

In situ conservation

Poplars and biodiversity

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Floodplain forests, the natural habitat of indigenous black poplar (*Populus nigra* L.), are among the most diverse ecosystems in Europe (Gepp *et al.* 1985). In Austria, for example, it was estimated that at least 12 000 species of animals and plants regularly inhabit the floodplains of the Danube (Gepp *et al.* 1985). According to Gerken (1988) more than 1000 species of beetles, most of the indigenous amphibians, 400–500 species of large butterflies (more than one third of all existing species) and between 150 and 200 species of birds occur in different floodplain habitats. Table 1 shows the numbers of invertebrates that have been recorded in the floodplains of the Rhine.

Table 1. Number of species of invertebrates in the floodplains of the Rhine, according to Tittizer and Krebs (1996)

Order	Number of species
Mollusca (land snails)	>60
Mollusca (water snails and mussels)	30–40
Odonata (dragonflies)	50
Coleoptera (beetles)	>1000
Lepidoptera (butterflies)	1000
Arachnida (spiders)	>100

Many of the species are highly specialized and depend on alluvial habitats. For example, 29% of the amphibians, 27% of the carabids, 20% of the reptiles and 12% of the dragonfly species in Switzerland occur uniquely or primarily in alluvial habitats (Walter *et al.* 1998). Undisturbed floodplain ecosystems are not only very rich in species, but also provide a unique or very important habitat for numerous threatened species and thus play a crucial role for species conservation. For insects, mammals, birds, reptiles and amphibians in Switzerland, for example, 17.5% of extinct species, 27% of those that are nearly extinct, 19% of highly threatened species and 11% of threatened species live exclusively, or primarily, in alluvial habitats (Walter *et al.* 1998).

Floodplains support a high level of biodiversity because they themselves represent a broad range of habitats with very different structures which are temporally dynamic. The small-scale mosaic of various habitats, in combination with varying water levels and frequent disturbances, creates a diversity of vegetation types which vary across the habitat to provide horizontally as well as vertically structured forests in various stages of development. The various animal and plant species which are characteristic of each particular succession stage may thus be found in close proximity. Although there are constant changes within the floodplain ecosystem, the number and area of the different habitats are astonishingly constant over time. This continuity, in combination with the high diversity of habitats, different stages of maturation and a mosaic of different horizontal and vertical structures, permits the maintenance of high and stable species richness over time (Gepp *et al.* 1985).

In contrast, poplar plantations are often criticized as they are considered to be highly unnatural. The use of non-indigenous species, hybrids and clones which are not integrated

into the natural ecosystems are thought to have detrimental effects on the native fauna (Blab and Kudrna 1982; Dickson and Whitham 1996; LFU 1996; Waltz and Whitham 1997). In addition, the unnatural stand structures of such plantations, which are commonly monospecific with little or no vertical structure as compared to natural floodplain forests, are also thought to have negative effects on fauna (Gerken 1980; Späth 1981; Handke and Handke 1982; Dorsch and Dorsch 1991; Twedt *et al.* 1999) and flora (Hügin 1981; Schuldes and Kübler 1991).

Poplars are often cultivated in alluvial habitats where site conditions are optimal for their growth. The natural floodplain forests are replaced by stands with a different, highly artificial structure and composition. Specialized and threatened species depending on alluvial forests may be negatively affected by such plantations.

This paper attempts to give a brief overview of the current state of knowledge regarding poplars and their role and importance for the biodiversity and conservation of associated plant and animal species. The paper primarily addresses three major topics: (1) the value of poplars as a food source or habitat for herbivores and other species, (2) the role and impacts of poplar hybrids (*P. × euramericana*) and (3) of poplar plantations on biodiversity.

Poplars and biodiversity

Black and white poplars are natural elements of a highly diverse ecosystem. The role and importance of poplar species in contributing to the high biodiversity of alluvial forests is, however, poorly understood for a variety of reasons. Firstly, associations between tree species and biodiversity are difficult to investigate because a number of factors other than the species itself affect biodiversity. Factors such as climate, soil and water conditions, quality and distribution of habitats, age, structure, abundance and quality of the host species, as well as the demography of a given herbivore, form a complicated web which is difficult to disentangle. Furthermore, information available on species–host relationships in the literature has not been collected systematically. Since certain species or groups of species have been studied in more detail than others, these species or groups are clearly overrepresented while others are completely lacking. This is especially true for poplars. The literature on species–host relationships concentrates almost exclusively on insects and fungi which cause economically significant losses in poplar plantations (for an overview, see FAO 1979 or Delplanque 1998). The general literature dealing with species–host relationships, on the other hand, is mostly based on field observations made by entomologists. Many of the observations are rather general and lack proper scientific verification. Information on poplars, for example, is generally available only at the level of the genus (*Populus* ssp.), including planted hybrids. Finally, a difficulty arises from the fact that monophagous herbivores are rather an exception. Many so-called monophagous herbivores feed on a whole genus and are thus oligophagous in a strict sense. Moreover, certain herbivores will use a given host plant in certain situations but abandon it as a food source under a different set of conditions. These limitations must be borne in mind when interpreting the following results and statistics.

According to Grechkin and Vorontsov (1962, cited in Georgiev and Beshkov 2000), more than 700 insect species have been recorded as being associated with the genus *Populus*. Delplanque (1998) lists more than 650 species of insects which are associated with poplars (Table 2). However, many of these species are polyphagous and feed on poplar species as well as a number of other hosts. Although poplars may play an important role for a high number of unspecialized (euryphagous) herbivores, these polyphagous herbivores are not part of the following overview. It concentrates on the faunal biodiversity which exclusively or primarily depends on poplar species as a food source.

Table 2. Insects associated with poplars, according to Delplanque (1998)

Insect families	Number of species associated with poplars	Insect families	Number of species associated with poplars
Scolytidae	11	Cephalidae	1
Buprestidae	16	Cimbridae	3
Cerambycidae	17	Tenthredinidae	22
Chrysomelidae	30	Vespoidea	1
Curculionidae	56	Apidae	1
Lucanidae	2	Thysanoptera	9
Meloidae	5	Cicadidae	3
Rutelidae	4	Flatidae	1
Meloidae	1	Cercopidae	3
Nymphalidae	5	Membracidae	2
Nepticulidae	10	Cicadellidae	24
Cossidae	2	Aphididae	28
Cochlididae	1	Ortheziidae	1
Lyonetidae	1	Pseudococcidae	1
Gracillariidae	8	Coccidae	6
Phyllocnistidae	3	Diaspididae	9
Oecophoridae	4	Pentatomidae	8
Coleophoridae	3	Coreidae	2
Gelechiidae	3	Tingidae	1
Yponomeutidae	2	Lygaeidae	5
Sesiidae	3	Miridae	6
Tortricidae	43	Tetranychidae	3
Cochylidae	1	Eriophyiidae	9
Pyralidae	3	Phytoseiidae	32
Lasiocampidae	6	Coccinellidae	10
Attacidae	1	Carabidae	10
Thyatiridae	4	Staphylinidae	1
Geometridae	27	Chrysopidae	1
Sphingidae	2	Hemeribiidae	1
Notodontidae	19	Syrphidae	4
Lymantriidae	7	Sphecidae	64
Arctiidae	3	Formicidae	6
Noctuidae	32	Pentatomidae	2
Agromyzidae	7	Nabidae	3
Cecidomyiidae	24	Reduviidae	1
Panphiliidae	2	Anthocoridae	5
Xiphidriidae	1	Miridae	4
Sicidae	1	Total	663

Heydemann (1982) has published the numbers of specialized (stenophagous) species of herbivores which are associated with the most important trees and shrubs, including *P. nigra*, *P. alba* and *P. tremula* as well as the genus *Populus* in Central Europe (specifically Schleswig Holstein) (Table 3).

