# Do abandoned tree plantations resemble natural riparian forests? A case study from northeast Greece

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# Abstract

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The conversion of a riparian forest to plantations of fast-growing, exotic species (Populus  $\times$  canadensis, Robinia pseudoacacia) may alter the floristic composition and soil properties, which may prevent the regeneration of natural forests when plantations are abandoned. Along the Nestos River in northeast Greece, we investigated how former plantations differ from natural forests after at least 14 years of abandonment. We carried out 60 vegetation relevés and took soil samples in each plot to determine soil texture and chemical properties. Relationships between the forest type (natural vs. abandoned plantations), the floristic composition of the understory and soil properties were analysed with classification (TWINSPAN) and ordination (DCA). There was a clear floristic differentiation between natural forest and abandoned plantations, especially those of Robinia pseudoacacia. The topsoil of abandoned plantations had a lower content of organic matter and nitrogen, and the tree layer was still dominated by the formerly planted species. However, there was a similar floristic gradient, related mainly to soil texture (sandy vs. loamy sediments), in both the natural forest and abandoned plantations. Thus, even though the establishment of natural riparian forest species in the former plantations was scanty, their present floristic composition sufficiently reflects the natural ecological gradient to serve as a basis for a management plan to restore the natural riparian forest.

Key words: Exotic tree plantations, forest restoration, forested wetlands, Nestos River, ordination, *Populus*  $\times$  *canadensis, Robinia pseudoacacia*, soil degradation.

## Introduction

Riparian ecosystems are characterized by complex environmental gradients, which vary in space and time (Ward 1998; Ward et al. 2002; Renöfält et al. 2005). This results in a large variety of plant communities and high species diversity. Large parts of riparian ecosystems are naturally occupied by forests (Lugo 1990). Riparian forests perform important functions such as reducing bank erosion (Micheli et al. 2004), improving water quality (Doyle 1990; Sagers and Lyon 1997; Hughes et al. 2001), and creating a complex mosaic of micro-habitats harboring a diversity of organisms (Doyle 1990; Fleishman et al. 2003).

Most riparian forests in Europe have been heavily modified by river regulations or destroyed by the conversion to agricultural, urban or industrial land (Dierschke 1980; Décamps et al. 1988; Ward et al. 2002). Large areas of natural riparian forests have been replaced by plantations of fast-growing, exotic tree species (Décamps et al. 1988; Hartley 2002). This has caused the loss of habitats and therefore the reduction of biodiversity as well as the alteration of soil properties (Lugo et al. 1990).

Nowadays, efforts are made to restore natural riparian forests (Ward 1998; Ward et al. 1999, 2002; Hughes et al. 2001), which raises the question whether the impact caused by the previous land use change is reversible. Zerbe (2003) suggested that poplar plantations in northeast Germany are reversible, i.e. they will develop towards natural riparian forests after their abandonment. This author also used the present floristic composition of the plantations to indicate which natural forest communities should be targeted by restoration management on former poplar plantations. A relevant question in this context is whether the plantations can host natural forest species. Some studies indicated that plantations can maintain a high biodiversity (Laquerbe 2000) and can be spontaneously recolonized by natural forest species (Lust et al. 2001), while other studies pointed to the floristic differentiation between plantations and natural forests (Michelsen et al. 1996; Ramovs and Roberts 2005).

This study investigates the differentiation in the floristic composition and soil properties between plantations that have been abandoned for at least 14 years, and remnants of a natural riparian forest in the Delta of the Nestos River (northeast Greece). The aim was to determine: a) how the floristic composition of the abandoned plantations differs from the natural forest, b) if there are differences in the soil properties between the plantations and the natural forest, and c) if the type of natural forest likely to develop on abandoned plantations can be derived from their present floristic composition and soil properties.

#### Materials and Methods

#### Study area

The study area is located in northeast Greece and is defined by coordinates  $40^{\circ}$  52' to  $40^{\circ}$  55' N and 24 $^{\circ}$  46' to 24 $^{\circ}$  50' (Fig. 1). The riparian forest of the Nestos River used to be called "Kotza Orman" (great forest) and covered an area of 12700 ha at the beginning of the  $20<sup>th</sup>$  century (Efthimiou 2000). This area was reduced to 7200 ha until 1946, and to 2700 ha between 1946 and 1953 (Papaioannou 1953). Deforested areas were converted to agricultural land and plantations of either Populus  $\times$  canadensis or Robinia pseudoacacia. Between 1980 and 1990, after two rotation cycles (approximately 30

years), several plantations were abandoned because of the loss of their productivity. Today, remnants of natural vegetation together with the secondary forest on abandoned plantations cover less than 800 ha, of which 500 ha are protected by the Greek State. The protected area is divided into two parts, which are on both sides of the Nestos River (Fig. 1). It includes remnants of natural forest vegetation as well as abandoned plantations of *Populus*  $\times$  *canadensis* and *Robinia pseudoacacia*. While the tree layer of the natural forests is dominated by Populus alba, Fraxinus angustifolia ssp. oxycarpa, Quercus robur ssp. pedunculiflora and Ulmus procera, the tree layer of the abandoned plantations consists almost exclusively of the formerly planted species.

