

## Niche shifts and seed limitation as mechanisms determining seedling recruitment in clonal plants

Posun nik a limitace dostupnosti semen jako mechanismus určující uchycení semenáčků u klonálních rostlin

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Dedicated to the memory of Leoš Klimeš

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This is a review of the evidence on seedling recruitment patterns in clonal forest plants, based on a previously used typology in which the occurrence of seedling recruitment is related to the performance of adult genets: repeated seedling recruitment (RSR), initial seedling recruitment (ISR), recruitment at windows of opportunity (RWO) and systematic spatial variation in seedling dynamics among local populations (RSR/ISR). Generally, seedling recruitment in clonal populations is common and the majority of species have the capacity to recruit within established adult populations. All four recruitment patterns are documented in studies, which include both genetic and demographic evidence that support the existence of a range of variation in seedling recruitment among clonal plants. However, it is suggested that this four-category typology should be replaced by a framework based on two continuously varying factors: the degree of niche overlap between juvenile and adult life cycle stages (uncoupling of juvenile and adult niches implies “niche shifts”) and of seed limitation during recruitment. This creates a hypothetical continuous space within which all recruitment patterns are placed and stimulates research to focus on identifying mechanisms determining the variation in the recruitment of clonal plants. Some further implications of this framework are briefly discussed.

**Key words:** forest plants, ontogenetic niche shifts, plant population dynamics, regeneration niche, repeated seedling recruitment

### Introduction

Clonal plants have attracted a lot of interest in evolutionarily oriented population ecology. Most clonal plants have two different modes of reproduction, sexual (with seeds) and asexual (clonal). For simplicity, here, the term “reproduction” is also used for clonal propagation. Clonal plants are thus suitable for studies on long-standing questions such as the evolution and maintenance of sex (e.g. Williams 1975) and clonal vs sexual trade-offs (e.g. Eckert 2002). For students of plant population dynamics, clonal plants offer a special challenge due to their dual modes of reproduction and because clonal reproduction generally is more local and associated with higher offspring survivorship than reproduction by seeds. Silvertown et al. (1993) based on a review of a range of demographic studies report that clonal reproduction is about ten times more important for local population growth than recruitment from seeds. It may therefore seem rather unexpected that studies of genetic variation in local populations reveal that there is no major difference between clonal and

non-clonal plants (Ellstrand & Roose 1987, Widén et al. 1994, McLellan et al. 1997). Although this may appear to be a result of several different processes, it indicates that seedling recruitment is prevalent in most populations of clonal plants. Indeed, modelling studies (Soane & Watkinson 1979, Watkinson & Powell 1993) suggest that even a very low rate of input from seedling recruitment may be sufficient to maintain considerable genetic variation in a population where clonal reproduction quantitatively dominates. Among clonal plants, self-incompatible species are genetically less variable than self-compatible species (Honnay & Jacquemyn 2008). Possibly, this indicates that self-incompatible species are more likely to suffer from “mate-limitation” resulting in low seed production, which results in limited seedling recruitment. As this mechanism assumes that mate-limitation occurs, it means that the local population initially must have been colonized by single or at least only a few genets.

A direct approach to studies of seedling recruitment in clonal plants is to observe and record the fate of seedlings in natural populations. Some decades ago, Eriksson (1989) made a summary of the then known observations of seedling recruitment in clonal plant populations and concludes that for the majority of species (60%) seedling recruitment is not recorded in established populations. Furthermore, there are differences between species inhabiting grasslands and forests. Among the forest species, seedling recruitment is recorded in just about 30% of the species, whereas it was more common in grassland species. Based on these findings, Eriksson (1989) suggests two main recruitment patterns in clonal plants: RSR (repeated seedling recruitment) and ISR (initial seedling recruitment). RSR implies continuous seedling recruitment within local conspecific populations. ISR implies that seedling recruitment only occurs when local populations are founded. In three later papers (Eriksson 1993, 1997, Eriksson & Fröborg 1996) this dichotomy was somewhat elaborated, incorporating also RWO (recruitment at windows of opportunity) and RSR/ISR (systematic large scale variation between RSR and ISR). RWO implies that continuous seedling recruitment occurs, but only under very specific conditions, “windows of opportunity”, that are spatially unpredictable within local conspecific populations. RSR/ISR implies that within a large region some local populations act as seed sources with RSR, but in many local populations in the region seedling recruitment only occurs at the initial colonization event, thus exhibiting ISR. This creates a regional population structure similar to source and sink population systems (Pulliam 1988) and the full genet dynamics can only be understood in a wider spatial context incorporating both kinds of local populations.

