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Effect of the *Quercus robur* L. Acorn Synzoochory by the Eurasian Jays *Garrulus glandarius* (Linnaeus, 1758) (Passeriformes: Corvidae) on the Shaping of an Orchard Landscape

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Abstract: Jays *Garrulus glandarius* play a major role in the synzoochorous dispersal of oaks in Europe, including Poland. Oaks have sprung up from acorns cached by jays not only in woodlands but also on meadows, pastures and fallow land. There are no reports as yet of acorn caching by these birds in orchards. This paper describes synzoochorous regeneration in orchards and attempts to evaluate its effect on the farming landscape. The research material was gathered from an area of 1.85 ha of fallow land in orchards (Poland, 51°41.712′N – 20°42.244′E). As a site for caching acorns, jays exhibited a preference for sour cherry orchards. The pedunculate oaks *Quercus robur* growing in these orchards were in very good condition. They may constitute a reservoir of good seeding material, which will also assist in the regeneration of the woodlands in the vicinity.

Key words: cherry orchard, fallow land in orchards, natural regeneration, seed dispersal, secondary succession, survival analysis

Introduction

There are two kinds of seed dispersal, i.e. autochory (self-dispersal) and allochory (vector dispersal) – the vectors in the latter being gravity, wind, water, animals and humans (Podbielkowski 1990, Kornaś & Medwecka-Kornaś 2002). Large-seeded species (oak, lime, hornbeam, hazel and walnut) are usually dispersed by animals, a process known as zoochory. If acorns were dispersed by autochory, they would never be able to reach areas beyond the driplines of their parent trees. Depending on the means by which seeds are carried, we can distinguish several types of zoochory; epizoochory, when seeds become accidentally attached to animals and are carried to a new site; endozoochory, when seeds are ingested and subsequently defecated in excreta at a new site; dyszoochory, when seeds are accidentally dropped before being consumed or stored (Olszewski 2015); synzoochory, when seeds and fruits are cached just beneath the soil surface or in clumps of herbaceous or bryophyte vegetation. If the dispersal vector is a bird, then we can talk about ornithochory. This phenomenon has been well documented in numerous publications (reviewed by Olszewski 2015).

The Eurasian jay *Garrulus glandarius* (L., 1758) (Passeriformes: Corvidae), henceforth jay, is a highly significant dispersal vector of oaks in Europe, including Poland (Danielewicz & Pawlaczyk 2006, Myczko et al. 2014). Oak regeneration via synzoochory occurs when jays fail to consume some of the acorns they have stored and their caches are not discovered by their foraging competitors, such as rodents (Kurek & Dobrowolska 2016). In

other tree species, e.g. Scots pine stands of different age classes and in clearings, synzoochorous regeneration is common (Pigan & Pigan 1999, Kurek & Dobrowolska 2016). Many oaks, presumably seeded by jays, grow alongside roads and paths (Vullmer & Hanstein 1995); oaks of this origin are also found on meadows, pastures and fallow land (Reif & Gärtner 2007). Acorn dispersal in orchards has not yet been recorded, however.

The present paper describes synzoochorous oak regeneration in orchards and attempts to define its effect on the shaping of the orchard landscape.

Materials and Methods

The study was carried out in a sour cherry orchard on the Rawa Upland in central Poland (Kondracki 2000). This site lies within a very wide area (c. 1.5 thousand km^2) of intensely-managed orchards around the towns of Grójec and Warka. The orchard surveyed was 1.12 ha in area and had the shape of an elongated rectangle (c. 570 m long x c. 26 m wide). The nearest forest complex with a substantial proportion of oaks *Quercus* sp. was c. 1.8 km distant. On its southern side, the orchard bordered on a gully overgrown mainly with blackthorn *Prunus spinosa*, hazel *Corylus avellana* and aspen *Populus tremula*, as well as a few single old oaks. The orchard in question consisted of c. 20-year-old sour cherry trees *Prunus cerasus* of the "Łutówka" variety. The trees had been planted every 4 m in rows 5.5 m apart. The orchard ceased to be cultivated some 8 years ago. Some of the originally planted sour cherry trees had died off, so there were gaps in the rows, but some 550 live trees remained. To the north, a narrow strip of blackthorn bushes adjoined the orchard, while farther to the south there was an intensely-managed apple-sweet cherry orchard. Apart from the results of synzoochorous regeneration, we drew up an inventory of oaks and other tree and shrub species in 19 fallow orchards (0.7259 ha) situated in the vicinity of the study site.

