Hydrobiologia (2006) 565:71–86
R.S.E.W. Leuven, A.M.J. Ragas, A.J.M. Smits & G. van der Velde (eds), Living Rivers: Trends and Challenges in Science and Management
DOI 10.1007/s10750-005-1906-6

Succession and rejuvenation in floodplains along the river Allier (France)

G.W. Geerling[1,5,*], A.M.J. Ragas[2,5], R.S.E.W. Leuven[2,5], J.H. van den Berg[3,5], M. Breedveld[1], D. Liefhebber[1] & A.J.M. Smits[1,4,5]

[1]*Institute for Science, Innovation and Society, Centre for Water and Society, Radboud University Nijmegen, Faculty of Science, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands*
[2]*Department of Environmental Science, Radboud University Nijmegen, Faculty of Science, Institute for Wetland and Water Research, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands*
[3]*Department of Physical Geography, Utrecht University, Faculty of Geographical Sciences, P.O. Box 80.115, 3508 TC Utrecht, The Netherlands*
[4]*Erasmus Centre for Sustainability and Management, Erasmus University Rotterdam, P.O. Box 1738, 3000 DR Rotterdam, The Netherlands*
[5]*Participant of the Netherlands Centre for River Studies (NCR), P.O. Box 177, 2600 MH Delft, The Netherlands*
*(*Author for correspondence: E-mail: Gertjan.Geerling@science.ru.nl)*

Key words: aerial photographs, Allier river, ecotope dynamics, floodplain vegetation, GIS, meandering, meta-climax, rejuvenation, steady state mosaic, succession, transition rate

Abstract

The spatio-temporal heterogeneity of a meandering part of the Allier river was studied by analysing ecotope composition and dynamics using a series of aerial images covering a period of 46 years (1954–2000). The ecotope dynamics was exemplified by two time series showing rejuvenating hydro-geomorphological processes, i.e., meander progression, meander cut-off and channel shift. The mean rejuvenation rate was 33.8 ha per 5 years for the 5.5 km long study area. The ecotope transition rates varied from 18% surface area change per 5 years to 58.7% surface area change per 5 years for pioneer vegetation. The combination of hydro-geomorphological processes and ecological succession resulted in a temporal diversity of the riparian area. In the year 2000 half of the total riparian landscape was 14 years or younger and 23% was not rejuvenated in 46 years. Eighty percent of the pioneer vegetation was found on young soils (<14 years) while more than 50% of the surface area of low dynamic ecotopes like bush and side channels was located on parts, which were stable for more than 46 years. Examining the relation between river stretch size and ecotope diversity showed that the ecotope diversity remained stable above a stretch size of 1.5 meander lengths for the years 1978, 1985 and 2000. The spatial and temporal analysis of the study area showed evidence supporting the steady state or meta-climax hypotheses, but influences of long-term processes on landscape composition were also found. Some implications for floodplain management are discussed.

Introduction

Since the late 80s, floodplains of highly regulated rivers are being reconstructed to increase flood protection and to follow society's call for strengthening riverine nature (Nienhuis & Leuven, 2001; Wolfert, 2001; Nienhuis et al., 2002; Lenders, 2003; Buijse et al., 2005; Van Stokkom et al., 2005). Plans involve geo-morphological interventions to increase the discharge capacity and to create semi-natural floodplains by stimulating natural processes like spontaneous succession, sedimentation, and to a lesser extent, erosion (Amoros, 2001; Prach & Pysek, 2001; Vulink, 2001; Wolfert, 2001).

The landscape unit pattern in natural river systems is shaped by a combination of two main driving forces: succession and rejuvenation.

Succession is the local transition of a landscape unit to another by changing species composition (Forman & Godron, 1986), while erosion in outer river bends and sedimentation in inner bends rejuvenates the vegetation types to a previous stage. In natural systems, the continuous disturbance of succession by rejuvenation processes results in a diverse landscape pattern with a high biodiversity (Amoros & Wade, 1996). However, semi-natural floodplains in regulated rivers generally lack natural rejuvenation mechanisms. This may result in a landscape pattern dominated by climax succession stages, which has a relatively low biodiversity and high hydraulic resistance (Bravard et al., 1986; Amoros & Wade, 1996; Baptist et al., 2004). This explains why river managers want to incorporate artificial rejuvenation measures in their management strategies (Smits et al., 2000). It is anticipated that clever application of artificial rejuvenation measures may increase biodiversity and safeguard flood protection goals (Buijse et al., 2005). However, to sensibly embed rejuvenation measures in river management, knowledge of the dynamics and the spatio-temporal heterogeneity of natural river systems is required (Ward et al., 2001). The present paper analyses succession and rejuvenation processes in a freely meandering river stretch in order to obtain information relevant for river management.

In a meandering system, the hydro-geomorphological processes associated with river channel migration rejuvenate the units that comprise the riparian landscape. Existing landscape units are rejuvenated while pioneer landscape units arise and go into succession. Landscape units are continuously present but shift in space, creating a spatio-temporally heterogeneous landscape pattern. If the system is in process equilibrium, the overall landscape unit dynamics must be stable at a certain scale level. This concept is called the steady-state mosaic (Forman & Godron, 1986) or meta-climax concept (Amoros & Wade, 1996). The dynamics and scale of the steady-state mosaic are largely controlled by flow and sediment regimes and the geological, climatic and biogeographical character of the river sector. For example, process equilibrium of a braided alpine river could be manifest within years in contrast with decades or more for a low gradient meandering channel (Van der Nat et al., 2003).

The aim of this paper is to determine the dynamics of landscape units in a freely meandering stretch of the river Allier (France) and the consequences for the spatio-temporal constitution of its riparian landscape. A time series of aerial photographs spanning 46 years was analysed to answer the following questions: 1. What are the transition rates of the different landscape units? 2. What is the spatio-temporal distribution of rejuvenation? 3. What is the surface area covered by the landscape units and how does it vary over time? 4. Can a river stretch size be determined, on which the landscape unit distribution is stable in all years?

Material and methods

Study site

The study site is a 6 km stretch of the river Allier, south of Moulins (France, Fig. 1). This is a meandering gravel river with lateral erosion in the outer bends and gravel point bars in the inner bends. Local sources state that before the transition to a nature area in the 1990s, the floodplains were subject to extensive grazing. It comprises about 500 ha of natural floodplain along a bit more than three meander lengths. The river is not used for navigation and the main channel in the research area is not regulated or excavated. These characteristics make it an interesting site to study meander processes in relation to riparian landscape composition and dynamics.

The Allier river's source is Lozère (1500 m altitude) located in the French 'Massif Centrale' (Wilbers, 1997). After 410 km, the river converges with the Loire river at Bec-d'Allier (186 m altitude). The Allier is a rain fed river with an unpredictable discharge course. The mean annual discharge is 160 $m^3 s^{-1}$ over the period 1850–1980 at Moulins (Gautier et al., 2000). Normally, peak discharges up to 1200 $m^3 s^{-1}$ (occurrence once every 10 years at Moulins) occur in winter and spring while the discharges are generally low in the summer with a minimum of 12 $m^3 s^{-1}$ (Gautier et al., 2000; Fig. 2).

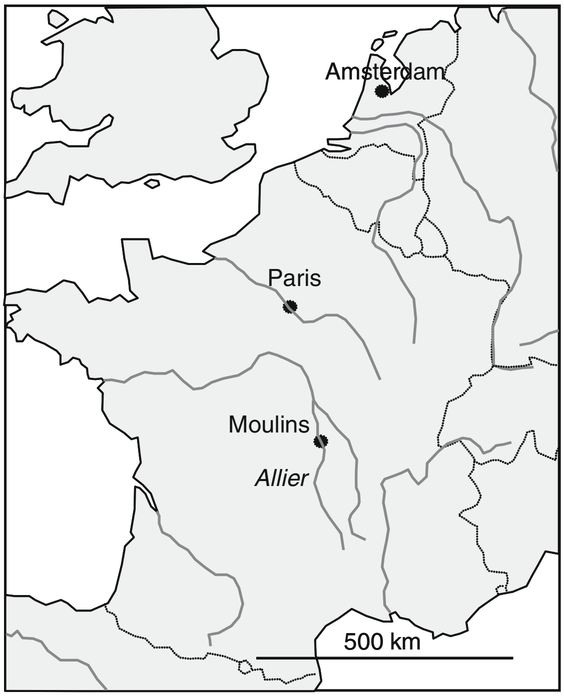

Figure 1. Location of the river Allier in Europe. The research area is located just south of Moulins. The north-west corner of the research area is (675330, 2170300) and the south-east corner is (678400, 2164550) in French national grid coordinates (Lambert zone II).