In Eriksson (1997) the implications of these recruitment patterns are summarized and some relationships with regenerative traits suggested and examined. The conclusions are as follows: (i) Even though evidence from genetic studies suggests that seedling recruitment in long-lived clonal plants generally is underestimated, there seems to be a considerable inter-specific variation in seedling recruitment patterns. (ii) Two general life history features seem to be associated with seedling recruitment pattern: RSR is associated with selection for competitive ability in the recruitment phase, for example manifested so that species with RSR possess relatively large seeds. ISR is associated with selection for dispersal ability, for example manifested so that species with ISR possess specialized dispersal attributes. The evidence for these trends is however weak. (iii) Seedling recruitment patterns are associated with genet dynamics acting on different spatio-temporal scales. RSR implies that genet dynamics are comparatively “small-scale” in both space and time,

whereas RWO, ISR and RSR/ISR imply that genet dynamics occur at a wider spatio-temporal scale.

The objective of this paper is first to briefly summarize what is revealed by recent studies of recruitment in clonal plant populations, and then to suggest a new conceptual framework for further studies on recruitment and genet dynamics in clonal plants. In order to avoid complications resulting from comparing species from many different kinds of habitats, the overview is restricted to forest plants of temperate and boreal zones. The suggested framework is however applicable also to clonal plants in other habitats.

## Methods

A search was made in the Web of Science database using different search words related to seedling recruitment in clonal plants: “clonal plant recruitment”, “clonal diversity”, “repeated seedling recruitment” and “initial seedling recruitment”, focusing on papers published during the last two decades. Only studies on species in temperate or boreal forests were recognized. Some papers were also found from reference lists. It is likely that the search did not result in a complete cover of existing studies. However, there is no reason to suspect that the sample is biased, meaning that emerging generalities should be valid. In the following, the concepts RSR, ISR, RWO and RSR/ISR are used as defined above in the introduction (following Eriksson 1997). Both demographic and genetic evidence are considered. The strongest evidence comes from studies using both these approaches. Most studies only analyze genetic structure. The methods used vary and include isozymes/allozymes, RAPD, AFLP, RFLP, chloroplast DNA markers, microsatellite markers and morphometric analyses. Any differences in reliability between these methods are not considered. Generally, a genetic pattern cannot be used to make strong inferences about the process responsible for the pattern. A large and variable initial cohort may suffice to maintain a high local genetic variation, indistinguishable from variation resulting from continuous seedling recruitment. In some cases genetic patterns are related to population development, which strengthens the interpretation. For example, increasing genetic variation over time implies that input of new genets is likely. However, for studies just reporting genet diversity in local populations, the interpretation of the authors, assuming field-based insights of the biology of the target species, is accepted. One should recognize though, that inferences of RSR based on single reports of high genet diversity may be misleading. Despite the increasing number of papers on genet diversity in clonal plants, there is still a need for studies incorporating both genetic and demographic approaches.

## Repeated seedling recruitment (RSR)

As mentioned above, it is well established that there is a high genetic diversity in many clonal plant populations, which is not generally different from non-clonal plants (Ellstrand & Roose 1987, Widén et al. 1994, McLellan et al. 1997). In many of the studies where such high genet diversity has been found this has naturally been interpreted as a result of RSR. Table 1A lists nine species for which RSR is suggested based solely on genetic evidence. In a few cases there is additional support for this conclusion. Verburg et al. (2000) found low genetic diversity in young populations of *Circaea lutetiana* but high diversity in

Table 1. – Evidence of four different types of seedling recruitment recorded in clonal forest plants. The table lists species and references for each type of recruitment, based on genetic and/or demographic evidence.

