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Seasonal dynamics of small mammals in an isolated woodlot and its agricultural surroundings

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The seasonal dynamics of small mammal populations was studied in an isolated 2.6–ha woodlot surrounded by agricultural "desert" in central Germany in 1984–88. The CMR method with monthly live trapping was used in 1984–86. In the autumn of 1986 all captured animals were removed and the recolonization of the woodlot was monitored until the spring of 1988. The bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) were dominant species in the woodlot. Wood mice exhibited a seasonal habitat change between woodlot and field, together with the less abundant yellow-necked mouse (*A. flavicollis*). The striped field mouse (*A. agrarius*) normally occurred in the forest in low numbers. During high densities of the common vole (*Microtus arvalis*) on the surrounding fields it also penetrated the inner parts of the woodlot. Contrary to expectation *Clethrionomys* was the most effective colonizer of the woodlot after the removal of rodents. The sex ratio of *Clethrionomys* was 1:1 at all seasons, that of *Apodemus*-species male-biased during the autumn immigration. The total densities of the rodent community were much higher during the autumn and winter than during the breeding season. The number of shrews was very low during the entire study and these seem to have a poor ability to colonize isolated areas. The study supports the idea of the importance of isolated woodlots in the agricultural mosaic, especially as overwintering refugies for rodents.

1. Introduction

Habitat patchiness affecting population dynamics has been a subject for several ecological studies (e.g. Wiens 1976, Abramsky & van Dyne 1980, den Boer 1980) – including the use of isolated woodlots in agricultural landscapes as study sites (e.g. Tischler 1958, Roth 1964, Wegener & Merriam 1979, Middleton & Merriam 1981, Fahrig &Merriam 1985). The special character of these 'islands' inside the intensive cultivated agricultural areas was appreciated early (Pflug 1955). Studies on small rodent dynamics in patchy agricultural habitats have mainly been carried out in the temperate zone of Europe and North America (Geuse et al. 1985, Gottfried 1979, Wegner & Merriam 1979, Middleton & Merriam 1981, Fahrig & Merriam 1985, Szacki 1987, Gliwicz 1988). Some sites (see Gottfried 1979) have been used to test the island biogeographical models of McArthur & Wilson (1967), or the workers have partially initiated models for pest control (e.g. Levin 1969, Stenseth 1977, 1981).

However, most field studies consider only rodent densities during the breeding season, giving an incomplete picture about the dynamics of the rodent community of such an island. We studied the seasonal dynamics of rodents in an isolated woodlot in central Germany in 1984–88. We used an intensive monthly live trapping technique throughout the study. The present paper deals with the following aspects of rodent dynamics in the woodlot:

1) What is the seasonal pattern of the occurrence of different rodent species inside an isolated woodlot?
2) What is the seasonal dynamics of small mammals between the woodlot and its agricultural surroundings?
3) How is an isolated forest patch colonized by small mammals after a local extinction or strong decline of the populations?

2. Study area, material and methods

The study area, an isolated forest area of 2.6 ha, was situated about 10 km southwest of the town of Halle in central Germany. It was surrounded by an intensively cultivated agricultural area sown with different crops each year. The surrounding vegetation varied from fodder production with lucern (*Medicago sativa*) and clover (*Trifolium* sp.) cultures on the north side of the woodlot to the man-high corn and poppy plantation on the south side. The surrounding agricultural areas showed great seasonal changes; after harvesting and reploughing in the autumn the area was desert-like without any cover until the spring sowing and formation of new vegetation.

The nearest areas with tree vegetation lay in the villages of Gröbers and Dieskau, both about 2 km from the study area. An old deep brown coal quarry used for dumping lay about one kilometre south of the woodlot. Its slopes were covered by ruderal vegetation with some bushes. Apart from hedges, small forest pockets and deciduous forest strips along the river valleys the district around the town of Halle has very little closed forest areas.

