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ORIGINAL PAPER

Regeneration of woody plants in beaver inhabited river valleys

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ABSTRACT

The aim of this research was to characterize the tree and shrub regeneration that has developed on beaver ponds and to identify factors that have a significant impact on the development of this regeneration.

Studies were conducted at 11 beaver ponds in lowland part of Poland. These ponds varied in the amount of time that had elapsed since their creation (from 5 to 16 or more years). Within the boundaries of each pond, tree regeneration and dead wood stocks were recorded on 6 circular plots of 25 m^2 and the percentage of plots occupied by sites inaccessible to plants was determined. Data were analyzed using generalized linear mixed models (negative binomial GLMMs).

The renewal was found on 85% of the sampling plots. Its density was 7151.5 ±1073.6 pcs/ha, and 74% of the seedlings and saplings were observed on dead wood. The average renewal height was 1.14 m (*SE*=0.04). The species composition of regeneration was dominated by *Alnus glutinosa* (80.8% of the total). The density of natural regeneration is higher the older the beaver pond is. More than the age of the pond, the density of regeneration is positively influenced by the stock of dead wood.

The results indicate that it is possible to initialize new forest stand generation with the species composition typical for riparian forests in beaver pond areas. This process takes at least 10-15 years and depends on the availability of areas suitable for regeneration that contain mainly dead wood with an adequate decomposition rate. In the highly variable conditions of beaver ponds, it is dead wood that appears to be the main factor affecting the establishment and development of regeneration of woody species. However, its future may be uncertain if beavers recolonize the area.

KEY WORDS

beaver ponds, *Castor fiber*, dead wood, forest regeneration

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Introduction

The European beaver *Castor fiber* L. is widely distributed in Europe (Wróbel, 2020). Beaver's activity which mainly consists of damming watercourses and creating beaver ponds, is beneficial for water retention and river renaturation (Westbrook *et al.*, 2006; Gorczyca *et al.*, 2018). But within the boundaries of a beaver pond, as a result of flooding, there is a decrease in the ground cover of the tree layer. In the short term a degeneration of the forest phytocoenosis is observed, not only in structure of the vegetation layers but also in the species composition of the undergrowth (Anderson *et al.*, 2005; Boczoń *et al.*, 2009; Hood and Bayley 2009; Gawryś *et al.*, 2021). However, the changes observed in the phytocoenosis are not permanent. As stated by Fryxell (2001), only 20% of beaver dams are inhabited for more than 10 years. Once the flooding subsides, conditions for forest regeneration reappear (Nummi and Kuuluvainen, 2013). Admittedly, beaver can return to the same places and interrupt the regeneration of the forest phytocoenosis. For example, Remillard *et al.* (1987) observed the repopulation of a beaver pond after 30 years. Kivinen *et al.* (2020) report in their paper that 61% of beaver ponds in an area of southern Finland, were recolonised during 49 years of observation, with the timing varied greatly from case to case. These authors consider beavers to be an important factor in the restoration of riparian forests and do not see them as a threat. According to them beaver activity in river valleys is not a long-term obstacle to the growth of young trees. As a result of the decay of the stands, numerous elevated places are created by lying wood, which, when sufficiently decomposed, could be a good substrate for the development of regeneration (Naiman *et al.*, 1998; Gawryś and Gabrysiak, 2020). Dead wood further impedes the flow of water, and the slowed flow is accompanied by an increased sedimentation of debris and thus the formation of shallows (Giriat *et al.*, 2016). All of this transforms the narrow watercourse into a meandering valley in which the water spills widely flowing in multiple streams (Wohl, 2013). The work of Gawryś and Gabrysiak (2020) confirms that it is possible to develop tree renewal even during the flood period, with deadwood playing an important role. However, a little is known about the causes of variability in regeneration density between different beaver ponds and within a single pond.

The aim of this study was to identify and quantify the habitat conditions that facilitate the emergence and development of woody plants regeneration in beaver ponds.

