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A quantitative survey of the propagation strategy of *Populus nigra* L. stands and its relation to successional processes within a riparian ecosystem along the lower river Allier (France).



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Abstract

The European black poplar (*Populus nigra* L.) is a riparian tree species that dominates the early successional stage of alluvial floodplain forests throughout Continental Europe. In the past decades, river management activities and the plantation of hybrid poplars contributed substantially to the loss of this species. Measurements to preserve *P. nigra* are of everincreasing importance but must relate to the restoration of its natural habitats and the concluding natural dynamics. *P. nigra* is able to propagate either generative or vegetative and therefore enhances its chance to be preserved in riparian forests in the future. The aim of this work was to quantitatively assess the dominant propagation strategy of black poplar stands and related successional processes within the floodplains of the lower river Allier. Two main approaches were taken for this assessment: Firstly, the analysis of the structural organisation of stands, regarding the age distribution within stands and, secondly, the retrospective analysis of successional processes and how they are related to the applied propagation strategy. Structural stand patterns have been proven to be valuable indicators to determine the dominant propagation strategy of black poplars, as if vertical heterogeneity within a stand indicates the occurrence of clones. From a total of 329 ha that have been analysed, 71 ha have been identified as sites where *P. nigra* established dominantly in an asexual manner. Furthermore it was proven, that grassland areas within the study reach are rather colonized by vegetatively recruited *P. nigra* individuals than by generative recruits.

Keywords: *Populus nigra* L., propagation strategy, floodplain age, vegetation succession, clonality, stand structure

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1 Introduction

Natural riverine floodplains number among the most precious ecosystems on earth, regarding their high biological productivity and diversity (Tockner & Stanford, 2002; Dickmann & Kuzovkina, 2013). As a consequence of river regulation many large European rivers have been physically degraded in the past (Buijse et al., 2005). Nowadays, unaltered floodplains count for the most threatened living spaces worldwide (Tockner & Stanford, 2002) and are as a consequence hard to find.

With the loss of natural/ semi-natural river systems, poplars (*Populus spp.*), simultaneously become less abundant (Cottrell et al., 2005) and loose suitable habitats for regeneration (Mahoney & Rood, 1991; Braatne et al., 1996; Shafroth et al., 1998; Barsoum, 2001; Benjankar et al., 2014). The European black poplar (*Populus nigra* L.) dominates, together with other Salicaceae species and *Alnus incana*, the early successional stage of alluvial forests in many temperate floodplain areas (Vanden Broeck, 2003). Within the riparian zone, the black poplar acts as an ecosystem engineer. By trapping and stabilizing sediments it is able to influence fluvial geomorphology, facilitate (even its own) colonization and change local physical conditions within the colonized floodplain areas (Gurnell, 2014; Corenblit et al., 2016). The black poplar is widely spread throughout Europe (excluding Scandinavia) with a distribution ranging from North Africa in the south to West Asia in the east (Aas, 2006). However, it counts for the rarest and most vulnerable tree species in Western and Central Europe (Cagelli & Lefèvre, 1997; Pospíšková & Šálková, 2006). According to Lefèvre et al. (1998) three main factors are driving the threat of black poplars in Europe. First, the modification of riparian ecosystems, by displacing native stands for the purpose of agriculture or other human causes. Further, hydraulic engineering practices, such as flood regulation, that favour later successional hardwood forests over black poplars in the remaining wild areas. Second, fast growing hybrid poplars replace autochthonous black poplar resources, or these resources have been overexploited, and have therefore been removed. Third, gene introgression from cultivated hybrid poplars leads to the loss of this species.

Populus nigra L. is a dioecious pioneer tree species with wind or water dispersed seeds, covered in lightweight hydrophobic cotton (Legionnet et al., 1997), that are released between June and July (Reichholf, 2006). Generative recruitment is episodic

and even along natural/ semi-natural rivers relatively rare because seedling viability is short (Aas, 2006) and closely linked to soil moisture (Mahoney & Rood, 1998). When germination is successful, seed propagated individuals colonize floodplains, wastelands or other open or barren sites, that are dominated by moist and sandy soil as it is exposed after seasonal flood events (Dickmann & Kuzovkina, 2013; Egger et al., 2015). Within riverine landscapes, generative recruits establish on low-lying point bars (Corenblit et al., 2016) and mainly form linear belts along the rivers' shoreline (Legionnet et al., 1997). Adult black poplar stands are not able to germinate and establish below their own canopy, what results in a decrease of age variety among established stands (Fierke & Kauffman, 2005), overaged floodplain forests (Brunnering & Reichholf-Riehm, 2011) and the evolvement towards hardwood forests (Lefèvre et al., 1998).

Apart from generative reproduction, the black poplar is capable of asexual propagation. So called, clonal propagation can either occur by shoots, growing as the extension of an adult plant, or independently, when fragments of a parent plant are relocated, or the shoots/roots are disconnected from another plant (Barsoum et al., 2004). The trophic relatedness of adventitious shoots to a parent plant is favourable and results in an enhanced vitality of these cohorts (Legionnet et al., 1997). Besides that, vegetative recruits do have advantages over seed distributed individuals: e.g. a higher potential survival rate at high elevations, away from flood waters, but as well at low elevations with rapidly receding groundwater tables, or at river reaches that are disturbed by high magnitude floods during the phase of seedling establishment (Barsoum, 2002; Braatne et al., 2007). Contributing to that, several studies ascertain that asexual recruits are favoured over seed distributed individuals because of their lower susceptibility for fluvial dynamics, resulting from a higher initial growth and even higher survival rate (Legionnet et al., 1997; Barsoum et al., 2004; Douhovnikoff et al., 2005; Moggridge & Gurnell, 2009).

These results offer vital evidence for the role of vegetative propagation contributing substantially to the rejuvenation strategy of black poplars. However, their propagation strategy is highly adapted to the riparian environment. Seedlings can establish at freshly exposed sites, whereas clonal individuals facilitate recovery from fluvial disturbances and provide intra-stand maintenance (Gom & Rood, 1999b). Though, micro-environmental conditions such as water availability, substrate composition and the disturbance regime are contributing factors for sites, favouring either seedlings or

vegetative rejuvenation (Braatne et al., 1996; Legionnet et al., 1997).

Legionnet et al., (1997) stated, that the occurrence of asexually recruited individuals can be predicted by the nature of the stand. Dense, homogeneous stands are characteristic for seedling recruitment, while less dense stands with rather shrubby trees indicate the occurrence of clones. Vegetative sprouting is frequent beneath the canopy of mature stands and results in a heterogeneous age and heterogeneous vertical stand structure. Besides that, a higher amount of clones within a population leads to a higher degree of heterogeneity concerning the spatial distribution of individuals within a stand (Gom & Rood, 1999b). Until present, numerous studies have analysed black poplar stands regarding their genetic diversity or cross-population gene flows (Legionnet & Lefèvre, 1996; Legionnet et al., 1997; Imbert & Lefèvre, 2003; Pospíšková & Šálková, 2006; Smulders et al., 2008). Gom and Rood (1999a) used morphological and phenological characteristics and subsequently related their results to the structural organization of analysed populations (Gom & Rood, 1999b). Wendelgaß (2016) investigated the manner of reproduction on the basis of four reference areas within the current research area. The results show, that higher amounts of vegetatively rejuvenated black poplars more frequently occur in dry areas (concerning soil moisture conditions) and that with an increasing amount of clones a heterogeneous stand structure (concerning age, height and horizontal organisation of poplars within stands) is concomitant. However, previous work has failed to draw quantitative conclusions regarding the applied rejuvenation strategy of black poplars at large-scale, or even beyond stands' boundaries.

Because of the significant ability of black poplars to rejuvenate either vegetative or generative, it enhances its chance to be preserved in floodplain forests in the future (Legionnet et al., 1997). But the most important measures to ensure regeneration and the preservation of this species is to restore its natural habitats and the concluding natural dynamics (Smulders et al., 2008; Rood et al., 2005), as they can still be found along the natural/ semi-natural Allier river.

Within the floodplains of the Allier, vigorous populations of the European black poplar appear in stands of all size and age classes. This fact makes the Allier a reference system concerning biological functioning and hydromorphology (Van Looy et al., 2008). Besides that, it is an up to date reference system to study near natural riparian plant succession (Garófano-Gómez et al., 2017). Furthermore, there is proven evidence that, within the current research area, hybridisation is absent. Wendelgaß (2016) genetically

determined, that all analysed black poplars (n=383) belonged to the *Populus nigra* L. species. This fact classifies the Allier as a unique opportunity to study black poplar individuals or stands and their contributing structural patterns within its natural living environment.

The Allier is a highly dynamic river that transports large amounts of bed-load during flood events (mainly sand and gravel) and therefore permanently changes its morphology (Baptist & de Jong, 2005). Extensive gravel areas are resulting riverscape features that evolve after the vegetation on previous alluvial bars was destructed (Corenblit et al., 2014). According to Garófano-Gómez et al. (2017) these gravel areas are, especially during the summer months, extremely dry and stay open for a long period of time. One of a few riparian plants that are able to colonize these harsh areas is the black poplar, in this case, mainly by vegetative propagation. Apart from gravel areas, large grassland areas can be found throughout the floodplains of the Allier. Garófano-Gómez et al. (2017) further stated that these grassland areas could evolve when fresh soil was deposited over former gravel bars where no favourable conditions for seedling establishment of the black poplar could be found. The aim of this thesis is to investigate if either vegetative or generative reproduction was the dominant propagation strategy of *Populus nigra* L. stands within the floodplains of the lower river Allier and which successional processes are related to the manner of reproduction.

Concluding from this main approach we hypothesize that:

- i.) The establishment of black poplar stands proceeds at a varying pace, in terms of either dominantly vegetatively or dominantly generatively reproduced stands.
- ii.) The age distribution of *Populus nigra* stands is different in regard to either vegetative or generative recruitment.
- iii.) The age of the sites on which *P. nigra* stands occur either sexual or asexual is different.
- iv.) The successional processes that either dominantly vegetative or dominantly generative stands run through are different.
- v.) Present grassland areas within the study site are rather colonized by dominantly vegetatively rejuvenated *P. nigra* individuals than by dominantly generatively rejuvenated individuals.

To achieve this, two approaches were applied: i.) the development of a scheme to assess clonality among established black poplar stands by combining the genetically derived results of Wendelgaß (2016) with an area-wide mapping of black poplar stands and their contributing structural organisation patterns; and ii.) the interpretation of aerial-images covering the past 60 years with a subsequent retrospective analysis of successional pathways.

2 Study site and methods

2.1 Study site and hydrometeorological characterisation

The river Allier has its source at 1485 m.a.s.l. in Lozère, situated in the Massif Central (southeast France) flowing south to north with a total flow length of 425 km. See Figure 2 for an overview map and the location of the river Allier within France. The Allier is the left tributary of the river Loire and is joining it at Bec d'Allier (67 m.a.s.l.). The climate is temperate and characterised by warm summers and the lack of a dry season (Cfb, Köppen-Geiger climate classification) (Peel et al., 2007). It is as a rain fed river with an unforeseeable discharge course (Geerling et al., 2006). The annual rainfall averages at 779.5 mm (based on the years 1981-2010) with highest precipitation rates in May (98,2 mm) and lowest in February measured at the meteorological station in Vichy (source: www.meteofrance.com, 2017). The mean annual discharge is $134 \text{ m}^3\text{s}^{-1}$ over the period of 1968-2017 at Moulins. Peak discharges up to $1600 \text{ m}^3\text{s}^{-1}$ occur once every 50 years and $1000 \text{ m}^3\text{s}^{-1}$ once every five years at Moulins (source: www.hydro.eaufrance.fr, 2017). According to Gautier et al. (2000) intense flood events occurred before the 20th century and induced major changes in the riparian corridor.

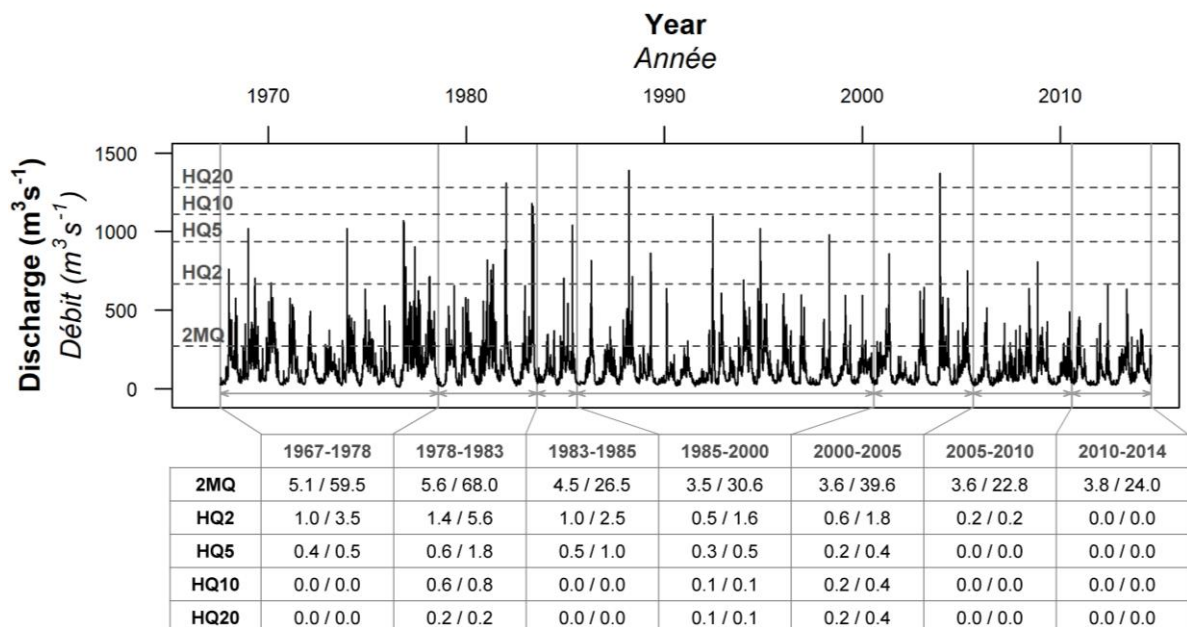


Figure 1: Mean daily discharge of the Allier (1968-2014) measured at Moulins and partly reconstructed from discharge registered at Cuffy station for missing periods at Moulins (produced by Garófano-Gómez et al., 2017; source: Banque Hydro)

The study site encompasses a 3.7 km long and 0.5- 1.5 km wide river stretch that is located within the *Réserve Naturelle du Val d'Allier* (<http://www.reserves-naturelles.org/val-d-allier>) which is declared as such since 1994. The area is situated 8 km south of Moulins and has an average altitude of 210 m.a.s.l. Before the 1990s the area was used for intensive grazing (Garófano-Gómez et al., 2017). The river system of the Allier can be denoted as climate sensitive which responds to glacials by aggradation in a braided river system and incision in a rather meandering system whilst interglacials (Veldkamp et al., 2004). There is no navigation and the main channel within the study site is not regulated or excavated (Geerling et al., 2006). Though, two upstream dams alter the discharge regime: Naussac, working since 1983 and Poutès, constructed in 1941.