The field work was carried out in November 2016 and October 2019. Carried out in November 2016, the fieldwork involved compiling an inventory and describing selected features of 182 pedunculate oak trees growing in association with "Łutówka" sour cherry trees. The following features were measured:

- diameter at breast height (DBH), within the interval < 7 cm and > 7 cm, as suggested by Olszewski (2015);
- spread above and below 1.3 m, indicative of the number of primary roots;
- tree height, split into 0.5 m intervals;
- vitality: live, dead, moribund;
- trunk form: A – straight trunk, vertical or slightly inclined with permissible slight curvature, B – strongly curved trunk, crooked or strongly inclined (<60-70^o), C – shrubby form (procumbent and umbrella-shaped), i.e. with atrophied primary shoot;
- crown form: A – regular and/or split or forked, but with a distinctly straight or slightly curved primary shoot, B – strongly branched crown, with a very crooked primary shoot, C – shrubby form (procumbent and umbrella-shaped), i.e. with atrophied primary shoot.

In addition, the distances between the oak trunks and sour cherry trees were measured (up to 50 cm, 50.1-100 cm, 100.1-200 cm, 200.1 and more), and the neighbourhood of other tree and shrub species was assessed, as was the habit of an oak, depending on its distance from a sour cherry tree (d+ very good, d good, d- weak, sł the weakest).

In October 2019, an inventory of oaks was carried out in other fallow orchards up to 1.8 km from the sour cherry orchard described here. It was assumed that farther away from the study orchard (>1.8 km), the number of orchards colonised by oaks and the numbers of such trees growing in them would be proportionally insignificant because of the very great scatter and exceptional occurrence of seed trees as well as fallows.

The statistical analyses, i.e. χ^2 tests and Fisher's exact tests, were performed in IBM SPSS Statistics 23. The level of significance was taken to be $P < 0.05$.

One-way ANOVA was performed in the intergroup scheme in order to assess whether the density of oaks varied in different kinds of orchards (apple, sour cherry, plum/plum-sour cherry and currant). χ^2 test was used to check whether the shape of the oak is related to the presence of blackberries nearby.

Results

The inventory carried out in the orchard showed the presence of 182 pedunculate oaks *Quercus robur* growing in association with the sour cherry trees. The oaks were of different ages, predominantly with DBH > 7 cm (62.6%), i.e. more than 3-years old. The maximum DBH measured was 45 cm, which translates to an approximate age of c. 15-18 years. This implies that some of the oaks must have been growing while the orchard was still in use. We checked whether the forms of the trunk and crown differed between oaks that were growing in the last 3

years (DBH < 7 cm) and since before 2012 (DBH > 7 cm) using Fisher's exact test. It turned out that the trunk form did not differ with respect to oak DBH (P = 0.111), neither did the form of the crown differ with respect to DBH (P = 0.155).