Materials and methods

Data were collected in year 2020 at 11 beaver ponds distributed in the lowland part of Poland. The geographical coordinates of the studied beaver ponds are presented in Table 1. This are the same places as analysed in Gawryś *et al.* (2021). The study sites were located in places where the beaver pond was present in the stand with a predominance of black alder *Alnus glutinosa* (L.) Gaertn. trees over 40 years old. As a result of flooding, 90% of the trees died. The analysed beaver ponds differed in age (time since the pond was created), so three categories were distinguished: (i) young ponds (ponds created from 5 to 10 years ago); (ii) medium-aged ponds (ponds created 11 to 15 years ago); (iii) old ponds (ponds created 16 or more years ago). Data on the age of the ponds were obtained from the managers of the land on which the ponds were located.

For each pond, the type of valley was determined based on the slope of the valley banks, categorising them as deep valleys (valley bank slope angle greater than 30%) or flat-bottomed valleys (slope angle less than 30%).

Six sample plots of 25 m^2 each were established at each beaver pond. The distribution of the sample plots was randomised on the nodes of a 10 m grid superimposed on the surface of

Table 1.
Geographical location and major characteristics of the studied beaver ponds

No	N	E	Age categories	Valley shape
1	52.821560	23.834352	old	flat
2	52.486252	23.328996	medium-aged	flat
3	54.159703	22.110483	young	deep
4	52.562818	19.455006	medium-aged	deep
5	52.744326	22.779928	medium-aged	flat
6	53.808518	23.226908	old	flat
7	51.562146	20.246954	young	deep
8	53.242917	23.485442	young	deep
9	52.781990	23.688643	old	flat
10	52.566092	19.458021	old	deep
11	52.492727	14.889613	young	deep

the beaver pond. The extent of past flooding was estimated on the site by visual inspection taking into account the terrain, traces of stagnant water on the ground and trees and the vegetation structure. The estimated extent of maximal flooding was almost always greater than the actual flooded area. The exception to this were ponds located in deep valleys. The length and thickness (at half-length) of the dead wood fragments were measured. Only wood fragments with a thickness >10 cm at the thinner end were considered. The volume of dead wood was calculated using the cylindrical formula, based on a circle with a diameter equal to the thickness at half the length of a given piece of wood. Stumps with a thickness at the upper end >10 cm and a height of up to 1.3 m were counted. The percentage of each area occupied by sites unsuitable to woody plants and the percentage of the area occupied by herbaceous vegetation including floating vegetation were estimated visually. By places unsuitable to woody plants an area that was flooded or swamped at the time of observation was meant. Accessible sites (on which regeneration could potentially occur) were exposed, undrained soil, sedge clumps, dead wood, etc. The frequency of the sample plots with stumps was only 51.5%. As plots with one stump dominated in this group (82%), the data were used in the analyses as a categorical variable with two levels, *i.e.* stumps present or not. In each plot regeneration was counted and its height was measured, differentiating the species. The origin of the regeneration (vegetative or generative) was not recorded, as exclusively generative regeneration was found.

All calculations were performed with the R program (R Core Team, 2022). Negative binomial GLMMs (generalized linear mixed models) were used to determine the relationship between density of sapling and the explanatory variables (pond age, valley shape, stumps, contribution unsuitable area for samplings, plant cover, volume of lying dead wood). For this purpose, the function 'glmer.nb' from the package 'lme4' (Bates *et al.*, 2015) was used. The use of a GLMM with a Poisson distribution was not possible due to the occurrence of over-dispersion. First the influence of only one explanatory variable was analyzed. Then all explanatory variables were used in a joint model. In order to reduce the number of variables in the model, variables which impact was insignificant were removed from the model. The variables used in the analysis were checked for the presence of collinearities by calculating the Variance Inflation Factor using the 'vif' function from the 'car' package (Fox and Weisberg, 2019). If the VIF was 3, the variables were considered collinear and thus were discarded. The relationship between unsuitable area and plant cover was determined using Spearman`s rank correlation (as the variables did not have a normal distribution), using the 'cor.test' function from the 'stats' package.

Results

The regeneration of woody species was observed in 56 of the total 66 plots. The height of the seedlings and saplings ranged from 0.01 m to 10.30 m, with a median of 0.70 m and an arithmetic mean of 1.14 m (*SE*=0.04). The density of natural regeneration was 7151.5 ±1073.6 pcs/ha (median=3600 pcs/ha). The saplings found on dead wood accounted for 74% of the total natural regeneration. In young and medium-aged ponds their share was 86% and 94%, and in old ponds it was 62%.