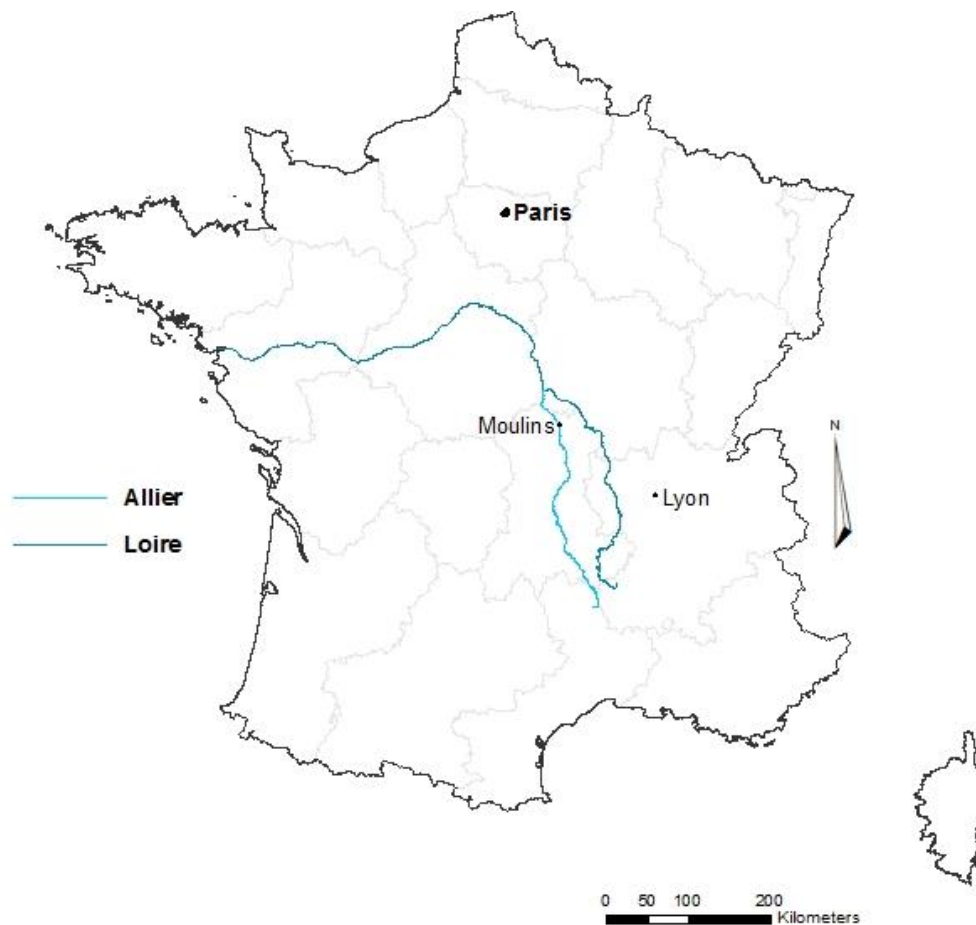


Figure 2: Location overview. River Allier, France. Coordinate System ETRS 1989 LAEA. Coordinates of study area: NE: 725732, 6602220; SW: 724814, 6598499 (Data source: www.eea.europa.eu).

2.2 Rejuvenation strategy assessment

2.2.1 Field mapping

In 2014, Metz (2015) defined homogeneous polygons (patches) and mapped ecologically functioning types, organized into succession series as well as 18 different vegetation types and primary/secondary succession phases throughout the current research area. These polygons and an aerial image from 2013 (source: Centre Régional Auvergnat de l'Information Géographique) were used to map *Populus nigra* L. stands area-wide in the field (1:2000, November 2016). The following variables were recorded: vegetation cover of tree, shrub, herb and moss layer. Further the coverage of black poplars within each polygon as well as the average percentage of individuals within a height class (<1m, 1-5m, 5-15m, 15-25m, >25m).

For each polygon the largest and thickest, as well as the smallest individual of target tree species have been selected to measure diameter at breast height, height (Nikon Laser 550 AS) and to sample increment cores for a subsequent dendrochronological analysis of the tree age. The sturdiest poplar of a stand was considered to be the oldest, as well, the smallest was considered to be the youngest tree within an assessed homogeneous stand (see chapter 2.3.4 for correlating height and age characteristics of analysed poplars). Small individuals of which no increment cores could be sampled, the diameter was measured at ground height and the age was estimated by counting the number of annual shoots or growth rings. Additionally, the percentage of black poplars with multiple trunks within each mapping unit was recorded.

In the course of the area-wide mapping, a scheme was applied to classify stands into three different age ranges: young stands (< 15 years), medium to old stands (15- 80 years) and old single individuals within young hardwood forests (> 80 years). Further, medium-old stands were assigned into four categories, depending on their vertical stand structure (see Table 1). Young stands were divided into primarily vegetative, primarily generative or mixed type stands. On a random basis roots of saplings were dug out to examine subterranean connection to parent trees, as mentioned by Legionnet et al. (1997).

Table 1: Categorisation scheme for the mapping of medium-old black poplar stands

Type 1	>60 % coverage (closed stands), homogeneous vertical structure (trees of a stand are approximately within the same height class, three or less height-classes)
Type 2a	25-60 % coverage, homogeneous vertical structure
Type 2b	25-60 % coverage, heterogeneous vertical structure (stand with three or more height- classes)
Type 3	<25 % coverage (open stands), heterogeneous vertical stand structure

2.2.2 Structural parameters for clonality

In the wake of a previous study, Wendelgaß (2015) assessed coordinates, age, height, crown diameter, diameter at breast height, the propagation strategy followed, geographical minimum distances and the genetic relationship of *P. nigra* individuals within four predefined stands (reference areas). The results and the derived data of this baseline study have further been processed and were used to quantitatively assess clonality within the current research area by means of the vertical organization of black poplar stands.

In the first instance, a graphical display of the amount of height classes and the percentage of clonal individuals within an aforementioned reference stand was carried out (see Figure 3).

Derived from these results, a scheme was developed that included the percentage of individuals within a height class of each stand mapped in the field (see chapter 2.2.1), the occurrence of saplings (individuals < 1m height) and a heterogeneous vertical stand structure, as an indicator for clonal reproduction. As dense, homogeneous stands (concerning age and height) are characteristic for seedling recruitment (Legionnet et al., 1997; Gom & Rood, 1999b) the appearance of more than three height classes was used as an indicator for clonality. This classification was exclusively applied to medium-old black poplar stands. By considering only stands with more than three height classes as stands that propagated dominantly vegetative, poorly grown individuals, due to e.g. interspecific competition, have largely been excluded. The assignment of categories and the graphical display have been processed in *Excel*, *ArcGIS 10.4.1* and *SPSS* (IBM v.21, 2012).

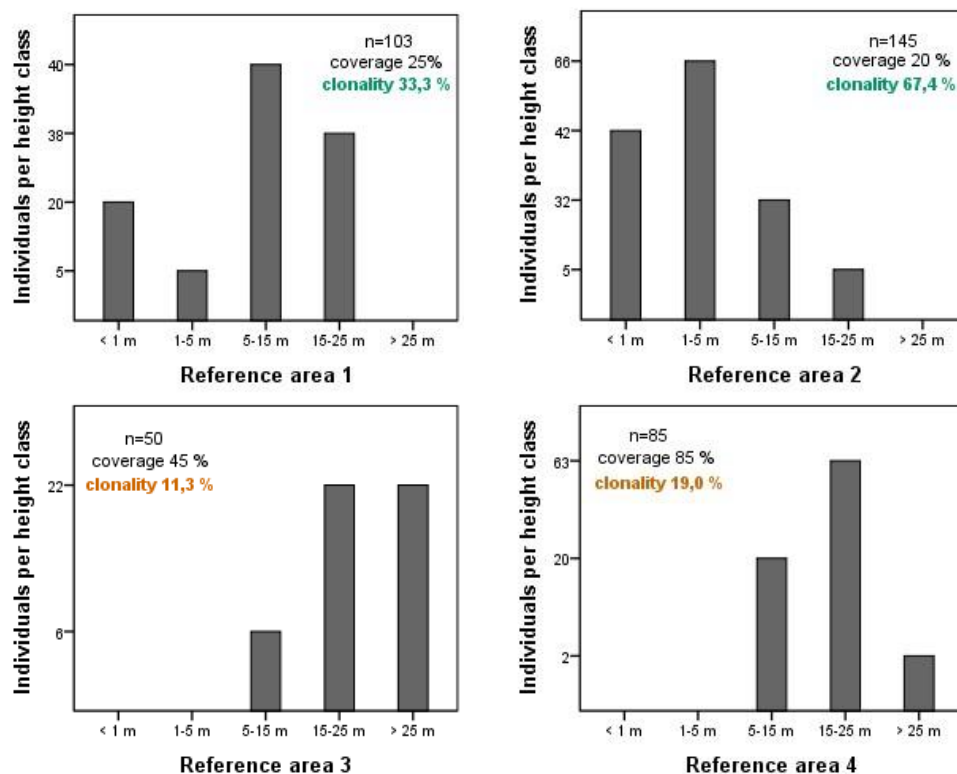


Figure 3: Amount of individuals per height class and percentage of clonal individuals within assessed areas (raw data: Wendelgaß, 2015).

2.3 Retrospective analysis

Geerling et al. (2006) ecotope mapped historical aerial images covering the current research area. Schwarzmeier (2015) and Garófano-Gómez et al. (2017) extended the time span of interpreted aerial images, now comprising the years 1954, 1960, 1967, 1978, 1983, 1985, 2000, 2005, 2010 and 2014.

Garófano-Gómez et al. (2017) further classified the ecotopes of Geerling et al. (2006) by vegetation types (see Table 2). These types were used to complement the time series and interpret a missing aerial image from 1992 (data: www.géoportail.gouv.fr) with *ArcGIS 10.4.1*.

Table 2: Classified ecotopes by vegetation types (Garófano-Gómez et al., 2017)

Ecotope	Vegetation type
Water	River & stillwaters
Bare soil	Gravel, Sand, Silt/mud
Pioneer	Pioneer grass, Pioneer sedum, Pioneer forbs, Pioneer shrubs
Grassland	Reed, Forbs, Grasslands
Bush	Willow shrub, Cottonwood shrub, Willow-cottonwood shrub, <i>Prunus/Crataegus</i> shrub
Forest	White willow forest, Black cottonwood forest, Willow-cottonwood forest, Willow/cottonwood-oak-elm forest, Oak-elm forest, Oak-Robinia forest

With a consistent set of digitised historical maps, shapefiles have been rasterized (5*5m) converted to points and spatially joined to amalgamate historical data into point features. Though, time gaps between analysed historical maps existed and consequently impeded to state the exact amount of years, the floodplain age (chapter 0) as well as the duration of constantly remaining vegetation types (chapter 0) were defined as a minimum and maximum amount of years.

By assigning codes to the ecotopes and vegetation types (Table 2) an analysis of the historically preceding ecotopes was carried out by using *Excel* and the statistical program *R*. For the analysis in *R* a script was written by the statistical expert Pamela Baur, including if-else queries, loop-functions and calculations.

2.3.1 Floodplain age

Along unregulated rivers and by the absence of forestry, riparian softwood trees as of the *Salix* spp. and *Populus* spp. can be considered as high-quality indicators for the age of a site (Alestalo, 1971 cited in Corenblit et al., 2014), as primary succession of riparian vegetation starts with the colonization stage on barren alluvial bars (=age 0) (Egger et al., 2015). Concluding from that, the ecotope type 'bare soil' was used for the analysis of the sites' minimum age. To obtain the maximum age the ecotope type 'water' was considered as the earliest starting point for successional processes. Each patch mapped in the field was divided into point features, as mentioned in chapter 2.3, and was then retrospectively analysed to obtain the year in which each point most recently was in its 'bare soil' or 'water' phase.

Egger et al. (2013) defined three succession stages valid for northern hemisphere floodplains which consist out of several phases sequencing as: Initial Phase, Pioneer Phase, (Herb-) Shrub Phase, Early Successional Woodland Phase, Established Forest Phase and Mature Forest Phase. Patches of which their attributed vegetation type did not follow these approved succession phases have been excluded from the analysis. Every time step back to the past, beginning with the year 2014, has been tested towards its sequence of succession phases. To avoid the exclusion of a data record because of the misinterpretation of a single year (historical image), a record was kept if there was merely one interpreted successional phase divergent to the phases in the years before. Evaluated data has been visualized in SPSS (IBM v.21, 2012) and displays the minimum (Figure 14) and the maximum (Figure 15) age per assessed vegetation type.

2.3.2 Constant vegetation type

To assess the amount of time of vegetation types remaining unchanged as this type, another query was defined to retrospectively analyse the historical data. Starting point of the analysis was the year 2014 wherefrom each record was traced back to the past until another vegetation type appeared. E.g. vegetation type 'grassland' in 2014, 'grassland' since 1985, 'bare soil' in 1983: equals 29 years minimum and 31 years maximum of how long this point constantly remained as a 'grassland' area (see Figure 16).

2.3.3 Succession duration

By deducting the average amount of years of the constant vegetation type (chapter 2.3.2) from the minimum age of a site (chapter 0), the succession duration of specific vegetation types could be acquired. It is supposed that the time-span between the latest starting point of successional processes (bare soil) and the earliest time, each vegetation type started to ground, reveals how long the vegetation type needed to establish (see Figure 17).

2.3.4 Dendrochronological analysis

The maximum tree age of *P. nigra* individuals of analysed stands was determined by a dendrochronological assessment. For each polygon mapped at least one increment core was sampled and analysed with a digital positiometer Type 1 by K. Johann. The age of poplars of which no increment core could be sampled was determined by counting the number of annual shoots or growth rings (see appendix for the share of black poplars within a height class).



Figure 4: Correlation of the height and the evaluated tree age of black poplar individuals within a polygon assessed in the field.

The highest value ($R^2 = 0.896$) has been obtained by correlating the measured height and the dendrochronologically evaluated maximum tree age (see above). This correlation was used to apply the categorisation scheme for clonality and to classify stands regarding their approximate age distribution in the field (Chapter 2.2.1.).

2.3.5 Point of establishment

To assess the starting-point of stand formation and its relation to the dominant propagation strategy of black poplar stands, calculations were carried out, involving the minimum floodplain age (Chapter 0) and the dendrochronologically assessed maximum tree age (Chapter 2.3.4). It is assumed that age margins, that result when deducting the maximum tree age from the minimum floodplain age, reveal how long stands needed to ground, after the river left its previous course and created new habitats. Calculations refer to point features (see chapter 2.3) that have been processed in *ArcGIS 10.4.1*. and individually represent an area of 0.025 hectare. An Example for this calculations can be found in the appendix. The results of this assessment have been combined with the previously described assessment of the dominant propagation strategy of stands within the research area (see Chapter 3.1.3).