The tree layer of the woodlot was formed mainly by four *Acer*-species, *Fraxinus exelsior, Populus nigra, Sambucus nigra, Carpinus betulus, Ulmus carpinifolia, Aesculus hypocastanum* and *Robinia pseudacacia*. The field layer was also very diverse and relatively dense, especially during spring before the formation of the leaf cover on the trees. Characteristic species were *Chaerophyllum temulum, Urtica dioica, Geum urbanum, Alliaria petiolata, Aegopodium potagraria, Galium aparine, Ballota nigra* and *Glechoma hederaceum*. The woodlot was relatively uniform, with only an old field road and a small open meadow area between the trees. The edges of the woodlot, where there was more light, had a more diverse bush vegetation with creeping species like *Vicia cracca* and *Humulus lupulus*. The soil of the woodlot was smooth and easy for rodents to dig holes in.

We began the study in March 1984 and continued the intensive monthly live trapping until August 1986. Most of the woodlot (2 ha) was covered with a trap grid with 90 Ugglan Special multiple capture live traps. A long narrow easterly part of the woodlot (0.6 ha) with two small water holes was not included in the study area as this was almost isolated from the main area.

We marked each captured animal individually by toe-clipping before releasing it again. Each trapping session consisted of ten trap checkings during five days. Animals captured during that time were considered to be present in the wood that month. Using ten trap checkings we assumed it was possible to capture every individual of the rodent community at least once and the numbers presented in this paper represent total densities in the woodlot. On the basis of the data we determined the densities of each species, the sex ratios and the survival of different individuals in the woodlot. The total data for 1984–86 consists of 15 601 observations of ten species, six rodent species, three soricids (*Sorex araneus, S. minutus* and *Crocidura leucodon*) and the least weasel (*Mustela nivalis*). Weasels were removed from the study plot.

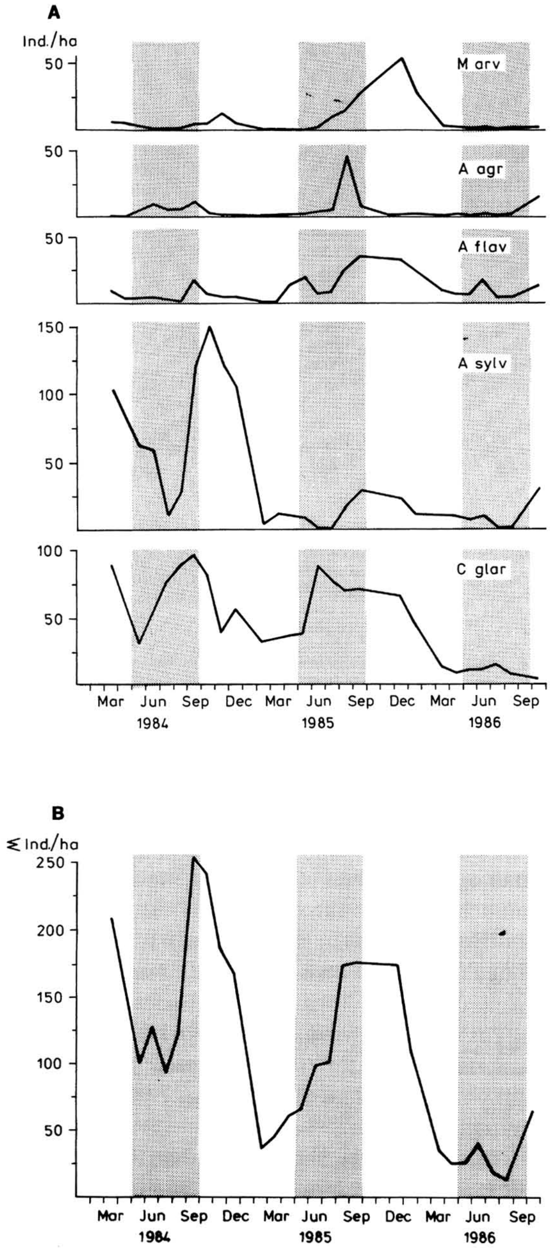

Fig. 1: Population density of different rodent species (A) and the total density of the rodent community (B) of the woodlot near Halle, in central Germany in 1984–86. The breeding season is shaded.

Between July and September of 1985 we also made an attempt at trapping outside the woodlot using three traplines of 200 m length. However, the trap type we used did not work in the totally open habitat. Obviously horizontal holes did not attract the mice and voles in an almost bare area. For example, *Microtus arvalis* seldom entered the traps in the open clover field, although its density was so high that several voles were observed between the traps during the trap checkings (see Nabaglo et al. 1984).