The genus *Populus* appears in the upper fourth of the ordered table (in seventh position), being host to 88 stenophagous species of herbivores. This compares with *Salix* and *Quercus* which respectively host twice and three times the number of specialized species. While *P. tremula* hosts a comparatively high number of species, *P. alba* and *P. nigra* are situated in the lower half of the table with 25 and 18 species of associated herbivores, respectively.

Somewhat higher but comparable numbers of stenophagous species associated with the genus *Populus* were reported by Southwood (1961) for the United Kingdom and Sweden. In

Table 3. Number of species of stenophagous phytophagous insects associated with important tree and shrub species in Central Europe (Schleswig-Holstein), based on data published by Heydemann (1982)

Tree/shrub species	Insect groups																		Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
<i>Quercus</i> spp.	12	12	5	3	0	4	0	75	10	16	70	15	2	16	8	22	24	4	298
<i>Salix</i> spp.	17	9	6	1	1	7	0	0	33	16	38	6	3	16	6	23	25	11	218
<i>Betula</i> spp.	8	10	4	3	1	3	1	0	18	11	27	10	2	17	6	30	9	4	164
<i>Pinus sylvestris</i>	22	5	4	3	0	2	2	0	1	16	42	54	0	1	1	6	1	2	162
<i>Picea abies</i>	17	4	12	1	0	1	0	0	1	10	44	44	0	1	1	11	2	1	150
<i>Fagus sylvatica</i>	6	2	1	2	0	1	0	0	0	6	38	19	0	7	3	7	4	4	100
<i>Populus</i> spp.	7	0	4	2	0	3	0	0	15	0	24	15	0	7	4	0	6	1	88
<i>Ulmus</i> spp.	2	4	6	4	0	2	0	0	0	3	28	19	2	0	2	1	5	1	79
<i>Corylus avellana</i>	6	3	1	0	1	2	0	0	15	7	25	10	1	1	0	3	0	1	76
<i>Populus tremula</i>	2	4	1	0	0	0	0	0	0	17	0	9	2	12	0	0	12	8	67
<i>Prunus spinosa</i>	2	0	5	3	0	0	0	0	0	9	15	0	2	5	0	16	7	3	67
<i>Alnus</i> spp.	0	0	0	4	0	5	0	0	0	3	24	10	0	5	2	0	5	3	61
<i>Crataegus</i> spp.	2	1	7	0	1	0	0	0	5	6	10	2	1	4	0	12	6	3	60
<i>Carpinus betulus</i>	0	5	1	4	2	1	0	0	0	3	23	14	0	2	1	0	0	3	59
<i>Abies alba</i>	1	0	9	1	0	0	0	0	0	0	19	28	0	0	0	0	0	0	58
<i>Tilia</i> spp.	6	3	1	1	0	4	2	0	0	3	18	4	0	3	2	1	4	5	57
<i>Alnus glutinosa</i>	9	10	2	2	0	0	0	0	7	10	0	0	0	0	0	14	0	0	54
<i>Larix</i> spp.	3	0	1	0	0	2	0	0	1	2	9	31	0	0	0	1	0	0	50
<i>Fraxinus excelsior</i>	6	0	1	3	1	2	0	0	0	2	10	12	0	1	2	2	2	3	47
<i>Malus sylvestris</i>	5	0	5	3	0	0	0	0	0	10	0	8	1	4	1	4	3	1	45
<i>Pyrus piraster</i>	3	0	6	1	1	0	1	0	0	9	9	5	1	0	0	6	1	2	45
<i>Vaccinium myrt.</i>	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	18	16	2	40
<i>Rosa</i> spp.	0	1	9	2	1	0	1	10	1	3	8	0	0	0	0	0	1	1	38
<i>Prunus padus</i>	0	0	3	3	0	0	0	0	0	4	15	2	2	4	0	3	0	0	36
<i>Salix alba</i>	0	6	7	0	0	0	0	0	0	19	0	0	0	0	0	0	0	3	35
<i>Salix aurita</i>	0	67	3	0	0	0	0	0	0	16	0	0	0	0	0	0	0	9	35
<i>Salix cinerea</i>	0	2	7	0	0	0	0	0	0	14	0	0	0	0	0	0	0	11	34
<i>Salix caprea</i>	0	2	6	0	0	0	0	0	0	17	0	0	0	1	0	0	0	7	33
<i>Rubus</i> spp.	0	2	3	0	1	0	0	1	1	2	2	1	0	0	2	5	10	2	32
<i>Prunus avium</i>	0	2	3	3	0	0	0	0	0	10	0	7	2	4	0	0	0	0	31
<i>Salix viminalis</i>	0	3	5	0	0	0	0	0	0	18	0	0	0	0	0	0	0	3	29
<i>Lonicera</i> spp.	0	0	3	2	2	0	0	0	0	0	2	0	1	0	2	6	5	3	26
<i>Sorbus aucuparia</i>	1	1	3	3	0	0	0	0	1	0	2	6	0	0	1	5	1	2	26
<i>Populus alba</i>	0	4	2	0	0	0	0	0	0	11	0	4	0	1	0	0	0	3	25
<i>Acer</i> spp.	0	3	0	0	2	0	1	1	0	1	0	4	0	0	0	7	2	3	24
<i>Ribes</i> spp.	2	0	8	3	0	0	0	0	0	0	0	0	1	0	1	3	0	1	19
<i>Populus nigra</i>	2	0	5	0	0	0	0	0	0	9	0	0	0	0	0	0	2	0	18
<i>Salix repens</i>	0	3	2	0	0	0	0	0	0	2	0	0	0	1	0	0	0	9	17
<i>Frangula alnus</i>	1	0	1	0	0	0	0	0	0	0	6	4	3	1	0	0	0	1	17
<i>Acer campestre</i>	0	1	4	0	1	0	0	0	0	0	0	7	0	0	0	0	0	3	16
<i>Rhamnus cathart.</i>	0	0	1	0	0	0	0	0	0	0	6	4	0	0	0	4	0	0	15
<i>Euonymus erop.</i>	0	0	4	0	0	0	0	0	0	0	6	0	0	0	0	1	0	0	11
<i>Salix pentandra</i>	0	0	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0	4	9
<i>Sambucus</i> spp.	0	0	3	0	0	0	0	0	0	0	1	0	0	1	1	1	1	2	9
<i>Viburnum opulus</i>	0	0	4	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	7
<i>Juniperus comm.</i>	0	1	0	0	0	0	0	0	0	0	2	0	0	0	1	2	0	0	6
<i>Vaccinium uliginos.</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	2	0	5
<i>Ligustrum vulgare</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	5
<i>Syringia vulgaris</i>	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	1	0	5
<i>Hedera helix</i>	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	1	0	0	5
<i>Hippophae rhamn.</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ilex aquifolium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1