The species composition of the regeneration was dominated by *Alnus glutinosa*. This species accounted for 80.8% of the total regeneration and occurred in 78.8% of the plots. The next species in terms of contribution to the number of regeneration were *Salix* spp. (5.2%, frequency (*F*)=31.8%), *Betula pendula* Roth and *B. pubescens* Ehrh. (aggregated share 4.1%, *F*=16.7%), *Padus avium* Mill. (3.1%, *F*=10.6%), *Carpinus betulus* L. (2.4%, *F*=4.5%), *Fraxinus excelsior* L. (1.6%, *F*=3.0%), *Picea abies* (L.) H. Karst. (0.4%, *F*=6.1%). The share of each of the other species: *Acer platanoides* L., *Corylus avellana* L., *Euonymus europaeus* L., *Frangula alnus* Mill., *Padus serotina* (Ehrh.) Borkh., *Populus tremula* L., *Quercus robur* L., *Ulmus minor* Mill. did not exceed 1% in renewal abundance and the frequency did not exceed 5%.

The median renewal abundance in medium-aged ponds was almost five times higher than in young ponds, and in old ponds almost three times higher than in medium-aged ponds (Table 2). However, the effect of pond age class on regeneration abundance was only significant between young and old ponds (Table 3). The median density of seedlings and saplings in ponds in flat-valleys was more than twice as high as in ponds in deep valleys, but the influence of this factor on the renewal rate was insignificant (Table 3). Sample plots where stumps were found, have a lower median but a higher arithmetic mean of the density of regenerations compared to plots without stumps. The effect of this variable was also not significant.

The coverage of sample plots by herbaceous vegetation ranged from 50% to 100% (86.3 ±1.5%). The unsuitable area for saplings ranged from 10% to 100% (81.8 ±3.0%). The volume of lying dead wood ranged from 0 to 2.07 m^3/plot (0.34 ±0.05 m^3/plot) that is from 0-827.09 m^3/ha (135.74 ±19.33 m^3/ha).

An increase in saplings abundance was significantly associated with an increase in the volume of dead wood (Table 3). The higher values for the coverage of the sample plot by herbaceous vegetation and the unsuitable area for saplings were associated with a lower regeneration abundance, but these variables were also not significant. In contrast, an increase in saplings abundance was

Table 2.
Density [pcs/ha] of tree and shrub regeneration in beaver ponds and its frequency (*F*)

Variable	Level	*N*	Mean	*SE*	Median	*F* [%]
Pond age	young	24	3866.7	1402.2	800	70.8
	medium-aged	18	5977.8	1286.0	3800	88.9
	old	24	11316.7	2192.5	10200	95.8
Valley shape	flat	30	9506.7	1894.3	7000	90.0
	deep	36	5188.9	1097.7	2800	81.6
Stumps	present	32	8237.5	1982.7	2600	78.1
	absent	34	6129.4	930.9	4800	91.2
	Total	66	7151.5	1073.6	3600	84.8

Note: *N* – number of plots, *SE* – standard error significantly associated with an increase in the volume of dead wood. The Spearman rank correlation coefficient between plant cower and the unsuitable area for samplings was 0.29 (p=0.02).

The multi-variable model including all independent variables (Table 3) achieved an *AIC* value of 492.5. Removing irrelevant variables from the model improved its fit to the *AIC*=489.3 (Table 4). Finally, two variables remained in the model: size of an area unsuitable for saplings and amount of lying dead wood. Therefore, the model was simplified to the form shown in Table 4. The total explanatory power of the model was moderate (conditional R^2=0.67) and the part related to the fixed effects alone (marginal R^2) was 0.33.

Discussion

The density of regeneration of woody species in young beaver ponds is relatively low and varies greatly from case to case. In medium-aged and old ponds, the regeneration density was many times higher than in young ponds. This shows that there is no linear relationship between the age of the pond and the density of natural tree and shrub regeneration. This proves that regeneration can develop into a future stand. The amount of regeneration also varies. The median is typical for sample stands a few years old, and the maximum for trees a dozen years old. However, this occurs relatively late, about fifteen years after the beaver pond appears, as beavers usually utilize a given area for up to about 10 years (Fryxell, 2001; Kivinen *et al.*, 2020) and can actively change

Table 3.