After commencing intensive trapping in the autumn of 1986 we started to remove all the animals captured in the woodlot. The isolated 0.6 ha part of the woodlot was included in this trapping. We removed all rodents and soricids during two trapping sessions in October and December 1986 in an attempt to completely empty the woodlot of small mammals. After this we trapped three times — in April and November 1987 and in March 1988 — in order to monitor the recolonization of the woodlot.

3. Results

3.1. Population dynamics

The most abundant species in the woodlot were the bank vole (*Clethrionomys glareolus*) and the wood mouse (*Apodemus sylvaticus*). Bank voles reached maximum densities of up to 96 voles/ha during late summer and wood mice a maximum density of 148 mice/ha in October 1984 (Fig. 1). The third species permanently present in the woodlot, the yellow-necked mouse (*A. flavicollis*), reached, especially during the first study year, only very low densities (maximum 17 mice/ha in September) compared to *A. sylvaticus*. Autumn densities of *A. sylvaticus* and *A. flavicollis* in 1985 were much more similar (Fig. 1).

The pattern of the population fluctuation between these two *Apodemus*-species was similar, with a low density phase during summer and a strong increase during autumn (Figs. 1 and 2). The mice captured in autumn were almost entirely adult individuals not previously captured in the woodlot (Fig. 3). The number of mice declined from autumn to spring and continued to do so during the early summer, too. Only a few new offspring were captured in the woodlot until al-

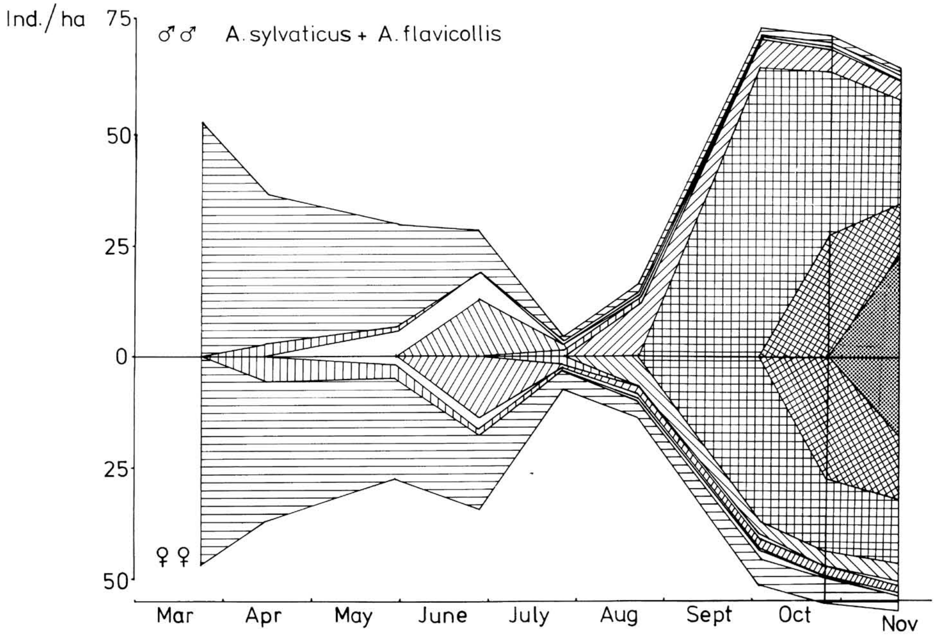

Fig. 2: Recruitment and survival of marked wood mice and yellow-necked mice in the woodlot population in the high density year of 1984. Differential shading shows the appearence of new individuals in the population every month and their survival until late autumn.

most all *Apodemus* individuals disappeared from the wood during June and July (Figs. 1 and 2). In the preceding autumn only a few of those *Apodemus*–individuals marked in the woodlot during spring were recaptured in the wood (Fig. 2).

The density fluctuation of the *Clethrionomys* population differed from that of the two *Apodemus*–species (Figs. 1 and 3.). After the spring decline and the onset of breeding the bank vole density began to grow, reaching its maximum during late summer (Fig. 1). The recruitment of new individuals to the population was more continuous in *Clethrionomys* than in *Apodemus* (Fig. 3) and the overwintering population was formed by individuals marked (born) in the woodlot.

