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ON THE ECOLOGY OF *SORBUS AUCUPARIA* (ROSACEAE) WITH SPECIAL REGARD TO GERMINATION, ESTABLISHMENT AND GROWTH

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Abstract: *Sorbus aucuparia* L. is a short-lived tree species very common throughout Europe, often occurring as a pioneer tree in open habitats as well as forest. Its life history traits are discussed on the basis of a case study in the Solling Mts (northwest Germany), with special regard to germination, establishment and growth. Investigations covered an old-growth spruce stand and a birch-rowan pioneer forest, the latter having developed spontaneously after storm damage in 1982. To emphasize the specific character of *S. aucuparia* among short-lived tree species it is compared with *Betula pendula* Roth, a short-lived tree species also very common in Europe, which is well studied biologically and ecologically. In its early life history, rowan should be considered a very shade-tolerant tree species, able to germinate in old-growth spruce forests under poor light and on thick layers of raw humus. There is no evidence that germination of rowan is slowed down or impeded by dense cover of *Deschampsia flexuosa* (L.) Trin. For birch the most suitable site conditions for germination and establishment are provided by moist sites with high relative light intensities and naturally or anthropogenously loosened topsoil layers. Once established, rowan is able to build up a ramet bank through a 'guerrilla' type of clonal growth in the organic layer and can thus successfully penetrate into closed vegetation cover. Whereas rowan acts as a 'stress-tolerant competitor' in its early life history, birch tends to have a more ruderal strategy by very successfully colonizing severely disturbed habitats and growing rapidly.

Key words: *Sorbus aucuparia*, *Betula pendula*, clonal growth, forest regeneration, pioneer trees, short-lived tree species

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INTRODUCTION

Rowan (*Sorbus aucuparia* L.) is a short-lived tree species, widespread and very frequent throughout Europe. According to Oberdorfer (1994), rowan occurs in deciduous and coniferous forests, in swamp forests, and as a pioneer tree on clear cuttings, pastures, etc. In addition to its occurrence in these forests and open habitats, rowan is the most frequent pioneer tree in non-natural forests of Norway spruce [*Picea abies* (L.) H. Karst.] and Scots pine (*Pinus sylvestris* L.), covering large areas in the Central European mountains and lowlands, primarily on acidic soils (Zerbe & Meiwes 2000). Here, this pioneer tree has to be considered an indicator of a natural restoration process in purely manmade forests, initiating a change in the vegetation and the organic layer (Zerbe 1993a). Consequently, rowan has increasingly drawn attention in forestry and silviculture in the last decade because of its role in the restoration of natural forests as well as in the reforestation of anthropogenously disturbed and deforested sites in Central Europe (e.g., Leder 1992; Lettl & Hýsek 1994; Moravčík 1994; Hillebrand & Leder 1995).

Although much data is available on the biology of *S. aucuparia* (for review: Raspé *et al.* 2000), there are gaps regarding the ecology of rowan. This ecological study of rowan focusses on its germination, establishment, and growth. To emphasize the specific character of rowan among short-lived tree species, it is compared with birch (*Betula pendula* Roth). Birch is one of the most common short-lived tree species in Europe and is well studied biologically and ecologically (e.g., Kinnaird 1974; Nygren & Kellomäki 1983; Pigott 1983; Johansson 1986, 1996; Maurer *et al.* 1997). Here the available data on the life history of *S. aucuparia* is documented through a survey of the literature, and a case study in the Solling Mts (northwest Germany) is presented. The germination, establishment and growth of rowan was investigated in an old-growth Norway spruce forest and an adjacent birch-rowan pioneer forest which had developed spontaneously after storm damage to the former stand.

This study aims to contribute to knowledge of the biology and ecology of rowan. Knowledge regarding the germination, establishment and growth of this short-lived tree species is also of practical importance for silviculture in Central Europe, which is planning natural forest stands in the future (Rodwell & Patterson 1995; Olsthoorn *et al.* 1999).

ON THE LIFE HISTORY OF *SORBUS AUCUPARIA* – A LITERATURE SURVEY

Data on the life history of *Sorbus aucuparia* was drawn from the literature (for references see Table 1) and supplemented with field observations. The data on the life history of *Betula pendula* was taken from Leuschner (1994). Dispersal, germination and sapling growth were distinguished from the mature and old-growth phases of the tree species. Where possible, absolute values are given (e.g., for frequency of seed production and longevity). Relative assessments, ranging from very low to very high (e.g., for shade tolerance of seedlings and sensitivity of the tree to frost) follow the criteria of comparisons of native Central European tree species made by Leuschner (1994) and Ellenberg (1996).