Key to insect groups: 1 = Heteroptera (SH); 2 = Cicadina (SH); 3 = Aphidina; 4 = Coccoidea; 5 = Aleurodina; 6 = Thyanoptera; 7 = Copeognatha; 8 = Cynipidae; 9 = Chrysomelidae; 10 = Curculionidae; 11 = Cerambycidae; 12 = Scolytidae/Platypodiale; 13 = Rhopalocera (SH); 14 = Bombycoidea; 15 = Arctiidea, Sphingidea und small Lepidoptera families; 16 = Geometridea (SH); 17 = Noctuidea (SH); 18 = Cecidomyiidea.

SH = data from Schleswig-Holstein only.

the United Kingdom, 97 species of insects were found to live primarily on poplars (fifth position), among them 78 species of Lepidoptera and Coleoptera, while 114 species were reported for Sweden. Similar results for the United Kingdom were published by Carter *et al.* (1979). Their results are summarized in Table 4.

Table 4. Number of phytophagous insects feeding on the most important tree species in the United Kingdom, according to Carter *et al.* (1979)

Tree/shrub species	Insect groups					Total
	Heteroptera	Homoptera	Makrolepidoptera	Mikrolepidoptera	Coleptera	
<i>Quercus</i> spp.	37	10	106	81	50	284
<i>Salix</i> spp.	22	20	100	73	51	266
<i>Betula</i> spp.	12	4	94	84	35	229
<i>Crataegus</i> spp.	17	1	64	53	14	149
<i>Prunus spinosa</i>	4	2	48	43	12	109
<i>Populus</i> spp.	8	11	33	26	19	97
<i>Malus domestica</i>	18	3	21	42	9	93
<i>Pinus sylvestris</i>	15	3	10	28	35	91
<i>Alnus glutinosa</i>	14	8	28	27	13	90
<i>Ulmus</i> spp.	11	4	33	26	10	82
<i>Corylus avellana</i>	16	2	18	28	9	73
<i>Fagus sylvatica</i>	4	3	24	16	17	64
<i>Fraxinus excelsior</i>	10	2	16	9	4	41
<i>Picea abies</i>	9	1	6	13	8	32
<i>Tilia</i> spp.	7	2	15	5	2	31
<i>Carpinus betulus</i>	1	0	7	16	4	28
<i>Acer campestre</i>	2	2	8	12	2	26
<i>Juniperus comm.</i>	6	0	4	8	2	20
<i>Larix</i> spp.	3	0	6	6	2	17

In terms of the number of associated species, the genus *Populus* is situated in the upper third (sixth position) of the tree and shrub species listed, although it supports less than half the species richness found on *Quercus*, *Salix* or *Betula* (Table 4).

The best and most complete overview of associations of host trees and herbivores, including poplar species, is given by Hondong (1994). Unfortunately, this very valuable compilation has not been published and is available only as a manuscript. For this reason, the results are reported here in detail. Hondong's work is especially valuable because it compiles all information on species–host associations available in the German literature on phytophagous insects. Moreover, herbivorous insects were classified on the basis of how endangered they are, thus providing information on the importance of host species for the conservation of endangered species of herbivores. Although most information sources relate to Germany, Hondong's compilation provides very valuable and unique information on species–host associations which in most cases should closely reflect the situation in Central Europe. It is interesting to note here that poplar–biodiversity relationships as well as possible impacts of poplar cultivation on biodiversity have mainly been studied in Germany. These topics have been of special interest because of the criticism that poplar plantations have encountered from nature conservation organizations in this country.

For the higher butterflies (Rhopalocera), skippers (Grypocera) and burnets (Zygaenidae), the following results are based on data from Baden-Württemberg (Ebert and Rennwald 1991), Central Europe (Weidemann 1986, 1988), Switzerland (SBN 1991) and Germany (Blab and Kudrna 1982). The larvae of these insects generally feed on buds, leaves and needles. A total of 177 species have been recorded in Germany, of which 91 (or more than half) are classified as threatened and 2 are now extinct. The importance of the most common tree and shrub species as a food source for the mentioned groups is presented in Table 5.

Table 5. Importance of tree and shrub genera as hosts for the larvae of higher butterfly (Rhopalocera), skipper (Grypocera) and burnet (Zygaenidae) species (after Hondong 1994). The numbers indicate how many species feed on each host

Geographic area Endangerment	Baden-Württemberg ¹		Germany ²		Switzerland ⁴
	Total number	Red list species	Total number	Total number	Total number
Tree/shrub genera					
<i>Prunus</i>	6	6	6	8	6
<i>Salix</i>	6	5	9	3	5
<i>Populus</i>	5	5	3	3	2
<i>Frangula</i>	5	3	0	2	2
<i>Cornus</i>	3	2	1	2	1
<i>Lonicera</i>	3	2	3	3	2
<i>Rubus</i>	3	2	1	7	1
<i>Ulmus</i>	3	2	3	3	3
<i>Betula</i>	2	2	1	2	2
<i>Crataegus</i>	2	2	1	4	1
<i>Pyrus</i>	2	2	0	0	1
<i>Quercus</i>	2	2	2	2	2
<i>Rhamnus</i>	2	1	0	3	3
<i>Ribes</i>	2	1	0	2	1
<i>Humulus</i>	2	0	1	1	1
<i>Fraxinus</i>	1	1	1	1	0
<i>Malus</i>	1	1	0	0	1
<i>Rosa</i>	1	1	0	0	1
<i>Sorbus</i>	1	1	0	0	1
<i>Ulex</i>	1	1	0	2	0
<i>Corylus</i>	1	0	0	1	1
<i>Hedera</i>	1	0	1	0	0
<i>Ligustrum</i>	1	0	0	0	0
<i>Euonymus</i>	0	0	1	0	0
<i>Hippophae</i>	0	0	1	0	0
<i>Sambucus</i>	0	0	0	1	0

Source of information and groups included:

- 1 Ebert and Renewald (1991); Rhopalocera and Grypocera.
- 2 Weidemann (1986, 1988); Rhopalocera and Grypocera
- 3 Blab and Kudrna (1982); Rhopalocera, Grypocera and Zygaenidae
- 4 SBN (1991); Rhopalocera

On the basis of the data from Baden-Württemberg (based on actual, verified field observations, while the other sources are based on literature records only), the genus *Populus* is an important food source for three groups of Lepidoptera. It is ranked third after *Prunus* and *Salix*. Moreover, all recorded species depending on *Populus* are listed as threatened species. According to the other less reliable sources of information, *Populus* has an average importance as a food source for these groups of Lepidoptera.

