Forest Ecology and Management 331 (2014) 35–39

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native (Pedunculate Oak *Quercus robur*) and an introduced oak species (Northern Red Oak *Quercus rubra*) in Europe

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ARTICLE INFO

Article history:
Received 11 April 2014
Received in revised form 6 June 2014
Accepted 30 July 2014
Available online 20 August 2014

Keywords:
Acorn predation
Seed dispersal
Introduced species
Hoarding behaviour
Natural regeneration
Survival analysis

ABSTRACT

Invasive species have a substantial influence on the environment, especially through competition with local, native species. In Europe, oak trees provide a good example of competition between species native to the region and species introduced from elsewhere in the Northern Hemisphere. When introduced species start to have a negative impact they are considered invasive. Here we focus on the seed dispersal of a native (Pedunculate Oak *Quercus robur*) compared to an introduced oak (Northern Red Oak *Quercus rubra*) where the main animal disperser of acorns is the European Jay *Garrulus glandarius*. The study was conducted in two forests in western Poland by placing acorns of both species in trays and monitoring their removal, and by recording establishing oaks on transects. We showed that jays were about twice as likely to harvest the acorns of the native oak compared to those of the introduced oak. Nevertheless, the extent of dispersal by jays of the acorns of the introduced oak species will facilitate colonization of new areas. Establishment of young trees of the introduced species was much greater than that of the native species despite the former having lower dispersal and being considerably underrepresented in the canopy. Thus, consequences for patterns of oak survival and forest development seem very likely.

1. Introduction

Introduced species, whether deliberate or accidental, may have either a benign or negative impact on their new environment. If the latter they are considered as invasive species. Whilst increasing their range, invasive plant species interact with other plant species which previously dominated those environments. Most of these interactions are of a directly antagonistic character, which is based on the suppression of the native species (Callaway and Aschehout, 2000; Traveset and Richardson, 2006; Powell et al., 2013). Invasive plants can affect all components of an environment, from ecosystem processes to the diversity and composition of invaded ecosystems (Ehrenfeld, 2003; Hejda et al., 2009; Pyšek et al., 2012; Powell et al., 2013). The rapid increase of the population size of invasive species in the new area is often assisted by the lack of natural herbivores and pathogens, as well as the inability of existing herbivores and pathogenic species to control the invasive organisms (Agrawal et al., 2005; Liu and Stiling, 2006; Huang et al., 2010; Dai et al., 2014). However, most plants need interactions with animals for their proper development and reproduction. These interactions most often involve mutualists, which ensure effective transfer of pollen and assisted seed dispersal in the environment (Brown and Mitchell, 2001; Gosper et al., 2005; Bartomeus et al., 2008). A plant species that requires seed dispersal services must either expand into areas already inhabited by the disperser (or expand together with the disperser into new areas) or enter into novel interactions. In such cases, the success of an invasive plant in colonizing new habitats is determined not only by its flexibility and adaptability to the new environmental conditions but also by the presence of species able to replace those species responsible for the reproductive success of the plant in its native habitat. In the case of anemophilous oaks (*Quercus* spp.), which are one of the staple species in deciduous and mixed forests of the Northern Hemisphere, the critical step is seed dispersal (Janzen, 1971). Leaving the immediate surroundings of the parent plant significantly increases the chance of the seed surviving and developing (Velho et al., 2012). Most oak species produce acorns

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http://dx.doi.org/10.1016/j.foreco.2014.07.027
0378-1127/

with large energy reserves that allow their seedlings to successfully compete with other plants. However, long-distance dispersal of such heavy seeds is impossible without the participation of animals. The main taxa which ensure long distance dispersal of acorns are birds from the family *Corvidae*. The key disperser for European oaks is the European Jay (*Garullus glandarius*) (Bossema, 1979; Gómez, 2003; Pons and Pausas, 2007) which hides seeds underground, especially where seed predation risk is low. Suitable environmental conditions can then provide a high probability of germination and growth (Bossema, 1979).

Here we examine the foraging preferences of European Jays for two oak species; native Pedunculate Oak (*Quercus robur*), a common tree species in Central Europe, and the introduced Northern Red Oak (*Quercus rubra*). In Northern Red Oak's native range in North America, the Blue Jay (*Cyanocitta cristata*) and the Common Grackle (*Quiscalus quiscula*) are the main dispersers of Northern Red Oak acorns (Steele et al., 1993; Moore and Swihart, 2006), whereas in Europe, the European Jay is considered the primary long-distance disperser of all European oaks (Bossema, 1979; Gómez, 2003; Pons and Pausas, 2007). The introduction and natural regeneration of Northern Red Oak in forests significantly reduces native species richness and abundance. Co-occurrence with this species is not known to benefit any vascular plant, moreover the abundance of Northern Red Oak strongly limits natural restocking of all native woody species (Woziwoda et al., 2014).

