The importance of seed rain and seed bank for the recolonisation of gravel bars in alpine rivers

Norbert Müller [1] and Stefan Scharm [2]

[1] University of Applied Sciences Erfurt, Dep. Landscape Management & Restoration Ecology. Leipziger Str. 77, 99085 Erfurt, Germany
[2] Goldammerweg 18, 86420 Diedorf, Germany

Papers in Commemoration of Prof. Dr. Shigetoshi Okuda's Retirement : Studies on the Vegetation of Alluvial Plains, 127-140, 2001.

Gravel bars sparsely covered with herbaceous and shrubby pioneer vegetation are a typical habitat of braided rivers all over the world. Under natural conditions there grow a lot of highly specialised species which seem to have special strategies to survive the strong disturbances caused by the river-dynamics and to recolonise newly created gravel bars quickly. Due to civil engineering measures in the last fifty years this habitat has been destroyed or changed severely for most rivers in the industrialised countries and their specialised species were replaced by common wetland species. To explain the alterations of floodplain vegetation under human impact in this dynamic habitat it is important to understand seed dispersal and recolonisation processes.

At the Lech river flowing from the European Alps to the Danube, seed rain and seed bank were researched in the gravel bar vegetation to compare the recolonisation strategies of plants on gravel bars in natural and impacted river courses.

Important results are:

- In natural river courses stress tolerating species dominate with plumed seeds, which are able to be transported by wind over great distances. By this strategy newly created gravel bars can be colonised quickly. In contrast to impacted floodplains no persistent seed bank could be find out. This makes sense because it may be destroyed at any time in this dynamic habitat.
- In impacted courses were the river-dynamics is lowered competitive species dominate with seeds dispersed by gravity. They develop a persistent seed bank in the soil, from where they can regenerate immediately when the above ground biomass is destroyed by flooding.

The results show that natural disturbances are the central factor for the preservation of the characteristic gravel bar species and vegetation. If the vegetation has changed due to impacts in the river-dynamics a complete restoration will be difficult. Because the original species do not form a persistent seed bank, regeneration efforts from the seed bank will not work, as it is possible in other habitats.

Key words: braided river, European Alps, human impact, pioneer vegetation, recolonisation, seed bank, seed rain.

INTRODUCTION

Gravel bars are a typical amphibious habitat of braided rivers all over the world, which run from high mountains to foothill regions (compare Fig 2). This habitat is predominated by strong physical disturbances due to the alterations of accumulation and erosion of bedload (morphodynamics). Regarding to this habitat in different alpine areas of the northern hemisphere it is obvious, that under natural conditions it characterised by vascular plants and plant communities - the pioneer species and vegetation- which exist only in this ecosystem (Müller 1995a, b).

For example a typical species with an European-Asian distribution is *Calamagrostis pseudopragmites* (nomenclature of plant names in general according to Ehrendorfer 1973) which forms dominate stands

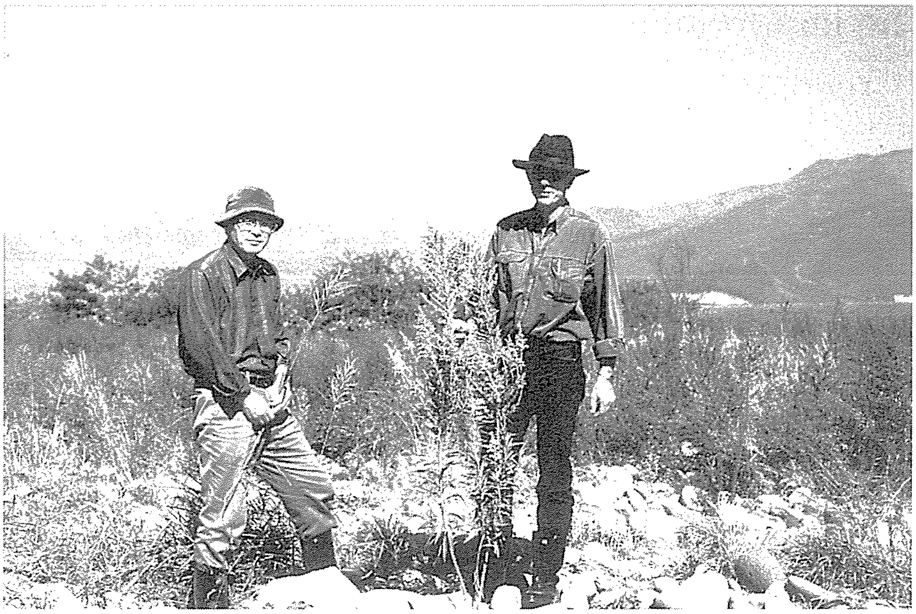

Fig. 1. Prof. Dr. S. Okuda (left) and the first author studying the ecology of native and alien floodplain species on gravel bars during an excursion in the Japanese Alps in the year 1997.

(*Calamagrostietum pseudophragmitis*) on newly created gravel bars with an high amount of sand.

Today within most alpine rivers in the industrialised countries these physical disturbances have been weakened or destroyed as a result of the construction of power plant dams in the last fifty years (Dynesius & Nilson 1994, Müller 1995b). Thus in most alpine rivers just as in lowland rivers hydrodynamics is the main ecological factor. In alpine rivers the pioneer species and vegetation has therefore been replaced by the inundation vegetation which is typical for lowland rivers and formed by common species of wetlands and ruderal sites. Also the fast invasion of alien plants in riparian landscapes can be explained with the change in the river dynamics (Müller & Okuda 1998).

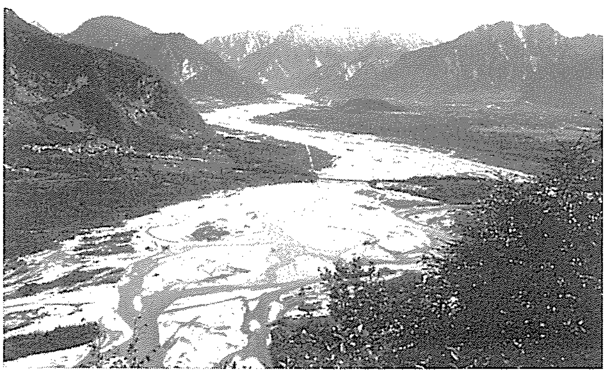

Fig. 2. Overview from the biggest remaining natural braided river in the European Alps-the Tagliamento (Southern Alps). Gravel bars sparsely covered with pioneer vegetation form large areas of the floodplains.