According to Koch (1984, cited in Brockmann 1991), 117 or 10% of the 1200 species of butterflies (Rhopalocera) are associated with the genus *Populus*. The number of butterfly species whose larvae feed on the different poplar species is listed in Table 6. From this table it can be seen that only a very small number of butterfly species associated with the genus *Populus* restrict themselves to indigenous black poplar alone. Most of them are able to feed equally on all poplar species and hybrids; they are thus oligophagous on the genus *Populus*. A rather large number of them even feed on *Populus* and *Salix*. Within the genus *Populus*, *P. tremula* seems to be by far the most important host for the monophagous Lepidoptera.

Table 6. Associations of butterfly species (Rhopalocera) with poplars (and willows) according to Koch (1984). The numbers indicate how many species feed on each host

All poplar species	78
<i>Populus alba</i>	2
<i>Populus tremula</i>	46
<i>Populus nigra</i>	11
<i>Populus nigra</i> subsp. <i>italica</i>	2
<i>Populus</i> × <i>euramericana</i>	5
<i>Populus deltoides</i>	1
<i>Populus</i> and <i>Salix</i> species	74

Food preferences of moth species belonging to the Bombycoidea and Sphingoidea were analysed by Peterson (1984). The study included 277 moth species of Central Europe, of which 255 were found in Germany with 104 of them being threatened. The larvae of most of these species are phytophagous and only occasionally feed on roots or wood. Table 7 lists the number of moth species associated with the most important genera of trees and shrubs.

The genus *Populus* is ranked second after *Salix*. More than two thirds of the associated 32 species feed exclusively or primarily on poplars. Together with *Quercus*, the genus *Populus* is a food source for the highest number of threatened moth species in Germany. *Populus* even hosts the highest number of threatened species which primarily depend on a genus.

Another group of important phytophagous species are the beetles (Coleoptera), especially long-horned beetles (Cerambycidae), bark beetles (Scolytidae), weevils (Curculionidae), fungus weevils (Anthribidae) and leaf beetles (Chrysomelidae).

A total of 175 species of long-horned beetles exist in Germany; 101 of them are listed as threatened or extinct. Only a small proportion of the Cerambycidae is phytophagous; most of the species live on decaying wood of dead trees and shrubs, which explains the high proportion of threatened species. Table 8 lists trees and shrubs which serve as food sources for the larval stage of phytophagous long-horned beetles in Central Europe, based on data from Koch (1992).

With 40 species of phytophagous long-horned beetles, the genus *Populus* is ranked in sixth position. Poplars seem to be a rather important host species for this group of herbivores, since half of these species are classified as threatened in Germany.

A total of 946 species of weevils (Rhynchophora) exist in Germany, with 318 species classified as threatened. While the fungus weevils (Anthribidae) and the bark beetles (Scolytidae) mostly feed on wood, the true weevils (Curculionidae) are mostly phytophagous.

Bark beetles are primarily associated with conifers (Table 9). As regards broadleaf species, *Populus* is ranked in fifth position having only three associated species fewer than *Quercus*.

The group of true weevils (Curculionidae) contains mostly species of phytophagous beetles which generally feed in a polyphagous manner on certain plants (Blab *et al.* 1984). An overview of species–host associations is presented in Table 10. Most species are polyphagous on broadleaves. For the mono- or oligophagous species, however, the genus *Populus* seems rather important, being the third most important host after *Salix* and *Quercus*. Of the species that feed primarily on *Populus*, however, only a small number are classified as endangered in Germany.

Table 7. Host genera for the larvae of moth species (Bombycoidea and Sphingoidea). The numbers indicate how many species feed on each host, differentiated according to their dependence and status of threat in Germany. After Hondong (1994), based on data from Peterson (1984)

Tree/shrub genera	Number of moth species			
	1	2	3	4
<i>Salix</i>	35	17	13	6
<i>Populus</i>	32	22	14	9
<i>Quercus</i>	30	17	14	8
<i>Betula</i>	25	9	12	5
Polyphagous on trees and shrubs	23	0	7	0
Polyphagous on broadleaves	22	0	4	0
<i>Fagus</i>	17	5	4	0
<i>Alnus</i>	13	4	5	3
<i>Prunus</i>	10	1	4	0
<i>Tilia</i>	9	1	5	1
<i>Rubus</i>	9	3	3	0
<i>Picea</i>	7	1	2	0
<i>Pinus</i>	6	2	2	1
<i>Abies</i>	6	0	2	0
<i>Sorbus</i>	5	0	2	0
<i>Corylus</i>	5	0	1	0
<i>Ulmus</i>	4	1	2	1
<i>Crataegus</i>	4	1	1	0
<i>Carpinus</i>	4	1	1	1
<i>Acer</i>	3	2	2	1
Polyphagous on conifers	3	0	1	0
<i>Larix</i>	3	1	0	0
<i>Lonicera</i>	2	0	1	0
<i>Fraxinus</i>	2	0	1	0
<i>Malus</i>	2	1	0	0
<i>Rosa</i>	2	0	0	0
<i>Ligustrum</i>	1	0	0	0
<i>Viburnum</i>	1	0	0	0
<i>Ribes</i>	1	0	0	0
<i>Euonymus</i>	1	0	0	0
<i>Juniperus</i>	1	0	0	0

1 = number of species feeding on the genus.

2 = number of species which primarily feed on the genus.

3 = number of species which are threatened in Germany.

4 = number of threatened species which primarily feed on the genus.

Table 8. Species of long-horned beetles (Cerambycidae) in Central Europe whose larvae feed on trees and shrubs. The numbers indicate how many species feed on each host, differentiated according to their dependence and status of threat in Germany. After Hondong (1994), based on data from Koch (1992)

Tree/shrub genera	Number of Cerambycidae species			
	1	2	3	4
<i>Quercus</i>	91	32	34	15
<i>Fagus</i>	56	7	24	2
<i>Pinus</i>	53	22	24	10
<i>Picea</i>	49	15	21	7
<i>Salix</i>	42	7	15	2
<i>Populus</i>	40	8	20	6
<i>Ulmus</i>	36	0	14	0
<i>Castanea</i>	35	2	14	0
<i>Prunus</i>	35	2	8	0
<i>Alnus</i>	34	2	15	1
<i>Betula</i>	33	1	7	0
<i>Tilia</i>	31	6	14	3
<i>Acer</i>	24	2	11	1
<i>Abies</i>	24	1	11	0
<i>Corylus</i>	24	2	8	0
<i>Pyrus</i>	24	0	2	0
<i>Carpinus</i>	20	0	9	0
<i>Juglans</i>	19	0	11	0
<i>Larix</i>	19	3	6	1
<i>Malus</i>	19	1	2	0
<i>Aesculus</i>	15	2	9	1
<i>Fraxinus</i>	15	0	6	0
Polyphagous on broadleaves	15	0	0	0
Polyphagous on conifers	9	0	1	0
<i>Robinia</i>	8	0	5	0
<i>Crataegus</i>	8	0	2	1
<i>Rhamnus</i>	5	1	2	1
<i>Euomyzus</i>	5	0	0	0
<i>Sorbus</i>	3	0	2	0
<i>Juniperus</i>	3	0	1	0
<i>Rosa</i>	3	0	0	0
<i>Lonicera</i>	2	2	1	1
<i>Rubus</i>	2	0	1	0
<i>Viburnum</i>	2	0	0	0

1 = number of species feeding on the genus.