Preparing GIS maps

Based on a set of aerial photographs, maps were produced to analyse the landscape changes in the research area using GIS (Miller et al., 1995; Muller, 1997; Green & Hartley, 2000; Mendonca-Santos & Claramunt, 2001). The photographic material consisted of stereographic coverage of aerial images of the years 1954, 1960, 1967, 1978, 1985, 2000 and a non-stereographic set of 1992 (Photothèque-Nationale, 2003). The photographic scale varied between 1:25 000 and 1:14 500 and all images were taken in the summer (July/August). For the years 1954–1992 black and white photographs were available; the photographs of the year 2000 were true-colour. The 1992 photograph set was not mapped and only used to determine a sinuosity value.

Through a combination of field knowledge and expert knowledge on the interpretability of the available aerial image time series, a set of ecotope types was defined to classify landscape units (Table 1). A distinction is made between cultivated ecotopes (cultivated forest and agriculture) and natural ecotopes formed by river dynamics. An ecotope is a spatial unit of a certain extension (usually 0.25–1.5 ha), which is

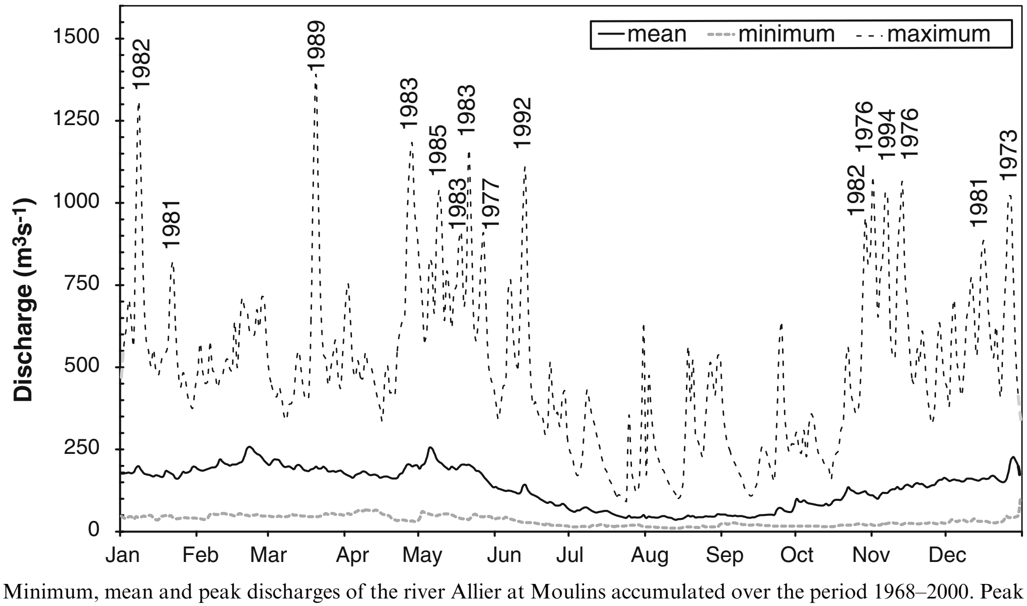

Figure 2. Minimum, mean and peak discharges of the river Allier at Moulins accumulated over the period 1968–2000. Peak discharges larger than 800 m^3 s^{-1} are labelled with the year of occurrence (data: l'agence de l'eau Loire Bretagne, France).

Table 1. The mapped ecotopes (landscape units)

Ecotope (landscape unit)	Horizontal density	Human influence
Forest		C
Agriculture		C
Water, main channel		N
Bare soil (pointbar)		N
Pioneer vegetation		N
Grassland vegetation		N
Herbaceous vegetation		N
Bush (shrubs and trees <5 m)	Open canopy (20–60% coverage)	N
	Closed canopy (>60% coverage)	N
Forest (>5 m)	Open canopy (20–60% coverage)	N
	Closed canopy (>60% coverage)	N
Water, (closed) side channel		N

C, Cultivated landscape; N, Natural landscape.

homogenous as to vegetation structure and the main abiotic factors on site (Forman & Godron, 1986; Klijn & Udo de Haes, 1994; Lenders et al., 2001).

The aerial photographs were scanned and geo-referenced to a 1:25 000 topographical base map yielding rectified images of all years with a resolution between 2.1 and 2.5 m (IGN, 1990; Erdas, 1999; Mount et al., 2002). The maximum geo-reference error found relatively within the time series was about 10 m. In digitising ecotopes using aerial images two kinds of errors can be made: errors in outlining the ecotopes and errors in ecotope identification (Küchler & Zonneveld, 1988; ESRI, 2000).

First, the minimal mapping unit was defined as 40×40 m, i.e., 0.16 ha. The outline of the ecotopes was identified using colour, texture and vertical structure (explored using a stereoscope on the original images). ArcGIS 8.3 was used to manually digitise the outlines applying a fixed on-screen scale of 1:7500 (ESRI, 2000). To minimise overlay errors in the analysis phase, the 2000 map was produced first and used as a basis for the older maps. Only borders of polygons that shifted more than the relative geo-reference error of 10 m were considered ecotope outline changes and the polygons were redrawn.

For ecotope identification and evaluation of the digitised ecotope outlines, the stereoscope was used to exploit the original quality and vertical information of the aerial photos. For this, the arcGIS polyline maps were printed on transparencies and were placed on top of the original aerial images under a stereoscope (Topcon Model 3). This process resulted in ecotope maps for the years 1954–2000, which were subsequently used for the analysis.

GIS methods

All GIS analyses were performed using ArcGIS 8.3 and ArcGIS 9.0. For the raster calculations, the vector maps were rasterised to a 5×5 m grid.

To derive ecotope transition rates from the ecotope maps, transition matrices were produced of each map transition, e.g., 1954–1960, 1960–1967, and so on (Forman & Godron, 1986; Miller et al., 1995; Van der Nat et al., 2003; Narumalani et al., 2004). Transition matrices show to which new ecotopes an ecotope is transformed during the time span between two successive photographs. To be able to compare transition rates between all the maps, the percentage change of each ecotope was computed and standardised to a 5-year period to compensate for the variety in years between maps. In this analysis, the main channel and the adjacent pointbars (bare soil) were grouped because fluctuations in water level influenced their relative surface areas.

To visualise ecotope dynamics, a general ecotope succession scheme was developed, based on the transition matrices and field expertise (Fig. 3;

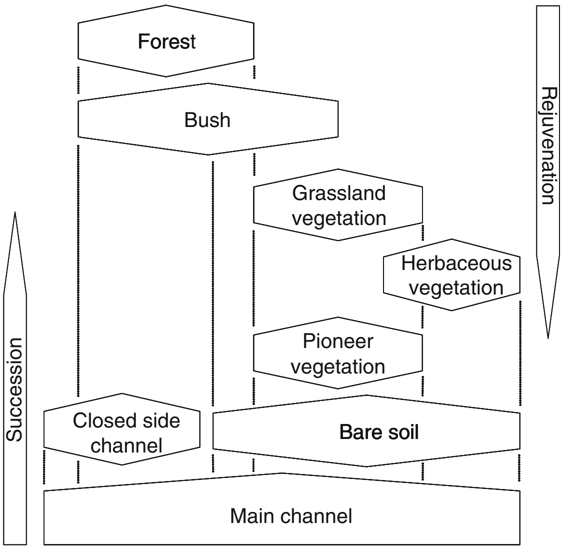

Figure 3. The succession scheme of the ecotopes along the river Allier.