Fig. 3. *Myricaria germanica* and *Salix elaeagnos* are typical species of the shrubby pioneer vegetation (*Salici-Myricarietum* and *Salicetum elaeagni*) on gravel bars in the European Alps and restricted to this habitat. They are being decreased rapidly in the last 50 years due to the loss of physical disturbances as a result of the construction of power plant dams.

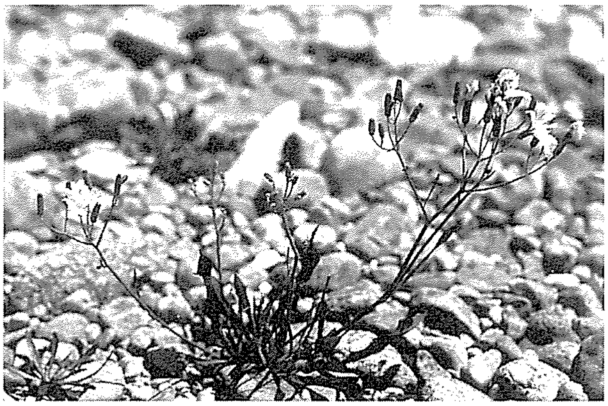

Fig. 4. *Chondrilla chondrilloides* is a typical species of the herbaceous pioneer vegetation in the European Alps.

Fig. 5. *Ixeris tamagawensis* is a typical species of the herbaceous pioneer vegetation in the Japanese Alps.

As a result of the human impact the typical species of the pioneer vegetation are being decreased rapidly or are becoming extinct as it is documented by the Red Data Books. Examples of endangered pioneer shrubs in Europe are e. g. *Myricaria germanica, Salix daphnoides* and *Salix myrsinifolia* which seem to have the same ecology as *Chosenia arbutifolia* in Japan. Examples for endangered herbaceous species are in Europe *Chondrilla chondrilloides, Erigeron acris subsp. angulosusa* and *Typha minima* and in Japan *Aster kantoensis, Ixeris tamagawensis* and *Potentilla chinensis* (Müller 1995, Okuda & al. 1997, Miyawaki & al. 1994) (compare Fig. 3 to 5).

To explain the alterations of floodplain vegetation under human impact in this dynamic habitat it is important to understand seed dispersal and recolonisation processes. In general, seed dispersal in rivers is considered to occur predominantly by transportation via water (e. g. Nilsson et al. 1991, Johansson et al. 1996), although this strategy can not explain the post-glacial recolonisation patterns of the alpine species, which show that they were travelling from the lowland areas to the alpine regions. Here is a lack of knowledge concerning the importance of seed rain and seed bank. Even though there has been some research into seed bank and seed rain of amphibious habitats at lowland rivers (e. g. Brugbauer & Bernhardt 1990, Bernhardt & Poschlod 1993, Poschlod 1993), there are only few data available about alpine rivers. Only recently some research projects started to fill this gap (Bill 2000, Müler & Scharm 1996, Takenaka et al. 1996).

This paper is an excerpt of studies in the European Alps concerning the vegetation-ecology of alpine rivers. Central ideas and questions were :

- How important are seed bank and seed rain for the recolonisation of newly created gravel bars in alpine rivers?
- As there is an obvious change in vegetation composition resulting from human impact in alpine rivers, is it possible to show that there is a change in seed bank and seed rain as well ?
- Is it possible to recreate the pioneer vegetation from the seed bank after the restoration of morphodynamics in an alpine river ?

INVESTIGATED AREAS AND HABITATS

The six study areas (SA) are located on the Lech river (Fig. 6), which rises in the Northern European

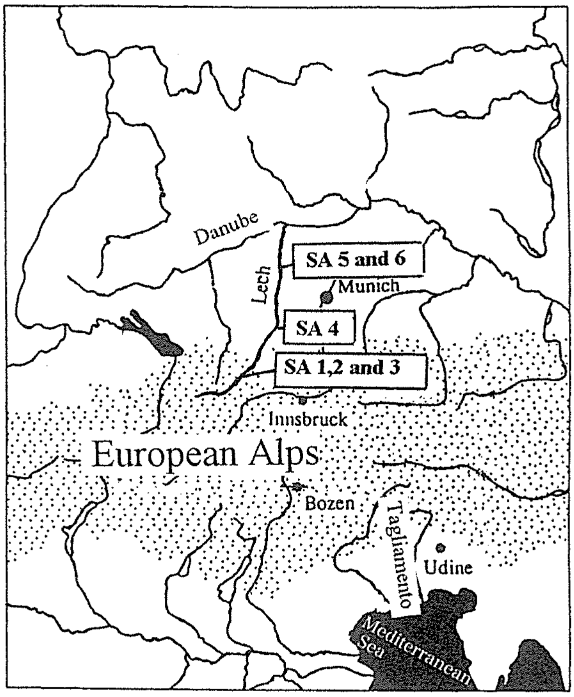

Fig. 6. Location of the Lech river and study areas (SA) in southern Germany and Austria.

Fig. 7. Study area 1 (natural floodplains at the upper Lech course) - Shrubby pioneer vegetation formed by *Myricaria germanica (Salici-Myricarietum)* in the areas with the strongest physical disturbances.

Alps (Austria) and flows to the Danube river (Southern Germany). The Lech river is exceptionally suitable for comparative studies because it shows natural floodplains as well as floodplains impacted by civil engineering measures, and because of the existence of basic data on vegetation before strong human

Fig. 8. Overview from study area 4 (strongly impacted floodplains at the middle course) - The loss of physical disturbances causes a dense vegetation cover where competitive species of the flooding vegetation pushes out the typical pioneer species.