Almost half (48.4%) of the acorns had been hidden at distances of up to 0.5 m from sour cherry tree trunks, and 76.9% up to 1 m away from them; barely 7.1% were found farther away than 2 m. Trees with straight trunks were predominant n=156 (N_{total} =182; 85.7%). Curved trunks or inclined ones made up 11.5% (n=21), while the occurrence of shrubby forms was marginal (n=5; 2.7%). Likewise, the form of the tree crowns was regular (n=157; 86.3%), less often strongly branched (n=20; 11.0%) or, exceptionally, shrubby (n=5; 2.7%). We assessed whether the form of the trunk and crown of a particular oak tree differed with distance from the surrounding sour cherry trees using Fisher's exact test. The results, however, were not even at the statistical tendency level (P = 0.405). Similarly, analysis of the combined results from groups B and C of trunk forms did not reveal any differences even at the statistical tendency level (P = 0.257). Then we checked whether the form of the crown differed with distance between a particular oak and a sour cherry tree. Here, the result was only at the statistical tendency level (P = 0.072). However, analysis of the combined results from groups B and C of crown forms showed that the difference was statistically significant (P = 0.002). No moribund oaks were found. The forms of the trunk (A – 85.7%) and crown (A – 86.3%) showed that these trees were in very good condition. The seed trees, standing at distances from the sour cherry orchard of 5–70 m, were from c. 40 to 60 years old.

Other species recorded in association with the sour cherry trees included European ash *Fraxinus excelsior* (11 ex.) and alder buckthorn *Rhamnus frangula* (5 ex.). Growing in the vicinity of the oak trees were bramble *Rubus* sp. (18 ex.), blackthorn (9 ex.), silver birch *Betula pendula* (2 ex.), hawthorn *Crataegus sp*. (2 ex.), rose *Rosa* sp. (1 ex.) and elder *Sambucus nigra* (1 ex.). The ground layer consisted mostly of small-reeds *Calamagrostis* sp.), common couch *Agropyron repens*, perennial ryegrass *Lolium cristatum*, mugwort *Artemisia vulgaris* and wild carrot *Daucus carota*. We checked to see whether the habit of an oak was related to the presence of brambles. This analysis was performed on a group of pre-2012 oaks using the χ^2 test and Fisher's exact test. The results, however, were not even at the statistical tendency level, regardless of whether four (P = 0.487), three (P = 0.307) or just two categories of oak habit were taken into account (χ^2 = 1.03; P = 0.311).

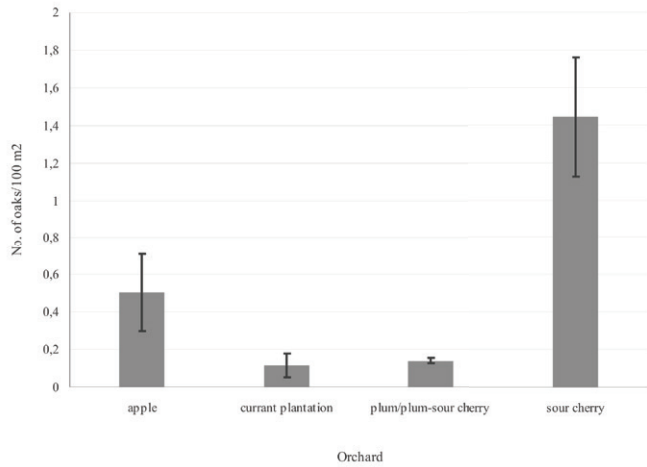

Fig. 1. Density of oaks at different sites. The plot shows means and standard deviations.

Oaks were found in all of the 19 fallow orchards surveyed (apple, sour cherry, plum/plum-sour cherry) and in the currant plantations. Their mean density was 0.51 /100 m^2 – the highest in sour cherry orchards (n=6; 1.53 /100 m^2) and the lowest in the currant plantations (n=2; 0.10 /100 m^2). There were oaks in five of the apple orchards but none in four others (0.45 oaks/100 m^2). The density of oaks varied in the different orchards F(3, 15) = 4.06; P = 0.027; a *post-hoc* analysis was therefore performed using the LSD test. Three statistically significant differences were found. The density in the sour cherry orchard was significantly higher than in the apple orchard (P = 0.014), the currant plantation (P = 0.022) and the plum-sour cherry orchard (P = 0.024). The other differences were not even close to statistical significance (Fig. 1).