Three other rodent species were captured in the woodlot: the striped field mouse (*Apodemus agrarius*), the common vole (*Microtus arvalis*) and the house mouse (*Mus musculus*). Of the last species only six individuals were captured during the whole study. *Apodemus agrarius* was present only during the summer and autumn and it entirely disappeared during the winter months. In August 1985 it had a short peak density of 45 mice/ha, which declined early in the autumn at the time of the immigration of *A. sylvaticus* and *A. flavicollis* into the woodlot (Fig. 1). *Microtus arvalis* occurred normally at low density (up to 10 voles/ha) in the small open area with tall grass vegetation. In the summer and autumn of 1985, with very high densities in the surrounding fields it also penetrated the inner parts of the woodlot and reached a peak density of 53 voles/ha in December (Fig. 1). The crash of the *Microtus* population was as dramatic as in the fields and the species remained totally absent during the trappings of the spring and autumn of 1988.

The whole rodent community had the highest densities of up to 250 individuals/ha during the autumn and early winter (Fig. 1).

The captures outside the woodlot in 1985 consisted of 112 individuals in all, of which *A. agrarius* made up 40.2%, *A. sylvaticus* 35.4% and *M. arvalis* 30.4%. *Clethrionomys* individuals were captured only three times in traps nearest to the woodlot.

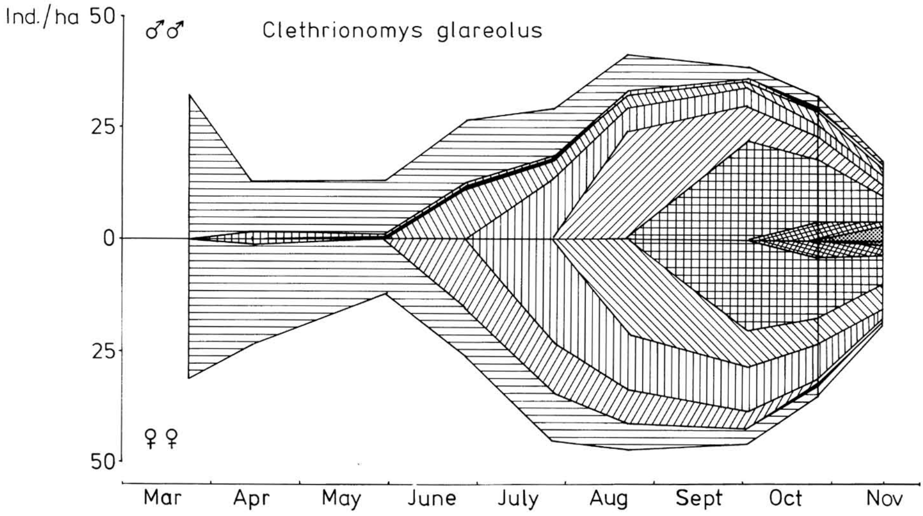

Fig. 3: Recruitment and survival of bank voles in the woodlot population in 1984. See legend to Fig. 2.

Soricids were rare in the woodlot; during the whole study only 33 *Sorex araneus*, five *S. minutus* and five *Crocidura leucodon* individuals were captured. The least weasel (*Mustela nivalis*) was captured eight times in 1984–86, and the captures were evenly distributed over the study period.

3.2. Sex ratio

In the pooled annual data the sex ratio of *Clethrionomys glareolus* was 1:1 (Fig. 4). *A. sylvaticus* and *A. flavicollis* exhibited a strong seasonal pattern of the sex ratio with significant deviations from 1:1 (July: $\chi^2 = 4.32$, $P<0.05$, September: $\chi^2 = 7.82$, $P<0.01$). During summer 70% of the mice remaining in the woodlot were females but during the autumn the invasion of mice from the fields was strongly male-biased (Fig. 4). The same pattern was observed during the removal trapping in the 1986 autumn: of 145 *A. sylvaticus* removed 59%, and of 46 *A. flavicollis* removed 61%, were males, but of 47 *A. agrarius* individuals only 49% were males. During *A. agrarius* and *M. arvalis* peaks in the summer and autumn of 1985 the sex ratios of the populations did not deviate from 1:1, either; (*A. agrarius*: 49% males, $\chi^2 = 0.005$, n.s.; *M. arvalis*: 54% males, $\chi^2 = 0.03$, n.s.).