The climate is coastal Mediterranean, with mild winters and dry and warm summers. The monthly average temperature varies between 5.5  $^{\circ}$ C (January) and 25.6  $^{\circ}$ C (July). The average annual precipitation for the period 1985 – 2002 is 425 mm, with a dry season of at least five months.

The watershed of the Nestos River belongs to the Rodopi massif, which consists of granite, gneiss and schist with marble intrusions (Mountrakis 1985). The study area lies in the lower part of the river delta and consists of alluvial deposits of the Quaternary period with a thickness of a few tens of meters.



Fig. 1. Map of the study area with the forest area in 1928 and 1952 (Kakouros and Dafis 2005). Vegetation and soil sampling was conducted inside the protected area.

## Vegetation survey

The vegetation was surveyed in spring and summer 2004, according to the Braun-Blanquet method (Dierschke 1994). A total of 60 relevés (each 300 m²) were taken in natural forest vegetation (26), as well as in abandoned plantations of *Populus*  $\times$ canadensis (27) and *Robinia pseudoacacia* (7). Relevés were selected subjectively to represent all vegetation types recognized visually in the study area. Fewer relevés were taken in abandoned plantations of Robinia pseudoacacia because this forest type covered a smaller area than the two others. Five vegetation layers were distinguished: herbs, low shrubs (height  $(2 \text{ m})$ , high shrubs (height between 2 and 5 m), understory trees and canopy trees. The cover abundance of all taxa was recorded for each vegetation layer using the 9-grade refined Braun-Blanquet scale (grade 2 being subdivided into 2m, 2a and 2b; Wilmanns 1989).

The nomenclature follows Tutin et al. (1968 – 1993), Greuter et al. (1984 – 1989), Strid (1986), and Strid and Tan (1991, 1997, 2002). A few species had to be aggregated because they could not be distinguished reliably (see App. 1).

#### Soil sampling and analysis

In each relevé, a soil profile was made to a depth of 50 cm, and samples were taken from each soil layer. Layers were distinguished visually on the basis of soil colour, texture and structure differentiation. In most profiles, four different soil layers were apparent, while in those with three layers, the last one was divided into two equal parts, so that four soil samples were taken from each profile. The thickness of each soil layer was measured.

The treatment of soil samples followed Carter (1993). Soil pH was measured in a 1:1 soil-water slurry for most samples and in a 1:5 soil-water slurry for those with a high proportion in organic matter ( $> 8\%$ ). Organic carbon was determined through wet oxidation (Nelson and Sommers 1982), and organic nitrogen with the Kjeldahl method (Bremmer and Mulvaney 1982). Particle size distribution (% of sand, silt and clay) was determined using the pipette method (Gee and Bauder 1982).

### Data analysis

Vegetation data were entered into TURBOVEG version 2.32a (Hennekens and Schaminée 2001). Taxa occurring in one or two relevés were omitted before the analyses. Additionally, if a taxon appeared in different vegetation layers but with very few occurrences in some of them, adjacent layers were pooled to avoid that such accidental 'structural differences' would distort the analyses (e.g. Smilax excelsa occurrences in the understory and canopy tree layers or Humulus lupulus occurrences in the understory trees, high shrub and low shrub layers). Furthermore, the occurrences of the six dominant tree taxa (*Populus alba, P.*  $\times$  *canadensis, Fraxinus angustifolia* ssp. oxycarpa, Quercus robur ssp. pedunculiflora, Robinia pseudoacacia and Ulmus procera) in the tree layers were omitted from the analyses so that we could test whether the species composition of the understorey was related to the composition of the tree layer, i.e. to the former land use.

To identify vegetation types and differential species, relevés were classified using the TWINSPAN method (Hill 1979) with four levels of divisions. The cover abundance of taxa was taken into account by using four pseudospecies cut levels, which correspond to cover values of 0, 5, 25 and 50%. The subdivisions given by the TWINSPAN analysis together with the composition of the tree layer and soil properties helped to identify ten floristically homogeneous and ecologically distinct vegetation groups. A phytosociological table representing this grouping was produced in JUICE version 6.3 (Tichy 2002). Soil variables were compared between abandoned plantations and the natural forest using the Mann-Whitney U test.

