**Verified hypotheses on the ‘nurse’ and ‘burial’ effects on introduced *Quercus rubra* regeneration in the European Scots pine forest**

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**Abstract:**

**1.** Recognition of favourable environmental conditions for seed germination and seedling survival in different types of forest sites is crucial both for effective regeneration of introduced tree and for control of its spontaneous spread. Studies on the encroachment of North American northern red oak *Quercus rubra* into European Scots pine forests revealed high abundances of seedlings and saplings under shrubs, with lower abundances in open areas or in clumps of bilberry *Vaccinium myrtillus*. It was unclear, does burying acorns by seed-hoarders in moss or soil in different microhabitats impact survival of red oak seeds and seedlings, and does acorn size matter?

**2**. Results of previous (observational) studies were verified in a 3-year experimental study: a pool of 900 sown acorns was monitored in natural conditions.

**3.** Study revealed that ~80% of sown acorns were lost due to pilferage, lack of germination, fungal infection, and death of sprouting acorns and leafed-out seedlings. The fate of acorns and seedlings depended largely on acorn size and differed among microsite types. Viable seedlings were twice as likely to develop from large- and medium-sized, than from small acorns. Surviving seedlings grew mainly from acorns sown under moss cover within bilberry clumps or in open area, confirming a positive ‘burial effect’. Less than 10% of acorns sown under shrubs developed into viable seedlings, contradicting former conclusions on their ‘nurse effect’.

**4.** The occurrence of extensive bilberry clumps and small clusters of shrubs in pine forests favours *Q. rubra* regeneration, but severe fluctuations of the warming climate limit the viability of red oak seeds and seedlings. Prognosed range shifts of native tree species and expected dramatic loss of *V. myrtillus* climatic optima will impact *Q. rubra* distribution in European forests. Meanwhile, to prevent red oak spread (if necessary), it is recommended to remove shrubs from pine stand.

**Keywords:** acorn germination, alien tree spread, early seedling growth, mesic Scots pine forest, northern red oak, weather fluctuations

**1. Introduction.**

Successful seed germination and seedling development are crucial for species survival, as the strongest selection for plant viability is observed in these two stages (Yan et al., 2015; Jia et al., 2020; Mattana et al., 2023). In the case of commercially important woody species intentionally planted outside their native range, successful development of juvenile specimens from seeds naturally dispersed or collected and sown directly to the ground, also have a fundamental meaning for forest management, due to the interest in less costly regeneration of stands (Pötzelsberger et al., 2020; Löf et al., 2019, 2021). Ongoing climate changes (IPCC, 2022) additionally force the development of more effective practices for forest regeneration, also with use of introduced trees (Brang et al., 2014; Dyderski et al., 2018; Badano and Sánchez-Montes de Oca, 2022; Puchałka et al., 2023a). The abundant uncontrolled encroachment of juvenile specimens into forest patches located outside areas of alien tree cultivation, however, can be undesirable if introduced species negatively impact native ecosystems (Richardson et al., 2000; Brundu and Richardson, 2016; Dyderski and Jagodziński, 2021). The recognition of favourable environmental conditions for alien seed germination and seedling growth in different types of the forest sites is essential for effective regeneration of introduced trees as well as for control of their ‘too spontaneous’ spread (Brundu et al., 2020).

Studying the North American northern red oak *Quercus rubra* L. (Sander, 1990) in Poland, we found that this species (introduced over 200 years ago; Woziwoda et al., 2014) is very common both in commercial and preserved forests, where it occurs in a wide range of the forest sites (Woziwoda et al., 2014; 2018a). Every year numerous *Q. rubra* stands, widely dispersed within forest complexes, produce an abundant crop of viable acorns (Gręda et al., 2022), variable in their size and mass (Woziwoda et al., 2023), and thus attractive for different native acorn consumers which are also involved in dispersion of oak seeds (Myczko et al., 2014; Wróbel et al., 2022). All factors mentioned above favour *Q. rubra* regeneration and its spontaneous spread in Polish (Woziwoda et al., 2019b; Chmura, 2020) and other European forests (Major et al., 2013; Bieberich et al., 2016; Nicolescu et al., 2018; Dyderski et al., 2020). The rate and scale of colonization of new forest patches by *Q. rubra,* however, vary both for types of the forest site and for different microsites within the same site (Jagodziński et al., 2018; Woziwoda et al., 2019b; Chmura, 2020; Nosko et al., 2022).

Our previous study on *Q. rubra* encroachment into the mesic Scots pine (*Pinus sylvestris* L.) forest (Woziwoda et al., 2018b) revealed abundant occurrence of red oak seedlings and saplings concentrated in nearby components of the forest understory (under shrubs), while many fewer specimens were noted in patches without a shrub layer or within spatially extensive clumps of bilberry (*Vaccinium myrtillus*L., a dominant component of the herb layer in pine forests). The inventoried juveniles were of different heights which indicated continuous regeneration for extended time periods and regular inflow of propagules from the adjacent red oak stand. We concluded that differences in the number and height of *Q. rubra* seedlings and saplings noted under shrubs, in the open areas and in bilberry clumps, resulted mainly from a different number of acorns deposited by animals in a specific type of microsite in subsequent years. The final distribution of the red oak juveniles, however, had to be related to different acorn and seedling ‘life-stories’, conditioned e.g. by the size of deposited acorn, post-dispersal acorn predation, pressure from herbivores, inter- and/or intraspecific competition, or by other factors. The lack of information on the initial number of acorns dispersed in the forest by acorn hoarders in specific sites was indicated as the cause of possibly erroneous conclusions on the efficiency of seed germination and seedling growth in different microhabitats (Woziwoda et al., 2018b).