Fig. 9. Study area 5 (strongly impacted floodplains of the lower course) with flooding vegetation during a highwater event. *Barbarea vulgaris* (yellow flowers) dominates in the areas flooded every year, whereas *Salix pupurea* (in the background) build up dense bushes in the areas which are flooded episodically.

impact (e. g. Müller et al. 1992).

Different areas were selected, from natural and moderately impacted floodplains (SA 1 to 3 in the upper course) to strongly impacted floodplains (SA 4 to 6 in the middle and lower courses) (Table 1 and Fig. 7 to 9).

In each area the plant communities on gravel bars were chosen as locations for experimental plots for seed rain and seed bank which are influenced by river dynamics most frequently. As a result of human impact there are two different types of gravel bar vegetation :

- the pioneer vegetation of the natural upper course which is predominated by different shrubs (shrubby pioneer vegetation) such as *Salix eleagnos* and *Salix myrsinifolia, Myricaria germanica* and several perennial herbs and grasses (herbaceous pioneer vegetation) like *Chondrilla chondrilloides* and *Calamagrostis pseudophragmites.* These species are restricted to natural alpine floodplains.
- the inundation vegetation (which has replaced the pioneer vegetation) in the strongly impacted middle and lower courses, where willows (shrubby inundation vegetation) like *Salix purpurea* and *Salix alba* and common herbs and grasses of wetlands and ruderal sites such as *Barbarea vulgaris, Poa palustris, Phalaris arundinacea and Stellaria media* (herbaceous inundation vegetation) predominate.

Studies were also carried out in the upper course of the river in sites without vegetation as large areas of bare or sparsely vegetated gravel bars are typical for natural alpine floodplains. In the following river dynamics and studied plant communities are described briefly ; for further information, see Müller et al. (1992).

Natural and moderately impacted floodplains of the upper course (study area 1 to 3)

In study area 1 (SA 1), the ecological conditions of gravel bars are dominated by periodical inundation, dessication and strong morphodynamic processes. The soil is typically nutrient-poor. One study site was established in the herbaceous pioneer vegetation on rough gravel (*Chondrilletum chondrilloidis*) with a vegetation cover of 15% (nomenclature of plant communities according to Oberdorfer 1992-1993).

Dominating species of this community were *Campanula cochlearifolia, Dryas octopetala* and *Hieracium staticifolium.*

Two study sites were surveyed in shrubby pioneer vegetation on rough gravel deposits (*Salicetum eleagni*). The vegetation cover was 15-25%. Main species of this community were *Salix eleagnos* and *Salix purpurea* growing to a height of up to 1m, as well as species from the herbaceous pioneer vegetation (*Chondrilletum chondrilloidis*). Another study site was surveyed in shrubby pioneer vegetation on sandy gravel (*Salici-Myricarietum*) with a cover of 40% (dominant species : *Myricaria germanica* and *Salix purpurea*).

In the less impacted study area 2 (SA 2), morphodynamics were weakened due to a lack of bedload, taken away from an upstream gravel pit. As a result, the succession of vegetation to floodplain forests, dominated by *Alnus incana* and *Salix* species had been accelerated on the gravel bars with the pioneer vegetation remaining only close to the main channel. Study sites were set up on bare gravel and in the shrubby pioneer vegetation (*Salicetum eleagni*) with a cover of 25%.

In the moderately impacted study area 3 (SA 3) hydro- and morphodynamics had been weakened since 1968 due to water draining. On gravel bars the share of pioneer vegetation had decreased as communities of advanced successional stages to floodplain forests had increased. Study sites were established on bare soil and in the shrubby pioneer vegetation on rough gravel (*Salicetum eleagni*) with a cover of 30%. In addition to the species mentioned above, *Calamagrostis pseudophragmites* a typical species of the pioneer vegetation on fine sediments, was also abundant.

Strongly impacted floodplains of the middle and lower course (study area 4 to 6)

In study areas 4, 5 and 6, gravel bars were characterized by reduced hydrodynamics and a lack of bedload due to the construction of upstream hydroelectric power plant dams. The river course in SA 4 had only been influenced indirectly by these dams built in the 1950ies while SA 5 and 6 were regulated immediately since 1920. As a result of the lack of morphodynamics gravel bars were fixed, soil development accelerated and the support with nutrients improved (Müller 1995a). Thus succession to floodplain forests (*Alnetum incanae*) proceeds on most gravel bars. The herbaceous and shrubby vegetation can only be found near to the main course, due to the strong fluctuation of water levels. However, the reduced river dynamics has caused the original pioneer vegetation on gravel bars to be replaced by inundation vegetation.

Study sites were established in all three study areas in the herbaceous vegetation (*Barbarea vulgaris community*). Vegetation cover ranges between 50 and 90%. *Barbarea vulgaris, Cirsium oleraceum, Agrostis gigantea, Deschampsia caespitosa, Phalaris arundinacea, Rumex obtusifolius, Myosoton aquaticum* and *Galium album* were the most frequent species with the highest cover.

Further sites were installed in the shrubby vegetation (*Salix purpurea* community) composed of *Salix purpurea* and *Salix eleagnos* and species of the *Barbarea vulgaris* community. Here the willows reached a height of up to 3m, in sharp contrast to the shrubby pioneer vegetation (*Salicetum eleagni*) in the upper course with a height of only 1m.

BASIC PRINCPLES OF SEED DISPERSALL AND OSEED BANK

Seed dispersal and the deposition of seeds in the soil or generally speaking the formation of a seed bank are two steps which follow each other in the cycle of life (Harper 1977). This investigation focuses on dispersal via gravity and via air streams, and in particular the dispersal of plumed seeds, characterized by flying organs consisting of plumes or a pappus. This enables them to be transported over greater distances, sometimes over kilometres (Harper 1977).

After the dispersal, the seeds rest in the soil and form the seed bank. Two main groups can be distinguished, the transient seed bank in which seeds germinate soon after their release and the persistent seed bank in which seeds remain viable in the soil for at least one year (Grime 1979). This research focuses on the persistent seed bank.