Discussion

Predicting the course and rate of woodland succession on post-agricultural land is far more difficult than at first thought (Szwagrzyk 2004). The species composition and structure of the woodland growing as a result of secondary succession is completely unknown. What we do know is that silver birch and pine play an important part in this process (Wójcik 1996). Future generations of Polish foresters will probably have to tackle the problems of managing and converting secondary stands of birch, aspen and false acacia. It is important to have some idea of what these new woodlands will look like and how they will function in the farming landscape (Szwagrzyk 1996); detailed studies of the second-

ary succession in orchards are thus becoming a matter of urgency.

Orchards are a specific type of plantation, where very large quantities of crop protection compounds and mineral fertilisers are applied (Surawska & Kołodziejczyk 2006): between 2002 and 2011 the use of such products increased (Jarecki & Bobrecka-Jamro 2013). When they are being applied, large amounts of pesticides enter the environment as a result of migration or settlement on the soil surface. Within the soil, however, the mobility of crop protection compounds is minimal: 1-2 m in the vertical and 20-60 cm in the horizontal per annum (Banaszkiewicz 2003). Following their application to plants or the soil, pesticides undergo physical, chemical and biological conversions, as a result of which they can contaminate the soil and water (Klimek 2000). While present in the environment they degrade ecosystems and affect the biological activity of the soil (Boligłowa 2011). It has been found that maintaining herbicide fallows retards the biological activity of soil (Kozanecka et al. 1996). All these aspects combine to produce the specific nature of soils in fallow orchards. To what extent this may affect the secondary succession of tree species is hard to judge today. The oaks in the fallow orchards described here are in very good condition and habit. The appearance of oaks in the orchard landscape is a sign that succession has started. Forecasting the further consequences for a landscape developing in this way may provide an answer to the question regarding the direction this succession is going to take. Is oak going to be the leading dominant tree or merely the initiator of succession? At what rate will it be replaced by other tree species? Do jays prefer a particular type of orchard (apple, sour cherry, pear, plum) or currant plantation for caching acorns?

European jays are woodland birds (Keve 1974), which is why they cache acorns under existing tree stands. At the same time, oaks are one of the principal woodland tree species disseminated by jays on grasslands (Kollmann & Schill 1996), although they prefer the acorns of pedunculate oaks than those of sessile oaks *Quercus petraea* and northern red oaks *Quercus rubra* (Olszewski 2015).

It was found that jays in woodlands mostly cache acorns under older trees (Kurek & Dobrowolska 2016). However, in the sour cherry orchard we surveyed, this was of no importance as the trees were of the same age. Jays select open terrain with vertical structures, such as tree trunks, in which to cache acorns (Bossema 1979). Nearly half the acorns in the sour cherry orchard have been concealed close to tree trunks (up to 0.5 m), which suggests that the jays preferred the proximity of a vertical object like a sour cherry tree trunk. At the same time, jays preferred sour cherry orchards as acorn caching sites. The reason for this was the fact that vertical structures like a sour cherry orchard were perhaps "better visible". Sour cherry trees lose their leaves earlier than apple or plum trees. From mid-October onwards, jays pick up large numbers of acorns (Olszewski & Brzeziecki 2019); at this time, the sour cherry trees no longer have any leaves, unlike other fruit trees. Most of the oaks were older trees with DBH >7 cm (62.6%). This implies that when an orchard has just fallen into disuse, jays take advantage of the as yet relatively low herb layer (weeds) for caching acorns. As the herb vegetation grew taller, the birds less often hid acorns there; some of those that had been stored there were found by rodents, which treat acorns as supplementary feeding. Land left fallow has a greater density of rodents than that which is intensively farmed (Sullivan & Hogue 1987, White et al. 1997, Massawe et al. 2003). This is probably also why barely 37.4% of the oaks were younger ones, with DBH <7 cm. In addition, 74.2% of the oaks had been growing for some 8 years since the orchard ceased to be cultivated; if we take just the six years since that point in time, that figure rises to 94.1%. Vullmer (1993) stated that jays preferred to cache acorns in areas with low vegetation. Where the herb layer was very lush, there were hardly any young oaks. This is confirmed by the results from the sour cherry orchard, where most of the oaks were older ones, which had grown from acorns left there while the orchard was still in use. Low, thin vegetation reduces losses of acorns as a result of their being destroyed by rodents, whereas tall vegetation retards the growth of saplings (Reif & Gärtner 2007).