Detrended correspondence analysis (DCA; Hill and Gauch 1980) was used to explore the main ecological gradients of floristic differentiation. For this analysis, cover abundances were square-root transformed and rare taxa were downweighted in proportion to their frequency to reduce their influence on the ordination. To help the interpretation of the ordination axes, soil properties and the relative cover values of the six dominant tree species were included in the analysis a posteriori. Soil organic matter and nitrogen content were converted into pools through multiplication by the thickness of the corresponding soil layer. DCA was performed using CANOCO version 4.5 software (ter Braak and Smilauer 2002).

#### Results

## Classification

The TWINSPAN classification revealed a clear floristic differentiation between abandoned plantations and natural forest. At the first level of division, relevés from plantations were distinguished from those of the natural forest, except for groups 5 and 6 (plantations), which clustered together with the natural forest. At the second level of division the relevés of *Robinia pseudoacacia* plantations were distinguished from those of the *Populus*  $\times$  *canadensis* plantations, and the relevés of groups 5 and 6 were distinguished from those of the natural forest. At the third level, groups 2 and 3 were distinguished from group 4 in the *Populus*  $\times$  *canadensis* plantations, and groups 7 and 8 were distinguished from groups 9 and 10 in the natural forest.

Group 1 included all the relevés conducted in Robinia pseudoacacia plantations. It was clearly differentiated from all other groups by the absence of species such as *Rubus* sanctus, Brachypodium sylvaticum/pinnatum, Periploca graeca, Clematis vitalba or Cornus sanguinea ssp. sanguinea, which were frequent in all other vegetation groups.

Groups 2 to 6 included all relevés in *Populus*  $\times$  *canadensis* plantations. Groups 2 and 3 had a dense herb layer, while the shrub layer usually had a relatively low cover. Group 3 presented a much higher species richness than all other vegetation groups of the study area. Group 4 was floristically similar to group 3, but structurally similar to group 5 because of a dense shrub layer composed mainly of Rubus species. Groups 5 and 6 had the highest floristic similarity to the natural forest vegetation, with the occurrence of Smilax excelsa, Tamus communis, Periploca graeca and Cornus sanguinea ssp. sanguinea in the shrub layer. Group 6 was differentiated through the high cover of Prunus spinosa shrubs and covered only a small area.

Groups 7 to 10 included all relevés in natural riparian forest. Group 7 represented softwood forest dominated by *Populus alba* in the tree layers; it occurred predominately in the eastern part of the study area. Group 10 represented hardwood forest dominated by Fraxinus angustifolia ssp. oxycarpa, Quercus robur ssp. pedunculiflora and *Ulmus procera* in the tree layers; it occurred predominately in the western part of the study area. Groups 8 and 9 represented intermediate forest types. Group 8 occured in the eastern part of the study area, and group 9 in the western part.

These ten groups correspond to a detailed classification of the vegetation. However, some of these groups (2 and 6) were very rare in the study area or represented intermediate conditions (groups 8 and 9). Furthermore, soil analyses showed that relevés of groups 2-4 and those of groups  $5-6$  were clearly distinguished by soil texture (sandy vs. loamy) in the three upper soil layers as well as by topsoil pH (Tab. 1). Soil texture also differed between relevés of groups  $7-9$  and those of group 10 (Tab. 1).

Based on the TWINSPAN classification, the ordination results (see below), the composition of the tree layer and soil analyses, the ten groups can be classified into five main vegetation units: abandoned plantations of *Robinia pseudoacacia* (group 1), plantations of *Populus*  $\times$  *canadensis* on sandy soils (groups 2–4), plantations of *Populus*  $\times$  canadensis on loamy soils (groups 5–6), natural softwood forest dominated by *Populus alba* on sandy soils (groups  $7-9$ ), and natural hardwood forest dominated by Fraxinus angustifolia ssp. oxycarpa and/or Ulmus procera on loamy soil (group 10).

Tab. 1. Median values of soil properties per soil layer (L) and vegetation unit. Abbreviations are: L.T.: soil layer thickness, O.M.: organic matter, O.N.: organic nitrogen. Vegetation units are (1) abandoned plantations of *Robinia pseudoacacia*, (2) plantations of *Populus*  $\times$  *canadensis* on sandy soils, (3) plantations of *Populus*  $\times$  *canadensis* on loamy soils, (4) natural softwood forest dominated by Populus alba on sandy soils, and (5) natural hardwood forest dominated by Fraxinus angustifolia ssp. oxycarpa and/or Ulmus procera on loamy soil.