Parameters of negative binomial GLMMs model predicting density of saplings including ID of Beaver Pond as a random effect

	Variable	Coefficent	*CI*	*p*-value	*Exp*	*AIC*	*Disp.*
Age	young (intercept)	1.53	0.64, 2.42	<0.001	4.62	498.8	0.74
	medium-aged	1.15	–0.17, 2.46	0.087	3.13		
	old	1.74	0.53, 2.96	0.005	5.70		
Valley shape	flat (intercept)	3.07	2.20, 3.94	<0.001	21.54	500.4	0.66
	deep	–1.10	–2.29, 0.10	0.071	0.33		
Stump	absent (intercept)	2.42	1.64, 3.20	<0.001	11.25	503.3	0.68
	present	0.08	–0.64, 0.80	0.826	1.08		
	(intercept)	3.88	2.25, 5.51	<0.001	48.42	499.9	0.79
	unsuitable area for samplings [%]	–0.02	–0.04, 0.00	0.066	0.98		
	(intercept)	5.24	1.85, 8.63	0.002	188.70	500.6	0.69
	plant cover [%]	–0.03	–0.07, 0.01	0.099	0.97		
	(intercept)	1.78	1.04, 2.52	<0.001	5.93	491.7	0.62
	lying dead wood [m^3/plot]	1.73	0.70, 2.76	<0.001	5.64		

formula: Density of saplings ~ variable + (1 | ID Beaver Pond)
Note: CI – 95% confidence interval, Exp – exponents of the coefficient value, AIC – Akaike information criterion, Disp. – Dispersion ratio

Table 4.

Parameters of a negative binomial GLMM showing relationships between density of saplings and selected environmental variables

Variable	Coefficient	*CI*	*p*-value	*Exp*
(Intercept)	3.16	1.70, 4.61	<0.001	23.57
Unsuitable area for saplings [%]	–0.02	–0.03, 0.00	0.035	0.98
Lying dead wood [m^3/plot]	1.72	0.73, 2.71	<0.001	5.58

Density of sapling ~ Unsuitable area for saplings + Lying dead wood + (1 | ID Beaver Pond); R^2 conditional=0.67, R^2 marginal=0.33, *AIC* (Akaike information criterion)=489.3, dispersion ratio=0.73
Note: *CI* – 95% confidence interval, *Exp* – exponents of the coefficient value

the structure of the phytocoenosis during this time. For a new generation of woody species to emerge, there must be places where the tree vegetation can regenerate, *i.e.* the water level must be lowered or elevations must be formed, for example, in the form of clumps of sedges, broken and fallen trees or sufficiently decomposed dead wood. Older ponds generally contain more sediments than those that have only recently been created (Rossel *et al.*, 2005). As a result of lowering water levels, 'islands' are formed in them, which can result in more abundant regeneration of woody species in old ponds. Organic material accumulates in beaver ponds, the decomposition of which is slowed down by the anaerobic conditions in the flooded areas (Pollock *et al.*, 1995). The organic material and sediments derive from the stream flow, from bank erosion, from the excavation of burrows and channels, from primary production in the pond, and from organic material from riparian vegetation that could be introduced by beavers or supplied by other natural means (Rosell *et al.*, 2005). As the regeneration develops on localized elevations, it will be resistant to the occurrence of high groundwater levels in the future. Although flooding prevents the development of seedlings, it also has a negative impact on the undergrowth, which is a strong competitor for tree regeneration (Pusłowska-Tyszewska *et al.*, 2014). As soon as the flooding recedes, woody vegetation will probably recover. The prospects for forest recovery are promising, but it should be borne in mind that future beaver activity may be a key damaging factor here. For example, according to Kivinen *et al.* (2020), about 60% of beaver ponds in Finland have been re-inhabited. On reoccupied locations, browsing by beavers could play a larger role here than the reflooding of the area. But the results of a study from northeastern Poland show that after an average of 15 years of beaver presence in areas that have been repeatedly settled and abandoned by beavers, the proportion of healthy woody plants is as high as 73% (Misiukiewicz *et al.*, 2016). So the damage is not extensive.