Brambles are regarded as facilitating the regeneration of oak stands (Kuiters & Slim 2003); these plants were growing in close proximity to 18 oaks in the cherry orchard. However, these particular oaks were neither the oldest nor the youngest ones, so the effectiveness of brambles is hard to assess unequivocally. Be that as it may, the oaks' habit was not associated with the near neighbourhood of brambles.

It is thought that birds carrying acorns to open terrain and hiding them there is a rare occurrence (Kurek & Dobrowolska 2016), although Pons & Pausas (2007) have found that in cork oak *Quercus suber* communities, birds prefer open terrain such as fields lying fallow. Tree stands such as orchards (with regular vertical trunk structures) appear to be preferred by jays, which frequently scatter acorns in

this type of landscape. This is probably why there were very few oak saplings in the currant plantations. Another reason for the small number of oaks in those plantations could be the lush growth of small-reeds *Calamagrostis* sp. (up to 1.5 m in height), the tall herbaceous vegetation and the absence of distinct vertical structures. In contrast to orchards, crop fields that have been left fallow initially become quickly overgrown with mainly herbaceous vegetation. The lack of distinct vertical structures like tree trunks may be why jays ignore them in as potential acorn caching sites. It is only some years later that these abandoned fields become colonised, primarily by gymnosperm trees (Wójcik 1996). Nonetheless, it is thought that there are many advantages for oak trees in open terrain. Bakker et al. (2004) claimed that less damage was caused by insects and disease in young plants in open areas than in old forests. The emerged seedlings, are exposed to damage by granivorous animals, since the emergence of the primary shoot acts as a flag to attract seed predators. Jays, wood mice and wild boar will all feed on the remaining cotyledons. Jays and wood mice generally damage only a fraction of the seedlings when they remove the cotyledons, and the seedling is well able to survive since seedling growth is not affected when remaining cotyledons are removed (den Ouden et al. 2005). At the same time, germination and oak sapling growth may be retarded by allelopathic secretions from various grasses and sedges, such as tufted hair-grass *Deschampsia cespitosa*, purple moor-grass *Molinia caeruleae* and *Carex brizoides* (Frost & Rydin 1997). According to Lampen (1994), jays prefer to cache acorns in mown areas with low grass.

It would seem that jays also deposited acorns in active orchards, although this is hard to confirm unequivocally, because farmers would no doubt have removed the oak saplings, since these would otherwise be competing with the fruit trees. Such cases of oak sapling removal were witnessed in neighbouring orchards.