L	Unit	L.T. (cm)	pH	O.M. $(\%)$	O.N. $(\%)$	Sand $(\%)$	Silt $(\%)$	Clay $(\%)$
	1	2.5	6.79	6.10	0.30	47.6	29.6	21.2
	$\overline{c}$	5.0	6.87	4.77	0.24	79.5	8.2	13.0
$\mathbf{1}$	3	3.0	7.11	6.08	0.31	42.5	29.0	29.1
	4	4.5	6.98	14.40	0.54	71.3	18.8	8.9
	5	4.8	6.84	11.11	0.46	55.8	25.4	18.1
	$\mathbf{1}$	12.0	7.15	2.32	0.16	49.7	29.3	20.9
	$\overline{c}$	10.0	7.14	2.03	0.11	81.8	9.6	12.2
$\overline{c}$	3	12.0	6.73	3.07	0.14	46.6	25.5	29.7
	4	8.0	7.20	1.58	0.11	80.5	11.8	5.9
	5	12.5	7.08	3.13	0.15	58.5	19.2	18.5
	$\mathbf{1}$	15.0	7.39	1.38	0.09	64.6	20.9	14.5
	$\overline{c}$	16.0	7.32	1.40	0.07	84.9	9.1	9.4
3	3	15.0	7.03	1.43	0.08	54.0	24.8	25.7
	4	18.3	7.43	0.57	0.03	84.4	10.3	5.0
	5	15.0	7.50	0.89	0.04	75.1	14.1	8.9
	$\mathbf{1}$	21.0	7.55	0.69	0.03	77.5	10.9	12.2
	2	17.0	7.50	0.51	0.02	81.2	8.7	9.8
$\overline{4}$	3	18.0	7.54	0.84	0.02	68.6	12.8	15.4
	4	19.8	7.39	0.34	0.02	81.8	12.0	6.8
	5	16.4	7.59	0.73	0.02	78.7	10.6	10.8

## Soil characteristics

Soil properties of the five main vegetation units are presented in Table 1. In Table 2, soil variables are compared between the plantations and the natural forest. The organic matter content and nitrogen content of the first soil layer were significantly higher in the natural forest. In contrast, organic matter content, nitrogen content and clay content of the third soil layer were significantly higher in the plantations (Tab. 2). The plantations have also significantly higher clay content in the second and fourth soil layers.

# **Ordination**

The DCA ordination of all 60 relevés revealed a fairly clear distinction of the two main vegetation types, i.e. natural forest vs. plantations (Fig. 2a, Tab. 3). The relevés of the natural forest clustered on the right side of the plot, while those of the plantations occupied the middle and left part of the plot, with the relevés of the Robinia pseudoacacia plantations forming a distinct group at the extreme left. Along the vertical axis, a less distinct differentiation was related to the dominance of hardwood species in the upper part of the plot.

A separate ordination including only abandoned plantations revealed three main groups of relevés (Fig. 2b): those of *Robinia pseudoacacia* plantations (group 1), those of groups 2 and 3, and those of groups  $4-5$  (at the right part of Fig. 2b), while the two relevés of group 6 appeared as outliers. The first axis was related to topsoil pH and soil

L	Forest type	L.T. (cm)	pH	O.M. $\frac{9}{6}$	O.N. (%)	Sand $(\%)$	Silt (%)	Clay $(\%)$
1	Plantation	4.0	6.95	$5.97*$	$0.26*$	70.0	16.2	14.7
	Natural	4.8	6.94	12.57	0.49	68.3	19.4	9.8
2	Plantation	11.5	7.08	2.51	0.12	72.1	12.8	$14.4*$
	Natural	10.5	7.12	1.74	0.11	77.7	13.5	8.7
3	Plantation	15.0	7.32	$1.39*$	$0.08*$	77.4	9.6	$11.4*$
	Natural	15.8	7.46	0.68	0.03	82.8	12.1	6.2
4	Plantation	18.8	7.53	0.53	0.02	78.4	8.8	$11.7*$
	Natural	19.3	7.52	0.47	0.02	80.5	10.9	7.9

Tab. 2. Median values of soil properties per soil layer (L) in abandoned plantations and natural forest. Abbreviations are as in Tab. 1. Asterisks indicate significant differences between the two forest types within a layer (Mann-Whitney U test;  $\alpha = 0.01$ )

Tab. 3. Eigenvalues, gradients length and total inertia obtained from DCA of the entire data set or from separate DCAs for either plantations or natural forests (cf. Fig. 2).