METHODS

Actual vegetation

In each study site the vegetation surrounding the experimental plots with a range of 300m was investigated to check for any possible correlation between actual vegetation and seed rain. Based on

Table 1. Location and plant communities of the study sites along the river Lech in Austria (A) and Germany (D).

River course study area	Short name of study site	Investigated sites & plant communities	Effects of human impact on river morphology
SA 1 upper course - Forchach (A)	SA 1.1	*Chondrilletum chondrilloidis*	no human impact
	SA 1.2	*Salicetum eleagni*	
	SA 1.3	*Salicetum eleagni*	
	SA 1.4	*Salici-Myricarietum*	
SA 2 upper course - Weißenbach (A)	SA 2.1	no vegetation	lack of bedload
	SA 2.2	*Salicetum eleagni*	
SA 3 upper course - Pinswang (A)	SA 3.1	no vegetation	reduced hydro- and morphodynamic
	SA 3.2	*Salicetum eleagni*	
SA 4 middle course - Schongau (D)	SA 4.1	*Barbarea vulgaris* community	reduced hydrodynamic, loss of morphodynamic
	SA 4.2	*Salicetum eleagni*	
SA 5 lower course - Augsburg (D)	SA 5.1	*Barbarea vulgaris* community	regulated, reduced hydrodynamic, loss of morphodynamic
	SA 5.2	*Salix purpurea* community	
SA 6 lower course - Augsburg (D)	SA 6.1	*Barbarea vulgaris* community	regulated reduced hydrodynamic, loss of morphodynamic
	SA 6.2	*Salix purpurea* community	

phytosociological studies, vegetation maps were drawn up. Finally the fructificating species in a range of 3m from every trap site were recorded. The intention was to find the potential source of the seeds recorded in the seed-traps.

The phytosociological relevees also served to erase the shares of different dispersal mechanisms in the surrounding vegetation.

1. Seed rain

The "liquid-trap" method (Ryvarden 1971) was used, in which seed-rain was registered by traps which were dug in the ground. Plastic cups (tubs) of identical size and an opening of 33cm were dug in until they projected 2cm above the ground. They were filled with 2cm of water to prevent seeds from being re-dispersed again. The cups were drained 2cm above the bottom to guarantee a regular water-level and to avoid water-overflow. 12 traps with a total capturing area of 396cm^2 were united to form a trap-group with four cups in the middle in direct contact, four cups in the corners and four between two corners of a square with a length of 0.5m. Each study site was equipped with 5 randomly positioned trap-groups a few metres away from each other. In such way in each study site an area of 1980cm was actually surveyed. Such a number of small traps is necessary to cope with the usual patchiness of the seed rain. The extension of the area investigated was decided upon work done by Fischer (1987) and Bernhardt (1993). The content of the traps was recorded every two weeks.

The selected seeds were divided into species spread via gravity and wind-dispersed species. The last were separated into species with plumed seeds and others (Harper 1977). Seeds with special fittings for water dispersal were not recorded.

2. Seed bank

The "germination method" (Roberts 1981, Numata 1984) was used to investigate the seed bank in the study sites. In this method soil samples are taken and exposed in a way that optimal germination conditions can break dormant states.

The samples were taken at the end of May 1994. The soil was investigated to 10cm below the surface. One single-sample covered an area of 290cm. Three single-samples taken from corners of one square metre were pooled to a collective sample. In every study site four collective samples were taken randomly a few metres away from each other, with a total area of 3480cm^2 surveyed in each study site. Debris and stones with more than a diameter of 6mm were removed after being passed through a dry sieve. The volume of this component was measured in order to make different samples comparable. With a layer of 2cm the samples were exposed in an unheated greenhouse, then supplied with water and stirred every sixth week. Emerging seedlings were removed as soon as they were discovered.

RESULTS

Seed dispersal mechanisms of species in the surrounding vegetation

Generally the vegetation of the study areas in the natural upper courses covered from 0% up to 40% of the surface, while in the strongly impacted middle and lower courses the cover was 70% up to almost 100%.

In the upper course (SA 1 to 3), on average 65% of species in the surroundings (up to 300m) of the experimental plots were species with plumed seeds. All other mechanisms including other types of wind-dispersed seeds amounted to 35%. The percentage of species with plumed seeds were lower only for the moderately impacted SA 3.

In the strongly impacted middle and lower courses the share of species with plumed seeds reached only 25% in the surrounding vegetation, and species with seeds dispersed by gravity predominated.

On the gravel bars of SA 1 (upper course) all willows showed no fructification during the year of investigation, only in greater distances of 100m and more fructificating willows could be found. In contrast, willows in SA 2 and 3 and as well in the middle and lower course produced large quantities of seeds.

1. Seed rain

As the period of observation ran from the end of May 1994 until early November 1994, very few seeds of *Alnus incana* were recorded and no seeds of other early fruiting species such as *Petasites paradoxus* and *Tussilago farfara* were found in the traps. Different species of *Salix* could not be distinguished and due to the method of trapping, species with very small seeds could not be found (e. g. *Campanula cochlearifolia*).

On average 6244 seeds/m² were captured in the natural upper course of the river (Fig. 10). The lowest quantity of seed rain was recorded in the herbaceous pioneer vegetation in SA 1.1 with 1716 seeds/m² the highest quantity reached 14299 seeds/ m² in the shrubby pioneer vegetation in SA 1.4. The seed rain was dominated by plumed seeds such as *Myricaria germanica, Calamagrostis pseudophragmites* and *Salix* spec., with 98,8% on average, ranging from 80,8% in SA 1.1, where in 3 trap sites *Agrostis gigantea* showed up to 70 fruiting individuals, up to SA 1.2 with 99,9% of plumed seeds (Fig. 2). Thus others than plumed seeds appeared only in small quantities in traps situated adjacent or close to the fruiting plants (e. g. *Poa alpina, Agrostis gigantea* and *Silene vulgaris*).