As seen in Table 1, the two tree species are similar in their high frequency of seed production, very low sensitivity to winter frost and late frost in the spring, and the very high decomposition rate of their litter. However, rowan and birch differ remarkably in the juvenile and mature phases. For example, high light intensity, loose topsoil and low competition in the herb layer have been shown to be essential for the germination and establishment of birch (Kinnaird 1974; Miles & Kinnaird 1979). Observation has shown, however, that rowan can germinate and establish successfully on thick layers of raw humus in relatively dense forest stands under poor light conditions. Nothing has been reported about the ability of rowan to germinate on dense swards of *Deschampsia flexuosa* (L.) Trin., which are typical for old-growth coniferous stands on acidic soils (Zerbe 1994) and are assumed to slow down or impede tree regeneration (Jarvis 1964; Bredemeier & Dohrenbusch 1985; Ellenberg 1996).

Rowan's capacity for clonal growth is not considered an important trait in its life history. According to Grime *et al.* (1989) and Raspé *et al.* (2000), rowan regenerates 'entirely by seeds.' Previously, lateral clonal spread has been recorded only occasionally (Kullman 1986).

To fill some gaps in knowledge of the early life history of *S. aucuparia* and to elucidate some aspects of the germination, establishment and growth of this short-lived tree species, investigations were carried out on an acidic forest site in Central Europe.

INVESTIGATION SITE

In the upper Solling Mts (northwest Germany), a 100-year-old anthropogenous coniferous forest of Norway spruce and an adjacent pioneer forest dominated by rowan were studied. The site is situated at alt. 420 m on acidic brown earth developed above red sandstone. With mean precipitation exceeding 1,000 mm per year, a mean temperature of 6.5°C, and frost possibly occurring in late spring, the climate of the upper Solling Mts is suboceanic and montane (Ellenberg *et al.* 1986).

The rowan pioneer forest, mixed with *Betula pendula* and a few specimens of *B. pubescens* Ehrh. in the tree layer, developed spontaneously after the spruce stand, now *ca* 100 years old, was partly damaged by storm in 1982. The relatively sharp boundary between the spruce stand and the pioneer forest (Fig. 1) is the result of clearance of storm-damaged trunks and some spruce specimens that were subsequently infected by bark beetles. The adjacent remnant of the spruce stand displays the typical vegetation and structure of *Galio harcynici-Piceetum*, a widely spread anthropogenous forest community on acidic mountain-

Table 1. Data on the life history of *Sorbus aucuparia* and *Betula pendula*: absolute values are given, where reported in the literature; relative assessment in accordance with Leuschner (1994) and Ellenberg (1996) with ❍❍ = very low, ❍ = low, ▲ = medium, ● = high, ●● = very high. Data on *Betula pendula* from Leuschner (1994) and data on *Sorbus aucuparia* from references given in the table and field observations.