3 Results

3.1 Rejuvenation strategy

3.1.1 Field mapping & vertical stand structure

The total analysed area of the free-flowing tract of the river Allier comprises 329 ha. By applying the categorisation scheme for clonality (Chapter 2.2.2) a total of 164 ha (50.2 %) have been identified as sites with the occurrence of *P. nigra* individuals or stands. By combining the results of the field assessment with the categorisation scheme, a map was created displaying the distribution of stands and their dominant propagation strategy, summarised into homogeneous polygons (see Figure 5). 71 ha (equals 21.6 % of the total area) dominantly rejuvenated in a vegetative manner, 70 ha (21.3 %) generatively and another 24 ha are characterised by the occurrence of single old trees (>80 years) within young successional hardwood forests.

Of all medium-old stands which have been propagated by seeds 83.3 % were determined to occur within closed softwood forests (>60% coverage). Young generative stands cover an area of 23.8 ha. About 56% of these generative stands established on bare soil (gravel) and 38 % on grassland areas. By comparing the map of the rejuvenation strategies with the map of floodplain ages (Figure 12 & Figure 13) it was found out that most of these grassland areas developed maximum four years ago (closed to the river grassland areas) and can therefore be considered as only recently evolved floodplain areas.

In total 94% (66.7 ha) of medium-old and vegetatively propagated *P. nigra* stands established on present (2014) grassland areas. These grassland areas tend to have a higher age, concerning the evolvement of sites (see chapter 0).

Table 3: propagation types of black poplar stands and share of preceding vegetation types

dominant propagation strategy	area [ha]	share of vegetation type assigned 2014 [ha]
vegetative (young)	4.7	Grassland 2.2 Pioneer grass 1.04 Silt/mud 0.9 others 0.56
vegetative (medium-old)	65.9	Pioneer 2.72 Pioneer forbs 0.9 Grassland 44.09 Prunus/Crataegus shrubs 3.6 Black cottonwood forest 7.57 Willow-cottonwood forest 5.67 others 1.35
generative (young)	23.8	Gravel 11.84 Sand 0.75 Grassland 7.35 Cottonwood shrub 2.7 other 1.16
generative (medium-old)	45.6	Prunus/Crataegus shrubs 0.7 Black cottonwood forest 37 Willow-cottonwood forest 1.5 Oak-elm forest 6.32 others 0.08
old single <i>P. nigra</i> individuals	24.4	Prunus/Crataegus shrubs 11.1 Willow/Cottonwood-oak-elm forest 5.8 Oak-elm forest 7.37 others 0.13

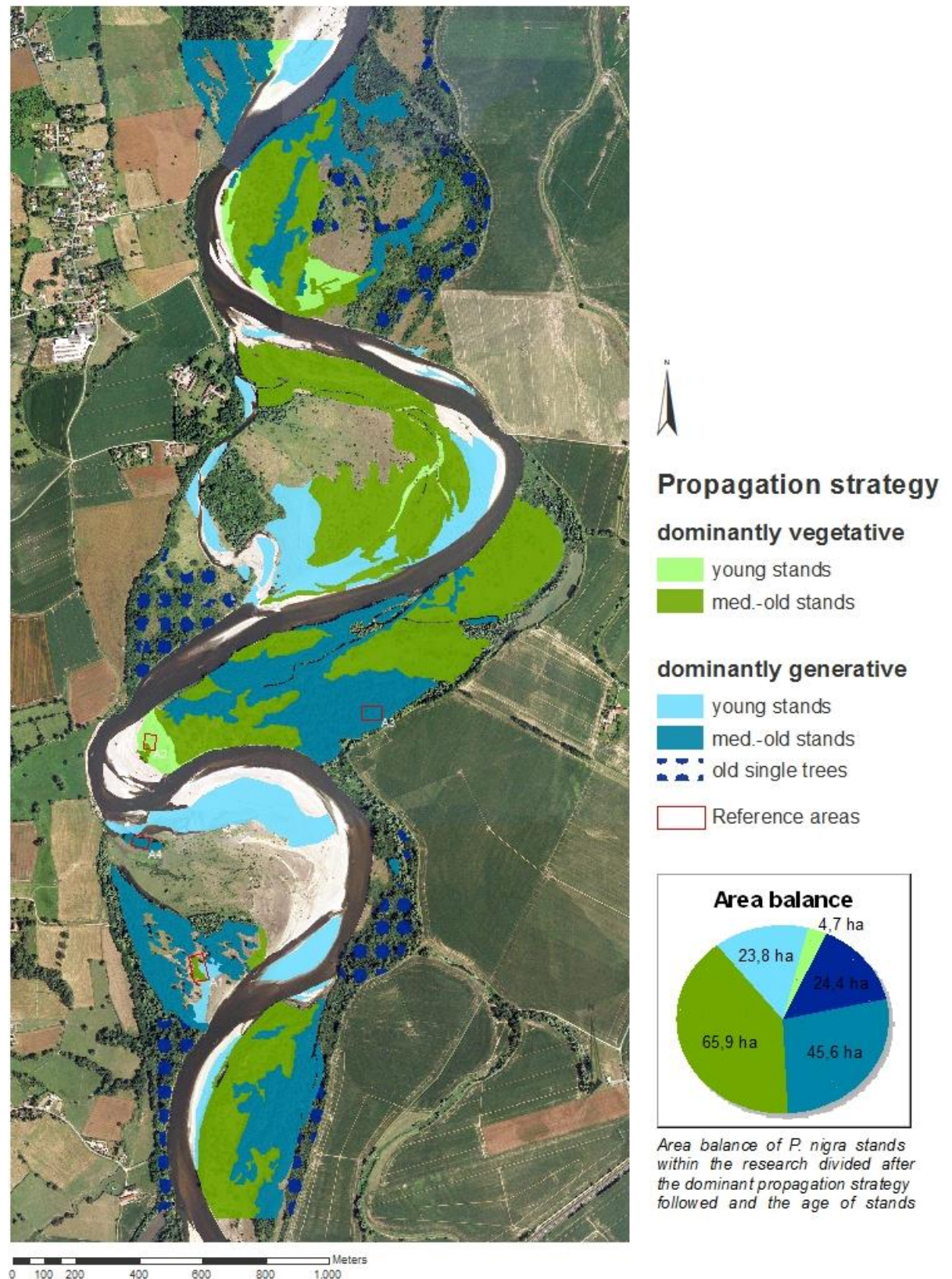


Figure 5: Assessed propagation strategy of *Populus nigra* L. stands within the research area, divided into homogeneous polygons. Areas not covered by black poplar stands have not been considered in this map.

3.1.2 Propagation strategy & Retrospective analysis

The following figures display results of the retrospective assessments divided into dominantly vegetatively (left) and dominantly generatively (right) propagated black poplar stands. In Chapter 3.2.1 another retrospective analysis can be found, including all vegetation types that have been mapped by Metz (2015) in 2014.

Figure 6 displays the minimum age of sites as mentioned in Chapter 0. Dominantly vegetatively established *P. nigra* stands, more frequently occur on grassland areas, wherefore only this figure illustrates the minimum age of grassland areas. The interquartile range lies between 4 and 29 years and therefore indicates a rather old minimum floodplain age of these areas. By comparing dominantly sexual and asexual black cottonwood forests, there is clear evidence that generative stands have a higher minimum age (interquartile range between 22 and more than 60 years) what states that the areas on which these stands were found evolved a longer timer ago (dom. vegetatively propagated stands between 9 and 36 years (interquartile range)). Willow-Cottonwood forests of dominantly generatively rejuvenated stands reveal an overall higher floodplain age as well.

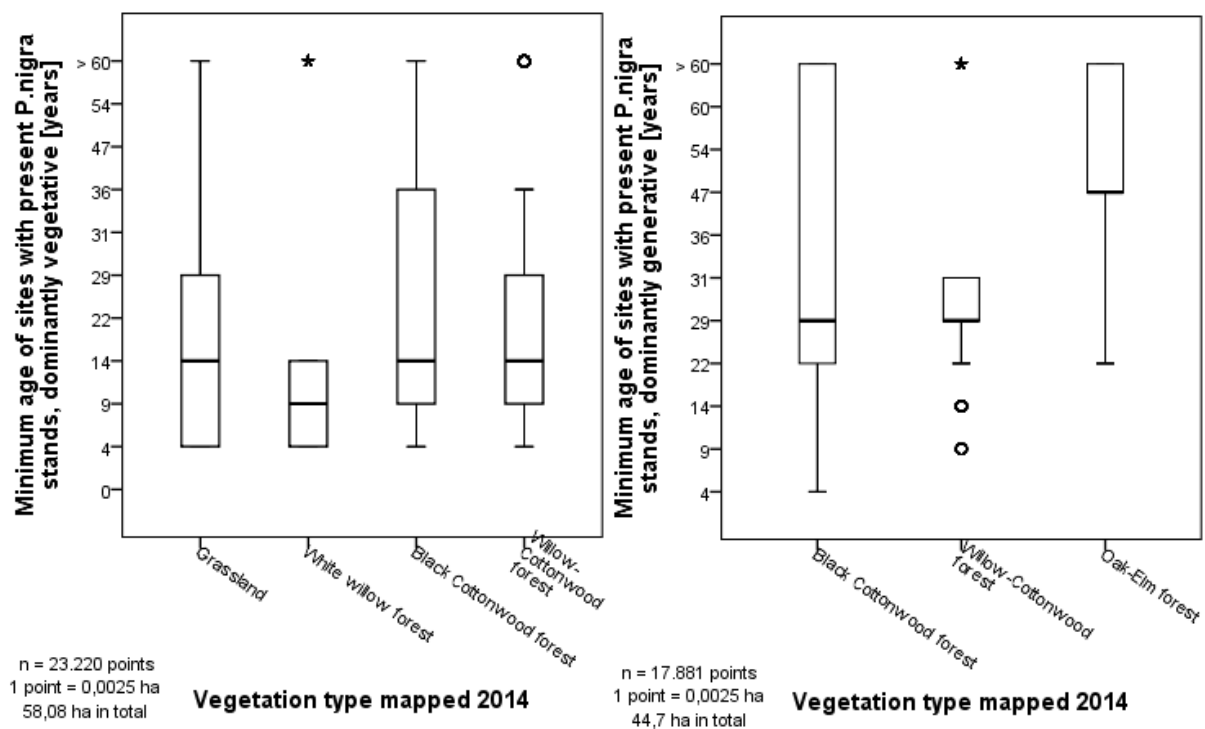


Figure 6: Retrospectively analysed *P. nigra* stands, divided into dominantly vegetatively (left) and dominantly generatively (right) propagated stands.

The maximum age of sites (Chapter 0) was derived by retrospectively looking for the formerly attributed type 'water'. Grassland areas on which vegetatively propagated black poplar stands occur, reveal a comparably high maximum age (median at 36 years). As if generatively propagated stands, hardly ever occurred on such sites, there is no evaluation of the maximum age of dominantly generatively rejuvenated stands.

Vegetatively propagated black cottonwood forests as well reveal a higher floodplain age when comparing it to generatively propagated stands (interquartile range: 31- 60 years, compared to 22- 47 years (vegetatively)). The overall areas tend to reveal higher ages when considering black poplar stands that established in a generative manner.

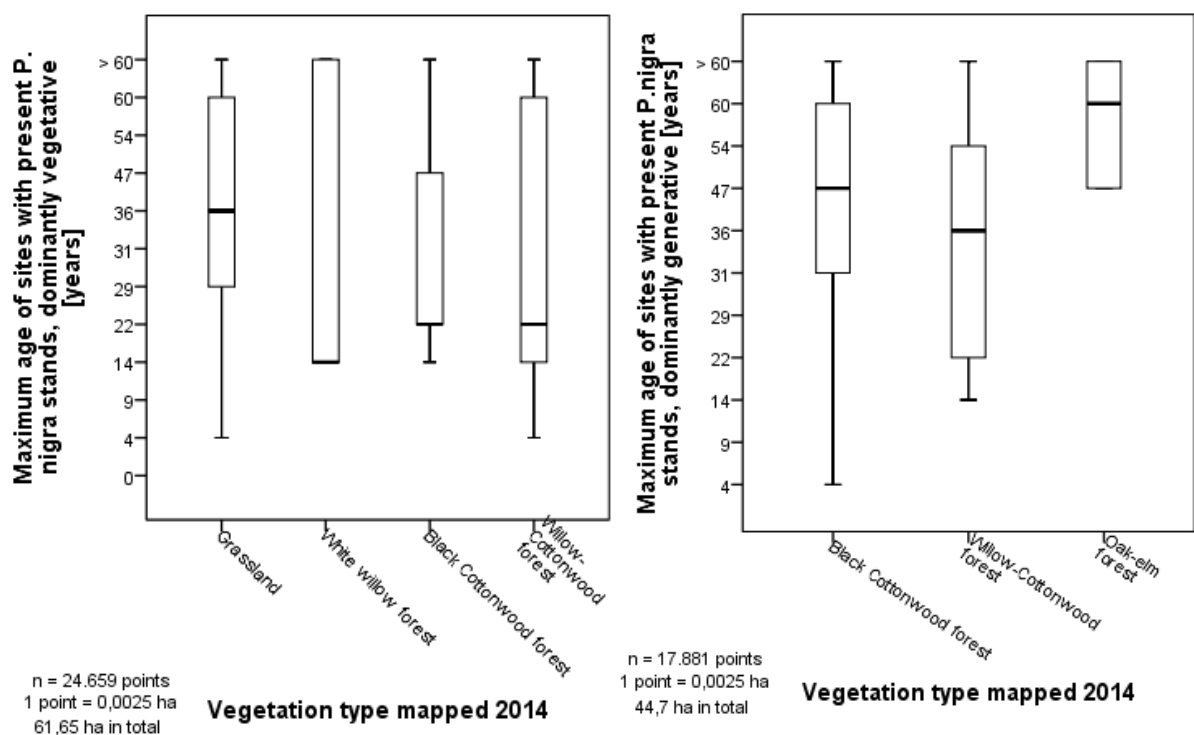


Figure 7: Maximum age of sites; divided into dominantly vegetatively (left) and dominantly generatively (right) propagated black poplar stands.

Figure 8 displays the amount of time of how long vegetation types remain constant before proceeding to another successional stage/vegetation type. Grassland areas on which dominantly vegetatively propagated stands occur, remain constant for mostly 3 and 18 years (interquartile range) and can therefore remain as such for a long time, compared to other vegetation types. As if black cottonwood forests and willow-cottonwood forests of dominantly generative origin reveal a constant time of about 12 years (median) the time of those types remaining constant is rather low. Vegetatively propagated black cottonwood and willow-cottonwood forests do not reveal representative outcomes because these stands predominantly occur on grassland areas (see Chapter 3.1.1).

