

# Hypotheses on the regeneration niche of fleshy-fruited species in natural forest gaps and edges in central Europe

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## Synopsis

The flora of central Europe contains 202 fleshy-fruited species of which 83% are shrubs and lianas (based on OBERDORFER 1994). In the same area the natural vegetation before human interference was predominantly forest in which the majority of the fleshy-fruited species were probably confined to temporary openings of the canopy (gaps), and to forest edges where trees are excluded for edaphic or climatic reasons, e.g. rocky outcrops, alpine timberline, riversides. Gaps are predictable in time, but rather unpredictable in space and undergo a quick succession. Therefore, gap species have probably evolved mechanisms to compensate for isolation in time. Forest edges, on the other hand, are predictable in space, but their formation is unpredictable in time, i.e. changes in the course of a river or a landslide creating a new cliff. Since edges are stable habitats with only minor successional changes, edge species are expected to compensate for isolation in space. The central hypothesis is that adaptations for isolation in space or time are reflected by the seed size, since seed size integrates several steps during regeneration of fleshy-fruited species. Actually, the seed size of gap species is significantly smaller than that of edge species. This result is discussed with respect to the effects on dispersal, predation, seed bank, germination and establishment of seedlings.

*isolation in space and time, primeval forest, seed bank, seed dispersal, seed predation, seed size*

## 1 Introduction

Dispersal and regeneration of fleshy-fruited species in central Europe have been analysed recently in a comprehensive study (KOLLMANN 1994). However, these investigations were conducted on abandoned grasslands in an anthropogenic landscape. Therefore, some adaptations of these species, which are part of their »regeneration niche« (*sensu* GRUBB 1977), remain cryptic, since they probably evolved in a different environment (HERRERA 1986).

The present contribution tries to reconstruct the origin of these species which became abundant in

central Europe due to human interference (ELLENBERG 1996). The central hypothesis is that seed size, a rather constant attribute of plants (HARPER & et. 1970), plays a key role within the regeneration niche of fleshy-fruited species, and that this trait can be used as an indicator of the original habitats. This approach is quite different from the usual methods in quaternary research, e.g. palynological records, extant distribution of species and their habitat requirements, or speciation of species-specific phytophagous organisms, as reviewed for hedgerow species in SCHWABE (1989). Concerning the functional significance of the seed size several hypotheses are presented that are supported by results reported in the current literature. However, some of these hypotheses bear more the character of open questions and will be discussed at the end of this paper. In this contribution the term »seed« is used for all dispersal units (»diaspores«), although some diaspores are actually fruits.

## 2 Fleshy-fruited species in central Europe

Fleshy-fruited species are mainly dispersed by frugivorous animals (VAN DER PIJL 1982). In central Europe most of them produce conspicuous fruits (96% are red or black) which are attractive, especially for birds, and their seeds are well protected against destruction in the gut of potential dispersers. Passerine birds are most important for the dispersal of these species, e.g. thrushes, warblers, and robins (SNOW & SNOW 1988, KOLLMANN 1994). Additionally, carnivorous mammals (red fox, badger, marten) are of some importance, especially for dispersal of species with rather large or tough fruits (*Malus sylvestris*, *Pyrus pyrastris*), which are less attractive for frugivorous birds (HERRERA 1989). Bird-dispersal of geophytic species (e.g. *Convallaria majalis*, *Paris quadrifolia*) is still a matter of debate (SNOW & SNOW 1988), but besides birds rodents and molluscs are probably involved in the transport of the seeds.

In central Europe 3320 cormophytic species occur according to OBERDORFER (1994), of which 202 are fleshy-fruited, i.e. 6% of the present flora. In this compilation occasional neophytes are excluded (e.g. *Lycium barbarum*, *Solanum cornutum*), whereas

27 species of the genus *Rosa* and 86 microspecies of *Rubus fruticosus* agg. are included.

These 202 species represent European plant life-forms in rather different numbers (Table 1). Most of them are lianas *sensu lato*, a group where 89 *Rubus* species are included. Another prominent group are shrubs (nanophanerophytes) with 70 fleshy-fruited species, whereas only nine tree species produce fleshy fruits. The remaining 24 species are dwarf

shrubs, hemicryptophytes, geophytes and one to two therophytes, epiphytes and helophytes. This analysis indicates already in which vegetation type fleshy-fruited species are most abundant in central Europe.