Myricaria germanica and *Salix* spec. grew frequently in the surroundings and produced enormous quantity of seeds. Due to their long distance dispersal they were detected in the seed traps in large numbers even if the nearest seed sources were situated 100m or more away from the trap (e. g: *Salix* spec. in SA 1.2, SA 1.3 and SA 1.4 from a distance of 140m to 200m). Due to the possibility of dispersal over far distances, the quantity of the seed rain showed no relation to the actual vegetation around the traps. Therefore the three study sites with the nearest willow-sources at a distance of 140m to 200m showed a similar quantity of seeds as other study sites with the nearest willow-source only a few metres away.

Calamagrostis pseudophragmites appears only locally but in large numbers corresponding to its distribution in the surrounding vegetation. All other species with plumed seeds appeared less frequently, but even these species grew everywhere in small quantities and could be found in nearly all traps.

Compared with the species composition in the vegetation around the traps, 33% of all seeds trapped originated from a distance of more than 10 m from the traps, and 20% from more than 100m.

In the strongly impacted middle and lower courses (SA 4 to 6) 15545 seeds/m² were trapped on average. The lowest quantity of seeds was observed in the willow communities, with 4574 seeds/m² in SA 4.2. The herbaceous inundation vegetation (SA 6.1) showed a remarkably high amount of seeds, with 65782 seeds/m² (Fig. 12).

Species with seeds dispersed by gravity such as *Barbarea vulgaris, Myosoton aquaticum* and *Poa palustris* dominated the seed rain. Species with

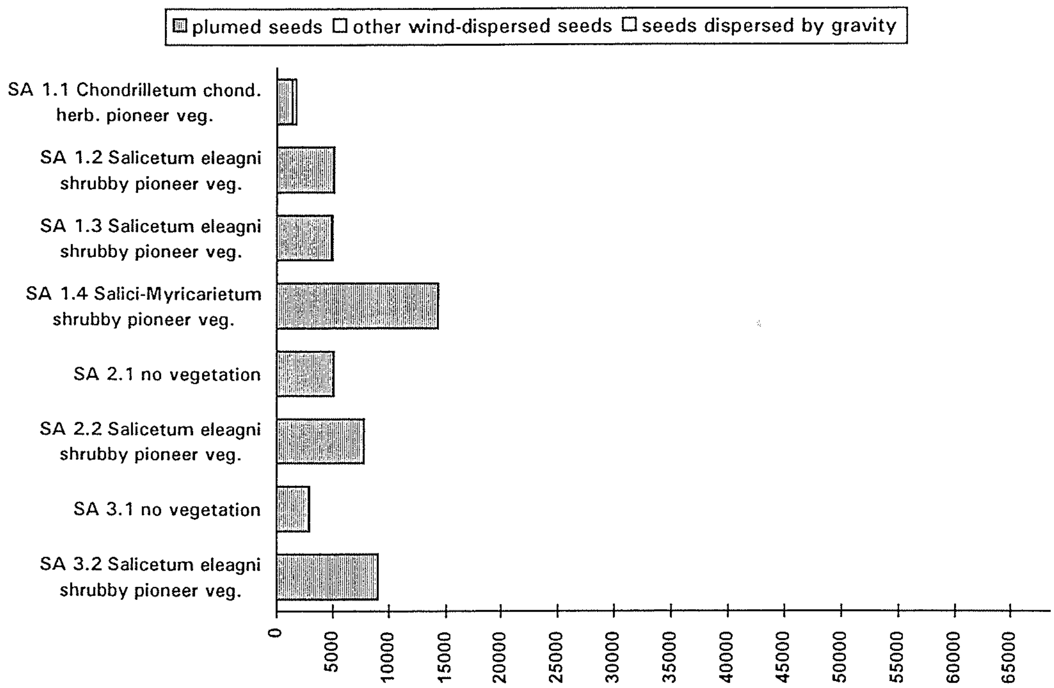

Fig. 10. Seed rain in the gravel bar vegetation (herbaceous and shrubby pioneer begetation) in the natural and moderately impacted upper course of the Lech river-shares of different dispersal mechanisms.

plumed seeds formed only 22% of the seed rain on average and were dominated by willow seeds. Shares of plumed seeds ranged from 2,4% in SA 6.1 to 77,4% in SA 6.2.

Only 18% of all trapped seeds originated from a distance of more than 10m. Most seeds simply followed gravity and fell into the traps situated directly below their sources. Species most frequent in the surrounding vegetation dominated the seed rain for that trap and area as well. For example *Barbarea vulgaris*, the dominating species around the trap in SA 4.1 had a share of 69% of the seed rain in this place.

2. Seed bank

The samples of the natural and of the less impacted upper course showed either no viable seeds in the soil or only very low densities. The results ranged from 0 to 35 seeds/m² corresponding with 0 to 3 emerged seeds/collective sample. All seedlings performed poorly so that identification was not possible. Neither a community related structure nor a persistent seed bank could be observed; seed densities were too small to distinguish significant differences (compare Fig. 11).

The strongly impacted middle and lower courses showed a well developed persistent seed bank (Fig. 11 and Fig. 13) ranging from 901 seeds/ m² in a *Barbarea vulgaris* community in the lower course (SA 6.1) to 9874 seeds/ m² in a *Barbarea vulgaris* community in the middle course (SA 4.1). 14 to 25 different species could be observed in the seed bank of the different sites with a total of 42 species in all trap sites of whole middle and lower course. The percentage of species that did not appear in the present vegetation but were nevertheless present in the persistent seed bank differed from 7% in the *Barbarea vulgaris* community in the lower course (SA 6.1) to 73% in the willow community of the middle course (SA 4.2). On average, the seed bank in all study sites consisted mainly of *Barbarea vulgaris, Poa palustris, Arenaria serpyllifolia* and *Eupatorium cannabium* (Fig. 13). *Barbarea vulgaris* and *Poa*

Fig. 11. Seed bank experiments in the glass house using the germination method:
- In front (no seedlings) from soil samples taken from the natural upper course (no permanent seed bank)
- Last row in the background from soil samples taken from the strongly impacted middlc and lower course where a permanent seed bank is well developed.