		Betula pendula	*Sorbus aucuparia*	References[1]
	DISPERSAL, GERMINATION, GROWTH OF SAPLING			
1	frequency of seed production in years	1–2	1–2	Raspé *et al.* 2000
2	lowest age of reproduction within the stand (in open habitats) in years	(10-)20–30	(5-)8–20	Aas 1997
3	mode of seed dispersal	anemochore	zoochore	Müller-Schneider 1986
4	sensitivity of seedlings to drought	●●	❍	Raspé *et al.* 2000
5	ability to germinate in raw organic matter	❍❍	●●	Zerbe & Meiwes 2000
6	sensitivity of seedlings to herb competition	●●	❍ to ❍❍	own observations
7	shade tolerance of seedlings	❍❍	●	Pigott 1983
8	liable to browsing	❍❍	●●	Prien 1997
9	clonal growth	no	yes	Zerbe 2000
10	capacity of stump sprouting	▲	●●	Leder 1992
11	max. growth height of sapling in cm/year	60–100	60–80	Prien 1965
	MATURE AND OLD GROWTH PHASES			
12	age of max. growth height outside of dense stand (within stand) in years	*ca* 20	*ca* 20(-30)	Hillebrand 1998
13	longevity in years (observed extremes)	100–150(-300)	80–100(-150)	Hillebrand & Leder 1995; Bernatzky 1978
14	max. recorded growth height in m	30	28	Raspé *et al.* 2000
15	max. recorded diameter at breast height in cm	150	> 60	Hillebrand & Leder 1995
16	sensitivity to late frost	❍❍	❍❍	Ellenberg 1996; Prien & Lemme 1997
17	sensitivity to winter frost	❍❍	❍❍	Barclay & Crawford 1982, 1984
18	old trees sensitive to drought	❍❍ to ❍	❍	Zerbe 1993b; Ellenberg 1996
19	tolerance of stagnating wetness	●?	❍ to ▲	Frye & Grosse 1992; Zerbe 1993b
20	endangered through storm damage	❍	❍	Prien & Lemme 1997
21	stem and branches sensitive to breakage through snow and ice load	▲	❍❍	Prien & Lemme 1997
22	endangered through bark burning	❍❍	●	Prien & Lemme 1997
23	favoured by nutrient richness	❍❍	❍❍ to ❍	Weihs 1993; Raspé *et al.* 2000
24	sensitivity to pests	❍	❍	Prien & Lemme 1997
25	radiation transmission through canopy in % light intensity on open land	9–12–20	10–20	Zerbe & Meiwes 2000
26	decomposition rate of litter	●●	●●	Wittich 1953
27	established strategy	intermediate between competitor and stress-tolerant competitor	stress-tolerant competitor	Grime *et al.* 1989

[1] references for the data on *Sorbus aucuparia*

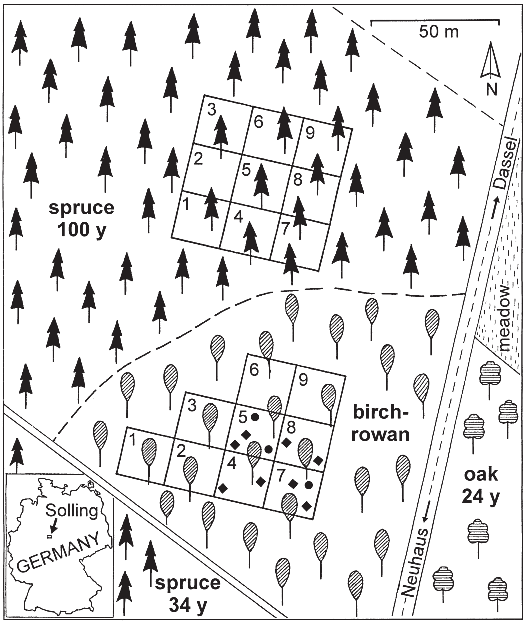


Fig. 1. Layout of the 18 sample plots (à 400 m^2) in the Norway spruce stand (y = age of stand in years) and the adjacent birch-rowan pioneer forest investigated in upper Solling Mts (alt. 420 m) N of village of Neuhaus (northwest Germany), with location of specimens (♦ = rowan, ● = birch) for tree ring analysis in plots 4, 5, 7 and 8.

ous sites in Central Europe (Zerbe 1993a). In the spruce forest, on a layer of raw humus up to 12 cm thick, *Deschampsia flexuosa* occurs as the dominant species in the herb layer, with cover of *ca* 20% in the dark center of the stand (canopy cover *ca* 60%) up to 100% at its light edge. In pioneer forest, with cover of tree layers between 20% and 50%, *Agrostis capillaris* L. is the most dominant species, with cover of up to 50% on a biologically more active humus layer *ca* 6 cm thick (Zerbe & Meiwes 2000).