Type of recruitment	Type of evidence	Species	References	
A. Repeated seedling recruitment (RSR)	Genetic	<i>Circaea lutetiana</i>	Verburg et al. (2000)	
		<i>Filipendula ulmaria</i>	Falińska et al. (2010)	
		<i>Vaccinium stamineum</i>	Kreher et al. (2000)	
		<i>Galium odoratum</i>	Ziegenhagen et al. (2003)	
		<i>Ilex leucoclada</i>	Torimaru & Tomaru (2005)	
		<i>Mercurialis perennis</i>	Vandepitte et al. (2009)	
		<i>Fragaria virginiana</i>	Wilk et al. (2009)	
	Demographic	<i>Anemone nemorosa</i>	Holderegger et al. (1998), Stehlik & Holderegger (2000)	
		<i>Uvularia perfoliata</i>	Kudoh et al. (1999)	
		<i>Mahonia aquifolium</i>	Auge & Brandl (1997)	
		<i>Oxalis acetosella</i>	Berg (2002)	
		<i>Allium ursinum</i>	Morschhauser et al. (2009)	
		Genetic and demographic	<i>Viola riviniana</i>	Auge et al. (2001)
			<i>Convallaria keiskei</i>	Araki et al. (2007, 2009)
<i>Maianthemum dilatatum</i>	Wilson et al. (2005)			
B. Initial seedling recruitment (ISR)	Genetic	<i>Cypripedium calceolus</i>	Kull (1998), Brzosko et al. (2000)	
		<i>Aegopodium podagraria</i>	Eneström et al. (2009)	
		<i>Empetrum hermaphroditum</i>	Szmidt et al. (2002)	
	Demographic	<i>Rubus chamaemorus</i>	Korpelainen et al. (1999)	
		<i>Vaccinium uliginosum</i>	Albert et al. (2005)	
		<i>Vaccinium angustifolium</i>	Bell et al. (2009)	
	Genetic and demographic	<i>Gaultheria procumbens</i>	Donohue et al. (2000)	
		<i>Oplopanax horridus</i>	Lantz & Antos (2002)	
	C. Recruitment at windows of opportunity (RWO)	Demographic	<i>Populus tremuloides</i>	Romme et al. (2005)
			<i>Hydrangea paniculata</i>	Kanno & Seiwa (2004)
		Genetic and demographic	<i>Vaccinium myrtillus</i>	Eriksson & Fröborg (1996), Albert et al. (2003, 2004)
			<i>Vaccinium vitis-idaea</i>	Persson & Gustavsson (2001), Eriksson (2002)
	D. Spatial variation in recruitment among populations (RSR/ISR)	Genetic and demographic	<i>Rubus saxatilis</i>	Eriksson & Bremer (1993)
			<i>Maianthemum bifolium</i>	Arens et al. (2005), Honnay et al. (2006)
Other combinations of evidence suggesting RSR/ISR		<i>Convallaria majalis</i>	Vandepitte et al. (2010), Eriksson (1997)	
		<i>Paris quadrifolia</i>	Jacquemyn et al. (2005)	
		<i>Linnaea borealis</i>	Scobie & Wilcock (2009), O. Eriksson (unpubl.)	

established populations suggesting that RSR is important during build-up of local populations. This result has an interesting parallel in a modelling study of *Asarum canadense* (Damman & Cain 1998) showing that the total number of genets (in the models) increased over time even though seedling recruitment had a small impact on population growth rate. In *Filipendula ulmaria*, Falińska et al. (2010) record high genet diversity, even in late stages of meadow succession, indicating continuous recruitment of seedlings during

30 years of population development. In *Anemone nemorosa*, seedlings are commonly observed in deciduous forests in Sweden (Eriksson 1995), which indirectly provides support for the interpretation of Holderegger et al. (1998) and Stehlik & Holderegger (2000). In *Uvularia perfoliata*, Kudoh et al. (1999) suggest continuous genet recruitment based on high genet diversity at two different spatial scales. However, under closed canopies seed production is very low, which implies that there is a “pulse-wise” seedling recruitment associated with gaps occurring in the canopy.

Support for RSR also comes from studies on three species, which focused on demography of recruitment (Table 1A). For example, Auge & Brandl (1997) record that RSR occurs in the invasive shrub *Mahonia aquifolium*, although the importance of seedling recruitment declines over time during the invasion. Morschhauser et al. (2009) created small gaps in stands of *Allium ursinum* and show that seedling recruitment responds to gaps, with the highest recruitment at intermediate densities of neighbours. They predict that the high genet diversity in these stands is due to RSR.