3.3. Recolonization

In the autumn of 1986 a total of 252 rodent individuals were removed from the woodlot (Fig 5.). An additional ten Soricids and one *Mustela nivalis* were captured during the removal trapping. *Apodemus* species seem to immigrate into the woodlot during the winter months, too, as after the removal of 117 *Apodemus* specimens in October 120 specimens were captured in December and 24 as late as in April 1987. Bank voles were removed completely in October and December (Fig. 5). The relatively low total number of removed animals compared with the densities during the previous two autumns was due to the already low density of *Clethrionomys* during the summer of 1986 (Fig. 1).

Until the trapping in November 1987 the populations of all rodent species except that of *Microtus arvalis* had recovered well (Fig. 5). The total density of the rodent community was 176 individuals/ha. All three *Apodemus*-species occurred in about the same density, but the proportion of *C. glareolus* was 49% of the total number of rodents in the woodlot. The sex ratios of all species were 1:1 in November. No shrews were captured in November 1987 or March 1988.

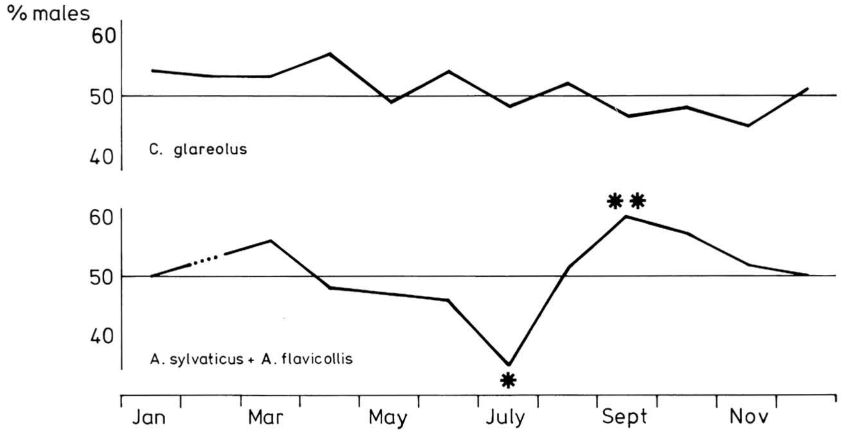

Fig. 4: Annual sex ratio (% of males in the population) for the bank vole and for the wood mouse and yellow-necked mouse combined (see Fig. 2). The data for each month is combined for the whole study period. Significant deviations from 1:1 are indicated with stars.

4. Discussion

The composition of the small rodent community of our study wood was similar to those found in previous studies on isolated forest areas or windbreaks (Ansorge 1983, Stubbe 1982, Geuse et al. 1985, Pelikan 1986, Gliwicz 1988) and resembles that of deciduous woodland (Gurnell 1985). The densities of *Apodemus sylvaticus* were similar to those found by Geuse et al. (1985) but the densities of *Clethrionomys* were much higher than found e.g. by these workers or by Gliwicz (1988) in small forest patches. The maximum densities in our study area outnumber those found in large woodland areas, too (review by Alibhai & Gipps 1985). This persistence of C*lethrionomys* could have been due to a lack of competition with *Apodemus* species during the main breeding season, as the mice moved to the fields during summer. The high maximum densities of rodents in the woodlot could have partly been due to the removal of captured weasels during the study (see Ryszkowski et al. 1971, Erlinge 1987).

Apodemus sylvaticus is known to be able to colonize very different habitats, from woodland to agricultural areas (Kikkawa 1964, Pollard & Relton 1970, Green 1979). In the present study it exhibited distinct seasonal habitat changes (Geuse et al. 1985). A. *flavicollis*, which is thought to be more dependent on mature woodland (Montgomery 1980, Gurnell 1985), took part in this shift between forest and field, too. The habitat change is supported by the facts that during the spring marked mice disappeared and were absent during the summer, an that the sex-ratio of autumn immigrants was male-biased with a high level of aggression between the individuals (many mice were tailless and wounded). Increasing aggression should indicate mutual unfamiliarity between the mice (e.g. Ferkin 1988).