2 = number of species which primarily feed on the genus.

3 = number of species which are threatened in Germany.

4 = number of threatened species which primarily feed on the genus.

Table 9. Species of bark beetles (Scolytidae) occurring in Central Europe whose larvae feed on trees and shrubs. The numbers indicate how many species feed on each host, differentiated according to their dependence and status of threat in Germany. After Hondong (1994), based on data from Koch (1992)

Tree/shrub genera	Number of Scolytidae species			
	1	2	3	4
<i>Pinus</i>	63	42	13	8
<i>Picea</i>	50	21	9	4
<i>Abies</i>	31	7	5	3
<i>Larix</i>	31	2	4	0
<i>Quercus</i>	17	8	2	0
<i>Fagus</i>	17	5	1	0
<i>Ulmus</i>	15	8	4	3
<i>Populus</i>	14	6	2	1
<i>Pseudotsuga</i>	14	0	2	0
<i>Carpinus</i>	12	0	1	0
<i>Acer</i>	11	0	3	0
<i>Fraxinus</i>	10	4	1	0
<i>Alnus</i>	7	3	3	1
<i>Corylus</i>	7	2	1	1
<i>Castanea</i>	7	2	0	0
<i>Tilia</i>	6	2	1	0
<i>Betula</i>	6	1	0	0
<i>Juglans</i>	6	0	0	0
<i>Juniperus</i>	6	0	0	0
<i>Salix</i>	4	2	2	0
<i>Pyrus</i>	4	0	1	0
Polyphagous on broadleaves	4	0	0	0
<i>Rhamnus</i>	3	1	1	1
<i>Sorbus</i>	3	0	1	0
<i>Crataegus</i>	2	0	0	0
<i>Malus</i>	2	0	0	0
<i>Robinia</i>	2	0	0	0

1 = number of species feeding on the genus.

2 = number of species which primarily feed on the genus.

3 = number of species which are threatened in Germany.

4 = number of threatened species which primarily feed on the genus.

A total of 463 different species of leaf beetles (Chysomelidae) occur in Germany. Of these, 183 are either extinct or classified as endangered. The species of this ecologically rather homogeneous group of beetles are mostly oligophagous herbivores feeding on different parts of the plants. The genus *Populus*, ranked in fourth position after *Salix*, *Corylus* and *Quercus*, provides important hosts for this group of herbivores (Table 11). A high proportion of these leaf beetles primarily live on the genus *Populus*, although only a few of them are listed as threatened.

For the fungus weevils (Anthribidae), which are a group with a rather restricted number of species, *Populus* is not an important host species (Table 12).

Table 10. Species of weevils (Curculionidae) occurring in Central Europe whose larvae feed on trees and shrubs. The numbers indicate how many species feed on each host, differentiated according to their dependence and status of threat in Germany. After Hondong (1994), based on data from Koch (1992)

Tree/shrub genera	Number of Curculionidae species			
	1	2	3	4
Polyphagous on broadleaves	108	0	11	0
<i>Salix</i>	66	41	8	5
<i>Quercus</i>	63	41	17	11
<i>Populus</i>	41	27	4	4
Polyphagous on conifers	37	0	1	0
<i>Alnus</i>	34	6	5	1
<i>Pinus</i>	32	23	6	4
<i>Betula</i>	28	10	2	1
<i>Picea</i>	27	8	6	4
<i>Fagus</i>	24	6	8	1
<i>Crataegus</i>	22	4	10	5
<i>Corylus</i>	18	3	3	0
<i>Rosaceae</i>	18	9	2	1
<i>Abies</i>	12	4	4	1
<i>Prunus</i>	12	5	3	2
<i>Ulmus</i>	11	7	2	0
<i>Acer</i>	10	7	6	4
<i>Rubus</i>	9	4	2	1
<i>Carpinus</i>	9	0	1	0
<i>Fraxinus</i>	8	6	1	1
<i>Castanea</i>	6	0	2	0
<i>Pyrus</i>	6	2	1	0
<i>Larix</i>	6	1	0	0
<i>Sorbus</i>	5	1	3	1
<i>Ligustrum</i>	4	1	0	0
<i>Rosa</i>	4	0	0	0
<i>Tilia</i>	3	0	0	0
<i>Euonymus</i>	1	1	1	1
<i>Juglans</i>	1	0	1	0
<i>Cornus</i>	1	1	0	0
<i>Lonicera</i>	1	1	0	0
<i>Frangula</i>	1	0	0	0
<i>Malus</i>	1	0	0	0

1 = number of species feeding on the genus.

2 = number of species which primarily feed on the genus.

3 = number of species which are threatened in Germany.

4 = number of threatened species which primarily feed on the genus.

In summary, the genus *Populus* hosts a rich complex of phytophagous herbivores. For many species of butterflies, moths and beetles, *Populus* is an important food source. Poplars are exclusive or primary hosts to a high proportion of threatened insect species, especially species of butterflies, moth and long-horned beetles. Poplars thus play an important role in the conservation of a large number of threatened species of herbivores and other species which are associated with them or depend on them.

The current base of knowledge does not permit the ranking in order of importance of the different poplar species as host plants. It seems, however, that monophagous herbivores are the exception rather than the rule. Long-horned beetles, butterflies, true weevils, fungus weevils and leaf beetles seem to utilize the whole genus. Many of the specialized species

even extend their potential hosts to the genus *Salix*. It is possible that the content of salic acid in the Salicaceae is responsible for the attractiveness of the two genera as a food source for many herbivores. It is known from a number of insects that they transform salic acid to a carbol-like substance which serves as a defence mechanism against predators. It is in fact striking that a number of genera in most of the mentioned groups of herbivores have become specialized to live on *Salix* and *Populus* (for example *Saperda*, *Trypophloeus*, *Zeugophora*, *Chalcoides* or *Melasoma*).