Fig. 2. Ordination biplot of the first two axes of detrended correspondence analysis of (A) all relevés, (B) abandoned plantations, and (C) natural forest. Symbols represent vegetation relevés; group numbers correspond to those of App. 1. Arrows represent explanatory variables included in the ordination a posteriori: Relative cover abundance of trees (P.C., R.P., P.A., U.P., F.A.: Populus  $\times$  canadensis, Robinia pseudoacacia, Populus alba, Ulmus procera and Fraxinus *angustifolia* ssp. *oxycarpa*) and soil properties;  $pH =$  soil acidity, OM, ON = percentages of organic matter and organic nitrogen, respectively, multiplied by the thickness of the corresponding soil layer, S, Si,  $C =$  percentages of sand, silt, and clay; numbers used as indices to the soil variables represent the soil layers. Only variables presenting correlations with at least one of the first two axes higher than  $|0.4|$  are drawn.

texture, with the relevés on more basic and more clayey soils in the right part of the plot. The second axis was mainly determined by the two relevés of the  $6<sup>th</sup>$  group, which had a lower soil pH in the second to fourth soil layers.

The DCA of relevés of the natural forest revealed two main groups of relevés: those in which *Populus alba* dominated in the tree layers (groups  $7-8$ ), and those where hardwood species dominated in the tree layers (groups  $9-10$ ). In group 9, although Populus alba dominated in the tree layers, hardwood species also occurred. The first axis was related to soil texture (more loamy soils in the hardwood stands and more

sandy ones in the softwood stands) and organic matter content (higher in hardwood stands). The second axis was not clearly related to any of the soil variables.

## **Discussion**

## Floristic differentiation between plantations and natural forest

For the protection and restoration of riparian habitats, an important question is how forest plantations could serve biodiversity conservation in addition to timber production (Laquerbe 2000; Lust et al. 2001; Hartley 2002; Zerbe 2003). The plantations investigated here have been abandoned for at least 14 years, so that the floristic composition of the understory is no longer affected by perturbations from cultivation practices. Still, the frequency and cover of typical species of natural riparian forests are low in the abandoned plantations. Considering the small distances between relevés carried out in plantations and in natural forest stands (in many cases less than 100 m), their strong floristic differentiation indicates the low degree of naturalness of the abandoned plantations. Most differential species of the natural forest vegetation are typical riparian forest species, which have been recorded with high constancy in other riparian forests in Greece (Ahtanasiadis and Drossos 1992; Athanasiadis et al. 1996). On the other hand, many differential species of the plantations are typical of ruderal vegetation.

However, the constancy and abundance of natural species was not equally low in all plantations. The 5th group included more natural forest species (especially shrubs and lianas) than groups  $2-4$ , while the *Robinia pseudoacacia* plantations (group 1) had the lowest frequency and cover of natural riparian forest species. This differentiation inside the poplar plantations may be attributed to soil factors (mainly soil texture), while the floristic difference between the two planted tree species probably results from stronger shading in the *Robinia pseudoacacia* plantations. The latter had the second lowest species richness of all vegetation groups. Additionally, their floristic similarity with Robinia pseudoacacia plantations in Central Europe (Pott 1992; Mucina 1993), indicates that the high shading of the tree layer and the enrichment of soil with nitrate through atmospheric N fixation create particular ecological conditions that govern the understory composition.

The differentiation between plantations and natural stands varied among plant groups (McCune and Antos 1981; Sagers and Lyon 1997; Guillaume 2002). Most of the natural riparian species occurring in the plantations were shrubs or lianas (e.g. Cornus sanguinea ssp. sanguinea, Smilax excelsa, Tamus communis, Periploca graeca), while many species occurring exclusively in either natural forests or plantations were herbaceous species. This may be attributed to the fact that the herbaceous species are more dependent upon the topsoil, which is more degraded in the plantations than the deeper soil layers. Therefore, the regeneration of tree and shrub species inside forest plantations should only be used with caution as an indicator of the degree of naturalness or ecological functionality (Lust et al. 2001; Hartley 2002; Zerbe 2003).

#### Soil conditions and restoration implementations

The restoration of riparian forests must address the issue of the alteration of physical and chemical soil properties caused by land use change. Plantations had significantly lower organic matter and nitrogen content of the first soil layer than natural stands. The site preparation for the establishment of plantations as well as the relatively low production of litter by the plantations and the periodic removal of organic matter from the ecosystem through wood cutting cause a long-term reduction of the organic matter and nitrogen content of the topsoil (Alifragis et al. 2000). The destruction of riparian forests generally causes huge losses of soil organic matter and nitrogen (Armentano 1980; Lugo et al. 1990; Alifragis et al. 2000; Efthimiou 2000).