2. Materials and methods

2.1. Study area

Observations were made in two forest complexes in the Wielkopolska region of western Poland at Strzeszyn (52°26′N 16°50′E) and Zielonka (52°30′N 17°03′E). Both sites were mixed forests dominated by Scots Pine (*Pinus sylvestris*) and Pedunculate Oak. Reproductive Northern Red Oak were present in both sites, but the frequency of mature trees was less than 1% of that of Pedunculate Oak. In 2012, we randomly established twenty-two 100 m long × 1 m wide transects at Strzeszyn only. All oak seedlings and young trees were counted in two size categories (⩽1.5 m and 1.5 m −5.0 m tall) on each transect to estimate establishment of the two oak species.

2.2. Experimental design

The study was conducted in the autumn of 2011 and 2012. In each year, 250 acorns were collected from the ground under each of 15 randomly selected trees of each species in each study site (a total of 15,000 acorns). Acorn collection coincided with maximum seed rain. Insect-damaged acorns were subsequently removed but there was no selection for size because we wanted the experiment to reflect the situation in forests. For each species, collected acorns were then thoroughly mixed and 30 of each species selected for each plastic dish from which monitoring would take place. To study dispersal, 20 dishes were placed at random in each study site on top of wooden posts 1.5 m above the ground. Dishes were separated by at least 500 m. The height of trays was a compromise between protection from ground predators and height above the ground surface where jays typically search for acorns. Predation by squirrels could not be eliminated but they are rare in our study sites. Furthermore, other *corvidae* species and other birds which may also take acorns were largely absent. The 60 acorns in each dish were mixed. In each study site we conducted the experiment both in early and late autumn to determine whether jay preferences were dependent on time and the abundance of acorns remaining in the environment. Trays where located in different plots in early and late experiments, but the same plots were used in the second year. A total of 9600 acorns were placed in dishes (4800 acorns from each oak species). We visited the dishes 2, 4, 6, 8, and 10 days after the initial installation to record the surviving numbers of each species. During each visit, we surveyed European Jays for 5 min. The mean number of birds detected in each plot was treated as an estimate of the relative abundance of European Jays during the experiment. For data analysis, we used only those dishes where at least one acorn was removed and also excluded one tray damaged by wild boar.

2.3. Data processing and analysis

Changes in the number of acorns remaining (survival of acorns) was examined using survival analysis (Kleinbaum, 1996) where "survival" and "death" are synonymous with acorns remaining or being removed. It was assumed that the probability of selection of either type of acorn by jays was identical. Therefore, all acorns exposed in each plot, in each year and in each period (early or late autumn) were treated as single cohorts.

Survival of acorns was analyzed using life tables (Kleinbaum, 1996). This method estimates survival functions where the life history (in this case, time present on trays) of acorns during the experiment is known. The major advantage of using life tables is that this method assumes that survival is a function of time, which is not the case when the simple proportion of surviving individuals is analyzed. This enables the identification of the 112 critical time points during the study period (Zduniak, 2010; Zduniak et al., 2011).

The survival time of acorns was estimated from the day when the experiment started until the 10th day when it ended. To determine the possible effect of different factors on acorn survival, Cox's proportional hazards model was applied (Cox, 1972). Though this method has not yet been commonly used by ecologists, it is suitable for studying a diversity of ecological phenomena occurring in space and time (Muenchow, 1986; Moya-Laraño and Wise, 2000; Reino et al., 2009). This model assumes that hazard rate (an element of life tables, defined as the probability per time unit that an individual that has survived to the beginning of the respective interval will not survive in that interval) is a function of the independent variables. Use of this model allows the estimation of regression coefficients for independent variables including categorical factors. In this case variables with positive coefficients for the selected category (e.g., species 1 – level of effect) are associated with decreased survival compared to the reference category (e.g., species 2), whereas variables with negative coefficients for a selected category are associated with increased survival compared to the reference category. Furthermore, values of hazard rate >1 for the selected level of the effect (e.g., species 1) indicate that species 1 has an increased risk of "death" compared to species 2, whereas, when the hazard rate is <1, species 1 has decreased risk of "death" compared to species 2. In this study, lower survival/higher hazard rate occurred when jays harvested and potentially dispersed more acorns. Using the model, several factors possibly influencing survival were tested: species of oak (Pedunculate Oak or Northern Red Oak), study site (Strzeszyn or Zielonka), year of study (2011 or 2012), time of season (early or late autumn) as categorical factors, and mean number of jays observed in the plots during the experimental period, as a covariate. All predictors were selected for inclusion in the final model by backward selection with the criterion for removal based on a significance level of 0.05. Multiple comparisons between pairs of species, year, site and time of experiment were made using the Cox–Mantel test (Cox, 1959, 1972; Mantel, 1966). A Bonferroni correction was used to adjust *P* values in multiple comparisons. All calculations were performed using