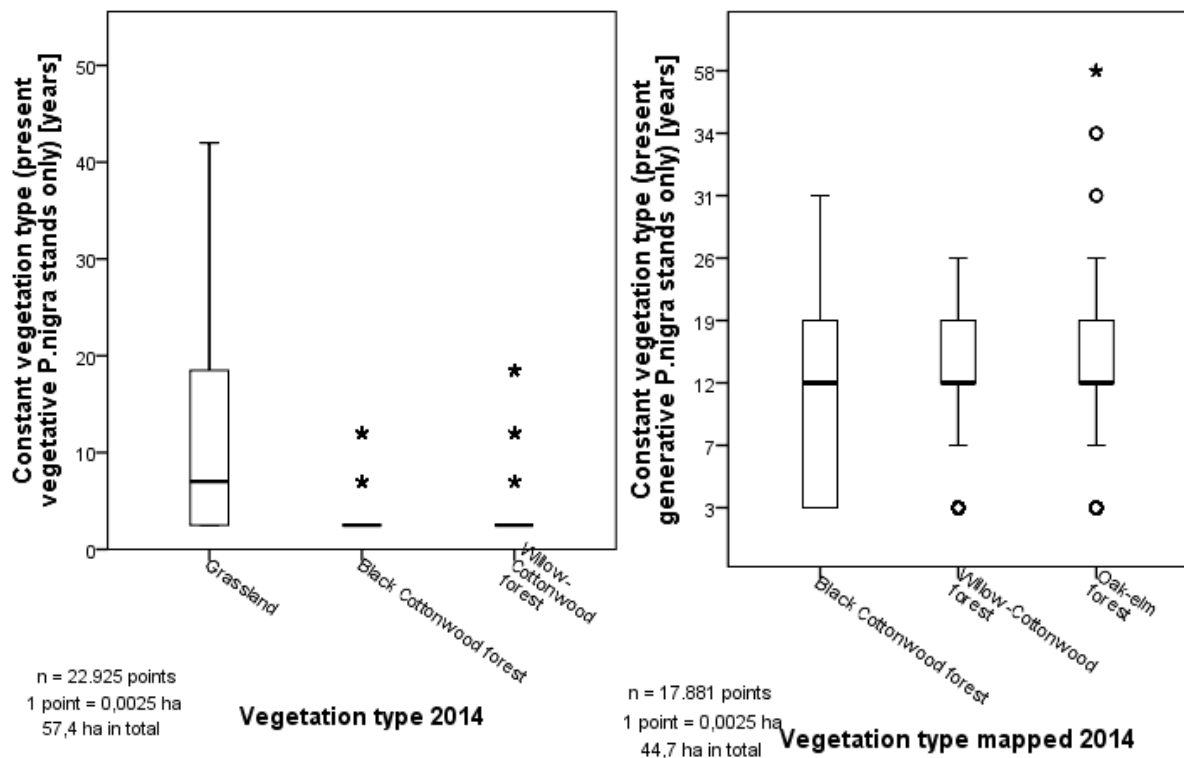


Figure 8: Time of vegetation types remaining constant before proceeding to another vegetation type; divided into dominantly vegetatively propagated *P. nigra* stands (left) and dominantly generatively *P. nigra* stands (right).

The succession duration of vegetation types shows the amount of time of how long black poplar stands, occurring on different vegetation types, needed to establish (Chapter 2.3.3). Black cottonwood forests of both propagation types established within the averagely same amount of time (vegetatively propagated stands have their median at 13 years and generative stands at 14 years). There is no significant difference in those two propagation strategies when it comes to the time of how long stands of these types needed to ground. The time it takes for grassland areas to establish is comparably low (median at 4 years) when considering their rather long period of remaining constant as such.

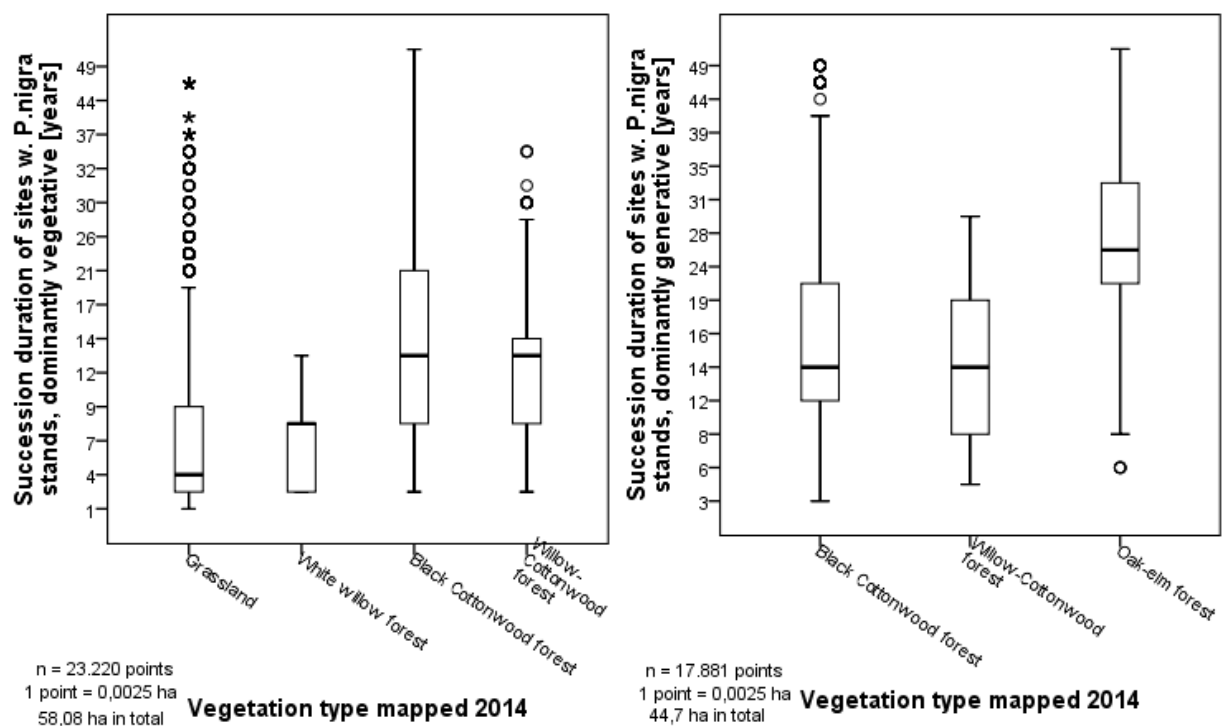


Figure 9: Succession duration of dominantly vegetatively and dominantly generatively propagated black poplar stands, occurring on different vegetation types.

3.1.3 Propagation strategy & point of establishment

Figure 10 shows, that there is no clear difference between the two propagation types of young black poplar stands, concerning the calculated age margins (as mentioned in chapter 2.3.5). Though, the statistical test is ascertained to be highly significant what can be attributed to the high amount of data used for this analysis. One data record (= n) is equating one point feature, derived in *ArcGIS 10.4.1* (see chapter 2.3.) and represents an actual area of 0.025 ha of the study reach. The age margins have been calculated by deducting the maximum obtained tree age from the minimum age of the site on which the target tree was found (Chapter 2.3.5).

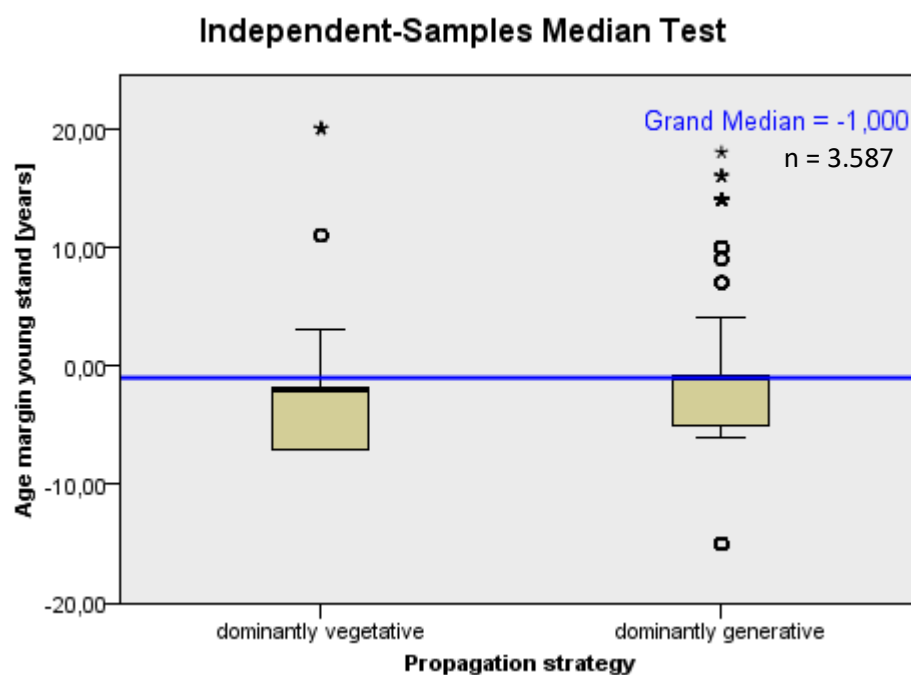


Figure 10: Boxplot with Median Test to display age margins of the dominant propagation strategy of young black poplar stands.

Test Statistic: $\text{CHI}^2 = 22.37$; $\text{df} = 1$; $p = 0.000$ [sign.]

Further, there is no broad dispersion that can be noted, both rejuvenation strategies show nearly equal results concerning the calculated age margins. Dominantly vegetatively propagated young stands have their median at negative two and therefore differ only one year from dominantly generative stands (median at negative one). Negative age margins have been achieved in cases where the maximum tree age was higher than the minimum age of the site. This can be explained by single old trees that withstood fluvial dynamics as floods, that created new habitats without destroying the overall prior vegetation.

Figure 11 pictures almost the same results as mentioned afore: there is no clear difference between the age margins of assessed propagation strategies. Due to that, the results can statistically be noted as equal. As well there is no broad dispersion of values and the statistical significance of results is high. But in comparison to young black poplar stands the assessed median of age margins is lower (Grand Median at negative ten) what indicates that the minimum age of a site is mainly 10 years less than the maximum age of a tree, that established on that site.

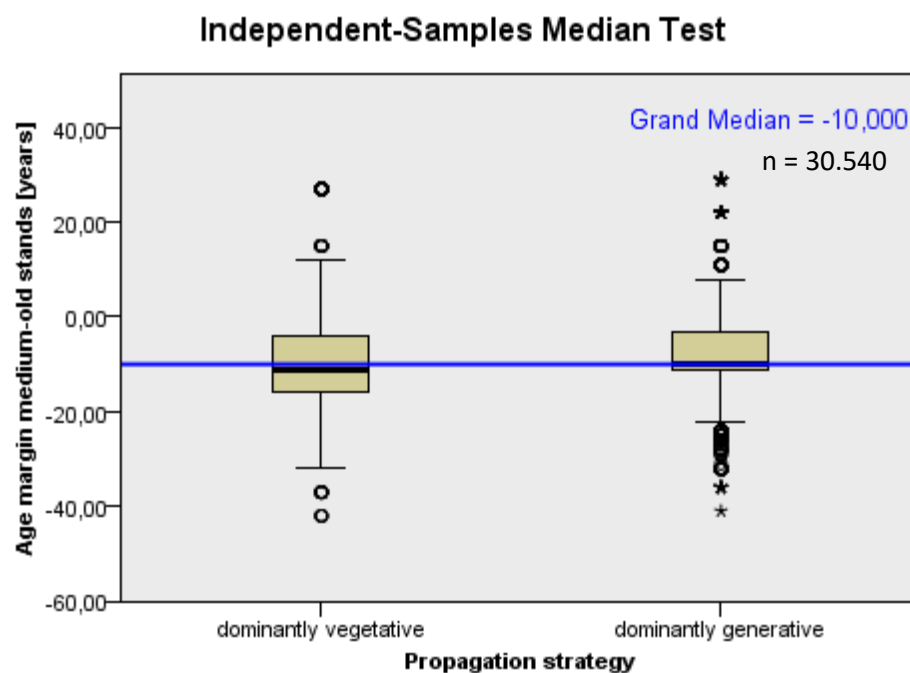


Figure 11: Boxplot with Median Test to display age margins of the dominant propagation strategy applied within medium-old black poplar stands.

Test Statistic: $\text{CHI}^2 = 43.27$; $\text{df} = 1$; $p = 0.000$ [sign.]

3.2 Successional processes

3.2.1 Floodplain age & Retrospective analysis

The Allier is characterised by the continuous relocation of its river bed (see Figure 12). Within the north-eastern part of the study reach the river steadily wanders (since about six decades) towards the north-western edge of the active tract. The area within the most extended meander bow (central, slightly northwards) more frequently changes its course direction but remains within its present river bed since about 2005. In this area the river broke through longitudinal in 1978 what might be attributed to a nearly 10-year-flood event occurring in 1976 with an average discharge of about $1060 \text{ m}^3\text{s}^{-1}$. After that interruption of the rivers previous course, it again oscillates eastwards. Within the currently southern meander bow the Allier remained approximately constant with no significant course changes between 1954 and 1967 but then started to shift its bed towards the active tracts' south-eastern boundary. In 1976 a 5-year-flood event occurred ($>1000 \text{ m}^3\text{s}^{-1}$) what might have influenced this channel shift. At present, in this area the river reached its' furthest eastern point since the past 60 years. Only comparatively small parts at the edge of the active tract (NE, W, SE) reveal a floodplain age of more than 60 years.

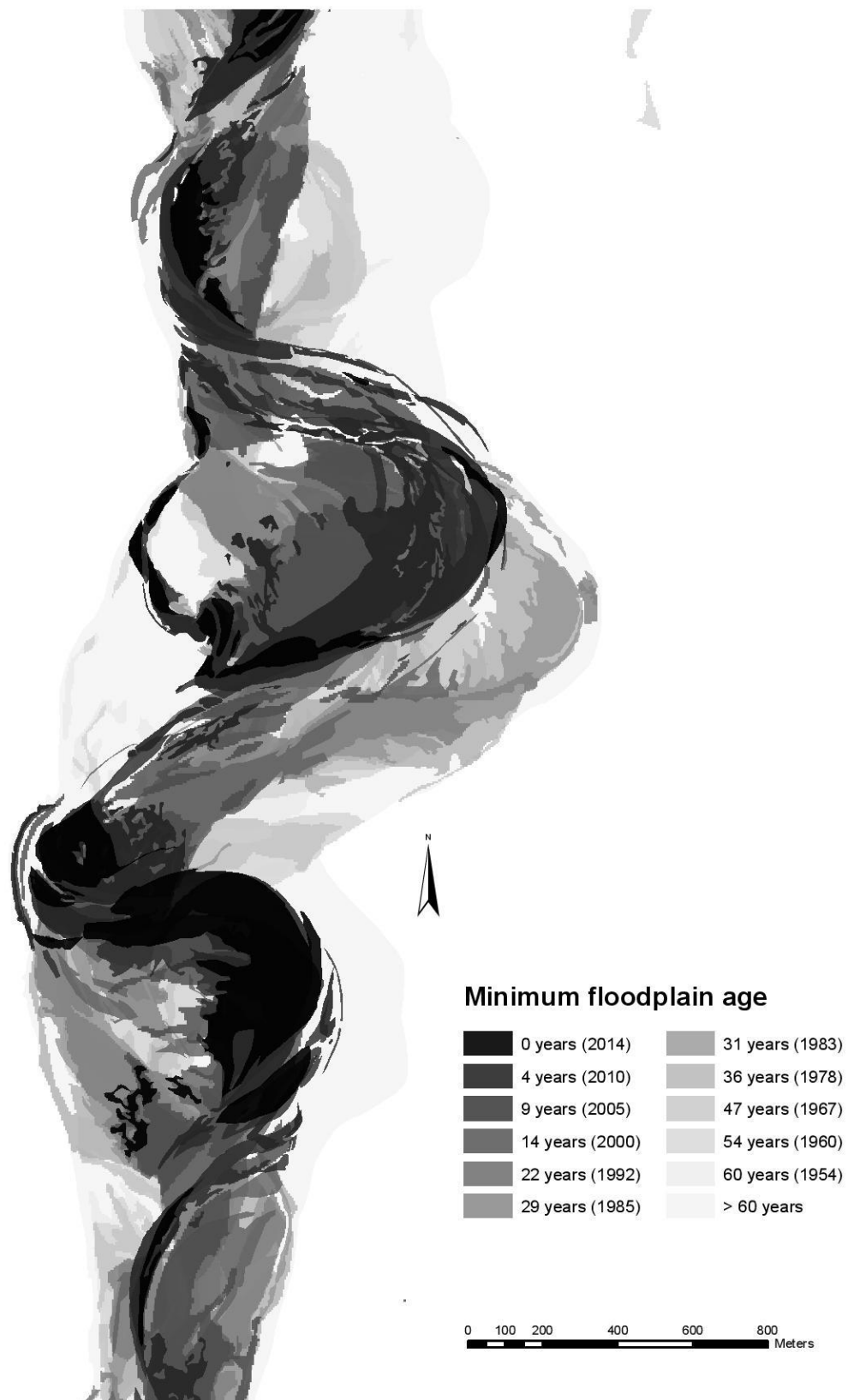


Figure 12: Map showing the minimum age of floodplain areas by using the ecotope-type 'bare soil' (1954-2014).