Van den Berg & Balyuk, 2004). The ecotope transition matrices were simplified by classifying every possible ecotope transition into three categories: succession, rejuvenation or stability. The classification was based on the direction of change in the succession scheme (Fig. 3). Per ecotope the percentage area in succession, rejuvenation or remaining stable was computed for all transition periods. These percentages were visualised in triangular ternary plots. These plots are widely used in (soil) chemistry, to illustrate the composition of a three compound chemical mixture. In this paper, the axes show the area (as a percentage of the entire ecotope area) being stable, in succession, and in rejuvenation.

To investigate the age distribution of the ecotopes in the year 2000, a map was constructed showing the year of last rejuvenation since 1954 by combining the ecotope types main channel and bare soil (pointbars) of the years 1954–2000. This floodplain age map was overlaid with the ecotope map of the year 2000 to determine the age distribution of each ecotope type in 2000. Parts of the floodplain, which were not rejuvenated within the time span of the photographic survey, were assumed to be in succession for more than 46 years.

To investigate scale in relation to ecotope diversity, a method was developed analogous to determining the minimum area size of vegetation quadrats in field vegetation surveys. Here, the quadrat size is increased until the species composition becomes constant; this is the minimum quadrat size (Kent & Coker, 1994). To accomplish this with ecotope maps, the maps were cut into regular stretches perpendicular to the meandering direction of the river. The Shannon Index (SI) was used as landscape diversity measure, because it relates to the relative ecotope surface area distribution (McGarigal & Marks, 1995). The SI is high when all ecotope types occupy a similar area and decreases when this ecotope area distribution becomes more uneven. Starting upstream, the SI was calculated for the first 600 m stretch of the mapped area. Subsequently, the area was stepwise enlarged in downstream direction and the SI was repeatedly calculated yielding SI values for a growing area until the area covered the complete map surface. Fragstats 3.3 was used to calculate the SI (McGarigal & Marks, 1995).

Results

Ecotope maps

Figure 4 presents a time series demonstrating ecotope succession and rejuvenation caused by the hydro-geomorphological processes. The meander grew and moved northward in the years 1954, 1960, 1967. Between 1967 and 1978 a bridge was constructed on the downstream border of the research area which probably caused or facilitated the cut-off shown in the 1978 excerpt, and so creating a side channel. The cut-off resulted in a peak in the rejuvenation activity (Table 2) and a drop in sinuosity (Table 3), but as the meandering process continued, sinuosity reached its former values again in 1992–2000. The mean rejuvenation rate within the 5.5 km straight (3 meanders long) research area is 33.8 ha every 5 years (Table 2).

Figure 5 illustrates the influence of hydro-geomorphological processes on the spatial distribution of ecotopes, in this case the formation of a black poplar (*Populus nigra*) niche by a shift of the river channel in 1967 and 1978. The main channel shift left a depression in the landscape and simultaneously rejuvenated older succession stages across the stream. Subsequently, the depression (i.e., the former river channel) functioned as an

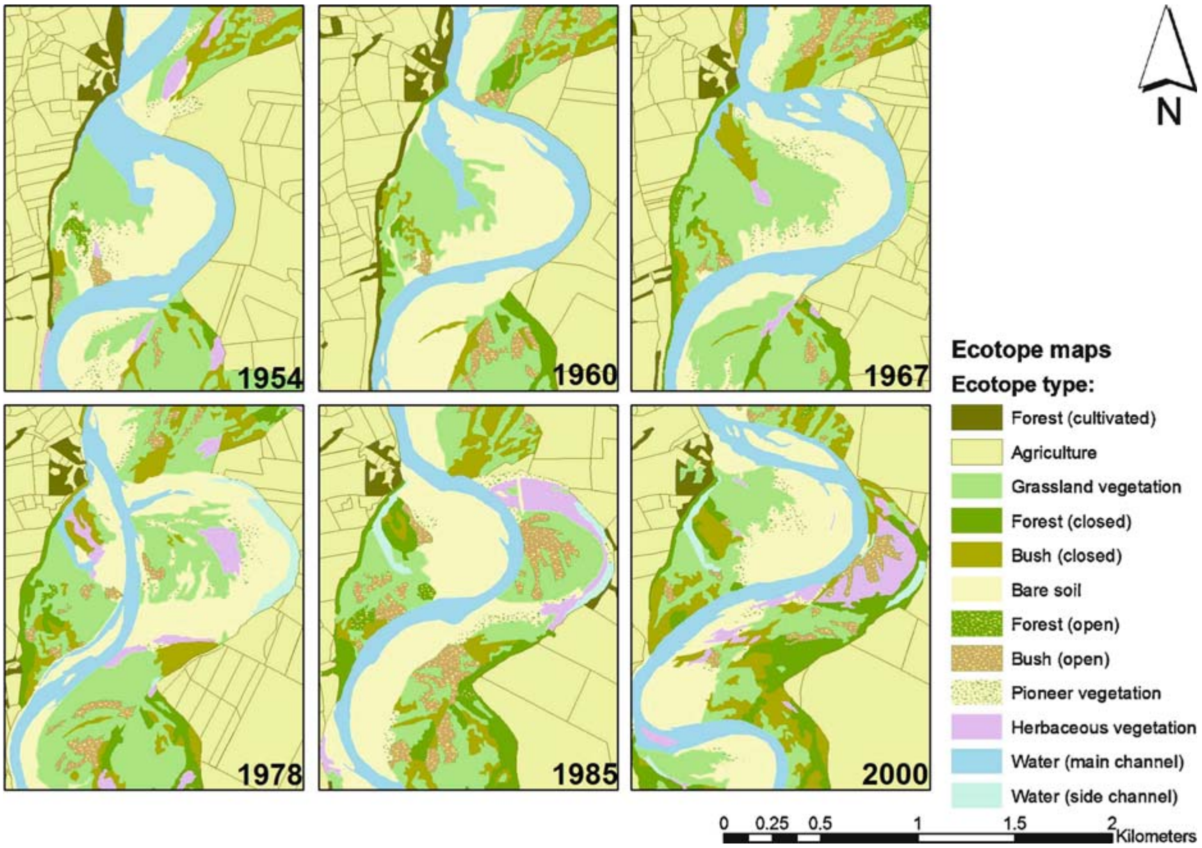

Figure 4. Meander progression in a part of the research area over the period 1954–2000. The river flows from South to North. From 1954 to 1967 a meander progression is visible. In the period 1967–1978 the meander was cut-off. The meandering process is restored in 1985 and 2000.

Table 2. Total rejuvenation in the research area

Time span (years)	54–60	60–67	67–78	78–85	85–00	Mean
Rejuvenation (ha)	31.5	57.8	68.9	72.9	80.1	
Rejuvenation (ha/5 year)	26.3	41.3	31.3	52.1	26.7	33.8

Table 3. Sinuosity of the studied river stretch

Year	Sinuosity
1954	1.35
1960	1.41
1967	1.45
1978	1.24
1985	1.27
1992	1.42
2000	1.47

environment for the settlement of black poplar. The small poplars grew from ecotope type bush to forest between the years 1985 and 2000.