Alder was the dominant species in the study plots. It was also the dominant species in the stand before the beavers colonized the watercourse. There were also other species not only of trees but also shrubs, which is a positive development. The high frequency of regeneration in the sample plots used in this study testifies to fairly widespread occurrence of renewal in the area. Gawryś (2019) observed that the floristic composition of the regeneration layer in the riparian forest resembles the species composition of a mature tree stand. This was also observed in the present study. Periodic flooding is a limiting factor on restoration abundance. McMaster and McMaster (2001) found that hydrological dynamics, including the frequency, duration and extent of flooding, had a greater influence than the depth of the water table. In this study the median value of the unsuitable area for samplings was up to 90%. This indicates that woody vegetation is found in clusters on elevations over a relatively small area.

Covering the area with herbaceous vegetation has a similar effect to the unsuitable area for sampling on the regeneration. The reason for the negative relationship could be competition (Pusłowska-Tyszewska *et al.*, 2014). The herbaceous vegetation in wet habitats develops very abundantly and can limit the space for the much slower developing tree seedlings, especially when the water level drops due to a dam failure. There was also a positive correlation between the size of unsuitable area for saplings and the plant cover. This indicates that the area inaccessible to seedlings is not identical to the location of the herbaceous vegetation, as herbaceous vegetation can also develop in water. In that case, the presence of herbaceous vegetation, mainly of the *Lemnetea* class, has a limiting effect as it is identical to presence of flooding. Sedges, whose tussocks are a good place for the development of the regeneration of woody species, can also develop in the water. However, they are not the dominant plant group in young beaver ponds (Gawryś *et al.*, 2021). Time is also needed for the development of new sedge clumps, as the current sedge clumps in front of the lagoon are lost under water.

Both the high water level and the high dynamics of its level do not allow tree seedlings to survive and grow (Hyvönen and Nummi, 2008). Woody vegetation is therefore limited to places that are not flooded and are not attractive substrates for herbaceous plants such as sedges and rushes. Dead wood has both of these properties. It is a relatively nutrient-poor substrate that forms local elevations. Lee and Sturgess (2002) found significant differences in the species composition of plant communities growing on dead wood and the surrounding forest floor. In contrast, the absence of a negative effect of vascular plant density on the abundance of *Cryptomeria japonica* (Thunb. ex L. f.) D. Don regeneration on *Pinus densiflora* S. et Z. logs was confirmed by Fukusawa and Komagata (2017). However, this example should be treated with caution due to the geographical location and different chemical composition of wood.

The presence of dead, especially lying, wood, is a very important factor that positively influences the development of forest regeneration at beaver ponds. However, it is important to note that not all dead wood is equally 'useful' for regeneration. As shown in the work of Gawryś and Gabrysiak (2020), regeneration on dead wood only develops several years after the stand has died, when it is sufficiently decomposed. This issue was also noted by Stroheker *et al.* (2018). Dead wood can also form the skeleton of 'islands' if silt is deposited on it (Rosell *et al.*, 2005). It is a common substrate in forested valleys. In valleys with a high degree of naturalness, where there is a continuity of dead wood resources in varying degrees of decomposition, it can play a key role in the formation of regeneration in the beginning of the existence of a beaver pond, when the stand is still in the dying phase. This was observed in the Orłówka River valley in the Białowieża National Park (Gawryś and Gabrysiak, 2020). According to the studies of the above-mentioned authors, this substrate is used mainly by alders and almost not at all by shrub species (occasionally *Salix* spp. and *Corylus avellana*), which are usually abundant in valleys not disturbed by beavers.

In the valleys where stumps were present, the restoration density was low, but regeneration clusters repeatedly appeared on the stumps, although regeneration of vegetative origin was rare. The stumps were created by man by cutting down dying trees. The presence of stumps therefore indicates a smaller volume of lying dead wood. Therefore, no collinearity was found between these variables. No vegetative regeneration was observed, as persistently high water levels led to the death not only of the above-ground parts of the trees, but especially of the root system. Regeneration could only occur on the rotted wood or sediment covering the stump. Vegetative regeneration therefore plays an insignificant role in the regeneration of beaver ponds. This is noticeable in the initial period, in contrast to the natural regeneration taking occurring in swamp and riparian forests uninhabited by beavers (Deiller *et al.*, 2003).

