hinder the population from reaching the density at which negative effects start to operate, the limits of the genet population will not be density regulated at all. This scenario is in striking contrast to the well known occurrence of density regulation at the ramet level in clonal plants (Hutchings 1979; Pitelka 1984). A prevalence of exogenic factors in combination with weak positive density dependent effects, such as the one described in this study, in the dynamics of genet populations of clonal plants illustrates the present lack of adequate population models for dynamics of these kinds of plants.

Acknowledgements

We are grateful to P. Gustafsson and L. Gustafsson for advice concerning the RAPD technique. G. Elmgren assisted in the laboratory, and comments from J. Ehrlén, J. van Groenendael and one anonymous reviewer improved the manuscript. This study was supported financially by grants from the Swedish Natural Science Research Council, and the Swedish Council for Forestry and Agricultural Research.

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Received 2 July 1992
Revised version accepted 15 January 1993

Appendix

Results of RAPD analysis of *Rubus saxatilis* ramets. The occurrence of bands on gels is indicated in the table (zero denotes 'no band'). Ramet numbers 2–25 refer to 'mixed semi-open forest', ramet numbers 31–50 refer to 'deciduous forest' and ramet number 26, 51 and 52 to 'road side patch'. (Numbers 27–30 were not used, and sample 1 was destroyed). Four different primers were used in the analyses.

Primers and approximate size (bp = base pairs) of fragments

Primer 1 (CAGGCCCTTC)
- Band A: 760 bp
- Band B: 850 bp
- Band C: 1380 bp
- Band D: 1900 bp

Primer 2 (AGTCAGCCAC)
- Band A: 770 bp
- Band B: 890 bp
- Band C: 1330 bp
- Band D: 1640 bp

Primer 3 (AATCGGGCTG)
- Band A: 575 bp
- Band B: 640 bp
- Band C: 890 bp
- Band D: 1020 bp
- Band E: 1410 bp

Primer 4 (AGGGGTCTTG)
- Band A: 690 bp
- Band B: 990 bp
- Band C: 1110 bp
- Band D: 1300 bp
- Band E: 1640 bp

Primer	1	2	3	4
Band	A B C D	A B C D	A B C D E	A B C D E
2		0 1 1 0		0 0 0 0 1
3		0 1 1 0		0 0 0 0 1
4		0 1 0 1		0 0 0 0 1
5		0 1 0 1		
6		0 1 1 0		
7		0 1 0 1		
8		0 1 1 0		
9		0 1 1 0		
10		0 1 1 0		0 0 0 0 1
11	1 0 1 0	0 1 1 1	0 1 1 0 1	0 0 0 0 1
12	1 0 1 0	0 1 1 1	0 1 1 0 1	0 0 1 1 1
13	1 0 1 0	0 1 1 1	0 1 1 0 1	0 0 1 1 1
14	1 1 0 0	0 1 1 0	0 1 1 0 1	0 0 0 0 1
15	1 1 0 0	0 1 1 0	0 1 1 0 1	0 0 0 0 1
16	1 0 1 0	0 1 1 1	1 1 1 0 1	0 0 1 1 1
17	1 1 0 0	0 1 1 0	0 1 1 0 1	1 1 0 0 1
18		0 1 1 1	0 1 1 0 1	0 0 1 1 1
19		0 1 1 1	0 1 1 0 1	0 0 1 1 1
20		0 1 1 1	1 1 1 0 1	0 0 1 1 1
21		0 1 1 0	0 1 1 0 1	1 0 0 0 1
22		0 1 1 0	0 1 1 0 1	0 0 0 0 1
23		0 1 1 1	0 1 1 0 1	0 0 0 0 1
24		0 1 1 1		0 0 0 0 1
25		0 1 1 0		1 0 0 0 0
31		1 1 1 0		0 0 1 0 1
32		1 0 1 1	0 0 1 0 0	
33		1 1 1 0	0 1 1 0 0	1 1 0 0 0
34		0 1 1 0	0 1 1 0 0	
35		1 0 1 1	0 1 1 1 1	0 0 0 0 1
36		0 1 1 0	0 1 1 0 0	0 1 0 0 1
37	0 1 1 0	1 1 1 1	0 1 1 1 1	0 0 0 0 1
38	1 0 1 0	0 1 1 0	0 1 1 0 1	0 0 0 1 1
39		0 1 1 1		1 0 1 0 0
40		0 1 1 1		1 0 1 0 0
41		0 1 1 1		
42		0 1 1 1		
43		1 0 1 0		1 1 1 0 0
44		1 0 1 0		1 1 1 0 0
45		0 1 1 0		0 1 0 0 0
46		0 1 1 0		0 1 0 0 0
47		0 1 1 0		
48		0 1 1 0		
49		0 1 1 0		
50	1 0 1 0	0 1 1 0	0 1 1 0 0	
26		1 0 1 0		
51	1 0 0 1	1 0 1 0	0 1 1 0 1	
52	1 0 0 1	1 0 1 0	0 1 1 0 1	