Table 11. Number of species of leafbeetles (Chrysomelidae) in Central Europe whose larvae feed on trees and shrubs. Given are the number of species feeding on the listed hosts, differentiated according to their dependence and status of threat in Germany. After Hondong (1994), based on data from Koch (1992)

Tree/shrub genera	Number of Chrysomelidae species			
	1	2	3	4
<i>Salix</i>	89	42	31	11
<i>Corylus</i>	39	2	16	2
<i>Quercus</i>	35	14	15	8
<i>Populus</i>	35	20	7	2
<i>Betula</i>	34	1	16	1
<i>Alnus</i>	20	3	8	1
<i>Crataegus</i>	20	5	3	1
<i>Prunus</i>	11	1	2	0
<i>Sorbus</i>	7	0	3	0
<i>Pinus</i>	6	5	3	2
<i>Ulmus</i>	5	3	3	2
<i>Rosa</i>	4	0	3	0
<i>Abies</i>	4	1	2	1
<i>Rubus</i>	4	1	1	0
Polyphagous on broadleaves	4	0	0	0
<i>Fraxinus</i>	3	0	2	0
<i>Juglans</i>	2	0	2	0
<i>Carpinus</i>	2	0	2	0
<i>Tilia</i>	2	0	1	0
<i>Rhamnus</i>	2	0	0	0
<i>Fagus</i>	2	0	0	0
<i>Pyrus</i>	1	0	1	0
<i>Mespilus</i>	1	0	1	0
<i>Ostrya</i>	1	0	1	0
<i>Picea</i>	1	0	1	0
<i>Larix</i>	1	0	0	0
<i>Juniperus</i>	1	0	0	0
<i>Viburnum</i>	1	0	0	0
<i>Cornus</i>	1	0	0	0
<i>Acer</i>	1	0	0	0

1 = number of species feeding on the genus.

2 = number of species which primarily feed on the genus.

3 = number of species which are threatened in Germany.

4 = number of threatened species which primarily feed on the genus.

Table 12. Number of species of fungus weevils (Anthribidae) in Central Europe whose larvae feed on trees and shrubs. Given are the number of species feeding on the listed hosts, differentiated according to their dependence and status of threat in Germany. After Hondong (1994), based on data from Koch (1992)

Tree/shrub genera	Number of Chrysomelidae species			
	1	2	3	4
<i>Quercus</i>	14	6	3	1
<i>Fagus</i>	12	3	3	0
<i>Alnus</i>	10	0	4	0
<i>Salix</i>	10	0	2	0
<i>Crataegus</i>	8	0	4	0
<i>Corylus</i>	7	0	1	0
<i>Betula</i>	6	1	4	1
<i>Prunus</i>	6	0	4	0
<i>Carpinus</i>	5	1	2	0
<i>Tilia</i>	5	0	2	0
<i>Malus</i>	5	0	2	0
<i>Pinus</i>	4	1	2	0
<i>Ulmus</i>	4	0	1	0
<i>Populus</i>	4	0	1	0
<i>Picea</i>	3	0	2	0
Polyphagous on broadleaves	3	0	1	0
<i>Frangula</i>	2	0	1	0
<i>Sorbus</i>	2	0	1	0
<i>Fraxinus</i>	1	0	1	0
<i>Abies</i>	1	0	0	0
<i>Acer</i>	1	0	0	0
<i>Rhamnus</i>	1	0	0	0
Polyphagous on conifers	1	0	0	0

1 = number of species feeding on the genus.

2 = number of species which primarily feed on the genus.

3 = number of species which are threatened in Germany.

4 = number of threatened species which primarily feed on the genus.

Poplar plantations and biodiversity

Poplar plantations are often criticized as being unnatural and highly artificial compared to natural forests. In Central Europe, especially in Germany and Switzerland, the cultivation of poplars has decreased drastically in the face of opposition from nature conservation organizations (e.g. Naturschutzbund Deutschland, Späth 1992; Allard and Dufour 1997). The main arguments against poplar plantations can be summarized as follows:

- Hybrid poplars are introduced species. Since they are not part of the natural ecosystems, they may have negative effects on the native fauna and flora.
- The monospecific, single age stand structures, compared to natural forests, have negative impacts on fauna, flora and the landscape.
- Poplars are often cultivated on alluvial sites, replacing highly diverse and highly structured floodplain forest with stands composed of one species, one or few clones and little or no vertical structure.

Hybrid poplars and their influence on biodiversity

The issue of negative effects of hybrid poplars on the native fauna was discussed by Blab and Kudrna (1982). They claimed that two species of butterflies, the lesser purple emperor

(*Apatura ilia*) and the poplar admiral (*Limenitis populi*) have become endangered as a direct result of the cultivation of poplar hybrids. They argued that the young larvae of both species starved because they were unable to feed on the thicker, tougher leaves of the introduced 'Canadian poplars'. It has subsequently been shown that no such negative effect exists and that Blab and Kudrna (1982) wrongly interpreted and generalized an earlier observation made by Friedrich (1966). Friedrich observed that the larvae of *Apatura ilia* did not consume the offered leaves of *P. balsimifera* for 2 days, grew less and developed faster into the next larval stage but performed normally when feeding on other poplar species (*P. pyramidalis*, *P. × canadensis*, *P. tremula* and *P. nigra*). At the same time he observed dead larvae on *P. balsimifera* trees in the field, although the females of this butterfly preferred *P. balsimifera* for oviposition, obviously attracted by its more intense scent. He speculated that *A. ilia* larvae may be 'trapped' by *P. balsimifera* since the females preferred it for oviposition but the larvae were not able to consume the leaves. *L. populi* females were also especially attracted by *P. balsimifera*, although eggs were also frequently found on *P. tremula*, *P. nigra* and *P. pyramidalis*.

In conclusion, Friedrich writes that, even if *P. balsimifera* seemed to be more attractive for both species for oviposition, both the size of the trees and their position in the stand as well as the microhabitat were much more important for the attractiveness to the butterflies than the species itself. Although Friedrich's observation has never been scientifically investigated, Blab and Kudrna (1982) reported Friedrich's observation of a possible 'trap effect' of *P. balsimifera* as if it were a scientifically proven fact. Moreover, they incorrectly extended his observation to both butterfly species and to 'Canadian poplars' without any proof or additional data. Blab and Kudrna were obviously unable to distinguish between balsam poplars (which in fact have thicker and somewhat tougher leaves) and 'Canadian poplars', a name which was commonly used for all *P. × euramericana* hybrids (i.e. crosses between *P. nigra* and either *P. deltoides* or *P. angulata*). Since then, hybrid poplars have had the reputation of having negative effects on the native fauna. It is interesting to note here that Friedrich (1966) came to exactly the opposite conclusion. He believed that the decreasing populations of both butterfly species were primarily a result of the diminishing surface of poplar plantations as an important food source. This example has been described in some detail because it illustrates that facts and assumptions regarding negative effects of cultivated hybrids are often not clearly separated, and that the arguments often lack a scientific basis and are merely misinterpretations or ill-founded generalizations.

There is in fact no scientific evidence for the belief that hybrid poplars or introduced species have negative effects on the native fauna because they are not part of the natural system. Instead, available data tends to suggest that specialized herbivore–host associations operate at the level of the genus rather than the species. Hybrid poplars seem to be utilized by herbivores as a food source in the same way as the native species. In some cases, the introduced species are even preferred over the native species, as the two examples of *Apatura ilia* and *Limenitis populi* mentioned above demonstrate. Moth species, for example, form the most significant group of invertebrates in poplar plantations that are presently known (Prater 1993). A wide range of macro-moths are also found on native poplars (Table 13). Since most of the planted hybrids have *P. nigra* as one parent, it can probably be assumed that most of these moth species also feed on plantation poplars. In fact, studies on leaf grazing by Dagley (1987, cited in Prater 1993) showed that a substantial number of the moth species listed in Table 13 were also present in poplar plantations. The caterpillars occurred on all cultivars examined although it was significantly less on 'Serotina' than on other cultivars. This is an indication that cultivars of hybrid poplars may differ in their value for biodiversity (see later).