A more reliable estimate of the habitat preferences of fleshy-fruited species is based on the phytosociological association of the species in the system of OBERDORFER (1994). This information is summarized on the level of phytosociological classes (Table 2);

Table 1  
Life-form spectrum among central European fleshy-fruited species (after OBERDORFER 1994).

Life-forms	Fleshy-fruited species
Phanerophyte (tree)	9
Nanophanerophyte (shrub)	70 (43)*
Lianas s.l.	97 (8)
Chamaephyte (dwarf shrub)	9
Hemicryptophyte	4
Geophyte	9
Therophyte	2
Epiphyte	1
Helophyte	1
Sum	202 (86)

\* In brackets without the genera *Rosa* and *Rubus*.

Table 2  
Characteristic extant habitats of fleshy-fruited species in

central Europe; the descriptions in OBERDORFER (1994) are summarized on the basis of phytosociological classes.

Phytosociological classes	Fleshy-fruited species
Rhamno-Prunetea**	134 (24)*
Quercu-Fagetea	24 (23)
Vaccinio-Piceetea	6
Artemisietea vulgaris	5 (4)
Betulo-Adenostyletea	5 (4)
Epilobietea angustifolii	5 (4)
Erico-Pinetea	3
Oxycocco-Sphagnetetea	3
Chenopodietea	2
Trifolio-Geranietea	2
Alnetea glutinosae	1
Asplenieta trichomanis	1
Phragmitetea	1
Pulsatillo-Pinetea	1
No phytosociological indication	9 (7)
Sum	202 (86)

\* In brackets without the genera *Rosa* and *Rubus*.  
\*\* after ELLENBERG & al. (1992)

nomenclature of plant species and communities follows OBERDORFER (1994). The result is that about 67% of the species are most abundant in scrub communities (Rhamno-Prunetea), even when the numerous species of the genera *Rubus* and *Rosa* are excluded. Fleshy-fruited species also occur in some deciduous forest communities (Quercofagetea), e.g. *Daphne mezereum* or *Polygonatum multiflorum*. Dwarf shrubs of the genus *Vaccinium* are characteristic for spruce forests. *Atropa belladonna* and *Sambucus racemosa* occur on clear-cut communities (Epilobieteae). *Sorbus chamaemespilus* and *Streptopus amplexifolius*, for example, are species of subalpine shrub and forb communities (Betulo-Adenostyletea), whereas *Rubus caesius* and *Sambucus ebulus* are members of ruderal vegetation (Artemisieteae). The remaining species belong to eight other phytosociological classes, and only nine species are described to have no specific association at all.

To sum up, fleshy-fruited species are found in about 14 of 49 phytosociological classes, i.e. only a small part of the central European vegetation. Fleshy-fruited species are particularly abundant in scrub communities, but they are rare among rock vegetation and absent from grasslands and water plant communities. Moreover, most species are not able to thrive in mature woodland. Species of the genus *Lonicera* and *Rosa arvensis*, for example, fruit only after canopy disturbance (WILMANN 1980). However, field observations show that several shrub species are able to persist vegetatively in moderate shade for decades, e.g. *Ligustrum vulgare* and *Viburnum lantana* (WILMANN & BOGENRIEDER 1987).

### 3 Natural habitats in a primeval landscape

It is not likely that the habitat demands of fleshy-fruited species have changed strongly under human influence on European vegetation, although some new species have evolved during this period, as has been reported for microspecies of the genus *Rubus* (MATZKE-HAJEK 1993). Therefore, it is reasonable to use extant habitat characteristics to reconstruct the original habitats of this species group, as has been suggested by SCHWABE (1989). The high light demands of most species (ELLENBERG & al. 1992) indicate that they were confined to open sites in the primeval landscape of central Europe, where forest was the predominant vegetation type (ELLENBERG 1996). The only exceptions were temporary gaps and permanent forest edges (Table 3).