Apodemus agrarius normally occurred inside the woodlot at very low densities but peaked once in 1985 when its densities were high in the surrounding fields. Its sudden disappearance during the autumn after the immigration of two other *Apodemus* species and *M*. arvalis implies competitive interactions among these species, which is contrary to suggestions by Pelz (1980). The occurrence of *Microtus arvalis* inside the woodlot was dependent on the fluctuation of its numbers in the surrounding fields (see Stubbe 1982). The few observations of *Mus musculus* were probably due to emigrants from the surrounding villages or from the landfill in the nearby quarry.

After the removal trappings in October and December 1986 either some *Apodemus*–speci-

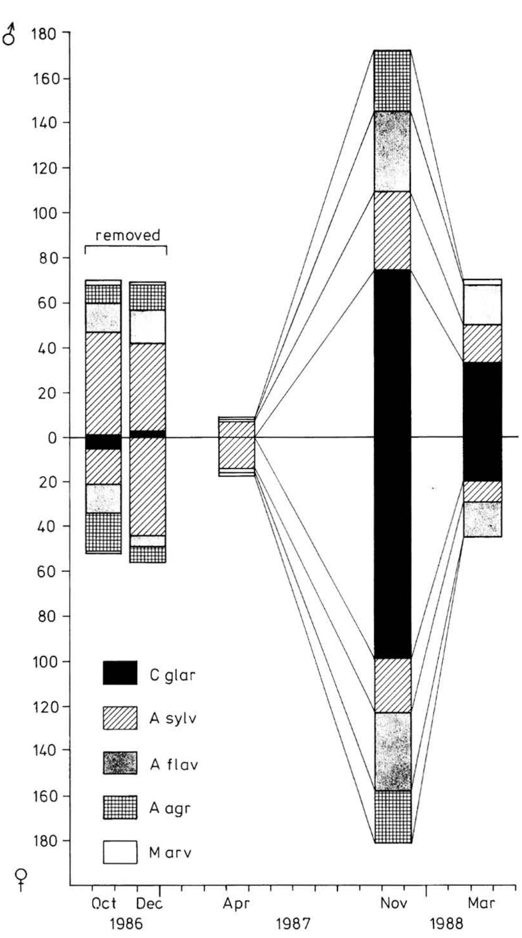

Fig. 5: The number of rodents removed from the woodlot during October and December 1986 and the recolonization of the woodlot during the subsequent year.

mens remained in the woodlot or these must have immigrated during the mid-winter. During the following April there were already six pregnant *A. sylvaticus* females present in the study area but *Clethrionomys* was absent. The rapid recolonization of the woodlot, especially by *Clethrionomys*, was not expected — one year after the removal its numbers (86 voles/ha) made up about half of the total density of the rodent community. This high colonization ability is contrary to the observations on the forest dependency of *Clethrionomys* (Geuse et al. 1985, Loman, unpubl. data).

An interesting point is whether recolonization already takes place during the spring and summer, or after harvesting, ploughing and harrowing in the autumn. In the first cases visual orientation would be almost impossible and the migratory movements of rodents should occur in any random direction. A harrowed field would be more like the surface of the sea and would allow visual orientation towards a woodlot silhouette. This has been shown to play a role e.g. in migrating lemmings crossing lakes or rivers (Myllymäki et al. 1962) and possibly in the colonization of islands by rodents and shrews (Hanski 1986).

Shrews occurred in low numbers in the woodlot throughout the study and were absent at least one year after the removal trapping. They seem to be relatively poor colonizers of isolated woodlots. For shrews an agricultural "desert" could act as a strong barrier to colonization in the same way as water in the annual colonization of small islands (Hanski 1986, Peltonen et al. 1989).

Strong winter declines in the rodent community can obviously be explained by climatic conditions and predation. Small isolated forest patches are much more exposed to severe climatic conditions (frost, wind, fall of wet snow as in the winter of 1984–85) than larger woodland areas. *Apodemus* species could be more sensitive to a changing climate than *Clethrionomys*. The diverse predator asemblage arround the study area resembled that studied by Erlinge et al. (1983) and Erlinge (1987) and it should have a strong impact on the winter decline, too.

The dynamics of the small mammal community with high densities during the nonbreeding season underscores the importance of these isolated woodlots as overwintering refuges for many mammal species. Beside the aesthetical aspects (Pflug 1955) and protection against wind erosion this is one of the main facets of the ecological importance of the woodlots in the agricultural landscape (Henderson et al. 1985).

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