MATERIALS AND METHODS

A grid comprising nine 400 m^2 squares was laid out in each stand (Fig. 1). The presence and abundance of all tree species were recorded within these grid squares using the Braun-Blanquet method (1964). Within a 5 × 5 m^2 subplot at the southeast corner of each 400 m^2 sample square, the individual numbers of spontaneous seedlings and saplings were counted and differentiated according to two growth height classes: (1) ≤ 10 cm and (2) > 10 cm growth height and up to stem diameter at breast height < 7 cm. Thus, the presence and abundance of tree rejuvenation was recorded for a total area of 3,600 m^2 and individual numbers for a total area of 225 m^2 in each stand. The mean differences of individual numbers in each stand were tested for statistical significance by the nonparametric Mann-Whitney rank sum test (Sachs 1999). In order to compare this data with data from other authors, the individual occurrences of tree rejuvenation were then converted into individuals per hectare. Up to 10 individuals of *S. aucuparia* with less than 10 cm growth height were checked randomly in each subplot for growth as a clone (cf. Begon *et al.* 1996 on clonal dispersal) or growth from seed. This sample plot design and statistical analysis were chosen because there was no similar pioneer stand in the Solling Mts comparable with the above-described birch-rowan forest.

In order to study the influence of dense cover of *Deschampsia flexuosa* on the germination and establishment of rowan, forty 1 × 1 m^2 subplots were laid out in the center of the spruce stand (see Fig. 1; grid squares 3 and 6), where patches of *D. flexuosa* occurred. In 20 subplots within these patches of dense *D. flexuosa* cover (100%) and 20 adjacent subplots free of *D. flexuosa* (total vegetation cover < 10%), rowan seedlings were counted. The mean differences of individual numbers were tested for statistical significance by the Wilcoxon matched-pairs signed-ranks test (Sachs 1999). This study was made on the assumption that there was most probably a similar input of mainly bird-dispersed (Turček 1961; Müller-Schneider 1986) rowan seeds in the subplots. As the old spruce trees in the coniferous stand offer birds the places to perch and defecate consumed rowan seeds (Vanha-Majamaa *et al.* 1996), subplots with similar distances to the nearest tree were chosen.

In the center of the birch-rowan pioneer forest (see Fig. 1: plots 4, 5, 7, 8), age and growth in diameter were analyzed dendrochronologically by taking cores at a stem height of 0.5 m from 3 specimens of birch with a diameter at breast height > 17 cm and from 8 specimens of rowan with a diameter at breast height > 10 cm. The mean growth height of both tree species forming the tree layers of the pioneer forest was drawn from forest documents with an inventory dated 1990 and was measured during field work in 1997 (Zerbe & Meiwes 2000).

The nomenclature of plant species follows Wisskirchen and Haeupler (1998).

Results

In the birch-rowan pioneer forest, four layers of woody species could be differentiated (Fig. 2). The upper tree layer, with growth height up to 15 m, consists mainly of *Betula pendula*, accompanied by a few specimens of *B. pubescens*. The cover of birch does not exceed 5% on average. The lower tree layer, with growth height up to 10 m, is dominated by *Sorbus aucuparia* with mean cover of 30%. In the upper shrub layer, with growth height between 3 and 5 m, rowan is the dominant species, together with *Frangula alnus* Mill. *Picea abies*, *Quercus robur* L. and *Salix caprea* L. also occur in the upper shrub layer, covering *ca* 7% on average. In the lower shrub layer, with growth height between 1 and 3 m, *Sorbus aucuparia* and *Frangula alnus* are the main species, with mean cover of *ca* 4%. Accordingly, rowan dominates the pioneer forest from the lower shrub (> 1 m) to the lower tree layer (< 10 m) and is absent only in the upper tree layer.

On the basis of tree ring analysis of specimens in the center of the pioneer forest, no difference in age between birch and rowan could be found. The oldest specimens of both tree species had ages between 17 and 21 years. Although no age difference between birch and rowan could be ascertained dendrochronologically, because of its more robust height growth birch was up to 8 m higher than rowan and it formed the upper tree layer (Fig. 2). Whereas rowan showed average yearly height growth of *ca* 0.5 m, birch grew 0.75 m annually. Tree ring analysis revealed that birch also had much greater diameter growth than rowan (Fig. 3).

Seedlings and saplings of *S. aucuparia* occurred most frequently in both the spruce stand and the pioneer forest (Table 2). On average, more than 35,000 individuals per hectare were found in the pioneer forest. In the spruce stand, even higher individual numbers were recorded for *Sorbus aucuparia*, reaching a maximum of 85,000 individuals per hectare. Additionally, seedlings and young trees of *Frangula alnus* were very frequent in both stands. Other tree species such as *Quercus robur* L., *Carpinus betulus* L. and *Acer pseudoplatanus* L. were only rarely observed. With the exception of *Picea abies* seedlings (growth height < 10 cm) which occurred significantly more frequently in the spruce stand, growing mostly on patches free of dense vegetation cover, no significant differences in mean numbers of tree rejuvenation could be found between the investigated stands (Table 2). Birch seedlings and saplings did not occur in any of the 400 m^2 plots or the 25 m^2 subplots. Thus, it is obvious that, although no birch seedlings and saplings were found within the investigated forest stands, this tree species dominates the upper tree layer of the pioneer forest.