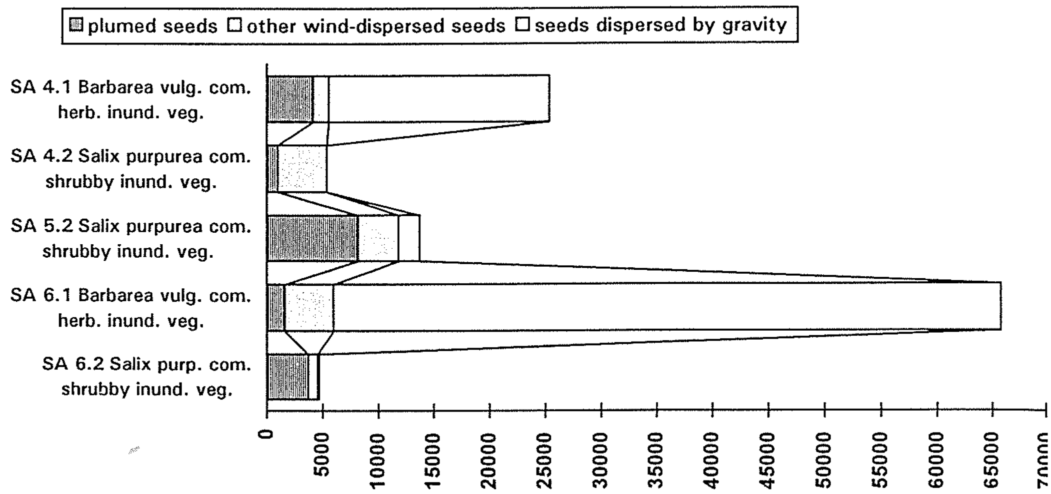

Fig. 12. Seed rain in the gravel bar vegetation (herbaceous and shrubby inundation vegetation) of the strongly inpacted middle and lower course of the Lech river-shares of different dispersal mechanisms.

palustris showed the highest average amount in all study sites, although *Urtica dioica* and *Myosoton aquaticum* were predominant in some sites.

Comparing the species in the seed bank and those present in the actual vegetation, a community-related composition could be detected in the herbaceous inundation vegetation (*Barbarea vulgaris* community) in contrast to the shrubby vegetation (Fig. 14). *Arenaria serpyllifolia* is most conspicuous of them with an extensive persistent seed bank in the middle course but no single individual in the recent vegetation. Whether this seed bank was developed by the seed rain, hydrochory or by formerly existing vegetation could not be determined.

DISCUSSION

Natural floodplains

In the natural alpine floodplains a persistent seed bank is almost non existent as the results above show. The absence of a persistent seed bank on gravel bars of natural alpine floodplains has also been detected in investigations carried out recently on the upper course of the Isar river (Bill 2000).

The seed dispersal is dominated by wind dispersed seeds. The dominant species with plumed seeds built a homogenous seed rain over large areas. The seed rain of different plant communities situated in close proximity thus showed no statisticly

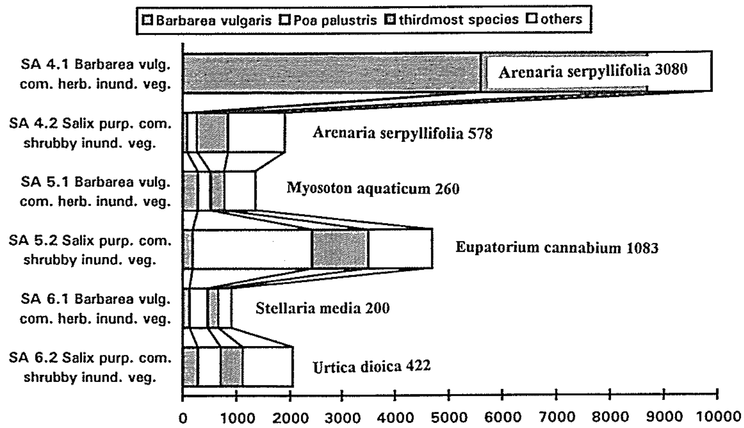

Fig. 13. Seed bank in the gravel bar vegetation (herbaceous and shrubby inundation vegetation) of the strongly impacted middle and lower course of the Lech river-shares of the predominant species. The thirdmost species is mentioned separately in the figure.

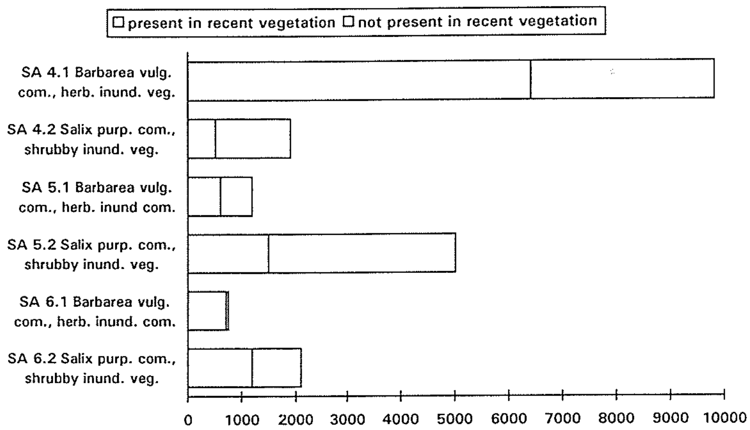

Fig. 14. Comparison of species present in the seed bank and in the actual vegetation (gravel bar vegetation of the strongly impacted middle and lower course of the Lech river).

significant difference whereas communities of the same type situated several hundred metres apart from each other differed significantly (U-Test Mann-Whitney $P < 0.01$, trap-sites compared).

How do these facts fit into the ecological conditions in these areas? In natural river courses flooding occurs with such energy that gravel bars may be eroded and destroyed completely and with them the seed bank. There must be reliable means of colonising gravel bars free of vegetation after a flooding event. Besides the transportation by water an excellent solution is provided by the long range dispersal capability of many pioneer species with plumed seeds.

Newly developed habitats may be reached from places more than 100 m away where vegetation has not been damaged or destroyed by flooding. Furthermore, successful plants have adapted to spatial isolation on single gravel bars by being able to germinate quickly. *Myricaria germanica* seeds begin to germinate within four hours under suitable conditions (Fig. 15). On the other hand however they survive only a few weeks in the soil (Müller 1995) and develop no persistent seed bank (Bill et al. 1997).