Table 13. Typical macro-moths found on poplars, according to Prater (1993)

<i>Xanthia ocellaris</i>	Pale-lemon sawfly
<i>Acronicta megacephala</i>	Poplar grey
<i>Furcula bifida</i>	Poplar kitten
<i>Eligmodonta ziczac</i>	Pebble prominent
<i>Pheosia tremula</i>	Swallow prominent
<i>Pterostoma palpina</i>	Pale prominent
<i>Clostera curtula</i>	Chocolate tip
<i>Cerura vinula</i>	Puss moth
<i>Smerinthus ocellata</i>	Eyed hawk
<i>Laothoe populi</i>	Poplar hawk

In contrast, there is evidence that host resistance to insect pests can affect associated species such as arthropods, fungi and birds. According to Dickson and Whitham (1996) or Campbell and Eikenbary (1990), plant resistance traits may affect aphid distribution and performance, for example. Aphids in turn may affect other species in different ways. Dickson and Whitham (1996) described such an interaction chain in natural hybrid cottonwood stands in northern Utah. Plant resistance traits affected the distribution of a common leaf-galling aphid (*Pemphigus betae*), which in turn influenced other community members. A richer arthropod community was observed on trees with high aphid densities relative to those with low aphid densities. Exclusion of the gall aphids on susceptible trees resulted in a 24% decrease in species richness and a 28% decrease in relative abundance of the arthropod community. In addition, exclusion of aphids also caused a two- to threefold decrease in foraging and/or presence of three taxa of aphid enemies, i.e. birds, fungi and insects. These results suggest that resistance traits may have a direct or indirect influence on associated species from different trophic levels. Removing certain genotypes from the populations, for example by breeding activities, or reducing the natural variability of resistance traits in the planting material may thus have serious indirect effects on the diversity of associated species.

While such negative effects may be a consequence of planting any improved material, they may be of special significance for poplars for the following reasons. Poplars are bred very intensively in Europe. According to Kleinschmit (2000), poplars come in fourth place after pine, spruce and oak regarding breeding activities. The reason for this is the high economic value of poplar plantations in Europe. France, for example, has 250 000 ha of poplar plantations which allow for an annual harvest of 3.4 million m³ of round wood. Regarding annual cut, poplar is the most important broadleaf in France followed by oak with 3.1 million m³ and beech with 2.3 million m³ (Villar 1998). Poplars are more susceptible to pests (insects, fungi, bacteria, virus and microplasms) which cause important economic losses than other commercial tree species (Villar 1998). In his compilation of insects associated with poplars, Delplanque (1998) lists more than 650 insects, most of which develop at the expense of the poplars. Consequently, the planting material used for plantations has been strongly selected for resistance traits against major poplar pests. Due to strong selections in the breeding programs, genetic variability is comparatively low in the employed material. Commonly, only a few clones are propagated and used for the plantations. For example in France, currently only 23 cultivars are nationally registered, only 10 of them are propagated and used for the plantations while only 5 make up 80% of the planted area (Villar 1998). Since resistance traits against parasites and fungi are important selection criteria in poplar breeding, and because genetic variation in the used planting material is very low, indirect effects on associated species are likely and probably more severe in poplars compared to other species.

According to Barkman (1958) and Hoffmann (1993), hybrid poplars support a rather high species richness of epiphytes. *P. × canadensis* (*P. × euramericana*) appears to be relatively rich in epiphyte species compared to other hosts, especially in polluted areas. In the moderately to slightly polluted areas in West Flanders, hybrid poplars were just as rich in epiphyte species as old *Quercus* and *Fraxinus* trees. Poplar cultivars with a rough, rather soft but grooved bark such as 'Robusta' supported a high species richness while very old, large and strongly grooved specimens with a hard bark and cultivars with a relatively soft and smooth bark were very poor in species (Hoffmann 1993).

In summary, poplar cultivars seem to have negative effects of on biodiversity of associated species. However, these negative impacts are rather a result of the genetic makeup of the planting material used (strongly selected material with very low genetic variability—few clones only) than a consequence of utilizing hybrids or foreign species to which the native fauna is not adapted.

Structural features of poplar plantations and biodiversity

There is some scientific evidence that both structure and composition of poplar plantations may have a negative effect on diversity of animals and plants. Poplar plantations are characterized by a much lower structural diversity than natural floodplain forests. In most cases, artificial plantations are monospecific, single-aged stands with little or no vertical structure. These structural features have a direct effect on associated species. It is a commonly observed pattern that mixed-aged stands have a higher level of biodiversity than even-aged stands. Waltz and Whitham (1997), for example, have demonstrated that plant development affects arthropod communities which may then, in a chain of interaction, have a cascade of effects on other species. Their investigation showed that mature zones of cottonwoods (i.e. crowns, flowering branches) supported 23% higher species richness and 108% higher relative abundance of arthropods than juvenile ramets of the same genotypes. In addition, of 17 common arthropod taxa, 8 showed a significantly higher abundance on one developmental zone over the others; 4 were more abundant on mature zones; while 4 were more frequent on juvenile ramets. These results suggest that habitat variability resulting from different developmental stages of host plants with varying levels of nutrition, chemical defence, leaf toughness and other factors affects species richness and abundance and contributes to increased biodiversity in uneven-aged stands. It is highly probable that other species of the food chain, such as predators, will also be affected. For example, Dickson and Whitham (1996) showed that within individual cottonwood trees, avian predators disproportionately foraged on branches where gall aphids (*P. betae*) were most abundant. After experimental reduction of the gall aphids, avian predation declined threefold relative to control branches. Plant development in time also alters branch architecture which, for example, can affect nest site selection by birds (McArthur and McArthur 1961; Martinsen and Whitham 1994; Waltz and Whitham 1997). Artificial poplar plantations have very little or no developmental variability, and consequently are expected to support less biodiversity than natural floodplain forests with their high structural diversity.

In fact, natural floodplain forests support a very high avian diversity and abundance (Table 14). They are very important for species conservation (Gepp et al 1985) and impacts of forestry, such as transformation into poplar plantations, have been well studied. Compared to natural floodplain forests, avian diversity and abundance is much lower in poplar plantations, as the following examples illustrate.

Table 14. Observed numbers of bird species in floodplain forests of Austria (Gepp *et al.* 1985)

Floodplain and location	Area of investigation (km ²)	Number of bird species
Enns/Trautfels	1	50
Donau/Petronell	4.1	64
Rhein delta	4	>70
Donau/Stopfenreuth	8.4	74
March–Thaya floodplains	40	117

A drastic reduction in the number of species and abundance of birds in poplar plantations has been described in floodplain forests of the Rhine in Baden, Germany by Späth (1981) (Table 15).