Ecotope dynamics

An example of the ecotope transition matrices that were produced is shown in Table 4. The rows show to what extent (percentage area) the 1967 ecotopes (row headers) developed into different ecotopes in

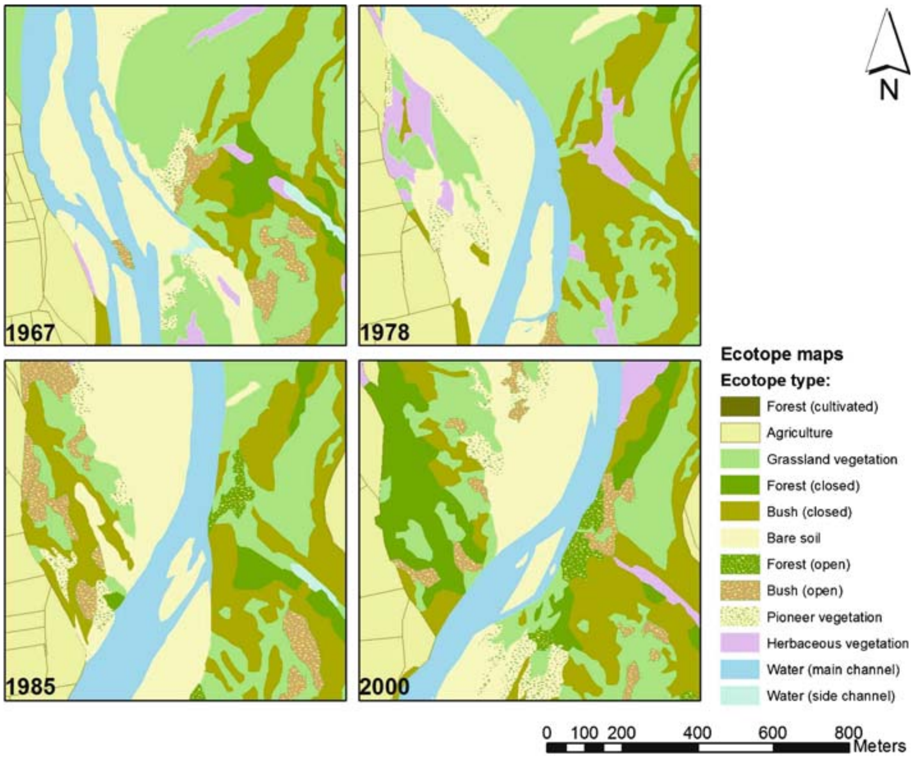

Figure 5. Meander shift rejuvenates ecotopes and creates niches for forest development over the period 1967–2000. The 1967–1978 shift rejuvenates ecotopes and creates niches for forest settlement in the former channels. In 1985 these channels are colonised by bush that grow to forest in the 1985–2000 period.

Table 4. Example of change matrix for one transition between the years 1967 and 1978, expressed as the percentage surface area change per ecotope type and total area for 1967

	Fcult	Ag	G	Fcl	Bcl	BS	Fo	Bo	P	H	MC	SC	Area (ha)
Fcult	36.98	47.11	0.53	1.43	6.90	0.00	0.00	0.00	0.05	6.99	0.00	0.00	51.59
Ag	1.18	97.28	0.86	0.18	0.27	0.02	0.02	0.00	0.02	0.12	0.04	0.01	954.96
G	0.00	1.39	62.20	0.88	2.17	19.99	0.44	2.92	3.50	0.85	5.30	0.36	148.72
Fcl	0.33	2.41	8.89	56.64	15.46	4.79	4.87	1.80	0.75	2.35	1.72	0.00	49.25
Bcl	0.00	0.60	18.30	10.63	45.79	1.41	0.10	13.20	0.56	2.16	7.20	0.05	59.56
BS	0.11	8.84	18.26	2.24	4.42	32.55	0.66	2.23	3.35	0.89	26.35	0.10	148.48
Fo	0.00	0.00	30.21	16.23	14.29	10.73	2.77	13.98	11.17	0.62	0.00	0.00	5.69
Bo	0.00	0.02	55.08	3.43	2.39	1.43	1.45	20.05	0.89	9.61	5.66	0.00	13.48
P	0.00	8.96	9.22	0.00	0.00	41.07	0.00	0.09	4.34	0.28	36.05	0.00	8.82
H	3.94	18.53	13.59	11.02	10.26	18.53	0.00	3.38	0.00	1.43	19.30	0.02	24.87
MC	0.08	8.43	23.64	2.04	6.86	21.65	0.49	1.91	3.53	0.05	31.10	0.21	57.45
SC	0.64	66.19	0.70	0.81	0.03	10.73	0.00	0.02	0.00	0.00	17.95	2.92	16.07

Fcult, Cultivated Forest; Ag, Agriculture; W & BS, Water and Bare soil; P, Pioneer vegetation; G, Grassland; H, Herbaceous vegetation; Bo, Open Bush; Fo, Open Forest; Fcl, Closed forest; Bcl, Closed bush; SC, Side channel.

1978 (column headers). Table 5 shows the ecotope transition rates for all time steps and standardised to a 5-year period. The four most dynamic ecotopes with more than 50% change per 5 years were open forest, open bush, pioneer vegetation, and herbaceous vegetation. Next to the surrounding

Table 5. Ecotope transition rates: percentage change to another ecotope for every map transition and standardised to a 5-year period. The data is numerically arranged based on the mean ecotope transition rate

Ecotope	Time span (years)					Mean	SD
	54–60	60–67	67–78	78–85	85–00		
Agriculture and cultivated forest	1.4	2.9	1.7	0.9	0.5	1.5	0.9
Main channel & bare soil	13.8	19.9	16.7	25.3	14.5	18.0	4.7
Forest (closed)	12.8	35.1	18.3	39.7	16.2	24.4	12.2
Grassland vegetation	47.3	13.5	20.7	40.9	19.3	28.3	14.8
Side channel	64.2	21.2	29.5	25.1	13.2	30.6	19.7
Bush (closed)	58.4	37.5	24.1	39.2	18.6	35.6	15.5
Bush (open)	58.3	46.5	39.7	56.6	29.6	46.1	12.0
Herbaceous vegetation	82.8	37.6	44.1	71.4	30.0	53.2	22.7
Forest (open)	81.1	71.4	44.0	52.4	31.9	56.1	20.0
Pioneer vegetation	77.5	68.0	44.2	70.6	33.3	58.7	18.9

SD, Standard deviation.

cultivated area, the main channel and point bar showed the lowest percentage of change and variability. Transition rates between the years 1954–1960 and 1978–1985 were higher than for other time spans.

The results of the visualisation of ecotope dynamics in ternary plots are presented in Fig. 6. Each data point represents the change of an ecotope in the period that lies between two successive maps. The most apparent example is the cultivated area, of which >95% of the surface area remained stable for each successive time span; all data of this ecotope type clearly show in the top corner of the ternary plot. The main channel and closed forest are opposites; their values lie, respectively on the succession axis and on the rejuvenation axis. Grassland and closed bush had a relatively low tendency for succession (<30%). They remained stable (>40%) or rejuvenated (>30%). The open bush ecotope varied in stability and succession, but rejuvenation remained constant around 40%. The open forest type, the pioneer vegetation and herbaceous vegetation showed low stability (<10%) and similar tendencies for succession and rejuvenation. The most diverse type in terms of succession, rejuvenation and stability was the side channel ecotope.

Floodplain and ecotope age

Figure 7 shows the year of last rejuvenation of the riparian area since 1954. Figure 8 shows the age distribution of the total floodplain area and of each ecotope in the year 2000. The age class >46 years consisted of the natural floodplain area that was not rejuvenated within the 46-year period

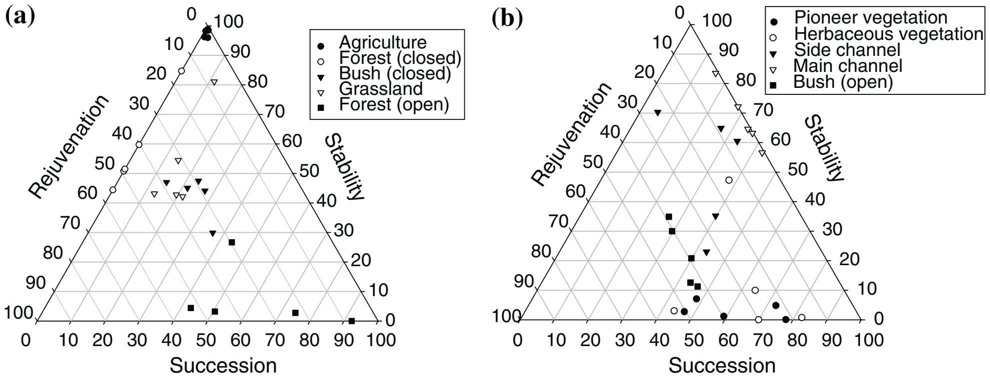

Figure 6. Ternary plots of ecotope stability, rejuvenation and succession.