Impacted floodplains

Here a persistent seed bank is well developed. For example, the seeds of *Barbarea vulgaris,* which showed the highest average amount in all study sites. Investigations in Japan, where *Barbarea vulgaris* is a successful invader in impacted floodplains showed that the seeds are still viable in the soil after two years (Tachibana & Itoh 1997).

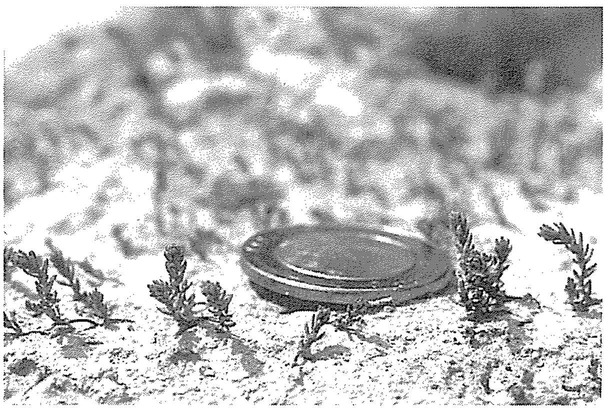

Fig. 15. Seedlings of Myricaria germanica on a sandy gravel bar. The species has the capability to germinate immediately under suitable conditions (wet sediment on newly created gravel bars)

Seed dispersal in the impacted middle and lower course in general is characterised by higher absolute figures which can be more than double the size of the natural upper course. As species with plumed seeds formed only a fifth of the complete seed rain in the strongly impacted courses, their absolute figures were half the size compared with natural courses. In consequence there were no significant differences between natural and strongly impacted courses concerning absolute figures of plumed seeds (U-Test Mann-Whitney, study sites compared). Thus the seed rain was dominated by seeds which might bridge only distances of a few metres or even only follow gravity and fall down next to the source, very significant differences between natural and strongly impacted courses (absolute figures) could be surveyed (U-Test Mann-Whitney $P < 0.01$, study sites compared). Consequently the percentages of plumed seeds showed very significant differences between natural and strongly impacted courses (U-Test Mann-Whitney $P < 0.01$, study sites compared).

Comparing the seed rain of different plant communities at the Lech river with that of other habitats, the enormous seed rain of the herbaceous flooding vegetation (*Barbarea vulgaris* community) stands out. The seed rain in all other communities investigated shows quantities typical for grasslands (Fischer 1987).

The quantity of the researched seed bank is similar to those of semi-arid grasslands (Poschlod 1991). However, it is very small when compared with the seed banks of oligotrophic wetlands or arable fields, where on average 100,000 seeds/ m^2 were observed (Albrecht & Bachthaler 1988, Poschlod 1990).

In strongly impacted river courses life strategies are appropriate for the ecological conditions. The flooding events show less force and gravel bars become fixed. Only the aboveground biomass is destroyed. More important, a persistent seed bank can be developed under these conditions and can also be present for a long time, facilitating a quick recolonisation of gravel bars hit by a flooding event. In addition improved nutrient supply allows faster

growth. As a result, pioneer species with a low growing rate and plumed seeds have no chance of withstanding the competition or even of establishing colonies. Other species emerging from a persistent seed bank on the spot are
already present and grow faster then the mostly light-requiring pioneer species.

Concerning the effects of human impact on river ecosystems from the point of view of population biology, changes in the habitat factors lead to a destruction of the "safe sites" (in the sense of Harper (1977)) of the original species with special adaptations to this habitat. The original species are ousted by species with other life strategies, resulting in a shift in the composition of species and vegetation.

Consequences for nature conservation and river restoration

Presently, natural river courses remain only in small parts of the European Alps (CIPRA 1992) thus many of their typical species and communities are threatened by extinction as documented by the Red Data Books for fauna, flora and vegetation. The habitat of gravel bars covered by pioneer vegetation is especially effected by the decline. Suggestions have been made recently to protect the last natural rivers and for river restoration (CIPRA 1992) in order to improve the situation of this ecosystem.

The following results and conclusions from this investigation are important for nature conservation and river restoration :

- Natural disturbances are the central factor for the preservation of the characteristic gravel bar species and vegetation in alpine floodplains (compare also Müller 1998, Plachter & Reich 1998).
- The complete restoration of floodplains especially of the gravel bar vegetation is very difficult where the typical pioneer vegetation has disappeared in strongly impacted river courses, even if the river dynamics are restored completely, because :
- natural floodplains with typical pioneer vegetation must be in direct contact to new gravel bars for the recolonisation by seed rain (The probability of a dispersed seed to bridge a certain distance diminishes exponentially with distance),
- most species of the pioneer vegetation do not establish a persistent seed bank. Regeneration efforts from the seed bank, while possible for the restoration of other habitats (Poschlod 1991), will not work in this situation.
- Courses influenced only recently by civil engineering measures in which the pioneer vegetation still exists, must be restored immediately before the pioneer vegetation is replaced by inundation vegetation.

Due to the actual situation and the difficulties in restoring alpine floodplain ecosystems, the last natural river courses with pioneer vegetation in the European Alps are especially in need of protection.

ACKNOWLEDGEMENTS

"Herzlichen Dank lieber Kollege Okuda fürdie wunderschönen Exkursionen und Ihre Untersützung während meines 1-jährigen Aufenthalts in Japan - Ihr Norbert Müller"

The first author is very grateful to Prof. Dr. S. Okuda (Yokohama National University, Japan) guiding him to several alpine floodplains in Japan during the years 1996 and 1997. These excursions and numerous discussions led to a deeper understanding of the ecology of alpine rivers as well as the Japanese landscape and people.

REFERENCES

Albrecht, H. & Bachthaler, G. 1988. The segetal flora of two bavarian agricultural sites, Z. Pfl.krankh. u. Pfl. schutz 11 (in German).