The strongest support for RSR comes from studies on six species, for which there is evidence for both high genet diversity and records of seedling recruitment (Table 1A). For example, in *Maianthemum dilatatum*, Wilson et al. (2005) found that the genet diversity increases with increasing patch size. Combined with their observations of seedling recruitment, this suggests that RSR contributes to local population development. Szmidt et al. (2002) recorded *Empetrum hermaphroditum* at three coniferous forest sites that had last experienced a wildfire 145 years, 375 years and 1720 years previously. The youngest forest stand had the highest genet diversity. Seedling recruitment was observed on decomposing wood and exposed mineral soil. Although there was a tendency that the colonization phase of genets was most pronounced in the early phase of forest development, this phase is so extended (100–300 years) that this pattern is here interpreted as RSR, but it might as well be considered as an extremely extended ISR. This study illustrates a scaling problem when interpreting recruitment patterns and this is further considered below.

### Initial seedling recruitment (ISR)

Unlike finding high genet diversity in local populations, which in principle can result from both RSR and ISR (with many genets in the colonizing cohort), single or few genets in a population most likely indicate that seedling recruitment only occurred when the local population was founded, or that genets were outcompeted soon after colonization (e.g. Hartnett & Bazzaz 1985). Three such cases are listed in Table 1B. If no seedling recruitment is recorded despite careful search for seedlings, this is also reasonably strong evidence for ISR, as in the shrub *Gaultheria procumbens* (Donohue et al. 2000). Demographic evidence for ISR (Table 1B) also comes from Lantz & Antos (2002) who used a chronosequence method to examine clonal dynamics in *Oplopanax horridus* in forest stands aged from less than 10 years up to more than 200 years. They found no evidence for seedling recruitment as most clonal fragments were older than the forest stand. Although there are scaling problems (seedling recruitment may be more infrequent than the length of an observation) this study indicates ISR.

There is a general paucity of studies that document the initial colonization by species with ISR. One exception, and indeed one of the most informative studies of recruitment patterns

in clonal plants, was done on *Populus tremuloides*. This species is known for its extremely long life span and rare seedling recruitment (e.g. Jelinski & Cheliak 1992). Romme et al. (2005) exploited the occurrence of a rare mass recruitment event following widespread wildfires in 1988 in Yellowstone National Park, described as a large scale “window of opportunity”. Such a mass recruitment most likely occurs only occasionally even at a time scale of a century. The majority of genets (65%) were established within the first 3 years after the fire, although occasional recruitment occurred up until 1996, i.e. 8 years after the fire. Still in the year 2000, the stands were composed of many genets, each having just a few ramets. Clonal reproduction (in aspen ramets are produced from roots) obviously commences at a later stage. Based on genetic studies of established aspen stands, where there are generally few genets each composed of many ramets, Romme et al. (2005) suggest that the cohort established after the fire was in the earliest developmental stage. Over time, competition among genets results in a reduction in genet number, along with an increase in the size of the successful genets. This study provides one of the few detailed insights into a colonization process most properly described as ISR. An important finding is that the initial recruitment proceeds over several years, but is clearly delimited in time.

As mentioned above under RSR, the colonization phase in *Empetrum hermaphroditum* may extend over more than a century (Szmidski et al. 2002) but it is a matter of definition whether this should be regarded as ISR or RSR. If the time window for colonization is related to the life span of probably extremely long-lived stands of *E. hermaphroditum*, the recruitment pattern of this species may perhaps most appropriately be described as ISR.

### **Recruitment at windows of opportunity (RWO)**

There are few studies on recruitment that might be interpreted as evidence of RWO (Table 1C). Recruitment at windows of opportunity is a term used by Jelinski & Cheliak (1992) for aspen and by Romme et al. (2005) to describe aspen recruitment after a widespread wildfire. However, as defined by Eriksson & Fröberg (1996) in a study of *Vaccinium myrtillus*, the RWO concept has a more narrow meaning. Experimental studies suggest that seedling recruitment in *V. myrtillus* occurs only on decomposing wood. This species produces enormous numbers of small seeds, potentially well dispersed by the berries, which are highly attractive to many birds and mammals. Decomposing wood, suitable for recruitment, occurs scattered in coniferous forests, implying that suitable recruitment conditions are temporally predictable (always exist) but spatially unpredictable. A “strategy” of producing many well-dispersed seeds would seem adaptive, although the likelihood that an individual seed is successful is very small. A relevant question is whether there is any difference between RSR and RWO, or whether this is just a question of how specific the recruitment conditions are relative to the general conditions in the local population. An argument for distinguishing these two variants of continuous seedling recruitment is that RSR implies a selective premium for competitive ability of seedlings (e.g. large seeds), whereas RWO favours maximizing the likelihood of finding recruitment windows (e.g. many small seeds). An extreme case of RWO may be found in species such as *Monotropa hypopitys* (Leake et al. 2004), which produces huge numbers of tiny dust-like seeds. Like other species with dust-like seeds, *M. hypopitys* is dependent on parasitizing a specific fungus and the likelihood per seed of successful recruitment is extremely small.