The fact that the plantations have significantly higher organic matter and nitrogen content in the third soil layer and clay percentage in the second to fourth soil layers may simply reflect the fact that the most sandy soils of the area were avoided when plantations were established. Alternatively, plants growing in plantations might be more deeply rooted (possibly because of the lower nutrient content of the topsoil). The decomposition of roots in deeper soil layers could then cause an increase in organic matter and nitrogen content.

Soil texture showed a parallel differentiation in plantations and natural stands. In both forest types, there was considerable variation in the clay content of the three upper soil layers. This differentiation was reflected in the species composition of the understory. Two main vegetation units were distinguished in the poplar plantations, occurring on sandy soils and loamy soils, respectively. Similarly, the two types of natural forest (softwood and hardwood stands) also differed in soil texture.

Therefore, the present floristic composition of the plantations can serve as a basis for a management aiming at the restoration of natural riparian vegetation. For example, the conversion of the plantations to natural forest could be assisted by the reforestation with native riparian tree species (Efthimiou 2000, Zerbe 2003). In this case, areas occupied by vegetation similar to that of the second unit (groups 2 to 4), should be reforested with Populus alba, while hardwood species should be regarded as more appropriate for the reforestation of areas with vegetation similar to that of the third unit (groups 5 and 6). Of course, the restoration of entire riparian communities, and not just of the tree layer, requires an increase in the organic matter content of the topsoil. For this reason, no tree biomass should be removed from the plantations, but it should be left on site (Efthimiou 2000, Hartley 2002).

The question whether the conversion of the plantations of the study area to natural forest is possible and, if so, how much time is needed, remains open. The regeneration of a natural riparian forest requires the restoration of hydrological and sediment input processes (Hughes et al. 2001). As the functional integrity of the river-floodplain complex is restored, biodiversity should follow (Ward et al. 1999). The regulation of the Nestos River has broken the abovementioned processes (Kotoulas 1991).

The remnants of the natural forest vegetation reflect ecological conditions existing before the river regulation; the more frequent occurrence of softwood stands in the eastern part of the study area can be explained by the old riverbed, which has now shifted 4 km westwards, in an area where fine sediments were being deposited in the past. Nevertheless, the river dikes prevent flood waters from affecting the forests of the study area. However, the natural forest stands seem to be well regenerated (Efthimiou 2000), probably because of the positive effect of a high water table. Today, there are initiatives for the restoration of a part of the natural forest of the Nestos River as well as

for the reflooding of certain areas, especially inside the protected area. This study as well as similar phytosociological studies could offer useful data and scenarios for the establishment of a biomonitoring plan aiming at the restoration of natural riparian forests and the investigation of the impact of management practices on the vegetation and biodiversity of riparian ecosystems.

#### Zusammenfassung

Die Umwandlung von Auwäldern in Plantagen schnellwachsender, nicht-einheimischer Baumarten (Populus  $\times$  canadensis, Robinia pseudoacacia) kann die Artenzusammensetzung des Unterwuchses sowie Bodeneigenschaften der Standorte verändern. Hierdurch wird möglicherweise die Regeneration natürlicher Wälder nach Aufgabe der intensiven forstlichen Nutzung verhindert. Am Nestos-Fluss in Nordost-Griechenland wurde untersucht wie sich ehemalige Plantagen mindestens 14 Jahre nach der Nutzungsaufgabe von natürlichen Waldbeständen unterscheiden. Wir führten 60 Vegetationsaufnahmen durch und bestimmten für jede Fläche die Bodenkörnung sowie chemische Eigenschaften des Bodens. Zusammenhänge zwischen dem Waldtyp (natürlich oder ehemalige Plantage), der Artenzusammensetzung des Unterwuchses und Bodeneigenschaften wurden mit Klassifikations-und Ordinationsmethoden analysiert.

Es gab eine klare floristische Differenzierung zwischen natürlichen Wäldern und ehemaligen Plantagen, besonders solchen von Robinia pseudoacacia. Der Oberboden der ehemaligen Plantagen enthielt weniger organisches Material und Stickstoff, viele Krautarten der natürlichen Wälder fehlten, und die Baumschicht wurde nach wie vor von den zuvor gepflanzten Baumarten dominiert.

Es gab aber auch einen natürlichen floristischen Gradienten in beiden Waldtypen, der durch die Bodenkörnung (sandige oder lehmige Sedimente) bestimmt wurde. Dieser Gradient wurde sowohl in den natürlichen Wäldern als auch in den ehemaligen Plantagen festgestellt. Obwohl sich in den ehemaligen Plantagen bislang nur ein Teil der natürlichen Waldarten angesiedelt hat, spiegelt deren Artenzusammensetzung den natürlichen Standortsgradienten bereits soweit wider, dass sie Hinweise für Massnahmen zur Wiederherstellung der natürlichen Wälder liefern kann.