In the dark center of the spruce stand, *S. aucuparia* is one of the first tree species occurring in succession, accompanied by *Frangula alnus* and *Picea abies*. Here, randomly checked individuals of rowan originated exclusively from seeds. In

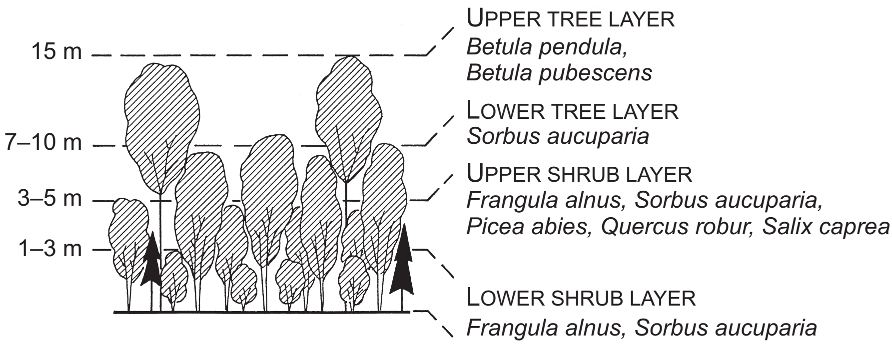


Fig. 2. Stand structure of the birch-rowan pioneer forest with four layers of tree species.

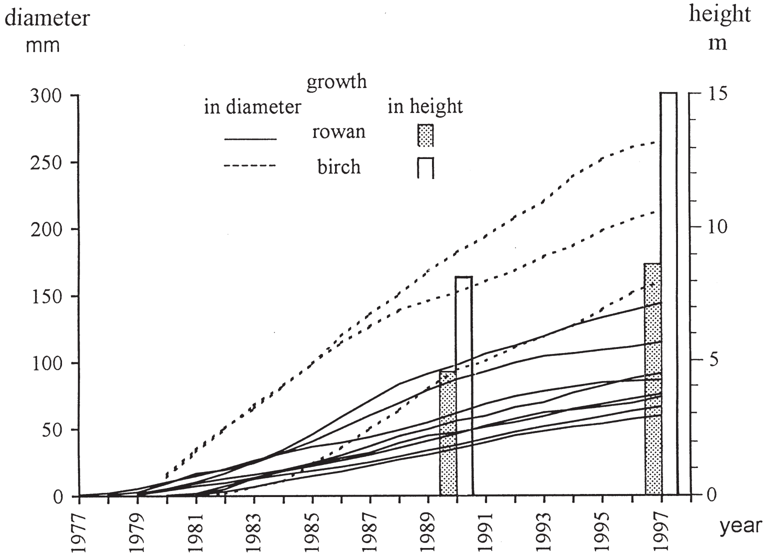


Fig. 3. Growth in diameter of three birch and eight rowan individuals through 1997 (results from tree ring analysis), and mean growth height of rowan and birch trees forming tree layers in the pioneer forest in 1990 (according to forest documents) and in 1997 (own observations).

contrast, in the pioneer forest *ca* 80% of the specimens < 10 cm checked within the subplots belonged to a clone. These specimens were sprouts from roots or else originating from stems that came to lie on the ground, were covered by litter, and rooted in the organic layer.

For *S. aucuparia*, no significant difference in the number of seedlings (Wilcoxon test, $p > 0.05$) was found in the spruce stand between patches densely covered with *Deschampsia flexuosa* (0 to 8 specimens/m^2, average 1.9) nor between patches without any dense vegetation cover (0 to 5 specimens/m^2, average 2.4).