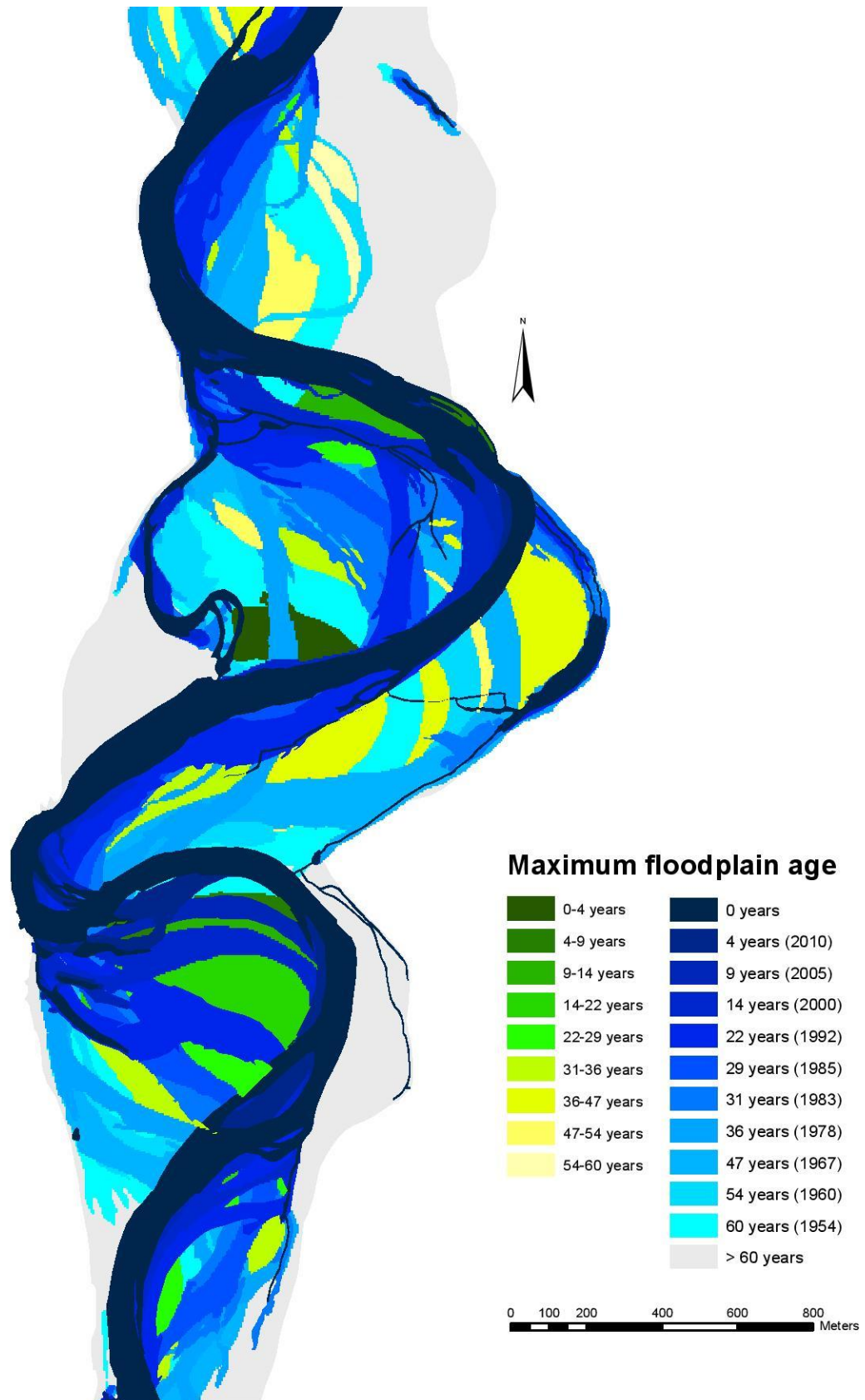


Figure 13: Map showing the maximum age of floodplain areas to display hydro-geomorphological activity within the active tract (1954-2014).

The following statistical evaluations show boxplots of the minimum floodplain age, the maximum floodplain age, the time of constant vegetation types and the succession duration, but refer to all analysed vegetation types, in comparison to the evaluations listed in Chapter 3.1.2, which refer to black poplar stands only and are divided after their dominant rejuvenation strategy.

The major part of the oldest areas within the floodplain is currently colonized by *Prunus/Crataegus* shrubs, mixed soft-/ hardwood and Oak-elm forests. Their minimum age mainly ranges between 36 to 54 years (interquartile range) (Figure 14). Furthermore, these areas reveal the longest period of time (predominantly >60 years) since the river left and the initial/pioneer phase could start (see Figure 15).

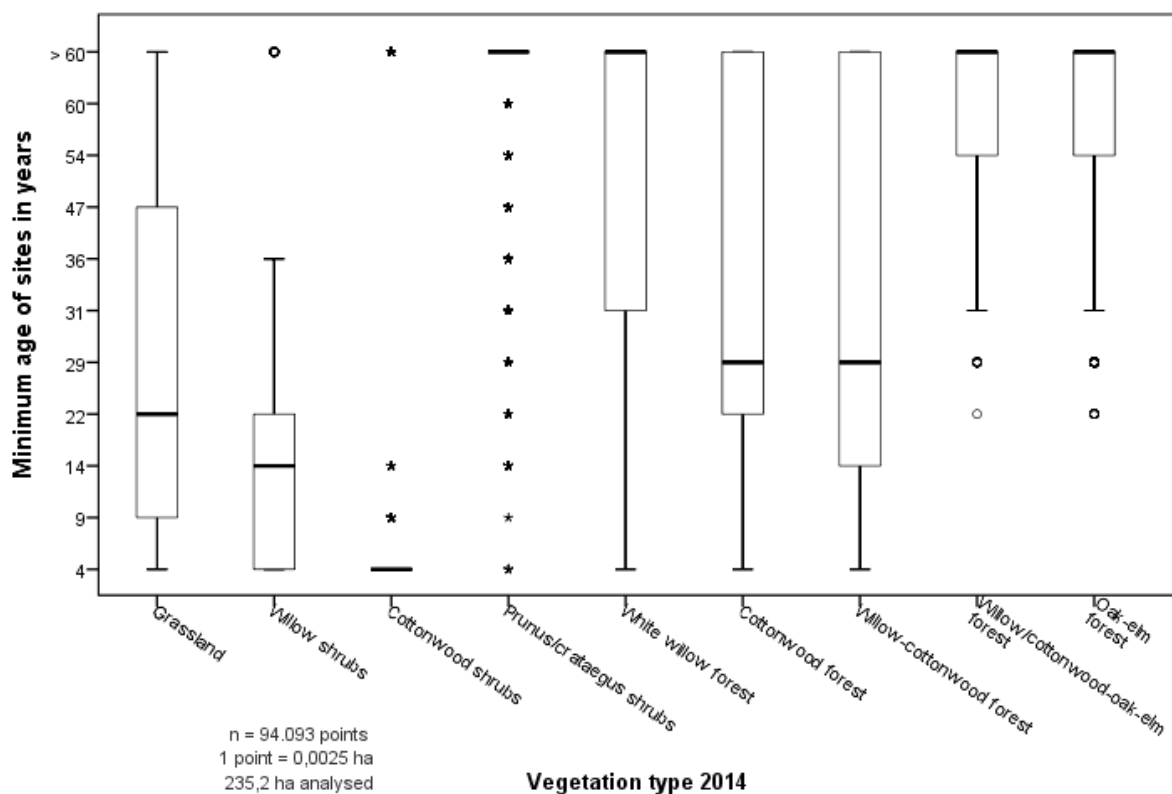


Figure 14: Boxplot displays the minimum age of sites (basis of the analysis: ecotope type 'bare soil').

Figure 14 shows that most areas, now covered by grassland vegetation, evolved minimum 9-47 years ago, whereas their maximum age ranges between 29 to 60 years (interquartile range) (see Figure 15). Due to that, nowadays grassland areas can be considered as sites with an apparently high floodplain age.

As previously assumed, areas with the present type gravel quickly evolved after the river created new habitats. Although Figure 15 reveals that it mainly was 4 to 14 years ago that the river left, it needs to be considered that these areas could have evolved in an even shorter period of time (e.g. one year ago).

Sites with established poplar forests tend to have a slightly younger age compared to sites with established white willow forests. Predominantly 22-60 years ago (interquartile range) these areas have been in their bare soil/pioneer phase and their maximum age ranges between 29 and 60 years.

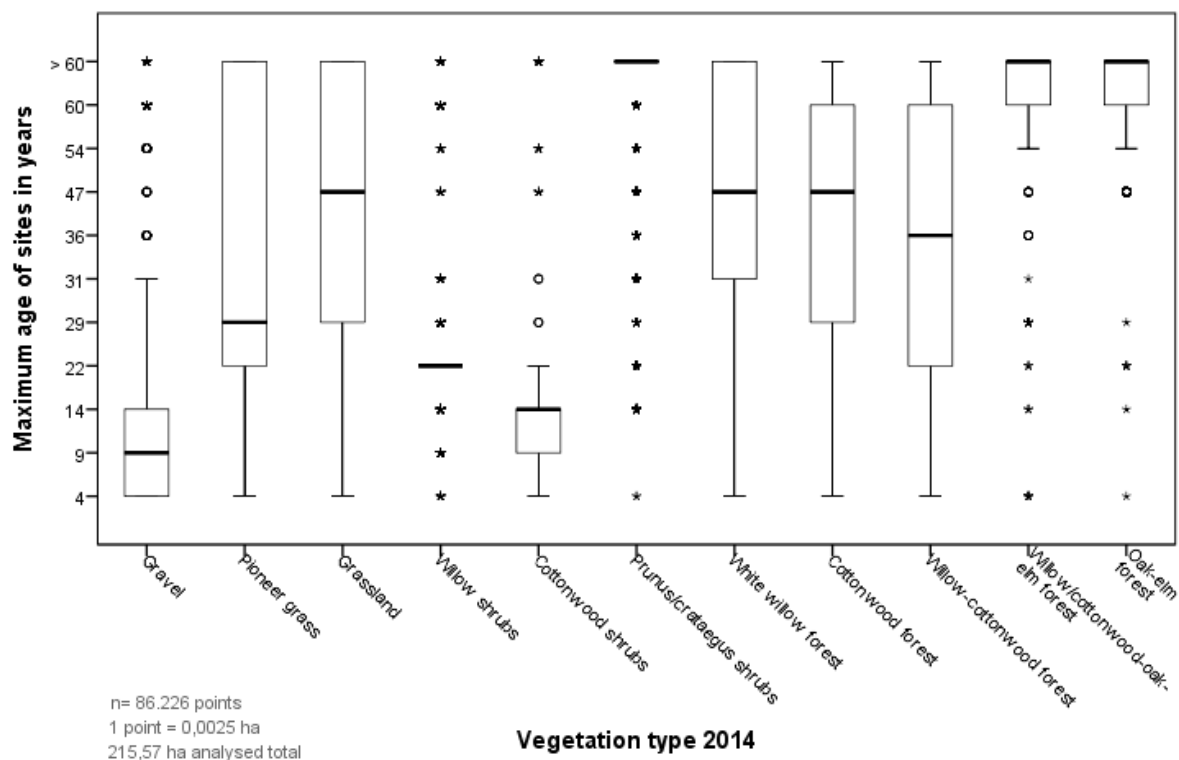


Figure 15: Boxplot displaying the maximum possible age of sites (basis of this analysis: ecotope type 'water')

3.2.2 Constant vegetation types & duration of succession

27.7 % (91.1 ha) of the total area mapped is dominated by grassland vegetation. Figure 17 displays, that these areas were comparably quickly colonized (mainly 3 to 7 years, interquartile range) within the past six decades. Once, grassland has established, it stays as such for a rather long period of time (interquartile range of 2.5-26 years).

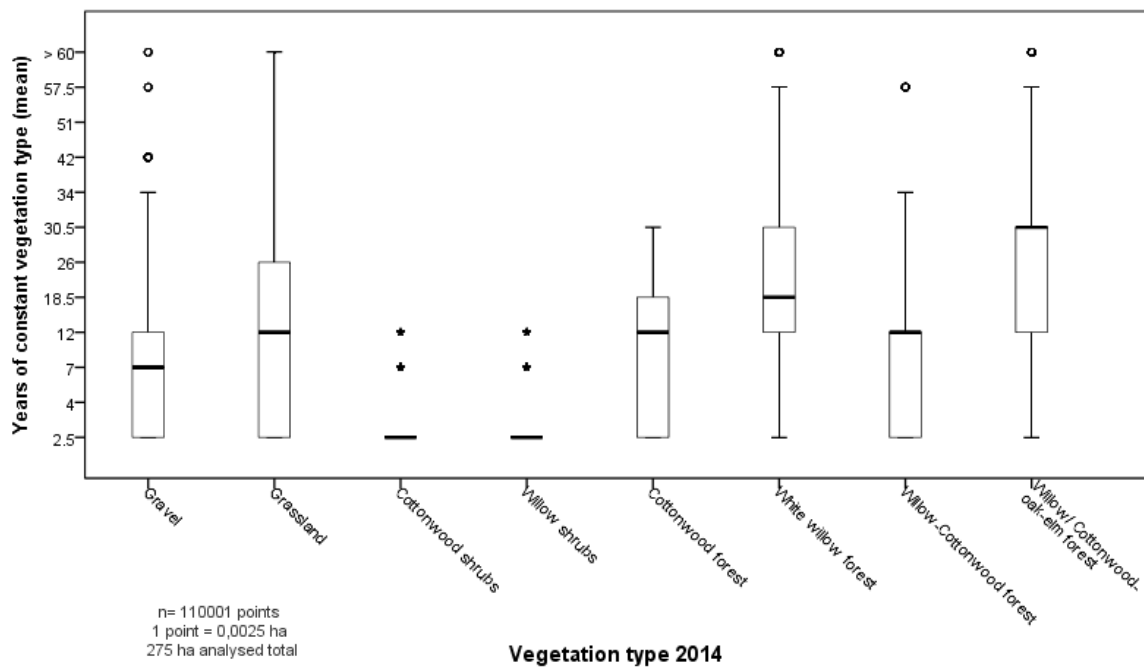


Figure 16: Time of vegetation types remaining constant.