Table 15. Number of bird species and breeding pairs in floodplain forests and poplar plantations, based on data from Späth (1981)

Type of stand	Age	Number of species	Number of breeding pairs/10 ha	Number of samples	Size of samples (ha)
<i>Quercus-Ulmetum</i>	100	36–40	155	2	11–12
<i>Quercus-Ulmetum</i>	40	32	144	1	12
<i>Quercus-Ulmetum</i> with hybrid poplars	80	25	142	1	9
<i>Quercus-Carpinetum</i>	93	31–35	111	3	9–10
<i>Salicetum albae</i>	50	35–36	109	2	10–15
Hybrid poplars	60	20	82	1	13
Hybrid poplars with understory	93	26–29	76	2	10–15
Hybrid poplar with understory	40	15	32	1	4.4

Similar results were also reported by Handke and Handke (1982) for floodplain forests of the upper Rhine in Germany (Table 16).

Table 16. Number of bird species and breeding pairs in floodplain forests and poplar plantations, after Handke and Handke (1982)

Type of stand	Number of species	Number of breeding pairs/10 ha	Number of samples	Area surveyed (ha)
<i>Quercus-Ulmetum</i>	48	238–296	4	20.5
<i>Salicetum albae</i> , rarely flooded	43	190–288	2	7.7
<i>Salicetum albae</i> , regularly flooded	35	75–130	2	3.9
Hybrid poplar plantations	33	46–87	2	23.0

Finally, Späth and Gerken (1985) reported results for floodplain forests in Baden, Germany (Table 17).

According to Bogliani (1988), 10 species of birds nested in poplar plantations even if the ground layers were completely absent (mechanically removed); they were primarily canopy or secondary cavity nesters. Six species nested in the lower strata but only if a shrub layer was present. Other species which commonly occur in natural floodplain forests were very scarce or absent in the plantations. The very low density of some forest passerines was obviously related to the low structural diversity of the poplar plantations.

Table 17. Number of bird species and breeding pairs in floodplain forests and poplar plantations, after Späth and Gerken (1985)

Type of stand	Number of species	Number of breeding pairs/ 10 ha	Number of samples	Area surveyed (ha)
<i>Quercus-Ulmetum</i>	32–40	103–144	3	38.7
<i>Salicetum albae</i>	35–36	103–118	2	25
<i>Ulmus-Carpinetum</i>	31–35	114–117	2	19
Hybrid poplar plantations	5–29	6–27	3	23

Both age and structure of the stands thus have an influence on species diversity and abundance. According to Karthaus (1990) or Dorsch and Dorsch (1991), the density of the understory is of special significance for bird density. Likewise, Anderson and Ohmart (1983) showed that vegetation density and diversity were both important predictors of avian community measures at the habitat level. Avian density was more closely related to variation in the vegetation than was avian diversity. Poplar plantations generally have no understory or only a poorly developed one, which has direct negative effects on the bird community. In addition, the arthropod community may be negatively affected (see above) which indirectly contributes to a decrease in avian diversity and abundance.

Similarly, Twedt *et al.* (1999) described higher species richness, diversity and territory density of birds in mature (> 30 years) bottomland hardwood stands than in young (6–9 years old) cottonwood (*P. deltoides*) plantations in the Mississippi alluvial valley. Tree species diversity, angular canopy cover, and midstory density were positively associated with bird species assemblage in the mature bottom hardwood stands, whereas vegetation density at ground level was positively associated with bird communities in cottonwood plantations. The authors conclude that mature hardwood forests are twice as valuable for bird conservation as cottonwood plantations, primarily because of the higher variability in composition and structure of the stands.

In contrast, a higher avian diversity in poplar plantations than in alluvial forests has been reported by Godreau *et al.* (1999). Their results, however, show a change in species composition in poplar plantations with semi-open landscape and urban park or garden species and less forest species.

Positive effects of poplar plantations on a number of bird species were also reported by Prater (1993) for the United Kingdom. In particular, the threatened golden oriole (*Oriolus oriolus*) and the barn owl (*Tyto alba*) were found to be associated with poplar plantations in fenland. While the barn owl did not nest within the woodlots but used the young plantations for hunting, the golden oriole is considered a key species for poplar plantations in this region. Its breeding population size has increased as a result of the increasing number of poplar plantations during the 1980s. It is interesting to note here that golden orioles prefer cultivars with big leaves and an early bud break like '*Robusta*' as nesting habitats and clearly select against cultivars with the opposite characteristics such as '*Serotina*'. According to Prater (1993), the positive effects of poplar plantations on bird species in fenland are partly a result of the small amount of suitable woodlands other than poplar plantations as breeding habitats. This example clearly indicates that the biological value of poplar plantations may differ according to the overall situation and always needs to be evaluated in a broader context.

Negative effects of the artificial poplar plantations on natural vegetation have been reported by Schuldes and Kübler (1991) and Hügin (1981). Due to the light crown cover of poplar plantations, neophytes such as *Solidago canadensis*, *Solidago gigantea*, *Reynoutria*

japonica, *Reynoutria sachalinense*, *Impatiens glandulifera*, *Helianthus tuberosus* or *Hertacleum mategazzianum* may develop optimally and become invasive in the stands, reducing the species richness of the original ground vegetation. Likewise, Schnitzler and Muller (1998) describe the invasion of *Fallopia japonica*, a close relative of *F. sachalinensis*, in plantations of cultivated poplars. It may be assumed that the invasion of these plants may not only change floral diversity but also faunal diversity.

According to Barnaud *et al.* (1996), poplar plantations lead to a 'simplification of the original ecosystem' (vegetation as well as animals, especially birds). The change in vegetation cover is the result of either soil treatment (tilled sites for planting), herbicide treatment, mechanical removal of vegetation competition (weeds and bushes) or the changes in light conditions due to the wide spacing of poplars compared to natural forest, or a combination of several of these factors. According to Daudon (1994), the proportions of nitrophilous species such as nettles (*Urtica dioeca*) and big-leaved species are much higher in artificial poplar plantations than in natural forests. In the Garonne valley in France, Karinski (1997) showed that 75 out of 182 plant species found in poplar plantations are typical followers of such artificial plantations.

In summary, there is some scientific evidence that biodiversity in poplar plantations is less than that of natural floodplain forests on the same sites. Negative effects are primarily related to two causes: firstly, the genetically rather uniform, highly selected planting material of low genetic variability used for plantations may negatively affect the arthropod community and all dependent species, such as birds and other predators, resulting in a reduced faunal diversity. Secondly, habitat variability, resulting from both different developmental stages (with varying nutrition, chemical defences, leaf toughness and other factors affecting species richness and abundance) and vertical structures, which contributes to a high biodiversity of arthropods and associated species, is much smaller in poplar plantations than in natural floodplain forest, resulting in a reduced biodiversity. Moreover, changes in arthropod diversity or light conditions result in changes of overall species composition in both animals and plants.

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