In effect, RWO creates a genetic pattern similar to RSR. As expected, populations of *V. myrtillus* are genetically very diverse (Albert et al. 2003, 2004). Persson & Gustavsson (2001) report similar high genet diversity in *Vaccinium vitis-idaea*, with the populations investigated composed of a few large and many small genets. No seedlings were observed, but the recruitment pattern was nevertheless interpreted as RWO. Eriksson (2002) found an ontogenetic niche shift in *Vaccinium vitis-idaea* (recruitment was more common at sites where there were no adults) whereas in *V. myrtillus*, the requirements for recruitment overlapped with adult occurrence. This may imply that *V. myrtillus* has a greater ability to recruit within established stands than *V. vitis-idaea*.

### RSR/ISR

RSR/ISR implies that there is a mixture of these two recruitment patterns. The rationale for recognizing this as a special kind of recruitment was the finding that some clonal species typically have genetically diverse local populations with high seed production, which at a landscape scale is mixed with local populations composed of single genets, which produce few seeds. This resembles source and sink populations (Pulliam 1988), but in a slightly different context than Pulliam envisaged. There are only a few good examples of RSR/ISR (Table 1D). In *Rubus saxatilis*, Eriksson & Bremer (1993) found genetically diverse source populations with many genets and high seed production enhancing local seedling recruitment and providing seed that disperses resulting in the founding of new populations, among which several remain isolated and comprised of single genets. Arens et al. (2005) found that most patches of *Maianthemum bifolium* are composed of single genets. This suggests ISR, a conclusion also reached after a small study on the same species by Lieske & Pfeiffer (2007). However, Honnay et al. (2006) found that some patches of *M. bifolium* contain several genets. These patches are also those with the highest fruit-set, suggesting a positive relationship between genet diversity and seed production. Most likely, as in *R. saxatilis*, this is mediated by mate-limitation in a self-incompatible species. At a regional scale, and particularly in landscapes where forests are fragmented, many local populations are the result of single colonization events and maintained by clonal reproduction.

In *Convallaria majalis*, Vandepitte et al. (2010) found that most populations (which are scattered in highly fragmented forests) are comprised of only single genets. However, other studies on *Convallaria*, including the closely related *C. keiskei* (Araki et al. 2007, 2009, Araki & Ohara 2008), indicate a RSR/ISR pattern is more likely. In Sweden, *C. majalis* occurs as scattered stands, often isolated in forests, but there are also stands in more open conditions, with a high fruit set and where seedling recruitment is frequently observed (both natural recruitment and experimentally induced) (Eriksson 1997, Ehrlén & Eriksson 2000, Ehrlén et al. 2006). There are no genetic analyses of these populations, but most likely they are highly genet-diverse. Another putative example is *Paris quadrifolia* for which Jacquemyn et al. (2005) found that dry sites harboured patches with few large genets and moist sites many small genets.

Honnay & Jacquemyn (2008) found that self-incompatible clonal species have a lower genotypic diversity than self-compatible species, indicating that the latter are more likely to possess RSR. Patches with single (or few) genets of self-incompatible species may thus

suffer from mate-limitation, as reported for *Rubus saxatilis* (Eriksson & Bremer 1993), *Maianthemum bifolium* (Honnay et al. 2006) and also most likely occurs in *Convallaria majalis* (O. Eriksson, unpublished). The clonal forest shrub *Linnaea borealis* may also be added to this list. In isolated stands of *L. borealis* in Scotland, Scobie & Wilcock (2009) found a very low fruit set (less than 8.5%) indicating that local populations were composed of few genets. As a comparison, in Sweden where *L. borealis* is much more common, fruit set is also higher. Over a ten-year period, fruit set was on average 23.2% based on a total of 9700 flowers, and seedling recruitment regularly observed (O. Eriksson, unpublished). Mate-limitation may also affect species that are self-compatible, as shown in an elegant study by Albert et al. (2008), who conclude that increased genet diversity decreases selfing rate in *Vaccinium myrtillus*. Possibly, this may lead to positive feedback, as increased seedling recruitment enhances genet diversity promoting outcrossing and most likely seed quality, further increasing the likelihood of seedling recruitment.