Beaver ponds bordered by steep escarpments have lower restoration densities and almost twice as high the proportion of sample areas without natural regeneration compared to ponds located in flat valleys. This is partly due to the retention capacity of these valleys. Ponds in flat valleys can hold much larger volumes of water at one time with a relatively small increase in depth. In ponds bordered by an escarpment, a sudden rise in water leads to a sharp rise in the water level, so that the local elevations favourable for the development of vegetation are also flooded. In addition, water stagnates longer under such conditions, which eventually leads to the death of vegetation typical of forests and to an increase in the proportion of floating plants and *Carex* spp. (Gawryś *et al.*, 2021). Since landforms can directly influence factors such as vegetation cover and the proportion of area unavailable for regeneration, this variable does not contribute nothing to the overall model and can be replaced by the variables mentioned above. The influence of the geomorphological shape of the valley on the effect of beaver activity is also highlighted by Robinson *et al.* (2020). Ponds in deep valleys may be less sustainable as the occurrence of high water levels after heavy rainfall can lead to dam failure (Burchsted and Daniels, 2014). Ponds in deep valleys also appear to be less attractive to beavers because they often have a smaller surface area and are directly adjacent to habitats that are less attractive to beavers in terms of their food base. Under such conditions, it is also more difficult to reach the food base outside the beaver pond. Therefore, the pressure of beavers on the vegetation in beaver ponds is higher than in ponds in flat valleys. These are thus relatively unfavourable locations for beavers and therefore quite short-lived (Ritter *et al.*, 2018). This is most likely a natural reason for the low proportion of ponds in deep valleys in the medium-aged and old age group.

Over time, the abundance of regeneration increases, as the flooding effect on the habitat diminishes. Eventually beavers move to a different location. Typically, beavers do not occupy a site for more than 10 years (Fryxell, 2001; Kivinen *et al.*, 2020). The dam, which determines the existence of the beaver pond, can function for at least 2-3 years after the beavers have left the pond (Hyvönen and Nummi, 2008). With the degradation of the dam, the damming it causes is no longer as high. Over time, the morphology of the watercourse also changes, the channel becomes wider, shallower and more meandering. The reason for this is the activity of beavers, which not only build dams but also dig channels and burrows and disturb the shoreline (Biały and Załuski, 1994; Burchsted and Daniels, 2014; Ritter *et al.*, 2019). In addition to water, the dam also retains sediment which forms localized plateaus that are accessible after the partial receding of the floodwaters. Over time, the stock of dead wood also increases, which decomposes and forms platforms on which regeneration can develop even in ponds that exist all year round. However, the speed at which these processes occur varies greatly and depends on both time and terrain. After 10-15 years after the occurrence of a beaver pond, a new generation of forest stands develops, with a species composition and density that offers prospects for the development of a forest phytocoenosis. However, at least a dozen more years is needed for its development, until the compactness of the crowns is reached. After 15 years after the occurrence of the beaver pond, the herbaceous vegetation still differs significantly in its composition from the vegetation typical of riparian forests (Gawryś *et al.*, 2021). Changes in the undergrowth towards a forest phytocoenosis are to be expected in the future if the light conditions deteriorate due to the spread of the tree layer (Ritter *et al.*, 2019). Another problem with unresolved effects on the regeneration of woody species is the impact of possible future recolonization of the river by beavers.

Conclusion

The natural regeneration of woody species at beaver ponds is dominated by *Alnus glutinosa* (80,8% of total) and occurred on 78.8% of the sites. In addition to alder, *Salix* spp., *Betula pendula*, *B. pubescens* and *Padus avium* also occur with frequency above 10%. The average woody renewal abundance in ponds created 16 or more years ago was almost three times higher compared to ponds created 5 to 10 years ago. But even more than the age of the pond, the density of regeneration was positively influenced by the volume of lying dead wood. Dead wood is the main substrate on which regeneration develops within the boundaries of the beaver pond, as 74% of all regeneration was found on it. In the highly variable conditions of beaver ponds, it is dead wood that appears to be the main factor affecting the establishment and development of regeneration of woody species. After 15 years of flooding a young tree population can be observed. However, its future may be uncertain if beavers recolonize the area.

Authors' contributions

Research concept – R.G.; material collection – R.G., M.W.; data analysis – R.G., O.H.; manuscript writing – R.G., O.H., M.W., K.A.G.; manuscript editing – K.A.G., O.H.

Conflict of interest

The authors declare no conflicts of interest.