Black poplar forests (44.6 ha) mainly remain constant for about 2.5 to 18.5 years (interquartile range). It predominantly took 14 to 22 years for this vegetation type to establish. In comparison, white willow forests mostly remain constant for about 18.5 years (median) and establish quicker (13-17 years, interquartile range).

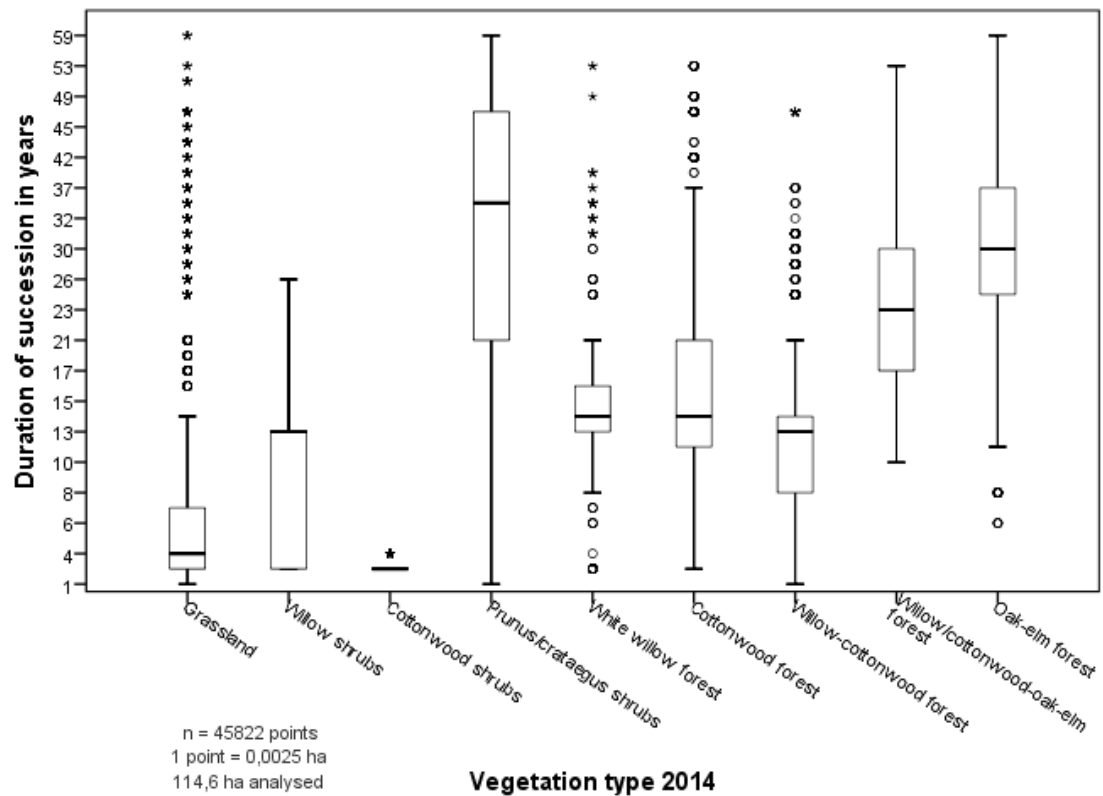


Figure 17: Boxplot showing succession duration of selected vegetation types (sites with a floodplain age of more than 60 years have not been considered in this analysis).

4 Discussion

4.1 Rejuvenation strategy & structural parameters

Wendelgaß (2015) evaluated that the majority of vegetatively reproduced black poplars within the four reference areas, indicated an age of less than 10 years, growing side by side with higher and differently aged individuals. Further, generative stock formation mostly happens within a short period of time involving (often thousands) young cohorts with the same age (Corenblit et al., 2016) which simultaneously proceed to a more mature stage. As well by considering that closed poplar forests hardly ever rejuvenate generatively within established stands (Legionnet et al., 1997; Gom & Rood, 1999b; Brunninger & Reichholf-Riehm, 2011) the occurrence of saplings, or individuals that are younger than the eldest generation, is an applicable indicator for vegetative recruitment. Legionnet et al. (1997) ascertained that most adult stands are likely to be of sexual origin. Contributing to that, the results of Wendelgaß (2015) demonstrate clear evidence that stands firstly established in a generative manner and at later point started to further colonize vegetatively. This fact might be attributed to intra-stand maintenance or the recovery from fluvial dynamics as described in Gom & Rood (1999b). Furthermore, age and height of black poplars within the research areas showed highest correlation values regarding the evaluation of age and structural patterns (Chapter 2.3.4). Using height classes to distinguish age variety within the analysed stands was practicable in the field and for subsequent analyses. Furthermore, the afore-mentioned findings confirm our hypothesis (ii.), that the age distribution, and the presence of a heterogeneous vertical structure, are an indicator for the propagation strategy of black poplar stands. However, the present work demonstrates that within the analysed study reach vegetative and generative recruitment of established medium-old black poplar stands is fairly balanced (71 ha vegetative, 70 ha generative). This comparably high amount of dominantly vegetatively rejuvenated stands might be attributed to the significant decrease of bare soil areas in the past fourteen years, as it was investigated by Garófano-Gómez et al. (2017). Furthermore, the disturbance regime and the therewith associated water availability are contributing factors for seedlings to successfully recruit (Legionnet et al., 1997). As the frequency and duration of moderate and high magnitude floods decreased within the

past decade (Garófano-Gómez et al., 2017), the amount of generative cohorts might have decreased concomitantly due to a lack of suitable habitats, as they are exposed after flood events (Dickmann & Kuzovkina, 2013; Egger et al., 2015). However, the findings of this present work offer indisputable evidence for the role of vegetative propagation. Table 3: propagation types of black poplar stands and share of preceding vegetation types shows, that 94% of all dominantly asexually recruited medium-old black poplars have been identified to occur on grassland areas (as mapped by Metz, 2015) which are, according to Garófano-Gómez et al. (2017) too dry for seeds of woody riparian species to be colonized. Therefore, we are able to confirm our hypothesis (v.), that the black poplar is conquering these harsh grassland areas rather by asexual propagation than by sexual propagation.

4.2 Floodplain age & Successional processes

Along the river Allier gravel point-bars can be considered as low-lying floodplain areas that are usually colonized by pioneer plants (Baptist & de Jong, 2005). Most of these areas are permanently relocated and therefore, the time-slot for sexual plant recruitment is small. Despite of that, the time that gravel areas remain constant is characterised by a rather wide range, as it can be seen in figure 8. This can be explained by close-to-the-river gravel bars that generally do not remain constant for more than 4 years (see Figure 16) and concomitantly higher-lying, dry gravel areas that are constant for a longer period of time and colonized by semi-arid grassland vegetation, which is able to establish fast (Figure 17). These grassland areas remain constant for a rather long period of time, what indicates a slow succession, and can be deduced from extreme habitat conditions (predominantly drought) (Metz et al., 2015).

White willow and black poplar shrubs (3.9 ha; 2.8 ha) count for merely 2 % of the areas present vegetation types. Though, it can be noted that poplar shrubs colonize suitable habitats in a shorter period of time compared to white willow shrubs (Figure 17). Both vegetation types quickly evolve into softwood forests and therefore remain constant for an only short period of time, as it can be seen in Figure 16.

Black poplar forests are widely spread throughout the analysed area. In some areas poplars build dense vegetation patches as mentioned in Corenblit et al. (2016), whereas in other parts of the floodplain stands appear more open with rather shrubby trees, as described by Gom & Rood (1999b). The retrospectively analysed *P. nigra* forests predominantly colonized sites after about 14-22 years (interquartile range, Chapter 0). Black poplar shrubs remain constant for mostly 2.5 years (median) before they proceed to a more mature phase, what would be black poplar forest.

The average dendrochronologically assessed maximum tree age of all analysed *P. nigra* stands equals 26 years. This can be noted as comparably young, when considering a 5.8 % share of old single individuals with an age of more than 60 years. Nevertheless, this fact corresponds well with the assessments of Wendelgaß (2015) and made us conclude that high dynamics occurred in the past century until the succession dynamics decreased about ten years ago, as evaluated by Garófano-Gómez et al. (2017).

Old floodplain areas, as described in chapter 3.2, are dominantly characterised by the occurrence of *P. nigra* individuals within young successional hardwood forests. These individuals occasionally reach ages of far more than 80 years and can mainly be found at the higher-lying edges of the active tract. In spite of that, these areas are comparably young and, within the study reach, no significantly old hardwood forests have been found. This assertion might be attributed to the time before the major part of the river was assigned to its current espace de liberté in 1993 (Hudin, 2010) and high dynamics that occurred in the past (before 2005) as it was found out by Garófano-Gómez et al. (2017).

Further, it is presumed that currently young hardwood forests within the research area did not evolve out of former softwood forests as described by Egger et al. (2013), but rather emerged out of *Prunus spinosa*/ *Crataegus laevigata*/ *C. monogyna* stands (Figure 17). According to Metz et al. (2015) *Prunus*/ *Crataegus* stands within the research area are often found on former pastured grassland and therefore could evolve within a few decades because of secondary succession. Currently these stands proceed towards a more mature phase, namely hardwood forests. Notwithstanding these interpretations, it has to be noted that concerning present *Prunus spinosa*/ *Crataegus laevigata*/ *C. monogyna* stands no conclusions can be drawn, regarding the time of their constant vegetation type (Figure 16). Such stands usually reach high ages and remain constant for a long period of time. The foremost cause of this discrepancy is due to misinterpreted aerial images (especially misinterpretation of areas covered by the vegetation type *Prunus/Crataegus shrub*) which have been edited by several persons, and affected aerial images from the years before 2014.

The results in chapter 3.1.2 reveal that the overall floodplain age of areas on which sexually recruited black poplar stands occur, is higher compared to asexually recruited stands. This evaluation might be as well, attributed to high dynamics in the years before 2005. However, these findings offer evidence to confirm our hypothesis (iii.), that generative and vegetative rejuvenation strategies differ in terms of the age of the sites on which those stands can be found.

4.3 Rejuvenation strategy & point of establishment

The calculation of age margins to draw conclusions towards varying paces between sexual and asexual recruitment of black poplar stands did not reveal clear differences between the two propagation strategies. Furthermore, the succession duration of the two propagation strategies (Figure 9) show that the average time of black cottonwood forests (dominantly vegetative and generative) needed averagely the same amount of time to ground. These findings are contributing substantially to make us reject our hypothesis (i.), that vegetatively and generatively propagated stands are characterised by a varying pace in succession. Though, it can be noted that, in comparison to generatively rejuvenated stands, vegetatively propagated stands predominantly occur on grassland areas, wherefrom we are able to deduct, that our hypothesis (iv.) can be confirmed: vegetative and generative recruitment differs in terms of the successional processes that are run through until adult black poplar stands are attained.

5 Conclusion

For the preservation of the European black poplar profound knowledge is required to preserve this threatened species and to ensure its regeneration. The most important measure to do so is to restore its natural habitats and the concluding natural dynamics (Smulders et al., 2008; Rood et al., 2005). But furthermore, the provision of suitable habitats requires approaches of holistic system thinking, especially in the sense of location requirements for either vegetative or generative regeneration. The existence of both, sexual and asexual propagation of a species enhances the chance of successful regeneration at different locations at the same time (Asaeda et al., 2011). Further, vegetative cohorts are able to manage a wider range of environmental influences and are characterised by a faster growth rate (Gurnell, 2014). Besides that, they are even able to support generative propagation by the accumulation of sediments and the subsequent trapping of seeds (Gurnell, 2014; Corenblit et al., 2016). Furthermore, vegetative propagation is crucial for the rapid development of landforms and vegetation units within highly dynamic rivers (Moggridge & Gurnell, 2009). These factors underline the need for a more comprehensive knowledge in regard to the propagation strategy of the European black poplar.

In the course of this study it was found out that structural stand patterns indicate the dominant propagation strategy of black poplars within established stands, as mentioned in previous studies (Legionnet et al., 1997; Gom & Rood, 1999b). Further, it was found out that vegetatively and generatively reproduced black poplar stands differ in terms of their successional phases, but do not differ in terms of a varying pace of establishment. Two of our approaches confirmed that there is no difference in time, but rather in space, when it comes to either sexual or asexual recruitment of the European black poplar.

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Appendix

Horizontal stand structure: Index of dispersion

In addition to the approaches mentioned in this work, the index of dispersion (grid: 10*10 m) was used to analyse a possible linkage between the horizontal stand structure and the applied rejuvenation strategy of *P. nigra* stands.

$$DI = \frac{s^2}{\bar{x}}.$$

By counting the amount of *Populus nigra* individuals within a predefined grid cell and by calculating the mean and standard deviation of counted trees within each reference area, values providing information about the spatial distribution of individuals within each reference area could be obtained (Lettner, n.d.).

Figure 18 displays the correlation of the index of dispersion and the amount of clones within the four reference areas, as assessed by Wendelgaß (2015). Index values higher than one state that the individuals are arranged in groups within predefined areas (Lettner, n.d.). All analysed areas show an index value above one, wherefore an increasing amount of clones within these areas led to a notably higher dispersion rate. Therefore it is assumed that if the stands rejuvenated clonal, the more significantly the stands are arranged in groups.

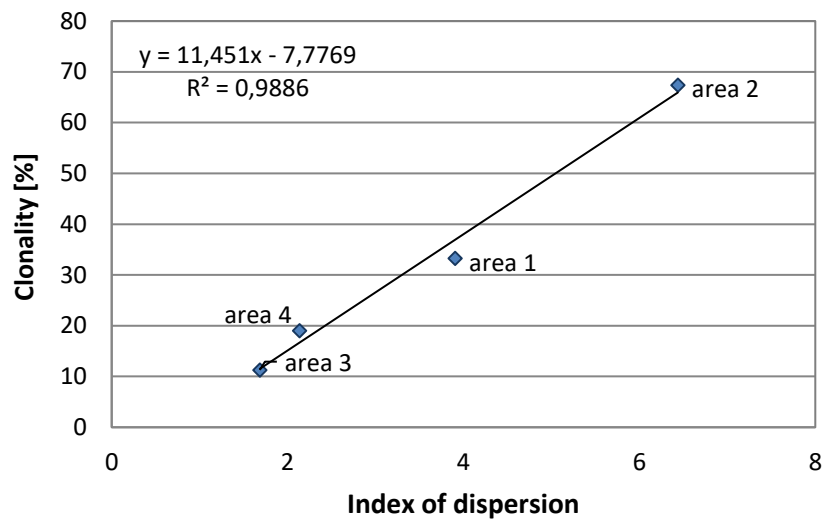


Figure 18: Index of dispersion for each reference area and percentage of each areas amount of vegetatively reproduced *Populus nigra* L. individuals.