Numerous studies showed that in the case of large-seeded species such as oaks *Quercus* spp., the larger the acorns, the higher the percent of germinated seeds, seedling growth rate and survival rate (e.g. Kormanik et al. 1998a, 1998b; Tecklin and McCreary, 1991; Bonfil, 1998; Clark et al., 2000; Ivanković et al., 2011; Löf et al., 2019). Large acorn size usually means more reserves in cotyledons necessary for seedling growth at the early stage of its development (Seiwa and Kikuzawa, 1991; Long and Jones, 1996), so the relationships mentioned above seem obvious. However, Long and Jones (1996) and Clark and Schlarbaum (2018) revealed that neither acorn size nor mass could be used reliably as morphological indicators of seedling quality or to predict survival of oak seedlings. Larger seeds deliver more resources at early stages of seedling development but they do not necessarily buffer young plants from the negative effects of environmental variation (e.g. from limitations in nutrients or water) or from competition of other plants (Jevon et al., 2021).

Larger acorns are attractive for seed consumers, so they can be more threatened by both pre- and post-dispersal predation (Crawley 2000; Buckley et al., 2006; Merceron, et al., 2017; Myczko et al., 2017; Mezquida et al., 2021). On the other hand, seeds with large size are often only partially damaged, so they still preserve ability to germinate and produce viable seedlings (Hopper et al., 1985; Steele et al., 1993; Branco et al. 2002; Yi and Yang, 2010). Dispersed acorns can be pilfered (stolen) and re-cached or consumed in large numbers by post-dispersal acorn predators (Wang et al., 2014). To reduce pilferage, seed hoarders chose landscape fragments with specific features, e.g. more open forest patches, or in contrast – forest fragments with a dense understory, and hide the food in the moss cover, litter or soil (Kollmann and Schill, 1996; Muñoz and Bonal, 2011; Sunyer et al., 2015). Acorn ‘hiding’ in the soil covered with the litter (mulch) is also used by commercial forestry during oak regeneration by direct seeding (García et al., 2002; Löf et al., 2019) or oak seedling production in forest tree nurseries (Crow, 1988; Dey and Parker, 1996).

Seed-hoarding also increases acorn protection against the negative impacts of weather (Sander, 1990; García and Houle, 2005; Zwolak and Crone, 2012) and, under favourable environmental conditions, acorns lost or unused by animals germinate and successfully develop into seedlings (Vander Wall, 1990, 2001; Bogdziewicz et al., 2020). In temperate forests acorns sown just after seed fall are naturally stratified (i.e. enzymes necessary for germination are activated) during frosty autumn or winter days (Suszka and Krawiarz, 1971; Bonner, 2008). Frosts which are too strong, however, can damage insufficiently protected oak seeds (Suszka and Tylkowski, 1981; Apostol et al., 2007). Late spring frosts can also be lethal for still dormant acorns, for germinating seeds, as well as for growing seedlings (Aizen and Woodcock, 1996). Extremely high summer temperatures and summer droughts are the next threat to young seedlings, as they can damage emerging leaves – the principal photosynthetic organs (Wright et al., 2004), and even seedling roots, when they develop shallowly underground (Apostol et al., 2009). Partial or complete plant defoliation may stunt the growth of a seedling or cause it to die (Wang et al. 2023, and references therein). However, effective photosynthesis guarantees the successful development of oak seedlings only in combination with effective uptake of water and nutrients from the soil (McGraw et al., 1990). Biomass allocation in roots is especially desirable in sites like coniferous forest, where the nutrient availability from acidic, oligotrophic soil is limited (Zwydak et al., 2011), water supply depends on rainfall levels, and the moisture content of the topsoil drops significantly during droughts (Buczko et al., 2005; Launiainen et al., 2022). There are three questions of interest. First, how does burying acorns in the moss, litter or soil in different types of microhabitats impact the red oak seed and seedling survival? Second, does the acorn size matter? Third, what is the proportion of the pool of *Q. rubra* acorns sown in natural conditions which successfully germinate and develop into vital seedlings?

In this experimental study we aimed to (i) identify the impact of the microsite on the fate of *Q. rubra* acorns and seedlings, (ii) compare the development of seedlings from acorns of different size sown in different microhabitats, and (iii) indicate the impact of external factors (weather and herbivory) on acorn germination and seedling growth and survival in the mesic Scots pine forest. We also wanted to verify two hypotheses formerly accepted by us as favourable for *Q. rubra* establishment and recruitment in the European mesic Scots pine forest (Woziwoda et al., 2018b), i.e. the ‘nurse effect’ of shrubs (García et al., 2002; García and Houle, 2005) and the acorn ‘burial effect’ (Briggs et al., 2009; Zwolak and Crone, 2012).