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STRESZCZENIE

Regeneracja roślinności drzewiastej w dolinach rzecznych zasiedlonych przez bobry

Działalność bobrów, polegająca m.in. na spiętrzaniu cieków wodnych i tworzeniu stawów bobrowych, sprzyja retencji wody i renaturyzacji rzek. W wyniku wystąpienia wieloletniego niekiedy zalewu terenu następuje rozpad drzewostanu. W krótkim okresie obserwuje się degenerację fitocenozy leśnej – nie tylko pod względem struktury pionowej, ale także gatunkowej. Zmiany te nie są jednak trwałe. Po ustąpieniu zalewu możliwa jest wtórna sukcesja roślinności w kierunku lasów łęgowych, a odnowienie gatunków drzewiastych może pojawić się jeszcze w czasie

trwania zalewu, pod warunkiem wystąpienia martwego drewna pochodzącego z okresu przed powstaniem zalewu i o odpowiednim stopniu rozkładu. Niewiele jednak wiadomo o tempie regeneracji i czynnikach kształtujących odnowienie drzew w obrębie stawów bobrowych. Celem pracy była charakterystyka odnowienia drzew i krzewów w obrębie stawów bobrowych oraz identyfikacja czynników mających istotny wpływ na jego rozwój.

Dane zbierano w 2020 r. na 11 stawach bobrowych rozmieszczonych w nizinnej części Polski (tab. 1). Wyróżniono 3 kategorie stawów: (i) stawy młode (powstałe od 5 do 10 lat wstecz); (ii) stawy średniowiekowe (powstałe 11-15 lat temu); (iii) stare stawy (powstałe 16 lub więcej lat temu). Dla każdego stawu określono typ doliny na podstawie nachylenia brzegów dolin, dzieląc je na doliny głębokie (kąt nachylenia brzegów doliny większy niż 30%) lub płaskodenne (kąt nachylenia brzegów poniżej 30%). Na każdym stawie na 6 powierzchniach próbnych o areale 25 m^2 każda liczono odnowienie z rozróżnieniem gatunku i mierzono jego wysokość. Ponadto dokonano pomiaru miąższości martwego drewna, odnotowano obecność pniaków, oszacowano procent powierzchni niedostępnej dla odnowienia roślin drzewiastych oraz procent powierzchni zajmowanej przez roślinność zielną. Za teren niedostępny dla odnowienia uznawano lustro wody i wymokliska. Natomiast za miejsca, gdzie mogłoby potencjalnie pojawić się odnowienie, uznawano nieuwodnioną glebę, jak też martwe drewno i kępy turzyc. W celu określenia zależności pomiędzy wybranymi zmiennymi środowiskowymi a liczebnością odnowienia wykorzystano uogólnione liniowe modele mieszane (GLMM).

Odnowienia gatunków drzewiastych stwierdzono na 56 z 66 powierzchni. Obserwowano wyłącznie odnowienia generatywne. Wysokość odnowienia wahała się od 0,01 m do 10,30 m (średnia arytmetyczna 1,14 ±0,04 m). Gęstość odnowienia wyniosła 7151,5 ±1073,6 szt./ha (tab. 2). Odnowienia rosnące na martwym drewnie stanowiły 74% ogółu stwierdzonych. W składzie gatunkowym odnowienia dominowała olsza czarna *Alnus glutinosa* (L.) Gaertn.

Określono parametry modeli GLMM opisujących wpływ pojedynczych zmiennych na liczebność odnowienia (tab. 3) oraz parametry modelu najlepiej opisującego zmiany liczebności odnowienia z uwzględnieniem wielu zmiennych (tab. 4). W modelu wykorzystującym wiele zmiennych liczebność odnowienia wykazywała pozytywny związek z miąższością martwego drewna, a negatywny z udziałem powierzchni niedostępnej dla roślinności drzewiastej. Wysoki poziom wody lub jego częste wahania uniemożliwiają odtworzenie się drzewostanu na gruncie. Natomiast kłody leżące na zalanym obszarze tworzą „wyspy”, na których może rozwijać się odnowienie. Tak więc w bardzo zmiennych warunkach stawów bobrowych to martwe drewno wydaje się głównym czynnikiem ułatwiającym powstawanie i rozwój odnowienia gatunków drzewiastych. Odnowienie to po 15 latach od wybudowania tamy i powstania zalewu wydaje się być wystarczające, by mógł rozwinąć się z niego drzewostan. Jednak jego przyszłość może być niepewna, jeśli bobry ponownie skolonizują ten obszar.