Even distribution:	$s^2 / \bar{x} < 1$
Random distribution:	$s^2 / \bar{x} \cong 1$
Group-wise distribution:	$s^2 / \bar{x} > 1$

The index of dispersion might be applicable to draw conclusions concerning the rejuvenation strategy in small-scale areas. But the basis is to well-know how individuals are arranged or distributed within an analysed area. As if it is hardly possible to assess the arrangement of trees (or their exact geographical location) in larger areas, this method was not practicable to draw a quantitative conclusions concerning the propagation strategy of target tree species.

Calculation scheme for the point of establishment

Example: The minimum floodplain age of a site is 54 years (this site/point feature has been in its bare soil phase in 1960) and the maximum, dendrochronologically assessed tree age (recorded for a polygon, comprising the aforementioned point feature) is 52 years, resulting in an age margin of two years.

minimum floodplain age	54 years
- maximum tree age	52 years
= age margin	2 years

Dendrochronological assessments

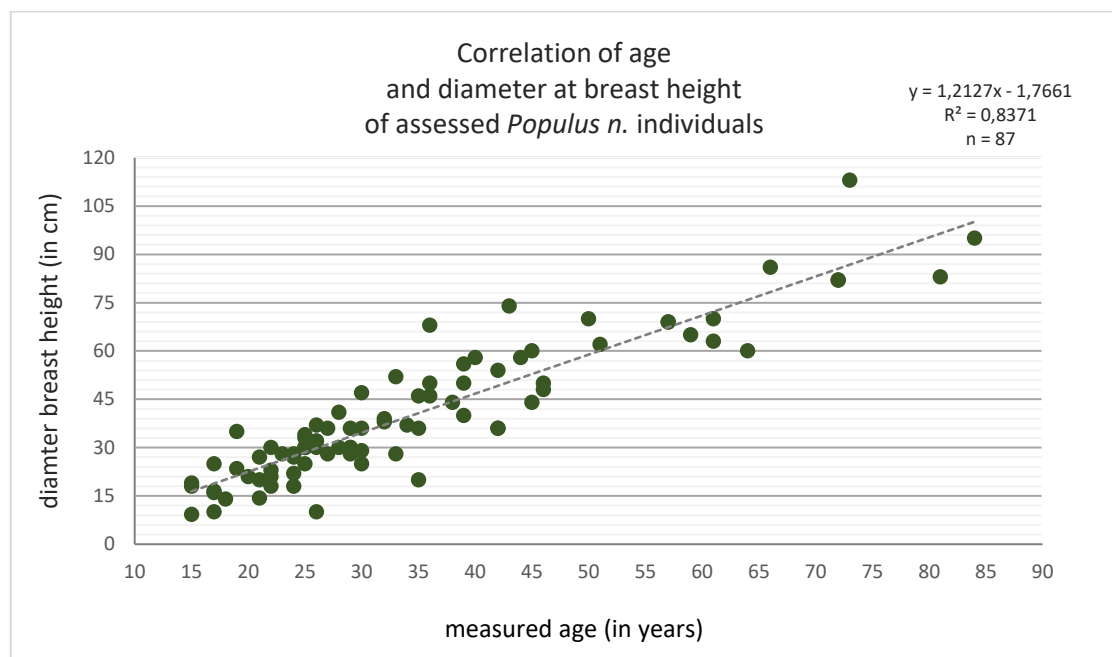


Figure 19: Correlation of the diameter at breast height and the evaluated tree age of black poplar individuals within a polygon assessed in the field.

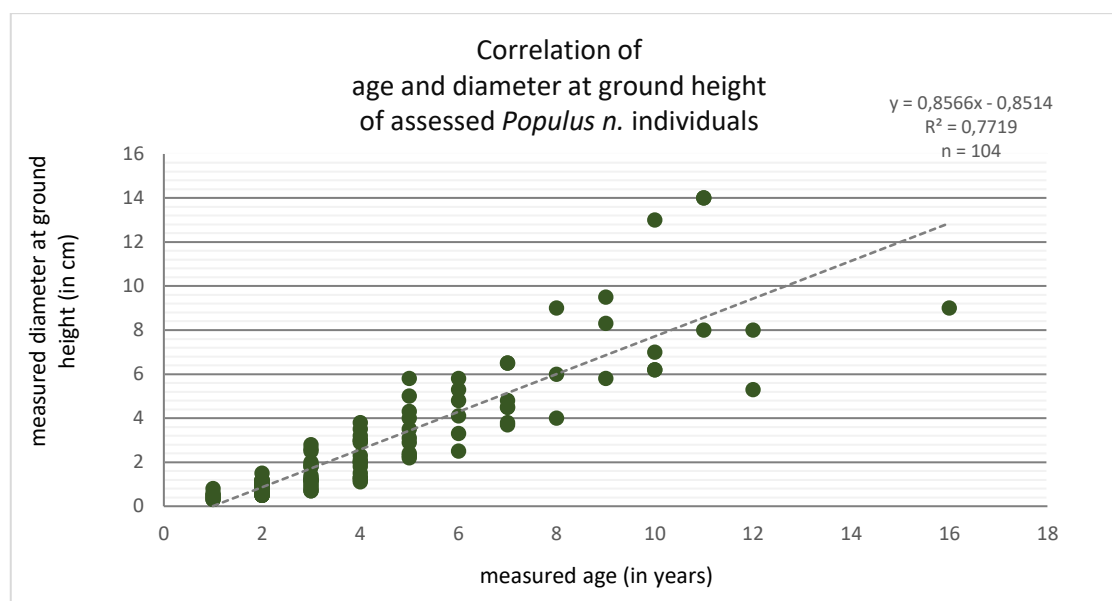


Figure 20: Correlation of the diameter at ground height and the evaluated tree age of black poplar individuals within a polygon assessed in the field.

The correlations of diameter measurements and the evaluated ages are lower, compared to the correlation of height and age characteristics (Figure 4) and have therefore not been considered for further evaluations.

Minimum and maximum floodplain age

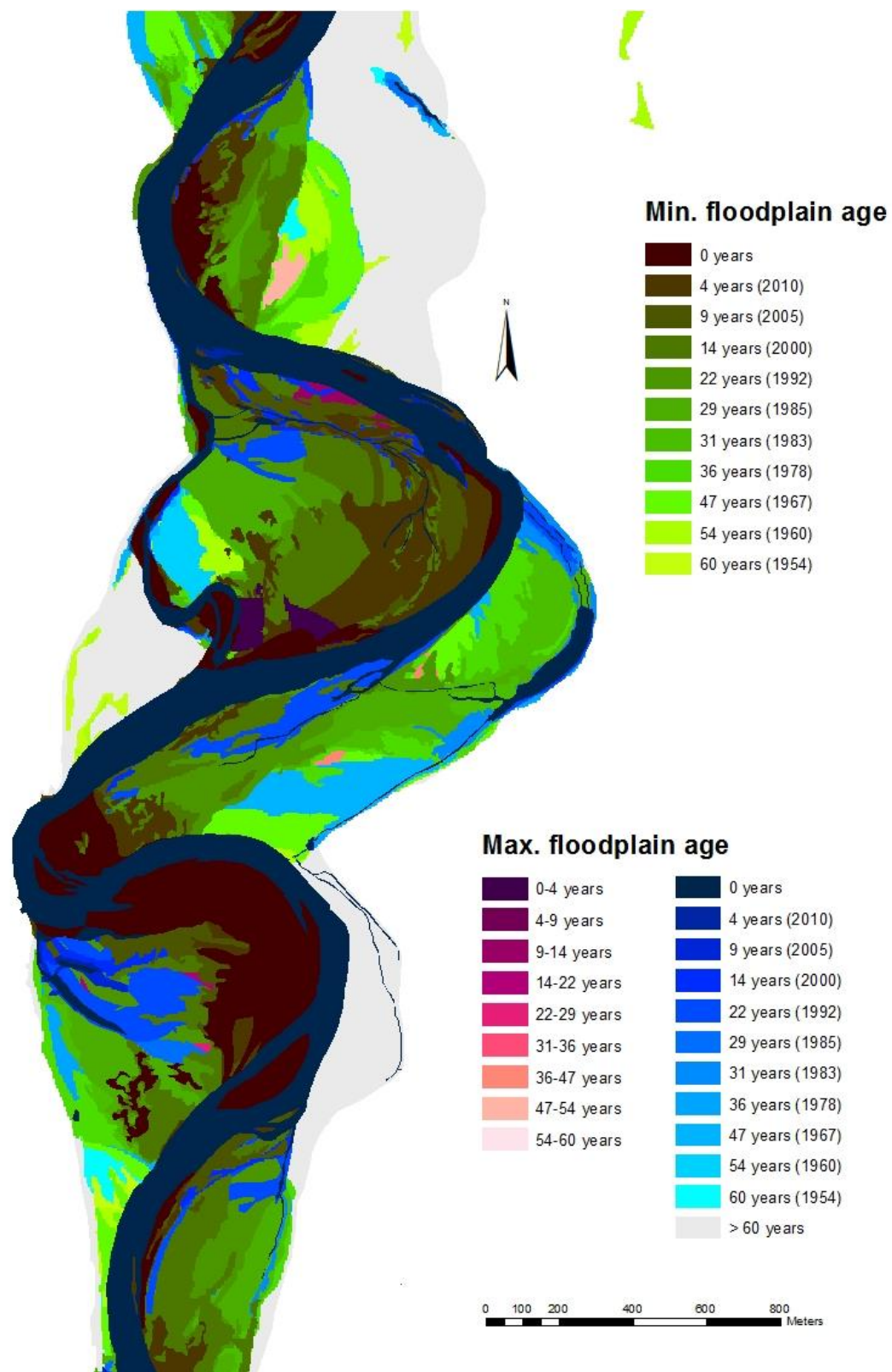


Figure 21: Displays the overlay of the assessed minimum and maximum age of floodplain areas, including the interpretation of areas between digitised historical maps (own display, 2017).

Assessed maximum tree/stand age

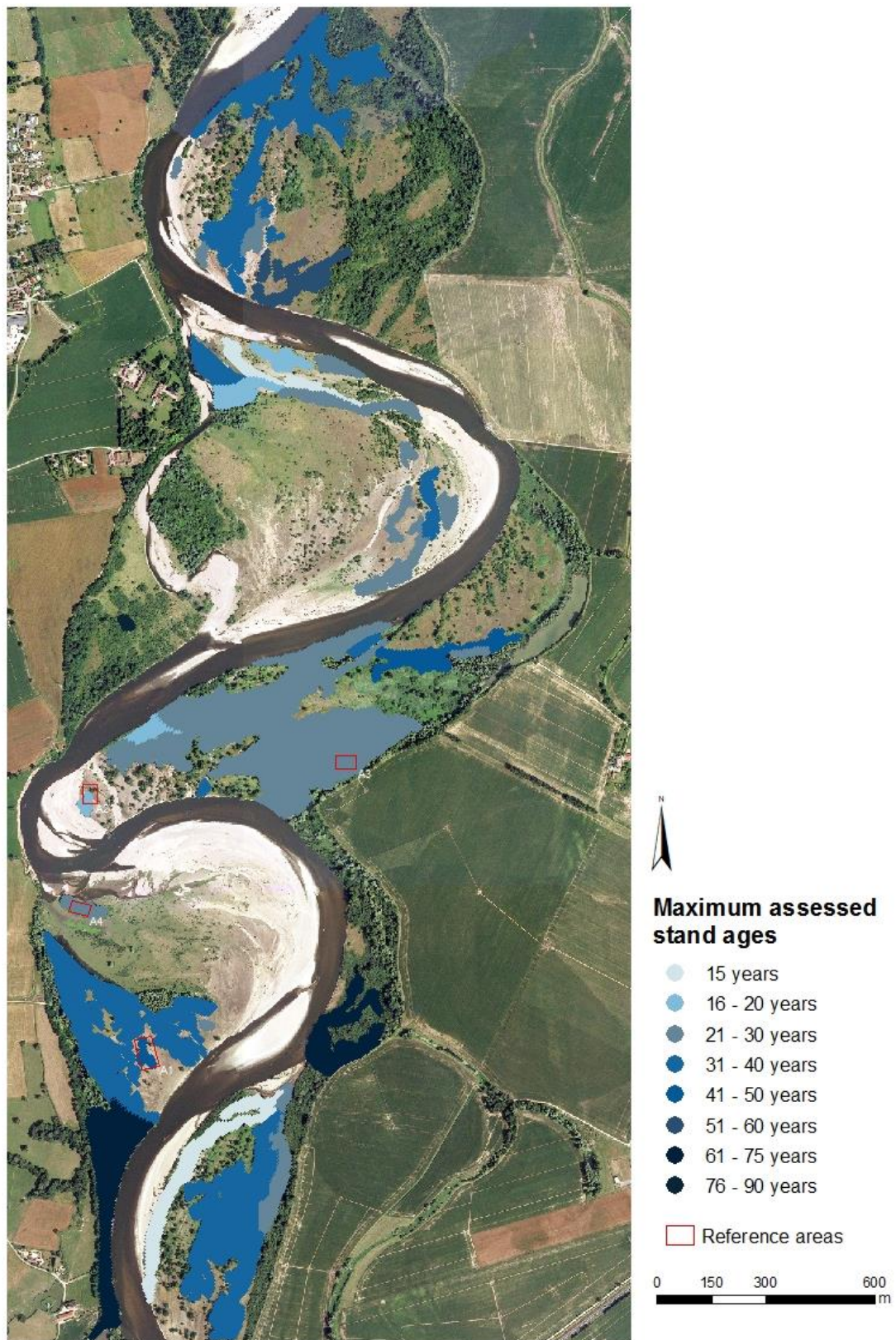


Figure 22: Dendrochronologically assessed maximum tree age within black poplar stands.