Insufficient light was found responsible for the low survival rate of sessile oaks in woodlands (Kelly 2002). Because of the greater crown transparency and rapid leaf fall, sour cherry orchards are better illuminated than other types of orchard. This promotes the growth not only of oaks but also of other tree and shrub species, and of tall herbaceous vegetation. Thus, when looking at neighbouring abandoned sour cherry orchards, one gets the impression that oaks lose out in competition with more quickly growing trees like birch. A competing influence was found in forest plantations of silver birch on the growth, habit and DBH of oaks when both species were growing side by side; at somewhat greater distances, birches stimulated oaks to faster growth (Andrzejczyk 2008). It is well-known that silver birch plays a very important part in secondary succession (Wójcik 1996); this was also the case in neighbouring fallow orchards. Birch is the dominant species in the natural regeneration of woodland (Dobrowolska 2008). Over time, it is replaced by *Pinus* sp. in coniferous and mixed woodlands. The proximity of woodland favours the expansion of pine: up to 75-85% of the seeds from a pine tree fall within a radius of 50-60 m around it, but just 2% at a distance of 90-100 m from it (Andrzejczyk 2000). Oak thus has to hurry, as it were, in order to become the dominant tree in stand structures forming in abandoned orchards. Being more resistant to fire (Szczygieł 2010, Greenler et al. 2019), it is more likely to survive if a fallow orchard should burn. Distinctly privileged are oaks growing on balks (strips of untilled land between fields), as they are not usually removed from them, being neither an obstacle nor competitor of fruit trees. They are the main suppliers of acorns in the farming landscape. Other competing species in orchards, in descending order of frequency, were hawthorn, aspen, pine and bird cherry *Padus avium*; together with birch these species make up 88% of these "competitors". Competition from softwood deciduous species like willow, aspen and black cherry *Prunus serotina*, as well as herbaceous plants, adversely affects the growth increment of oaks, though without compromising their quality (Ammer & Dingel 1997, Robakowski & Bielinis 2011). Of the 182 pedunculate oaks growing in association with sour cherry trees, not one was moribund. Nowadays there are numerous reports of oak dieback; although this decline has been observed in Europe since the early 18th century, it has greatly intensified in the last 25 years (Kuźmiński et al. 2007). Most authors point to a complex disorder, in which there is interplay of predisposition (acting over a longer period), initiation (the occurrence and development of the disease) and co-occurring factors that are directly responsible for oak death (Olszewski 2015). The usually mentioned causes of this process are disruption of hydrological relationships, the far-reaching effects of severe frosts, irruptions of defoliating insects and secondary pests (two-spotted oak buprestid beetle *Agrilus biguttatus*, air pollution, fungi and Oomycota – pathogens causing phytophthorosis (see the review in Olszewski 2015). It is not known whether dieback will continue to affect oaks or whether a period of regeneration will follow. Observation of this

process suggests that recurrent cycles of dieback and regeneration are highly likely. A disturbing aspect is the manifestation of symptoms of dieback and disruptions to development in various phases of tree growth, which may indicate that this disorder will persist for a longer time and complicate the cultivation of oaks in woodlands (Bernadzki & Grynkiewicz 2006). The good condition of oaks in the orchard landscape testifies to the fact that this disease does not appear to affect such habitats. Acorns are scattered on average several hundred metres from their parent trees (Chettleburgh 1952, Bossema 1979, Kollmann & Schill 1996, Gómez 2003), even as far as 20 km away (Olszewski 2015). Oaks thus constitute an important reservoir of good seed material which will promote tree regeneration in woodlands as well.

An inventory carried out in a fallow sour cherry orchard revealed pedunculate oaks growing together with the cherry trees. The presence of the oaks is the consequence of synzoochorous regeneration by jays. Although the oaks were of various ages, this factor did not affect the form of either trunk or crown. The distance of an oak from a sour cherry tree had no effect on the form of the crown, but did influence trunk shape. Oak habit and brambles were not associated. Jays cached acorns in the orchard regardless of the age of the fruit trees. Nearly half of the acorns had been hidden close to sour cherry tree trunks. In the first years after fruit cultivation in the orchard had ceased, when the herbaceous vegetation in it was still quite low, jays were more likely to deposit acorns there. These birds prefer tree stands like orchards because of their regular vertical trunk structures. The density of oaks measured in 19 fallow orchards (apple, sour cherry, plum/plum-sour cherry) was significantly higher only in the sour cherry orchards. Oak cannot compete successfully with rapidly growing birch in fallow orchards. Nonetheless, the good condition of the oaks in the orchard landscape indicates that they may constitute a reservoir of good seed material even for the woodlands in the vicinity.

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