Mature forests have been described as shifting mosaics of different-sized patches cycling through gap, building and mature phases (BROKAW 1985, REMMERT 1991). The frequencies of such regeneration cycles have been calculated for several forest types. Therefore, gap formation in these forests seems to be statistically predictable in time, but rather unpredictable in space. Exceptions are steep slopes or mountain ridges where gap formation is more frequent; the same is true for forest stands adjacent to existing gaps (LAWTON & PUTZ 1988, TANAKA & NAKASHIZUKA 1997). Natural gaps are produced by hurricanes, wild-fires or insect invasions on average every 100–200 years in tropical forests (BROKAW 1982), whereas gaps are probably less frequent in central European forests (KORPEL 1995). Gaps make up 1–5% of the area of primeval forests in the tropics (BROKAW 1986, LAWTON & PUTZ

Table 3  
Generalizations about the different habitat characteristics of gaps and edges in primeval forests, and hypotheses about

how the regeneration niche of fleshy-fruited species differs in these two habitats.

	Gap species	Edge species
Habitat	Temporary openings of the canopy, with succession towards forest; predictable in time, not in space	Long-term open sites without trees (e.g. rocky outcrops, river banks), no succession; predictable in space, not in time
Strategy	Compensation for isolation in time	Compensation for isolation in space
Seed size	Small (0.1–5 mg)	Large (10–200 mg)
Dispersal	By birds either not at all or widely, no secondary dispersal	Short-distance dispersal by birds (< 300 m), secondary dispersal by rodents (10–30 m)
Seed predation	Low, because seeds are small	High, leads to secondary dispersal
Seed bank	Extensive, long-term (> 2 years)	Small and short-term (< 2 years)
Germination	High, mostly without delay	Low, often with delay
Establishment	Shade-intolerant seedlings, with higher demands of soil humidity and nutrients	Seedlings more shade-tolerant, with lower demands of soil humidity and nutrients

1988, SCHUPP & al. 1989). These sites support a special vegetation for only about 5–10 years, since gaps give rise to a characteristic succession. This means that gap species are forced to develop adaptations which reflect habitat loss with time rather than isolation in space.

The occurrence of natural forest edges, on the other hand, is predictable in space but not on a time scale on which adaptations of plant species are selected (Table 3). These sites have distinct geomorphological, edaphic or climatic attributes which do inhibit tree growth but not the growth of herbs and shrubs (cf. SCHWABE-BRAUN & WILMANN 1984). Trees are excluded from these sites by abiotic factors, e.g. around lakes and bogs, in riverine systems, at the sea shore, near rocky outcrops and at the alpine timberline. However, it is unpredictable in which intervals these forest edges are created or enlarged. Besides, natural forest edges are more or less stable on an intermediate time scale and undergo no apparent succession (ELLENBERG 1996). Therefore, it is probable that species of these habitats have developed mechanisms for compensation of isolation in space rather than in time.

#### 4 The importance of seed size for regeneration

The pivotal hypothesis of this paper is that differences in seed size of fleshy-fruited species reflect adaptations to the suggested original habitats in natural forest gaps and edges, or more precisely, mechanisms for compensation of isolation in space and time. Therefore, we have to investigate the effects of different seed sizes on the regeneration of fleshy-fruited species, i.e. on the various processes between seed dispersal and establishment of seedlings (Table 3).

(1) The seed size affects the attractiveness of fruits for potential dispersers, since birds are restricted in the size of seeds which they are able to swallow (SNOW & SNOW 1988, DEBUSSCHE & ISENMANN 1989). Moreover, large seeds are often regurgitated after a relatively short time, whereas small seeds pass through the gut and are defecated after longer periods (LEVEY 1986, MURRAY & al. 1993). Therefore, small seeds are more likely to be dispersed over large distances. Nevertheless, dispersal by birds rarely exceeds 100–300 m (KOLLMANN 1994).

(2) A second point of importance is seed predation by rodents since this process destroys a high proportion of bird-dispersed seeds (60–80% of total seed rain; KOLLMANN 1994). However, rodents do not only feed on seeds, they also store a sizeable proportion in their burrows. Because some seeds are not recovered, this leads to secondary dispersal. Seed predation is size-dependent, as has been shown by several authors; and rodents generally prefer large seeds (review in HULME 1993) which are more profitable

to harvest. Of course, other factors, such as poisonous compounds within the seeds and the thickness of the husk, will interfere with this size effect.

(3) The next step in the life history of plants is the ability to produce a seed bank, and this depends on the survival of viable seeds in the soil due to avoidance of seed predation and dormancy (POSCHLOD 1991). Seed predation is most intense on the soil surface and decreases with the depth of seeds in the soil (KOLLMANN & SCHILL 1996). Small seeds experience a lower risk of predation, since they are less attractive and washed faster into the soil. Therefore, small seeds are more likely to develop an appreciable seed bank (THOMPSON & al. 1993).