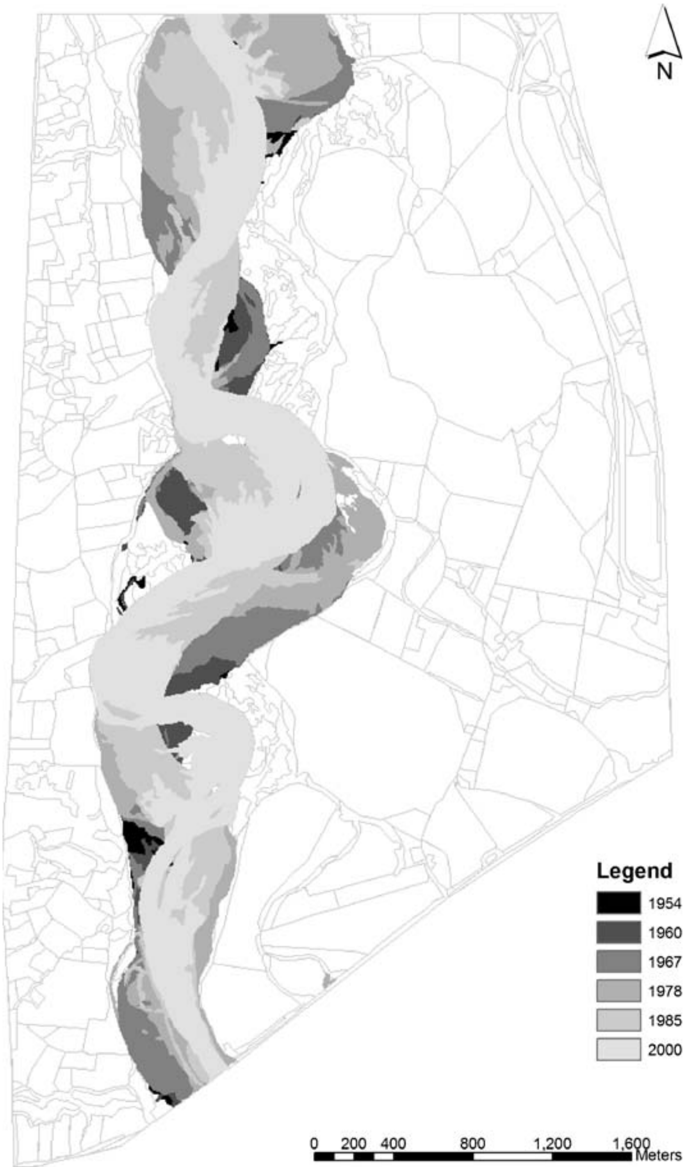

Figure 7. The floodplain age map illustrates the hydro-geomorphological activity of the research area by overlays of the ecotopes active main channel and bare soil (point bars) of 1954 to the year 2000. As background, the ecotope map of the year 2000 is used.

of the map series. Half of the natural floodplain consists of ecotopes of 15 years and younger and about 24% of the surface area is older than 46 years. Viewed per ecotope type, the age distribution is different when compared to the age distribution of the entire area. The youngest ecotope type is pioneer vegetation; more than 80% of its area is younger than 15 years. Grassland, herbaceous vegetation and open bush form an intermediate group with 50–60% of their area younger than 22 years. Side channel and closed bush are the oldest ecotopes with about half their area older than 46 years.

Ecotope areas over time

The temporal variation in the surface area coverage of different ecotope types is shown in Figure 9 and Table 6. The surface area of natural ecotopes (Table 1) vs. the surface area of cultivated

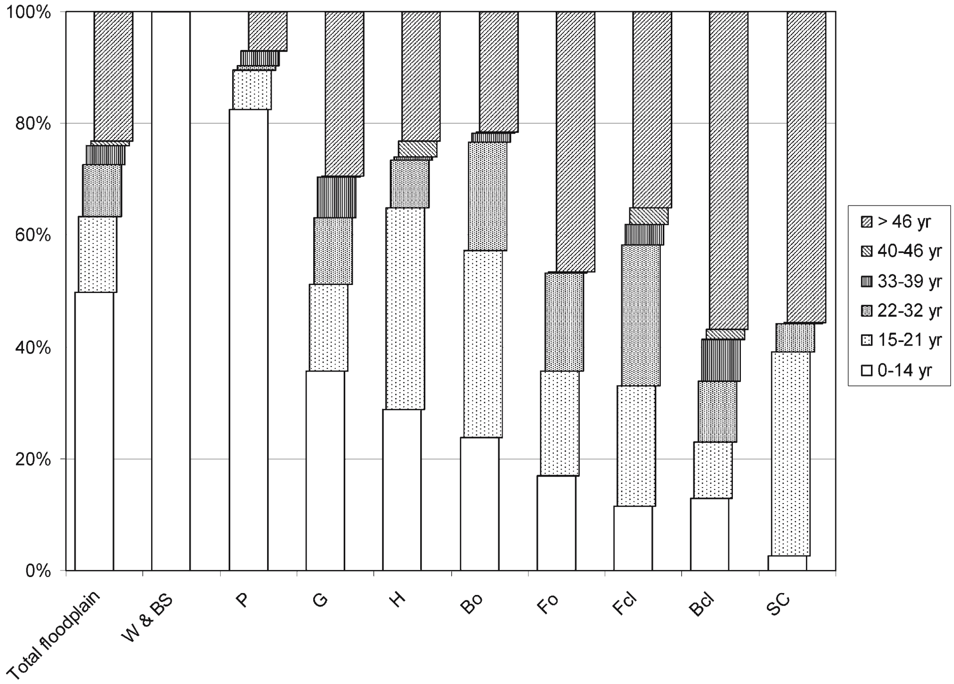

Figure 8. Floodplain and age distribution of natural ecotope types: W & BS, Water and Bare soil; P, Pioneer vegetation; G, Grassland; H, Herbaceous vegetation; Bo, Open bush; Fo, Open forest; Fcl, Closed forest; Bcl, Closed bush; SC, Side channel.

ecotopes changes on the local scale (Figs. 4 and 5) but fluctuates during the years at the river stretch scale only within a 10% range around a mean of 507 ha (see totals of Table 6). Grasslands and bare soil are the most variable, especially in the years 1954, 1960 and 1967, while for example the surface area of side channels is relatively stable. A decrease of open vegetation types like pioneer vegetation, grassland, herbaceous vegetation in favour of the closed types like

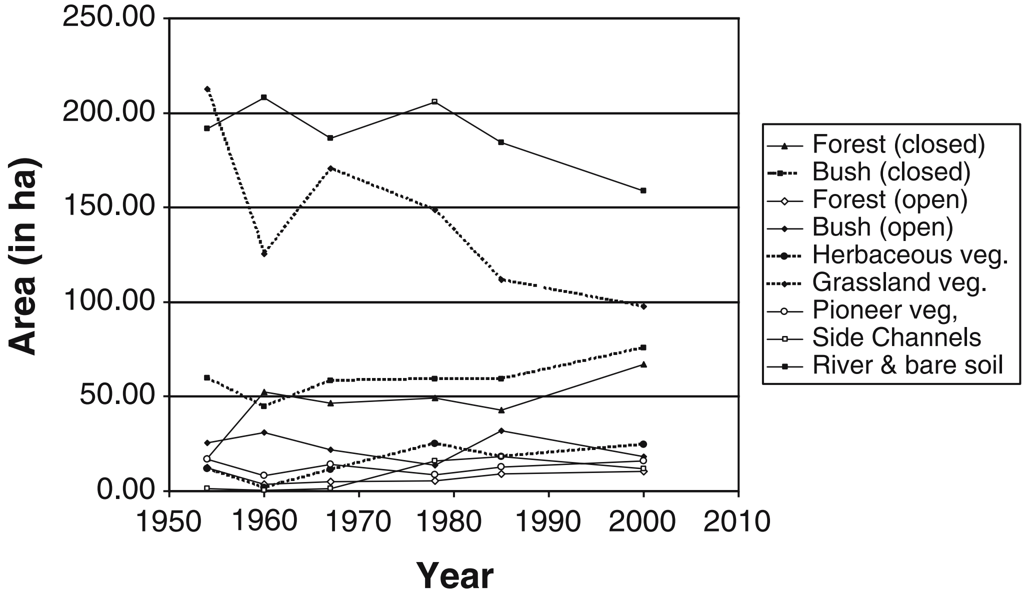

Figure 9. Total ecotope surface area (ha) over the period 1954–2000.