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### References

Alifragis D., Papaioannou A. and Smyris P. 2000. Soil conditions of the riparian forest "Kotza Orman" of the Nestos River. Proceedings of the 8<sup>th</sup> Panhellenic Pedological Conference, Hellenic Pedological Society, Kavala, 276 - 292 (in Greek, with English abstract).

Armentano T.V. 1980. Drainage of organic soils as a factor in the world carbon cycle. BioScience 30: 825 – 830.

- Athanasiadis N. and Drossos E. 1992. Leucojo-Fraxinetum parvifoliae Glavač and Pruno-Fraxinetum Oberdorfer 53 of the Thessalian Pinios Delta (Greece). Bot. Helv. 102: 159 – 170.
- Athanasiadis N., Theodoropoulos K., Eleftheriadou E. and Drossos E. 1996. Forest plant communities of delta of Thessalian Pinios river. Scientific Annals of the Department of Forestry and Natural Environment 39: 881 – 902.
- Bremmer J.M. and Mulvaney C.S. 1982. Nitrogen-total. In: Page A.L. et al. (eds.). Methods of Soil Analysis. Part 2: Chemical and Microbial Properties. 2nd ed. ASA and SSSA, Madison, WI., 595 – 624.
- Carter M.R. 1993. Soil Sampling and Methods of Analysis. CRC Press LLC, USA.
- Décamps H., Fortune M., Gazelle F. and Patou G. 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecol. 1: 163 – 173.
- Dierschke H. 1980. Zur syntaxonomischen Stellung und Gliederung der Ufer- und Auenwälder Südeuropas. Coll. Phytosociol. 9: 115 – 129.
- Dierschke H. 1994. Pflanzensoziologie Grundlagen und Methoden. Ulmer, Stuttgart.
- Doyle A.T. 1990. Use of riparian and upland habitats by small mammals. J. Mammol. 71: 14 23.
- Efthimiou G.Sp. 2000. Analysis of stand structure, dynamics and ecological interpretation of riparian forests of Nestos. Ph.D. Thesis, Aristotle University of Thessaloniki, Thessaloniki (In Greek, with German and English abstract).
- Fleishman E., McDonal N., MacNally R., Murphy D.D., Walters J. and Floyd T. 2003. Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed. J. Anim. Ecol. 72: 484 – 490.
- Gee G.W. and Bauder J.W. 1982. Particle-size analysis. In: Klute A. (ed.) Methods of Soil Analysis, Part 1: Physical and Mineralogical Methods. 2<sup>nd</sup> ed. ASA and SSSA, Madison, WI., 383-411.
- Greuter W., Burdet H.M. and Long G. (eds.) 1984 1989. Med-Checklist 1, 3, 4. Conservatoire et Jardin botaniques, Genève.
- Guillaume D. 2002. Patterns of plant species and community diversity at different organization levels in a forested riparian landscape. J. Veg. Sci. 13: 91 – 106.
- Hartley M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155: 81 – 95.
- Hennekens S.M. and Schaminée J.H.J. 2001. TURBOVEG, a comprehensive database management system for vegetation data. J. Veg. Sci. 12: 589 – 591.
- Hill M.O. 1979. TWINSPAN a FORTRAN Program for Arranging Multivariate Data in an Ordered Two Way Table by Classification of the Individuals and the Attributes. Ecology  $\&$ Systematics, Cornell University, Ithaca, New York, USA.
- Hill M.O. and Gauch H.G. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47 – 58.
- Hughes F.M.R., Adams W.M., Muller E., Nilsson C., Richards K.S., Barsoum N., Decamps H., Foussadier R., Girel J., Guilloy H., Hayes A., Johansson M., Lambs L., Pautou G., Peiry J.- L., Perrow M., Vautier F. and Winfield M. 2001. The importance of different scale processes for the restoration of floodplain woodlands. Regul. Rivers – Res. Manage. 17: 325 – 345.
- Kakouros P. and Dafis S. 2005. Implementation Study for the Restoration of the Riparian Forest of Nestos. Greek Biotope-Wetland Centre, Thermi.
- Kotoulas D. 1991. Nestos River, physiognomy and river activity regarding natural environment – consequences. Proceedings of the conference "Nestos: Natural Environment and its Problems". Geotechnical Chamber of Greece, Kavala, 27 – 37 (in Greek).
- Laquerbe M. 2000. Richesse spécifique et phytomasse des sous-bois de peupleraies cultivées en bordure de Garonne (Sud-Ouest de la France). Ann. For. Sci. 57: 767 – 776.