(4) The effect of the seed size on germination is less easy to estimate, since species react rather differently. However, some of the large-seeded species, e.g. *Crataegus* spp. and *Euonymus europaeus*, germinate not before the second or third spring after ripening, whereas small-seeded species tend to germinate immediately under favourable conditions, e.g. *Solanum dulcamara* and *Atropa belladonna* (KOLLMANN 1994).

(5) Seed size is also important during the establishment of seedlings, since most larger seeds provide seedlings with more seed reserves (HARPER & al. 1970). Therefore, seed size may function as a buffer against natural hazards in a difficult environment, i.e. enhance tolerance against nutrient shortage, drought or shade.

#### 5 Synthesis: seed size vs. natural habitats of fleshy-fruited species

At this point we have to compare the average seed weight of fleshy-fruited species that are believed to be characteristic for natural gaps in central Europe with those of forest edges (Table 4). For this comparison seed weight has been chosen because seed size is rather difficult to determine due to the variability in the shape of seeds (cf. BERTSCH 1941), and seed mass was significantly correlated with seed size for 12 fleshy-fruited species tested (Spearman rank:  $r_s = 0.99$ ,  $P < 0.001$ ). The statistical comparison includes only species that are associated with gaps or forest edges according to OBERDORFER (1994). Species of mature forest, e.g. geophytes or shade-tolerant shrubs, are arranged in a separate group. The statistical analysis reveals that gap species have significantly smaller seeds than species of natural forest edges (Kruskal-Wallis test:  $P < 0.01$ ). This result is true both for data from Spain (HERRERA 1987), and from southern England (SNOW & SNOW 1988), it also meets the hypotheses expressed in Table 3.

What is the effect of differences in seed size on compensation of isolation in time and space? – To answer this question, the various processes during re-

generation of fleshy-fruited species have to be considered again.

A few more words are necessary on fruit preferences of frugivorous birds. It is obvious from several observations that birds tend to ignore some species fruiting in gaps, e.g. *Atropa belladonna* or *Sambucus racemosa* (KOLLMANN 1994). Therefore, these species are hardly dispersed although they have small seeds, but they produce locally an abundant seed bank. Other species of gaps, on the other hand, are very attractive (*Sambucus nigra*, *Solanum dulcamara*) and are dispersed over large distances, e.g. into adjacent forest stands and to gaps nearby (cf. HOPPES 1988, SCHUPP & al. 1989). This is important since the creation of new gaps is more likely to happen in the neighbourhood of existing ones. Of course, there is also variation in the attractiveness of fruits among edge species (e.g. *Cornus sanguinea* vs. *Ligustrum vulgare*). However, the larger seed size of edge species, which translates into short-distance dispersal, seems to be not particularly suitable to compensate for isolation in space, whereas some small-seeded gap plants are dispersed over larger distances. Therefore, the issue of seed size and bird dispersal fits not convincingly into the needs of gap vs. edge species.

The effect of seed predation on large seeds of edge species seems to be much clearer, since these species, which experience only short-distance dispersal by birds, are additionally dispersed by foraging rodents. The distance of this secondary dispersal rarely exceeds 10–30 m (ABBOTT & QUINK 1970, JENSEN & NIELSEN 1986). This is a spatial scale over which shifts or enlargement of natural forest edges are most likely to happen.

The ability of small-seeded gap plants to develop a seed bank is probably the most important measure

to compensate for isolation in time. The absence of a seed bank among many edge species, on the other hand, matches with the temporal continuity of this habitat.

Many gap species have developed an immediate germination to take advantage of open sites as soon as they arise. The delay of 1–2 years in germination of some edge species, on the other hand, may be due to two reasons. Firstly, it increases the chances of secondary dispersal by rodents, and secondly, it spreads the risk for germination which seems to be sensible under habitat conditions where the growth of trees is limited by abiotic factors as it is along natural forest edges.