Table 6. The surface area of natural ecotopes and total natural floodplain (ha)

Ecotope	1954	1960	1967	1978	1985	2000
Forest (closed)	17.44	52.52	46.73	49.25	42.67	67.28
Bush (closed)	59.65	44.84	58.45	59.47	59.34	75.60
Forest (open)	12.20	3.63	4.91	5.67	9.12	10.62
Bush (open)	25.35	31.09	21.89	13.51	31.99	18.31
Herbaceous vegetation	11.91	1.94	11.50	24.89	18.08	24.56
Grassland vegetation	212.70	125.40	170.50	148.82	111.70	97.46
Pioneer vegetation	16.78	8.25	14.32	8.82	12.76	15.83
Side channel	1.58	0.61	1.39	16.05	18.45	11.86
Main channel and bare soil	191.80	208.25	186.50	205.91	184.27	158.78
Total	549.40	476.53	516.19	532.38	488.37	480.30

bush and forest is visible. In 1954, 79% of the research area was open, in 1978 76% and 64% in 2000. The drop in area of grassland vegetation between 1954 and 1960 was caused mainly by transition to agricultural area (34.5%, data not shown, but see Table 2 for years 1954 and 1960).

Ecotope diversity and scale

Figure 10 shows the landscape diversity of the study area, expressed as Shannon Index (SI), as a function of scale. The variation in SI values decreases when sliding from ecotope to river stretch scale. For the year 2000, the ecotope diversity remained stable if the floodplain surface area was about 250 ha, i.e., about 1.5 meander lengths. This seems to hold for the 1985 and 1978 results, but the 1954, 1960 and 1967 show an upward trend of SI values within the research area and no real stabilisation. An overall temporal trend of the SI values is also clearly visible, in time the overall landscape diversity is increasing.

Discussion

Mapping and GIS-analyses

The spatio-temporal heterogeneity of a meandering part of the Allier river was studied by analysing ecotope composition and dynamics using a series

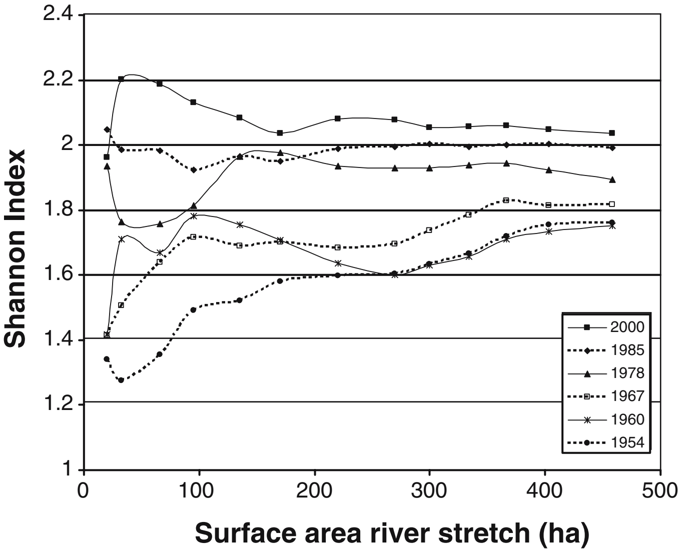

Figure 10. Landscape diversity in relation to the surface area of the river stretch that was used for calculation.

of aerial images covering a period of 46 years. Ecotopes were mapped starting with the aerial photograph of 2000 and retracing the changes in ecotope borders through time. This procedure worked well to overcome small geo-rectification differences of the different aerial photograph years. The overall quality of the aerial images was good but the quality and interpretability of early photos (1954, 1960) determined to some extent the resolution of the ecotope classification system.

The digitising process was optimised by a combination of digitising on screen and stereoscopic verification. In previous methods, the aerial images were viewed with a stereoscope and the ecotopes were traced on overlaid transparencies. Consequently, the minimal mapping unit depended on the trace-pen width. Subsequently the transparencies had to be scanned, geo-referenced and vectorised. Furthermore, before polygon vectorisation could start, the scan had to be checked and corrected manually for unclosed polygons using a drawing programme such as photoshop. This whole process was rather laborious and was shortened by digitising on screen. The verification and labelling of the on-screen digitising result was done by overlaying the digitised polygons (printed on transparencies) on top of the original aerial images under a stereoscope. In this way, the advantage of stereoscopic interpretation was kept.

Ecotope maps

The local dynamics are influenced by the succession speed of a particular ecotope and the local acting hydro-geomorphological processes. Figures 4 and 5 show the processes at work in the evolution of two small parts of the research area: rejuvenation of older succession stages by lateral erosion of outside bends, formation of new succession stages, formation of a side channel, and colonisation by vegetation of former channels. Figure 5 is a good example of the expansion and contraction events that steer riverine landscape heterogeneity (Tockner et al., 2000). The retracting water level followed the former channels in the point bar while seed dispersal took place and so steered the spatial distribution of vegetation settlement.

Ecotope dynamics

The mean ecotope transition rates (Table 5) follow the succession scheme illustrated in Figure 3 with dynamic ecotopes close to the main channel and less dynamic ecotopes to the climax stages, i.e., pioneer with the highest mean transition rate and closed forest with a relatively low mean transition rate. Two exceptions are grassland vegetation and open forest. Grassland is less dynamic than ecotope bush ecotope, probably because in the past the grasslands in the floodplains were used for grazing, so succession to open bush or open forest was inhibited. The open forest is relatively dynamic because in effect it is a mixed ecotope. Close to the river the ecotope type open forest consists of dynamic patches of young pioneer forest, so called softwood forest, and on well developed older stages it consists of low dynamic patches in succession to hardwood forest.

The ecotope transition rates in this study vary between 18 and 59% per 5 years. The mean rejuvenation rate is 33.8 ha per 5 years along the 5.5 km stretch of the study area. Studies presenting comparable values are scarce. As can be expected, the ecotope dynamics are lower when compared to dynamics in a braided alpine river where 80% of major landscape elements are rejuvenated within 3 years (Ward et al., 2001). A study on the river Ain (France) along a 40 km stretch of this river showed that rejuvenation rates decreased from about 100 ha per 10 years per 40 kms in the period 1945–1965 to 30 ha per 10 years per 40 kms in the period 1985–1991 (Marston et al., 1995). This river has a slightly lower mean annual discharge (130 $m^3 s^{-1}$) than the Allier. Between 1945 and 1991, the river dynamics decreased resulting in a single thread meandering river.

The transition rates of 1954–1960 and 1978–1985 transition are relatively high compared to the other years. In the period 1954–1960 the river channel was very active in the northern half of the research area. The limited availability of data on external pressures and influences that may explain this increase in activity, impede a satisfactory explanation. Possible explanations are listed below.

(1) A peak flow could be the cause, but discharge data on this period is not available for this

study, although in the Ubaye river in the Southern Alps about 400–500 km from the Allier catchment, a millennium flood is recorded in 1957 (Piégay & Salvador, 1997).

(2) An important factor is the sediment balance in the system; it can affect meander progression (Kondolf et al., 2002; Millar, 2005).

(3) The high activity could be a downstream geomorphological effect of the main channel running into a natural fixed bank and slowly passing this point in 1954–1967 (Fig. 4).