Discussion

As can be concluded from Fig. 4, the present study confirms the main site conditions favoring germination, establishment and growth of birch, that is, high disturbance of vegetation, high light intensity, and the occurrence of bare mineral soil. Throughout its life history, birch must be considered a light-demanding species (Kinnaird 1974; Pigott 1983), unable to germinate and establish in dense cover of vegetation. For example, data on succession collected by Prach & Pyšek (1999) from 15 series starting on bare ground in manmade habitats (e.g., ruderal urban sites, abandoned sand pit, bulldozed sites) revealed that *Betula pendula* was the most successful tree species, reaching maximum cover values of up to 50% and participating in more than 50% of the series investigated. Schmidt (1998) made similar observations on abandoned fields, where birch established most successfully on sites without any dense vegetation cover. Schmidt-Schütz & Huss (1998) investigated the reforestation of storm-damaged spruce stands with pioneer species in southwest Germany. There, the rejuvenation frequencies of birch correlated strongly with the occurrence of open ground, that is, low cover of the herb layer and loose mineral soil. These investigations, and soil analysis results in the birch-rowan pioneer forest in the Solling Mts which revealed a considerable mixture of the mineral soil with the organic layer (Zerbe & Meiwes 2000), suggest that the most favorable conditions for the establishment of birch

Table 2. Mean individual numbers per hectare (medians; min./max. in brackets) of tree seedlings (growth height < 10 cm) and saplings (growth height > 10 cm up to a stem diameter at breast height < 7 cm) in the spruce forest (n = 9 sub-plots à 25 m^2) and the birch-rowan pioneer forest (n = 9 sub-plots à 25 m^2); * = significant differences of mean numbers (Mann-Whitney test, p < 0,01).

Tree species	Growth height	Spruce forest	Pioneer forest
Sorbus aucuparia	< 10 cm	47,500 (2,500/85,000)	30,000 (17,500/67,500)
	> 10 cm	10,800 (400/20,400)	7,600 (2,800/11,600)
Frangula alnus	< 10 cm	17,500 (0/37,500)	15,000 (0/65,000)
	> 10 cm	2,400 (400/4,400)	2,000 (0/4,800)
Picea abies	< 10 cm	12,500* (0/42,500)	0* (0/0)
	> 10 cm	0 (0/2,800)	0 (0/1,600)
Quercus robur	< 10 cm	0 (0/400)	0 (0/400)
	> 10 cm	0 (0/400)	400 (0/1,600)
Carpinus betulus	< 10 cm	0 (0/400)	0 (0/1,200)
	> 10 cm	0 (0/0)	0 (0/400)
Acer pseudoplatanus	< 10 cm	0 (0/400)	0 (0/1,200)
	> 10 cm	0 (0/0)	0 (0/400)

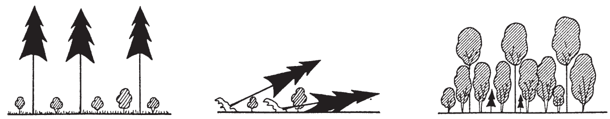
on the forest site studied should have occurred immediately after the occurrence of storm damage and the subsequent removal of wood.

Incorporating Kinnaird's (1968; see also Kinnaird 1974) investigations, we can summarize the conditions following storm damage and clearance which are highly suitable for colonization by birch: (1) surface vegetation is disturbed, (2) mineral soil is loosened and mixed with litter and humus, (3) soil moisture is increased, (4) soil temperatures are raised by more penetration of sunlight, and (5) mineralization of soil organic matter is accelerated (cf. other birch species, e.g., Godman & Krefting 1960 for *Betula alleghaniensis* Britton). Wind dispersal of seeds is often attributed to species with high colonizing ability (e.g., Grime 1979; Prach & Pyšek 1999); birch is a very successful pioneer tree in open habitats where this dispersal mode can perform best.

In contrast, our studies on forest sites in the Solling Mts have shown that rowan can germinate and establish under poor light conditions in the dark center of a spruce stand on thick layers of raw humus. There, rowan specimens originate exclusively from seeds. Thus, in its early life history rowan should be considered a very shade-tolerant tree. Moreover there is no evidence that germination is slowed down or impeded by dense cover of *Deschampsia flexuosa*; the old-growth spruce stand should be considered the initial stage of the establishment of rowan, subsequently succeeding to pioneer forest after storm damage (or silvicultural removal) of the upper tree layer.