- Lugo A.E. 1990. Introduction. In: Lugo A.E., Brinson M. and Brown S. (eds.). Forested Wetlands. Elsevier, Amsterdam, The Netherlands, 1 – 14.
- Lugo A.E., Brown S. and Brinson M.M. 1990. Concepts in wetland ecology. In: Lugo A.E., Brinson M. and Brown S. (eds.). Forested Wetlands. Elsevier, Amsterdam, The Netherlands, 53 – 85.
- Lust N., Kongs T., Nachtergale L. and De Keersmaeker L. 2001. Spontaneous ingrowth of tree species in poplar plantations in Flanders. Ann. For. Sci. 58: 861 – 868.
- McCune B. and Antos J.A. 1981. Correlations between forest layers in the Swan Valley, Montana. Ecology 62: 1196 – 1204.
- Micheli E.R., Kirchner J.W. and Larsen E.W. 2004. Quantifying the effect of riparian forest versus agricultural vegetation on river meander migration rates, Central Sacramento River, California, USA. River Res. Applic. 20: 537 – 548.
- Michelsen A., Lisanework N., Friis I. and Holst N. 1996. Comparisons of understorey vegetation and soil fertility in plantations and adjacent forests in the Ethiopian highlands. J. Appl. Ecol. 33: 627 – 642.
- Mountrakis M.D. 1985. Geology of Greece. University Studio Press, Thessaloniki (in Greek).
- Mucina L. 1993. Galio-Urticetea. In: Mucina L., Grabherr G. and Ellmauer T. (eds.). Die Pflanzengesellschaften Österreichs. Teil. 1. Anthropogene Vegetation. Fischer, Jena, 203 – 251.
- Nelson D.W. and Sommers L.E. 1982. Total carbon, organic carbon and organic matter. In: Page A.L. et al. (eds.). Methods of Soil Analysis. Part 2: Chemical and Microbial Properties. 2nd ed. ASA and SSSA, Madison, WI., 39 – 579.
- Papaioannou I. 1953. The Kotza-Orman Forest. Eklogi, Athens (in Greek).
- Pott R. 1992. Die Pflanzengesellschaften Deutschlands. Ulmer, Stuttgart.
- Ramovs B.V. and Roberts M.R. 2005. Response of plant functional groups within plantations and naturally regenerated forests in southern New Brunswick, Canada. Can. J. Forest Res. 35: 1261 – 1276.
- Renöfält B.M., Nilsson C. and Jansson R. 2005. Spatial and temporal patterns of species richness in a riparian landscape. J. Biogeogr. 32: 2025 – 2037.
- Sagers C.L. and Lyon J. 1997. Gradient analysis in a riparian landscape: contrasts among forest layers. For. Ecol. Manage. 96: 13 – 26.
- Strid A. (ed.) 1986. Mountain Flora of Greece, Vol. 1. Cambridge University Press, Cambridge.
- Strid A. and Tan K. (eds.) 1991. Mountain Flora of Greece, Vol. 2. Edinburgh University Press, Edinburgh.
- Strid A. and Tan K. (eds.) 1997, 2002. Flora Hellenica, Vols. 1 2. Koeltz, Königstein.
- ter Braak C.J.F. and Smilauer P. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, USA.
- Tichý L. 2002. JUICE, software for vegetation classification. J. Veg. Sci. 13:  $451 453$ .
- Tutin T.G. et al. (eds.) 1968 1993. Flora Europaea. Vols.  $2-5$  and Vol. 1,  $2<sup>nd</sup>$  ed. Cambridge University Press, Cambridge.
- Ward J.V. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. Biol. Conserv. 83: 269 – 278.
- Ward J.V., Malard F. and Tockner K. 2002. Landscape ecology: a framework for integrating pattern and process in river corridors. Landscape Ecol. 17: 35 – 45.
- Ward J.V., Tockner K. and Schiemer F. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regul. Rivers – Res. Mgmt.  $15: 125 - 139$ .
- Wilmanns O. 1989. Ökologische Pflanzensoziologie, 4, Aufl. Quelle & Meyer, Heidelberg.
- Zerbe S. 2003. Vegetation and future natural development of plantations with the Black poplar hybrid Populus  $\times$  euramericana Guinier introduced to Central Europe. For. Ecol. Manage. 179: 293 – 309.



App. 1. Relevés table. Taxa occurring in 1 or 2 relevés were omitted. L: vegetation layer (1: canopy trees, 2: understory trees, 4: high shrubs, 5: hour channels of the process indicated throw of the channel of the process



![](_page_15_Picture_16.jpeg)

![](_page_15_Picture_17.jpeg)

![](_page_16_Picture_9.jpeg)

![](_page_16_Picture_10.jpeg)

App. 1. (continued)

![](_page_17_Picture_9.jpeg)