(4) The meander progression is increased when river banks consist of agricultural grounds (Micheli et al., 2004). The meander, shown in Figure 4, flows past agricultural area in the outer bend.

The increased dynamics in the 1978–1985 period can be attributed to the bridge effect (discussed later) and to the accumulation of major flood events in the early 80s (Fig. 2: January and December 1981; January and October 1982; April and May 1983; May 1985).

Floodplain and ecotope age

As a consequence of the spatial distribution of rejuvenation in the floodplain as shown in Figure 7, the ecotopes present are spatio-temporally distributed (Fig. 8). This spatio-temporal distribution is a characteristic of the steady-state mosaic or meta-climax. Figure 7 also shows the separate and combined effect of rejuvenation and succession. The floodplain age shows the age distribution caused by hydro-geomorphological processes and without ecotope succession. Due to ecotope succession the ecotope-age distribution of separate ecotopes is different as compared to total floodplain age composition. For example, half of the total riparian area is younger than 15 years; the ecotope closed-forest is almost for 90% situated on parts older than 15 years.

In Figure 8 the order of the succession scheme (Figs. 3 and 6) can be identified. Generally, the ecotopes having lower transition rates are relatively abundant on the older floodplain parts. Interesting is the ecotope-age distribution of open forest, which was classified as a dynamic ecotope with low stability based on the transition rates. However, seemingly contradicting the dynamic nature of this ecotope, more than 40% of the ecotope is found on older grounds. But, on older parts, the ecotope is a recent development because the older areas are being colonised by trees, i.e., in succession to (hardwood) forest stages via the open forest stage. Unfortunately, photo interpretation did not permit recognition of different types of open forest.

Ecotope areas over time

As shown on the local scale, ecotopes are dynamic (Table 4, Fig. 6), shifting in space through time (Figs. 4, 5 and 7). Within the river stretch or functional sector the overall ecotope distribution is less dynamic (Fig. 9), as assumed by the steady-state mosaic or meta-climax hypotheses (Forman & Godron, 1986; Amoros & Wade, 1996).

A true (theoretical) steady state (or meta-climax) within a stretch homogeneous in processes and environment would show as a stable ecotope distribution time series. However, our study shows a general trend in decrease of the proportion of open, low structure ecotopes towards an increase of structure rich ecotopes, such as forest and bush (Fig. 9). This trend in the ecotope distribution is caused by long-term changes of acting processes. Most probably a decrease of the grazing intensities. The area became a nature reserve in the 1994 and all grazing was phased out.

Another bias is the construction of the bridge near Chemilly, just south to the research area. Although the meander pattern recovered (Figure 4, Table 3), the exact influence of the bridge near Chemilly is not known. It can be hypothesised that what the shift accomplished is similar to a major flood event, though now induced by human intervention of narrowing the channel downstream by building a bridge and short cutting the first meander (Wilbers, personal communication) and simultaneously a flood occurrence in 1976 (1,020 $m^3 s^{-1}$). This channel shift created niches for various vegetation types, e.g., a poplar settlement. Together with lower grazing intensities, this can explain the increase in bush ecotope in 1985 and in 2000 the increase in forest ecotope (poplar becoming higher than 5 m) found in Figure 9.

In general, over medium time scales (10–100 years) most river systems can be viewed as quasi-equilibrium states (Petts & Amoros, 1996) but the (theoretical) steady state (or meta-climax) is in populated areas likely to be biased by either human interventions or land use change. Furthermore, the larger the time scale of the steady-state dynamics of a particular system, like a continental scale river, the more influence can be expected of long-term processes like climate change or geological change which affect discharge, sediment regimes and rates of succession.

Ecotope diversity and scale

When sliding from ecotope scale to river stretch scale; the surface area proportion of each ecotope will change. However, will it change indefinitely? Under similar hydro-geomorphological conditions along the stretch, i.e., a steady-state situation, it should stabilise at a certain river stretch size. Therefore, the question is if this 'steady-state unit' in which the relative ecotope diversity is at a constant level over time, can be determined in space.

Our results indicate that the steady-state unit size has been decreasing over the years. It was smallest but stable for 1985 and 2000 at about one and a half meander length (Fig. 10). However, a spatially consistent area containing a steady state or stable meta-climax 'unit' is not found because the area should be the same through all the years. Similar to the trend found in Figure 9, these results again point to an underlying long-term process of change, like diminishing grazing intensities. This is also consistent with the rising SI values over the years (Fig. 10), indicating a trend towards a more heterogeneous landscape.

In this study, the sliding scale approach is used to investigate the scale on which landscape diversity stabilises. When focussed on changes in the SI curve, the approach could facilitate locating transitions in landscapes, indicating a change in acting processes.

Implications for floodplain management

In regulated systems, the hydro-geomorphological processes are restricted because the main (navigation) channel is fixed. Therefore, rejuvenation processes such as lateral erosion are inhibited. As succession of ecotopes still proceeds, the imitation of rejuvenation processes in regulated river systems has two main advantages. First, the absence of rejuvenation mechanisms in regulated systems causes the gradual disappearance of ecotopes with high turnover, leading to a lower biological diversity (Bravard et al., 1986; Amoros & Wade, 1996; Gilvear et al., 2000). The introduction of rejuvenation can increase biological diversity. Secondly, rejuvenating hydraulically rough vegetation, often the older climax stages, helps to maintain the discharge capacity, a major concern of the river manager (Smits et al., 2000; Baptist et al., 2004).

The combined effect of succession and rejuvenation brings about unique spatio-temporal patterns for different streams and rivers. The ecological successions vary with the biogeographical region and rejuvenation is connected to the fluvial setting. A high dynamic braided alpine river, constrained geologically, will give rise to a landscape with young ecotopes with high turnover rates, and few older elements like trees (or forests) will survive. In rivers with moderate dynamics, like the Allier or ever larger rivers, turnover rates drop, ecotope succession may reach climax stages and consequently the temporal pattern changes (Marston et al., 1995; Petts & Amoros, 1996; Ward et al., 2001; Van der Nat et al., 2003). It would be interesting to compare different rivers of various sizes on their landscape dynamics, but comparative material was hardly found in literature. The combined knowledge on succession and rejuvenation processes of natural rivers and knowledge of the former river dynamics of the managed river gives the river manager insight in possible management options (Buijse et al., 2005).

Important in sound ecological management is the spatio-temporal context on which the riparian landscape has to be viewed (Bravard et al., 1986; Ward et al., 2001). Therefore, the river and nature manager has to have knowledge on direction of change and information on the present day diversity in space and succession stage (time) before management options can be evaluated.

Conclusions

The results show that a freely meandering system generates a spatially and temporally diverse landscape. On the ecotope level, the dynamics are higher than on the river stretch. On the river stretch, the ecotope distribution was relatively stable, but showed long-term trends, generally changing towards a more closed and structure rich heterogeneous landscape.

The river Allier shows characteristics of a system in a steady-state mosaic or meta-climax but this equilibrium is influenced by long-term changes in processes affecting landscape composition.

Riparian landscapes have to be viewed in their spatio-temporal context. Process knowledge is important to be able to anticipate on riverine landscape changes and to make ecologically sound management choices. Therefore, reference studies of non-regulated rivers can provide a guideline for ecological management of regulated systems.

Acknowledgements

This study was funded by the Ministry of Public Works and Transport, Survey Department, Delft. We would like to thank the project leaders M. Vreeken-Buijs and R. Brügelmann for their support. We would like to thank B. Peters for valuable field excursions along the river Allier. Furthermore, we thank all the people which we have met during the summers 'au bord d'Allier': M. Baptist, L. van den Bosch, A. Wilbers, J. de Kramer, and all the students from Delft University (TUD) and Utrecht University (UU). Finally yet importantly, we thank our colleagues E. Kater and A. Bos for their stimulating discussions. This is CWE publication 420.

References

Amoros, C., 2001. The concept of habitat diversity between and within ecosystems applied to river side-arm restoration. Environmental management 28: 805–817.