### **A unified concept of seedling recruitment patterns**

In the majority of the studies of clonal forest plants reviewed here, there is evidence that seedling recruitment occurs regularly in local populations. Just counting the number of species (as in Eriksson 1989) at least 18 of the 32 species reviewed possess RSR. Including the eight species for which RWO or RSR/ISR is recorded implies that in 81% of these species seedling recruitment occurs within populations of established adults. Thus, as indicated by the conclusions of for example Widén et al. (1994) and McLellan et al. (1997) based on genetic evidence, it is likely that seedling recruitment in clonal forest plants has been overlooked and its importance underestimated. The suggestion by Eriksson (1989) that seedling recruitment is more common in populations of clonal species in grasslands than in forests is therefore probably wrong. Ehrlén & Lehtilä (2002) estimate plant life span based on an analysis of demographic data using matrix models and record that species inhabiting forests are generally more long-lived than species in open habitats. Thus, apart from the possibility that grassland species simply are more thoroughly investigated it may also be that seedling recruitment is more infrequent on an absolute time-scale in forests than in grasslands, reflecting that forest species are generally more long-lived.

A second conclusion is that there are studies using both genetic and demographic methods that support all four of the patterns of recruitment suggested by Eriksson (1997), RSR, ISR, RWO and RSR/ISR. But is this classification meaningful, or stated in another way, are there other ways to describe the existing range in variation in the patterns of seedling recruitment in clonal plants? An alternative approach is to determine whether there are ontogenetic niche shifts, i.e. the niche requirements of the regenerative phase are different from those of the adult plants. Although not explicitly phrased in these terms, this idea is included in the concept of the regeneration niche (Grubb 1977), which specifies that the regeneration phase of plant life cycles may incorporate a multitude of niche relationships that are not important for adult plants. This implies that it may be possible to uncouple the features of regenerative and adult life-cycle phases (Shipley et al. 1989, Grime et al. 1997) and this uncoupling deserves a general analysis based on clonal-trait databases, such as the CLO-PLA (Klimešová & Klimeš 2008, Klimešová & de Bello 2009), and information on regenerative traits.



There are few studies specifically on ontogenetic niche shifts in plants (e.g. Parrish & Bazzaz 1985, Eriksson 2002, Quero et al. 2008, Anderson et al. 2009), but the changing of niche requirements has for a long time been an essential concept in studies on succession and gap dynamics (e.g. Bazzaz 1979). Poorter (2007) found that tropical forest trees have leaf traits that are generally more adapted to the conditions during recruitment than during the adult stages and suggest that the realized adult niche partly reflects the regeneration niche. For clonal plants, it seems evident that a characteristic feature of species that regularly recruit by means of seedlings in adult stands is that the regeneration niche overlaps the adult niche. For species with ISR, like *Populus tremuloides* (Romme et al. 2005) it is likewise clear that the regeneration niche does not overlap the adult niche. Thus, the spectrum of variation in seedling recruitment patterns can be described as a gradient from complete niche overlap between juvenile and adult stages, to no-overlap in niche requirements of these life-cycle phases. RWO would in this respect be intermediate in that the conditions necessary for seedling recruitment is a subset of the adult niche space (as in *Vaccinium myrtillus*; Eriksson & Fröberg 1996). A decoupling of juvenile and adult niche requirements necessitates that the conditions fulfilling these requirements are separated in space (or in time). Thus, the relevant spatio-temporal scale for incorporating genet population dynamics in clonal species increases from overlapping to non-overlapping juvenile and adult niches.