The large seeds of edge species probably work as a buffer against natural hazards during seedling establishment. And this is an advantage especially in sites at the physiological limits of trees. Gap sites, on the other hand, are often richer in soil nutrients, moisture and light than the surrounding forest but competition is fierce (ELLENBERG 1996). Unfortunately, there exist only a few experimental results on establishment of fleshy-fruited species (KOLLMANN & REINER 1996, GRUBB & al. 1996), and the adaptive value of the seed size for establishment remains to be shown in several cases.

The conclusion is that the regeneration niche of gap and edge species, based on differences in seed size, is a useful concept, although some functions of the seed size remain to be tested. However, even if there are several exceptions from the various assumptions presented as a part of the regeneration niche of fleshy-fruited species, the net effect on the evolution in seed size will remain similar, since the selection pressure of the additional processes is still leading in the expected direction.

Table 4

Seed weight of fleshy-fruited species of natural forest gaps and edges (mean  $\pm$  1SE; Kruskal-Wallis test); means with different superscripts are significantly different (Dunn test;  $P < 0.05$ ). The comparison is based on data from (A) Spain (HERRERA 1987),

and (B) southern England (SNOW & SNOW 1988); average seed weight determined with 20–40 seeds per species, number of species in brackets. Additionally, examples of some characteristic species are given.

Seed weight (mg)			H
Gap species	Edge species	Others	
(A) 1.6 $\pm$ 0.3 <sup>a</sup> (7)	32.7 $\pm$ 10.2 <sup>b</sup> (25)	18.3 $\pm$ 4.3 <sup>b</sup> (21)	14.4***
(B) 2.3 $\pm$ 0.5 <sup>a</sup> (6)	50.8 $\pm$ 15.0 <sup>b</sup> (16)	57.2 $\pm$ 22.4 <sup>b</sup> (12)	12.4**
<i>Atropa belladonna</i>	<i>Berberis vulgaris</i>	<i>Actaea spicata</i>	
<i>Fragaria vesca</i>	<i>Bryonia dioica</i>	<i>Arum maculatum</i>	
<i>Rubus idaeus</i>	<i>Frangula alnus</i>	<i>Convallaria majalis</i>	
<i>Sambucus nigra</i>	<i>Ligustrum vulgare</i>	<i>Daphne mezereum</i>	
<i>Sambucus racemosa</i>	<i>Prunus spinosa</i>	<i>Hedera helix</i>	
<i>Solanum dulcamara</i>	<i>Rosa micrantha</i>	<i>Prunus avium</i>	

\*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$

## 6 Critical points

Although the majority of the several hypotheses fit into a comprehensive and convincing picture, several points remain critical. Firstly, a simple dichotomy of open sites in primeval forest clearly is too crude, since the effect of forest gaps is strongly size-dependent and several gap types may exist (LIEBERMAN & al. 1989). Forest edges, on the other hand, are also different in their spatio-temporal structure depending on the limiting factor for tree growth, and there are obvious differences between for example a riverside forest edge and the alpine timberline (ELLENBERG 1996).

Unfortunately, so far not enough information exists about undisturbed forests in central Europe, e.g. about microhabitats within natural gaps and along edges, and about vegetation dynamics in gaps and along edges. However, on the basis of the data in FALINSKI (1986), MAYER (1987) and KORPEL (1995) it is highly questionable that the mosaic-cycle concept of REMMERT (1991) is applicable for central European forests where beech is the most important tree species, also during the regeneration phase. We are also lacking knowledge about the timing of gap formation and the extent to which natural edges occurred in the primeval European landscape. Moreover, it is likely that some natural forest types (e.g. *Erico-Pinetea*) had a rather open canopy which enabled several fleshy-fruited species to persist vegetatively, with the option of flowering and fruiting as soon as gap formation happened in this site or adjacent to it.

It is also unclear under which circumstances the specific seed size of fleshy-fruited species has been developed (HERRERA 1986). This is especially unfortunate, since the number of fleshy-fruited species is rather small in central Europe compared to Japan or North America, which may lead to an interference between ecological constraints and phylogenetic ties. A rigorous test of the hypotheses proposed in this study has to apply phylogenetically independent contrasts within genera with both, species adapted to gaps and to edges (e.g. SAVERIMUTTU & WESTOBY 1996). This seems to be feasible within the *Rubus fruticosus* group which is the focus of a new research project.

Last but not least, the central hypothesis of this contribution needs to be tested in other areas with temperate climate, e.g. Japan or North America, and also in different vegetation zones.

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