Bernhardt, K.-G. 1993. Investigations on colonization and dynamic of sandy and mud sites, Diss. Bot. 202, Berlin, Cramer (in German with English summary).

Bernhardt, K. -G. & Poschlod, P. 1993. Biology of semi-aquatic habitats in botanical view - an introduction - in : Bernhardt, K. G., Hurka, H., Poschlod, P. (Edit.) Biology of semi-aquatic habitats - aspects of population biology, Natur u. Wissenschaft, pp. 9-15 (in German).

Bill, H. -Ch., Spahn, P., Reich, M. & Plachter, H. 1997. Distribution and patch dynamics of Myricaria germanica Desv. at the upper Isar (Bavaria), Z. Ökologie u. Naturschutz, Vol. 6, pp. 137-150, (in German with English summary).

Bill, Ch. 2000. Recolonisation dynamics and population biology of characteristic pioneer species of north alpine rivers, Marburg, Görich & Weihershäuser (in German)

Brugbauer, R. & Bernhardt, K.-G. 1990. Consequences of flooding and wind dispersal of seeds on composition of seed bank and vegetation in pioneer habitats on the banks of the river Ems, Verh. Ges. Ökol. Osnabrück 19 : 404-408 (in German with English summary).

CIPRA Edit. 1992. The last natural alpine rivers. CIPRA Kleine Schriften 11/92, 67 p., Vaduz.

Ehrendorfer, F. (Edit.) 1973. List of vascular plants in Central Europe, 2nd. ed., Stuttgart, Fischer (in German).

Dynesius, M. & Nilson, Ch. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science, 266 : 753-762.

Fischer, A. 1987. Investigations on population dynamics in the beginning of secondary succession, Diss. Bot. 110, Berlin, Cramer (in German with English summary).

Grime, J. P. 1979. Plant strategies and vegetation processes, Chichester, John Wiley.

Harper, J. L. 1977. Population biology of plants, London, Academic Press.

IUCN 1982, List of rare, threatened and endemic plants in Europe, Council of Europe, European Committee for the conservation of nature and natural resources 27, Strasbourg.

Johansson, M. E., Nilsson, C. & Nilsson, E. 1996. Do rivers function as corridors for plant dispersal?, Journal of Vegetation Science, 7 : 593-598.

Tachibana, M. & Itoh, K. 1997. Current status and management of naturalized weeds, *Barbarea vulgaris* R. Br. and *Anthemis cotula* L. in the Tohoku area of Japan, Proceedings Int. Workshop on Biological Invasions, Tsukuba, Japan, pp. 282-295.

Müller, N. 1995a. Alterations of flora and vegetation of north-alpine braided rivers under human impact, Ber. ANL 19 : 125-187 (in German with English summary).

Müller, N. 1995b. River dynamics and floodplain vegetation and their alterations due to human impact, Arch. Hydrobiol. Suppl. 101 Large Rivers 9 : 477-512.

Müller, N. 1998. Effects of natural and human disturbances on floodplain vegetation - in : Müller, N., Okuda, S. & Tama, N. (eds.) : Proceedings International Symposium for River Restoration, Tokyo, pp. 15-24

Müller, N., Dalhof, I., Häcker, B. & Vetter, G. 1992. Consequences of engineering measures on river dynamics and floodplain vegetation at the Lech river, ANL 16 : 181-214 (in German with English summary).

Müller, N. & Okuda, S. 1998. Invasion of alien plants in floodplains - a comparison of Europe and Japan, in : Starfinger, U., Edwards, K., Kowarik, I., and Williamson, M. eds., Plant invasions : Ecological Mechanisms and human responses Backhuys Publishers, Leiden, pp. 321-332.

Müller, N. & Scharm, S. 1996. Vegetation ecology of floodplains, Braunschweiger Geobotan. Arbeiten, 4 : 269 - 295 (in German with English summary)

Miyawaki, A., Okuda, S. & Fujiwara, K. 1994. Handbook of Japanese vegetation, Shibundo, Tokyo.

Nilsson, C., Gardfjeli, M. & Gelsson, G. 1991. Importance of hydrochory in structuring plant communities along rivers, Can. J. Bot. 69 : 2631-2633.

Numata, M. 1984. Analysis of seeds in soil, in : Knapp, R. : Sampling methods of taxon analysis in vegetation science, Handb. Veg. Sc. 4 : 161-169.

Oberdorfer, E. (Edit.) 1992-1993. Plant communities of Southern Germany 1-4, Fischer, Jena (in German).

Okuda, S. 1998. Characteristics of floodplain vegetation in Japan, - in : Müller, N., Okuda, S. & Tama, N. (eds.) : Proceedings International Symposium for River Restoration, Tokyo, 15-26

Okuda, S., Kobune, A. & Hatase, Y. 1995. The Floodplain (Plant communities, Vegetation) of the Tama River, Ministry of Construction eds., Tokyo, (in Japanese with English summary).

Plachter & Reich 1998. The significance of disturbance for populations and ecosystems in natural floodplains, in : Müller, N., Okuda, S. & Tama, N. (eds.) : Proceedings International Symposium for River Restoration, Tokyo, pp. 29-38.

Poschlod, P. 1990. Vegetation development in depeated moors of the bavarian alpine foreland focusing on population biology, Diss. Bot. 152, Berlin, Cramer (in German with English summary).

Poschlod, P. 1991. Seed banks in soils - basic items and importance, in : Schmid, B. & Stöcklin, J. (Edit.) 1991, Population biology of plants, Basel, Birk-häuser, pp. 15-35 (in German).

Roberts, H. A. 1981. Seed banks in soil, Adv. Appl. Biol., VI.

Ryvarden, L. 1971. Studies in seed dispersal. I. Trapping of diaspores in the alpine zone of Finse, Norway, Norw. J. Bot. 18 : 215-226.

Takenaka, A., Washitani, I., Kuramoto, N. & Inoue, K. 1996. Life history and demographic features of *Aster kantoensis,* an endangered local endemic of floodplains. - Biological Conservation, 78 : 345-352.

Thompson, K. & Grime, J. P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats, J. Ecol. 67 : 893-921.