Much of the variation in seedling recruitment pattern in clonal plants can be accounted for by using niche requirements for recruitment relative to those of the adult. However, there is a need for incorporating one further aspect, namely, seed production. As the examples of RSR/ISR show, in some species, especially those that are self-incompatible, there is a systematic mate-limitation in local populations composed of single or few genets. Thus, seedling recruitment may be hampered simply due to lack of seeds. Sowing experiments including some using species with RSR/ISR, for example *Convallaria majalis* (Ehrlén et al. 2006), support seed limitation for recruitment in this species. This aspect may seem less relevant for clonal species with numerous small seeds, for example *Vaccinium myrtillus* and *Populus tremuloides*. However, self-incompatible species with large seeds, such as *Convallaria majalis* (seed size: 17.0 mg), *Rubus saxatilis* (seed size: 10.3 mg) and *Maianthemum bifolium* (seed size: 9.1 mg), may regularly suffer from seed limitation (seed-size data from Eriksson & Ehrlén 1991). Lack of seedling recruitment may therefore not necessarily reflect that the regeneration niche requirements are not fulfilled. Although a low seed production may result from mate-limitation, as suggested by the comparatively low genetic diversity in self-incompatible clonal plants (Honnay & Jacquemyn 2008), a poor seed production may have other causes than mate-limitation, such as abiotic factors. In order to be general, it therefore seems most appropriate to describe the mechanism behind RSR/ISR as seed limitation (sensu Ehrlén & Eriksson 2000), which encapsulates all the mechanisms causing low seed production.

Thus, instead of four, rather arbitrary (and phenomenological) categories, RSR, ISR, RWO and RSR/ISR, the existing variation in recruitment patterns can be described using two continuous factors: the degree of niche overlap between juvenile and adult life cycle phases, and the degree of seed limitation (Fig. 1). Instead of labelling an observed recruitment pattern RSR, ISR etc., it is more informative to identify the underlying mechanisms. It is suggested that studies with this objective should focus on experimental assessments of the juvenile (regeneration) niche in relation to the realized niche exploited by adults and combined with experimental assessments of the degree of seed limitation.

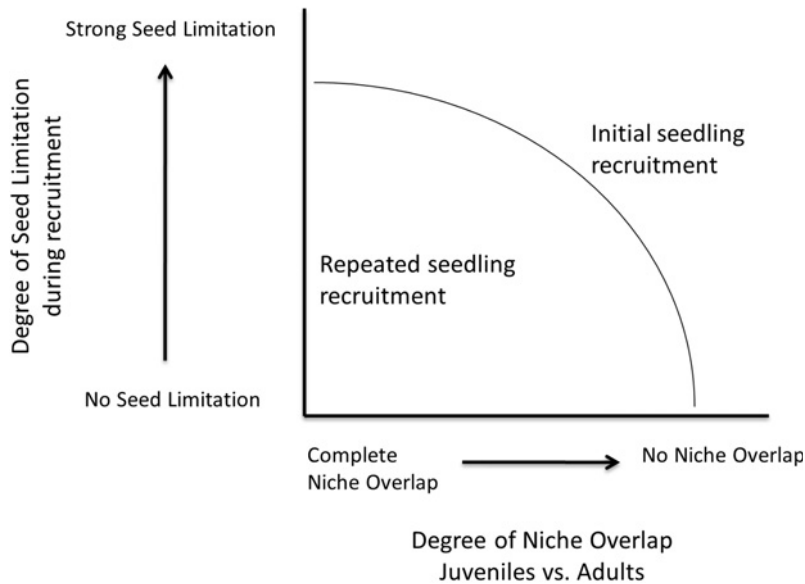


Fig. 1. – A framework of the mechanisms determining seedling recruitment patterns in clonal plants. The realized seedling recruitment depends on two factors, the degree of overlap between juvenile and adult niches (“juvenile” incorporates the process from germination to juvenile plant), and the degree of seed limitation during recruitment. The curve represents a boundary outside which only initial seedling recruitment occurs.