In the birch-rowan forest, *Sorbus aucuparia* expands mainly vegetatively (Fig. 4), a strategy very successful in relatively undisturbed environments (Grime 1979). With great ability to spread horizontally (up to 5 m recorded by Kullman

	Old-growth Norway spruce stand	Norway spruce stand, storm damaged	Birch-rowan pioneer forest after clearance



Mode of establishment			
rowan	• • •	• • •	(• • •)
birch	(• • •)	• • •	(• • •)
Disturbance intensity	low	high	low
Light intensity on the ground	low	high	medium to low
Bare mineral soil (frequency of occurrence)	low to very low	medium to high	low to very low

modes of establishment: • • • – through seeds, – clonal growth

Fig. 4. Modes of establishment of rowan and birch under three different site conditions: old-growth Norway spruce forest, storm-damaged spruce stand, and *ca* 20-year-old birch-rowan pioneer forest developed spontaneously after clearance. (●●●) – establishment through seeds possible but of minor importance.

1986), rowan corresponds to the 'guerrilla' type of growth, successfully penetrating closed vegetation cover (Lovett Doust & Lovett Doust 1982; Begon *et al*. 1996) and building up a ramet bank there [cf. Kowarik 1995 for *Ailanthus altissima* (Mill.) Swingle]. Rowan's high capacity for clonal growth in pioneer forest should be considered together with the conclusions of other researchers who stress the importance of increasing vegetative expansion in the later stages of succession when establishment from seeds becomes limited by dense vegetation cover and litter layers (Rydin & Borgegård 1991; Prach & Pyšek 1994).

The case study in the Solling Mts showed that, although the ability of birch to germinate and establish was very much restricted to the specific conditions immediately following storm damage to the former spruce stand, high growth rates in height and diameter enable this pioneer tree to compete successfully and prevail in the dense rowan stand. Fiedler (1962, 1965) documented similar growth rates in diameter and height on fresh to wet and oligotrophic to mesotrophic sites in Saxony (eastern Germany). There, growth rates were independent of stand density, as shown in the results obtained for young birch pioneer forests (max. 16 years old) dispersed by silvicultural treatments.

For the establishment and growth of rowan and birch, grazing or browsing should also be considered an important site factor. Where grazing or browsing is frequent, regeneration of birch is negatively influenced unless large numbers of seedlings populate the area (Kinnaird 1968) and/or the organic layer is damaged by intense treading by animals, providing open mineral soil for the germination of birch (Bonn & Poschlod 1998). Along with oak, rowan is one of the tree species most susceptible to browsing (e.g., Prien 1997). However, the much higher regeneration (clonal growth) and sprouting capacity of rowan compared to birch, as well as its high tolerance to damage (Miller *et al.* 1982; Raspé *et al.* 2000) enable it to endure even very high browsing pressure.

According to Grime *et al*. (1989), the established strategies are 'stress-tolerant competitor' for rowan and 'intermediate between competitor and stress-tolerant competitor' for birch. However, the differentiation into types of strategy suggested by Grime (1979) can only be a very rough and schematic characterization of plant species and populations (cf. Ellenberg 1996). In particular, comparing rowan and birch as short-lived species that often occur as pioneer trees in succession, it is obvious that species considered biologically and ecologically similar can perform very differently, especially when the different phases of the individual life history are examined. Whereas rowan acts as a stress-tolerant competitor in its early life history, for example by building up a ramet bank with extensive lateral spread below ground, birch tends to have a more ruderal strategy (see also Hampe & Bairlein 1999 for Central European *Frangula alnus* populations), colonizing severely disturbed habitats most successfully and growing rapidly.

CONCLUSIONS

The relatively undisturbed development of the birch-rowan pioneer forest over approximately two decades on a site formerly covered by a purely manmade coniferous forest stand can be taken as an example of the integration of spontaneous tree rejuvenation into the regeneration of natural forests in Central Europe (e.g., Mosandl & Kleinert 1998). Short-lived tree species such as rowan and birch can play a major part in these natural regeneration processes. Integration of spontaneous pioneer forest stages dominated by short-lived tree species into forest management strategies can have benefits for silviculture, for example an increase of species and structural diversity and the biological activation of raw humus layers (Zerbe & Meiwes 2000). Natural pioneer forests two or more decades old, situated in woodland managed for social and economic purposes, should be considered very rare and thus to have a high value for nature conservation.

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