Share of Poplars within a height class

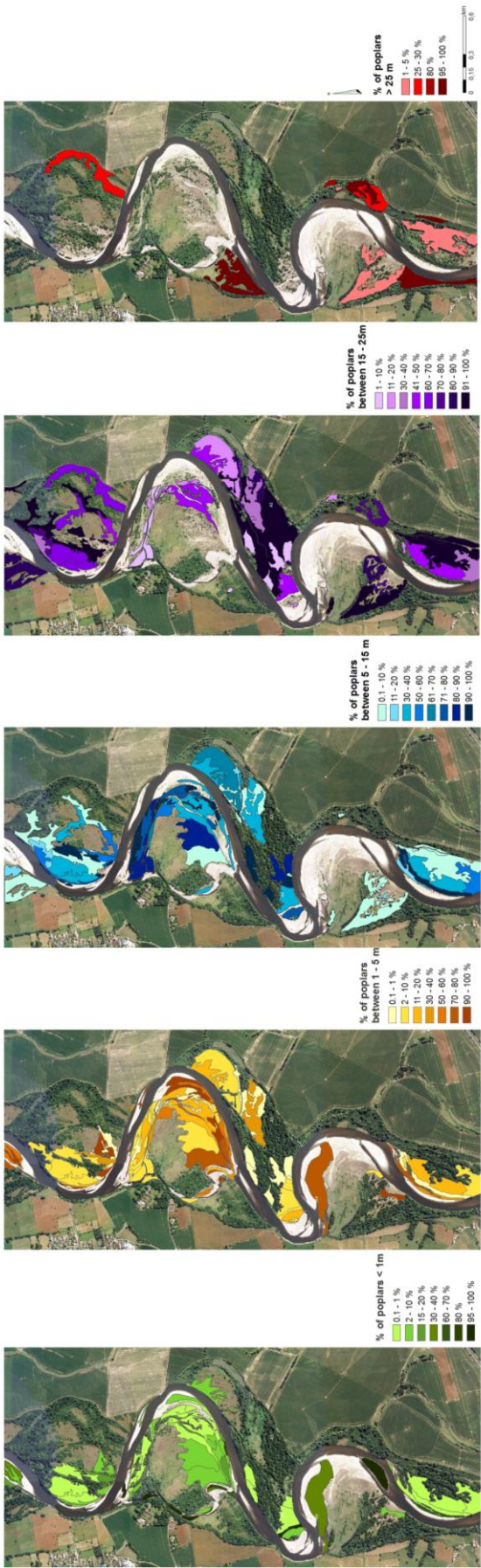


Figure 23: Assessed share of *Populus n.* individuals within a height class (< 1m, 1-5m, 5-15m, 15-25m, >25m) per polygon mapped.

Ecotope maps of subsequent years

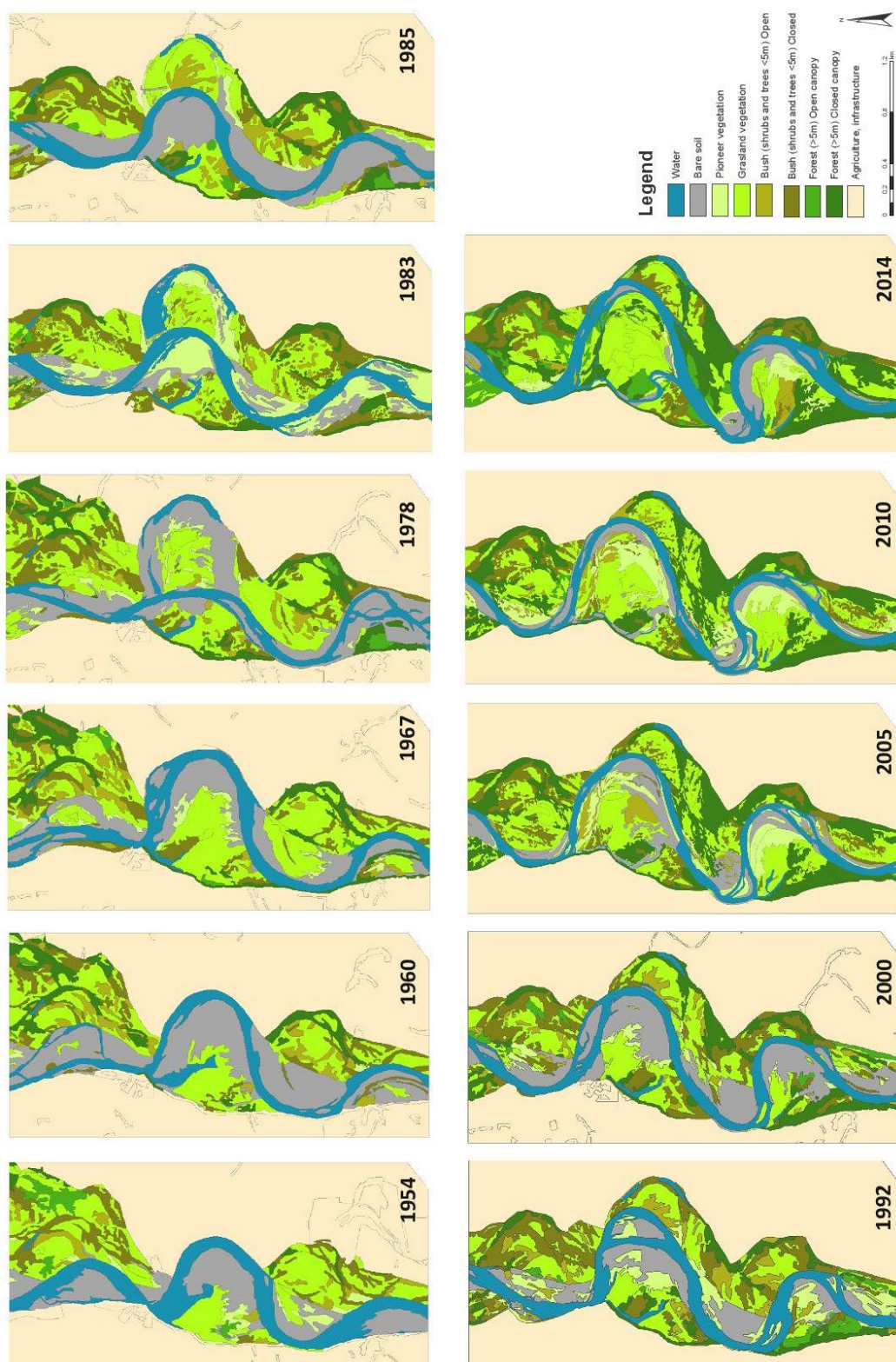


Figure 24: Interpreted aerial images (Geerling et al. (2006), Metz et al. (2015), 1992: own display (2017)).

Maximum age of floodplain areas

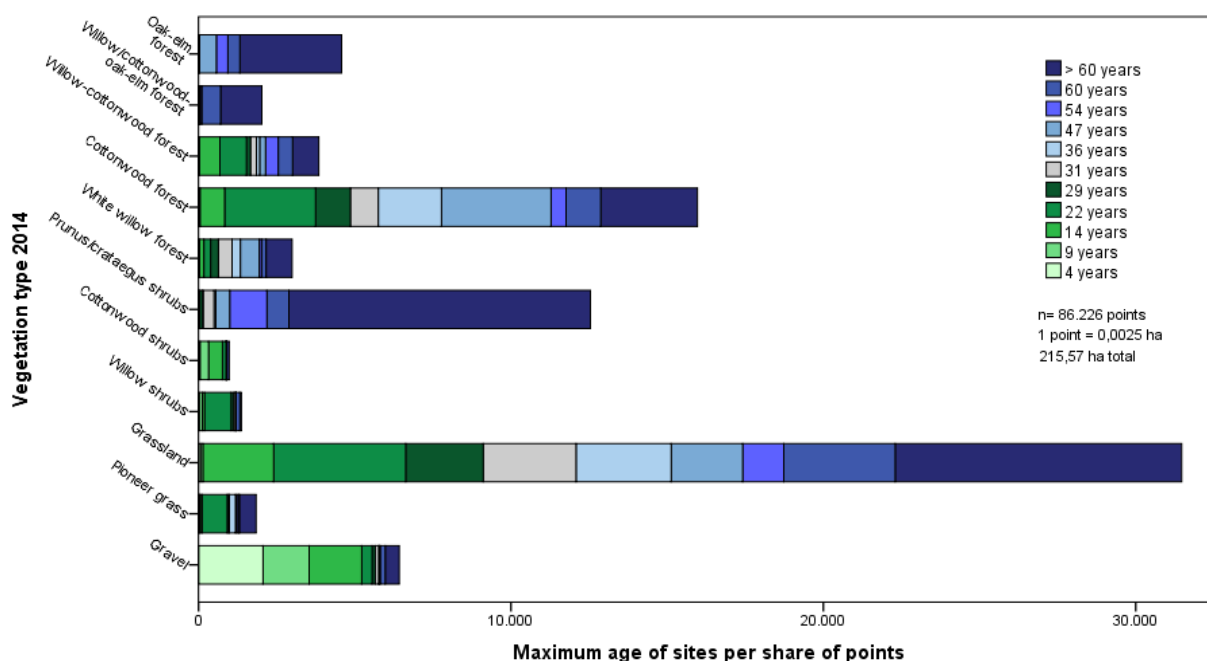


Figure 25: Bar chart of acquired point features (with *Arc GIS*), displaying the share of points related to the assessed maximum floodplain age.

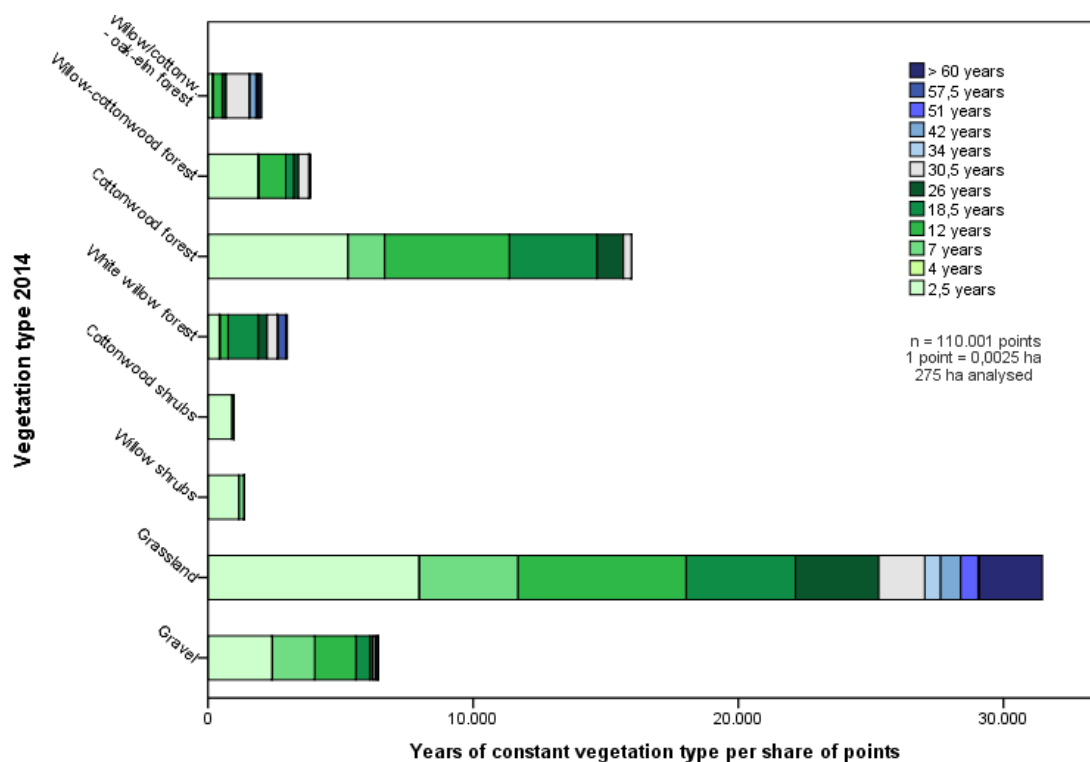


Figure 26: Bar chart of acquired point features (with *Arc GIS*), displaying the share of points related to the amount of time a vegetation type remained constant.

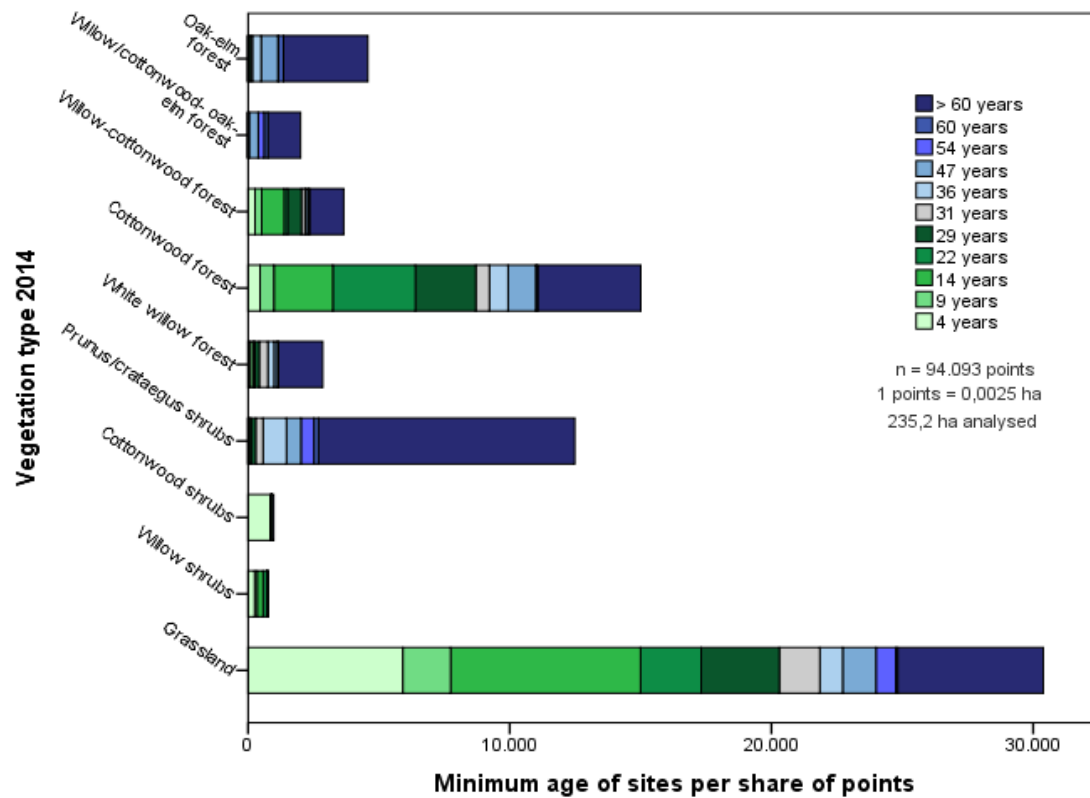


Figure 27: bar chart of aquired point features (with Arc GIS), displaying the share of points related to the assessed minimum floodplain age.

[illegible]

Figure 28: Mapping sheet used for the area-wide mapping of black poplar stands.

Statutory Declaration

I herewith declare that I have composed the present thesis myself and without use of any other than the cited sources and aids. Sentences or parts of sentences quoted literally are marked as such; other references with regard to the statement and scope are indicated by full details of the publications concerned.

This Master Thesis was not used in the same or in a similar version to achieve an academic grading or is being published elsewhere.

Furthermore I declare that the submitted written (bound) copies of the present thesis and the version submitted on a data carrier are consistent with each other in contents.

Place, Date

Signature