The first axis in Fig. 1 denotes the relationship between niche requirements in the regenerative and juvenile vs the adult life stages. A complete or partial niche overlap implies that seedling recruitment is possible within populations of adult genets, provided seeds are available. Moving along the first axis towards lower overlap between juvenile and adult niches implies that recruitment within adult populations becomes more and more limited. This may in effect represent the situation where seedling recruitment occurs within adult populations but only under special circumstances. If there is a complete uncoupling between juvenile and adult niches, the only possible recruitment is ISR, implying that the conditions change along with the growth and development of juveniles into adults, so that no further recruitment is possible irrespective of whether there are any seeds or not. Any mechanism that constrains seed production will force the population to move along the second axis. In extreme situations this may lead to a complete lack of seedling recruitment after the initial colonization event, not because conditions prevent it, but because there are no seeds. ISR is thus a boundary condition (indicated by the curve in Fig. 1), either due to uncoupling of juvenile and adult niches, or extreme seed limitation.

Attempts to identify all aspects of the fundamental niche for any species are possibly unrealistic. However, it is possible to design experiments to assess the realized niche space relevant for a local or regional population. The methodology for assessing seed limitation is rather well established (e.g. Ehrlén & Eriksson 2000) and what is now needed is to determine niche dimensions incorporating a range of microsite conditions, preferably located both inside and outside the local distribution range of conspecific adults. An important aspect to consider is that there may be different requirements for germination

and juvenile survival, and hence the experimental design should include both seed sowing and observations of a developing cohort of juveniles, or if it is necessary to be more time-effective, transplantation of juveniles (Eriksson 2002).

This framework does not alter one of the predictions made by Eriksson (1993, 1997) that continuous recruitment within populations of conspecific adults most likely favours competitive ability during the recruitment phase, whereas recruitment under conditions spatially uncoupled from the location of adults most likely favours dispersal ability. This would imply that the first axis in Fig. 1 (coupled to uncoupled juvenile and adult niches) also represents a gradient in the selection for competitive vs dispersal ability in the recruitment phase (cf. Shipley et al. 1989).

In conclusion, it is suggested that studies on recruitment in clonal plants should focus on the underlying mechanisms instead of just classifying the recruitment patterns. The two mechanisms suggested are essential for capturing the existing range of interspecific variation in seedling recruitment in clonal plants and the extent of niche decoupling between regenerative and juvenile vs adult life stages, and the extent of seed limitation. A recent study on aspen (*Populus tremuloides*) in the Rocky Mountains in Alberta, Canada, by Landhäusser et al. (2010) illustrates the importance of understanding mechanisms of recruitment. As a result of climate warming and forest management, which provide ample disturbed sites for recruitment, aspen is currently extending its range to higher altitudes. Due to its clonality aspen can dominate an area over long periods of time and may completely alter the forest ecosystems in the future. In many systems in temperate and boreal forests, clonal plants are among the dominant species. Thus, climate- or management-induced changes in recruitment may have a strong effect on developing ecosystems. In order to predict these changes, it is important to have an understanding of mechanism(s) of recruitment. It is hoped that the framework presented will advance such studies.

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## Souhrn

Článek přináší přehled literárních údajů o uchycování semenáčků lesních klonálních rostlin, založený na dosud používané typologii, ve které je výskyt semenáčků dán do souvislosti s genetickou strukturou dospělých rostlin v populaci: opakované uchycení semenáčků (RSR), počáteční uchycení semenáčků (IRS), uchycení semenáčků v tzv. „oknu příležitosti“ (RWO) a systematická prostorová variabilita v dynamice výskytu semenáčků mezi lokálními populacemi (RSR/ISR). Publikované práce dokládají, že uchycení semenáčků v populacích klonálních rostlin je běžné a většina druhů má schopnost semenného (generativního) obnovování v populaci dospělých rostlin. Všechny čtyři zmíněné způsoby uchycování semenáčků byly zaznamenány ve studiích zahrnujících jak genetické, tak demografické údaje o zkoumaných populacích, což podporuje představu o tom, že generativní obnovování populací klonálních rostlin probíhá různými způsoby. Předkládaná práce však navrhuje nahradit systém čtyř kategorií výstižnějším rámcem založeným na dvou variabilních faktorech: míře přesahu nik juvenilních a dospělých životních stádií téhož druhu a míře omezení populačního rozvoje dostupností semen. Tento rámec poskytuje hypotetický kontinuální prostor, ve kterém jsou umístěny všechny kategorie dosavadní typologie, navíc však identifikuje mechanismy, které k těmto typům uchycování vedou. Tento rámec by mohl stimulovat výzkumný zájem o identifikaci mechanismů ovlivňujících generativní obnovování u klonálních rostlin.

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