Amoros, C. & P. M. Wade, 1996. Ecological successions. In Petts, G. E. & C. Amoros (eds), Fluvial Hydrosystems. Chapman & Hall, London: 211–241.

Baptist, M. J., W. E. Penning, H. Duel, A. J. M. Smits, G. W. Geerling, G. E. M. van der Lee & J. S. L. van Alphen, 2004. Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. River Research and Applications 20: 285–297.

Bravard, J.-P., C. Amoros & G. Pautou, 1986. Impact of civil engineering works on the successions of communities in a fluvial system. Oikos 47: 92–111.

Buijse, A. D., F. Klijn, R. S. E. W. Leuven, H. Middelkoop, F. Schiemer, J. H. Thorp & H. P. Wolfert, 2005. Rehabilitation of large rivers: references, achievements and integration. Archiv für Hydrobiologie Supplement 155: 715–738.

Erdas, 1999. Erdas Imagine 8.x. Tour Guide. Erdas Inc., Atlanta, Georgia.

ESRI, 2000. ArcGIS 8.x and ArcInfo Workstation. Environmental Systems Research Institute, Redlands.

Forman, R. T. T. & M. Godron, 1986. Landscape Ecology. John Wiley & Sons, New York.

Gautier, E., H. Piégay & P. Bertaina, 2000. A methodological approach of fluvial dynamics oriented towards hydrosystem management: case study of the Loire and Allier rivers. Geodinamica Acta 1: 29–43.

Gilvear, D. J., J. Cecil & H. Parsons, 2000. Channel change and vegetation diversity on a low-angle alluvial fan, River Feshie, Scotland. Aquatic Conservation: Marine and Freshwater Ecosystems 10: 53–71.

Green, D. R. & S. Hartley, 2000. Integrating photointerpretation and GIS for vegetation mapping: some issues of error. In Alexander, R. & A. C. Millington (eds), Vegetation Mapping: From Patch to Planet. John Wiley & Sons Ltd, Chichester: 103–134.

IGN, 1990. Carte Série bleue Top25 de France. Map No. 26270 (Moulins), Institut Geographique National, Paris.

Kent, M. & P. Coker, 1994. Vegetation Description and Analysis: A Practical Approach. Wiley, Chichester.

Klijn, F. & H. A. Udo de Haes, 1994. A hierarchical approach to ecosystems and its implications for ecological land classification. Landscape Ecology 9: 89–104.

Kondolf, G. M., H. Piégay & N. Landon, 2002. Channel response to increased and decreased bedload supply from land use change: contrasts between two catchments. Geomorphology 45: 35–51.

Küchler, A. W. & I. S. Zonneveld, 1988. Vegetation Mapping. Kluwer Academic Publishers, Dordrecht.

Lenders, H. J. R., 2003. Environmental rehabilitation of the river landscape in the Netherlands. A blend of five dimensions. PhD Thesis, University of Nijmegen, Nijmegen.

Lenders, H. J. R., R. S. E. W. Leuven, P. H. Nienhuis, R. J. W. de Nooij & S. A. M. van Rooij, 2001. BIO-SAFE: a method for evaluation of biodiversity values on the basis of political and legal criteria. Landscape and Urban Planning 55: 121–137.

Marston, R. A., J. Girel, G. Pautou, H. Piégay, J.-P. Bravard & C. Arneson, 1995. Channel metamorphosis, floodplain disturbance, and vegetation development: Ain river, France. Geomorphology 13: 121–131.

McGarigal, K. & B. Marks, 1995. FRAGSTATS: Spatial Analysis Program for Quantifying Landscape Structure. Gen Tech. Rep., USDA Forest Service.

Mendonca-Santos, M. L. & C. Claramunt, 2001. An integrated landscape and local analysis of land cover evolution in an alluvial zone. Computers, Environment and Urban Systems 25: 557–577.

Micheli, E. R., J. W. Kirchner & E. W. Larsen, 2004. Quantifying the effect of riparian forest versus agricultural vegetation on river meander migration rates, Central Sacramento River, California, USA. River Research and Applications 20: 537–548.

Millar, R. G., 2005. Theoretical regime equations for mobile gravel-bed rivers with stable banks. Geomorphology 64: 207–220.

Miller, J. R., T. T. Schulz, N. T. Hobbs, K. R. Wilson, D. L. Schrupp & W. L. Baker, 1995. Changes in the landscape structure of a southeastern Wyoming riparian zone following shifts in stream dynamics. Biological Conservation 72: 371–379.

Mount, N. J., P. M. Zukowskyj, R. M. Teeuw & T. A. Stott, 2002. Use of aerial photography and digital photogrammetry in the assessment of river channel destabilisation. In Leuven, R. S. E. W., I. Pourdevigne, & R. M. Teeuw (eds), Application of Geographic Information Systems and Remote Sensing in River Studies. Backhuys Publishers, Leiden: 41–62.

Muller, E., 1997. Mapping riparian vegetation along rivers: old concepts and new methods. Aquatic Botany 58: 411–437.

Narumalani, S., R. M. Deepak & R. G. Rothwell, 2004. Change detection and landscape metrics for inferring anthropogenic processes in the greater EFMO area. Remote Sensing of Environment 91: 478–489.

Nienhuis, P. H., A. D. Buijse, R. S. E. W. Leuven, A. J. M. Smits, R. W. J. de Nooij & E. M. Samborska, 2002. Ecological rehabilitation of the lowland basin of the river Rhine (NW Europe). Hydrobiologia 478: 53–72.

Nienhuis, P. H. & R. S. E. W. Leuven, 2001. River restoration and flood protection: controversy or synergism. Hydrobiologia 444: 85–99.

Petts, G. E. & C. Amoros, 1996. Fluvial Hydrosystems. Chapman & Hall, London.

Photothèque-Nationale, 2003. Aerial images of years 1954, 1960, 1967, 1978, 1985, 1992 and 2000, Photothèque Nationale, 2/4 avenue Pasteur. Saint-Mandé Cedex.

Piégay, H. & P.-G. Salvador, 1997. Contemporary floodplain forest evolution along the middle Ubaye river, Southern Alps, France. Global Ecology and Biogeography Letter 6: 397–406.

Prach, K. & P. Pysek, 2001. Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. Ecological Engineering 17: 55–62.

Smits, A. J. M., H. Havinga & E. C. L. Marteijn, 2000. New concepts in river and water management in the Rhine river basin: how to live with the unexpected?. In Smits, A. J. M., P. H. Nienhuis & R. S. E. W. Leuven, (eds), New Approaches to River Management. Backhuys Publishers, Leiden: 267–286.

Tockner, K., F. Malard & J. V. Ward, 2000. An extension of the flood pulse concept. Hydrological Processes 14: 2861–2883.

Van den Berg, J. H. & T. Balyuk, 2004. Interaction of Vegetation and Morphodynamics in Pointbars of the Lower Volga (Russia) and the Allier (France). Inter-university Centre for Geo-Ecological Research, Utrecht.

Van der Nat, D., K. Tockner, P. J. Edwards, J. V. Ward & A. M. Gurnell, 2003. Habitat change in braided floodplains (Tagliamento, NE-Italy). Freshwater Biology 48: 1799 1812.

Van Stokkom, T. C., A. J. M. Smits & R. S. E. W. Leuven, 2005. Flood defense in the Netherlands, a new era, a new approach. Water International 30: 76–87.

Vulink, J. T., 2001. Hungry Herds. Management of Temperate Lowland Wetlands by Grazing. PhD thesis, Rijkswaterstaat Directie IJsselmeergebied/Rijksuniversiteit Groningen.

Ward, J. V., K. Tockner, U. Uehlinger & F. Malard, 2001. Understanding natural patterns and processes in river corridors as the basis for effective river restoration. Regulated Rivers: Research & Management 17: 311–323.

Wilbers, A. W. E., 1997. The Allier, a river with two patterns. MSc Thesis Utrecht University, Utrecht (In Dutch).

Wolfert, H. P., 2001. Geomorphological Change and River Rehabilitation. PhD Thesis Wageningen University, Alterra Green World Research, Wageningen.