**2. Material and Methods**

***2.1. Study area***

To verify the results of previous research (Woziwoda et al., 2018b), we set up an experimental study in the same locality, in the Małyń-Jerwonice forest complex (central Poland; 52°46′49″N, 19°02′42″E). The experimental plots were situated in the same forest fragment of the mesic Scots pine forest, and the sowing material (acorns) was collected from the adjacent Scots pine-Northern red oak stand. The tree stand was commercial (artificially planted 70 years ago; FDB, 2018), thus Scots pines were distributed regularly and the light conditions under the canopy were relatively uniform. The shrub layer was sparse, composed of scattered clumps of alder buckthorn *Frangula alnus* Mill., silver birch *Betula pendula* L., and single specimens of red and pedunculate oaks *Quercus robur* L. The herb layer was dominated by clumps of bilberry *V. myrtillus,* and the forest floor was covered by mosses, mainly by *Pleurozium schreberi* (Willd. ex Brid.) Mitt.

The soil of the site was mineral, with sandy-loams lying on top of sand subsoil, and classified as a ‘brunic podzol’. Soil was well-drained, but mesic, i.e. containing a moderate amount of moisture from precipitation. It was nutrient poor and acid (pH=4–5) (FDB, 2018).

During the three-year-experiment (from October 2017 to September 2020), the weather conditions varied (**Fig. 1**). Winters and springs were characterized by alternating warmer and cooler periods lasting several days, with decreases and increases above and below zero of the daily mean and maximum temperature, and minimum temperature at the ground level. The extremely low values of the latter were noted at the turn of February and March 2018 and in January 2019.



**Fig. 1.** Weather conditions (selected parameters) from 01/10/2017 to 30/09/2020 (based on data of The Institute of Meteorology and Water Management – National Research Institute, Poland, presented on: Meteo Data, 2023). \*We chose the minimum temperature at the ground level as this parameter is a good characteristic (better than a minimum daily temperature) of the environmental conditions on the forest floor, where acorns germinate and seedlings grow. This temperature was measured 5 cm above the ground, while the other air temperatures were measured at a height of 2 m above the ground (in shade).

As a result of temperature fluctuations, the snow cover alternately appeared and melted, especially in winter of 2017/2018 (the first winter after acorn sowing). In winter of 2019/2020, the mean and maximum daily temperature was usually above zero, and negative minimum temperatures at the ground level occurred periodically, so there was no snow cover. However, in spring 2020 the temperature at the ground level decreased to below zero (up to -11.7oC) almost each day in March and April, and occasionally in May, also when the daily maximum temperature was well above zero (up to 24.1oC). April 2020 was colder at the forest floor than March and each of three previous winter months (**Fig. 1**). Late spring frosts were also occasionally noted in the first 10 days of April 2018 (up to -5.6oC at the ground level) and from March to May 2019 (up to -7.9oC). Summer temperatures also fluctuated, and extremely hot days with temperatures above 30oC and above 15oC at the ground level were noted each year of study (**Fig. 1**). Early autumnal frosts occurred sporadically in September each year, and a few frosty days were noted in October and November 2019 and 2020. Precipitation varied with seasons and years, and episodes of heavy rain and drought occurred periodically (**Fig. 1**). However, the extremely dry and hot summer of 2019 was the characteristic feature of the studied period, as well as cold and dry springs (March-April) in 2019 and 2020, and the extremely cold and dry late winter and early spring (February/March) in 2018.

***2.2. Experimental material and treatment design***

Red oak acorns were collected from the ground in October 2017. Only acorns that appeared to be viable, with no visible external damage (e.g. weevil exit holes or black fungi mycelium), were collected. To examine the impact of acorn size on *Q. rubra* germination and seedling growth, acorns were divided to three size classes: large, medium, and small (the size classes were determined by spreading all acorns on a white plastic sheet on a flat surface and visually grouping them into three size classes). Next, a sample of 300 acorns was randomly selected from each size class (900 in total) and sown the same day as harvested to limit changes in seed quality (e.g. in their moisture).

To verify the results of former study (Woziwoda et al., 2018b), acorns were sown in three types of microsites: open spaces, within clumps of bilberry *Vaccinium myrtillus*, and under shrubs of the silver birch *B. pendula* and alder buckthorn *F. alnus*. To imitate behavior of animals in seed hoarding, acorns were buried under the compact moss layer in the open space, under a loose moss layer hanging on dense shoots of bilberry, and under shrubs – buried in the soil at a depth of 4-5 cm. Acorns, five per set, were sown regularly in 20 subplots for each of the conditions studied (100 acorns × 3 size classes × 3 types of microsite) and consecutively numbered (**Fig. 2**).

Obraz zawierający tekst, panorama, zrzut ekranu, drzewo

Opis wygenerowany automatycznie

**Fig. 2.** The scheme of distribution of large (L), medium (M) and small (S) acorns of *Quercus rubra*, sown (in five-acorn-sets) in the soil under shrubs (1) and buried under the moss cover within clumps of bilberry *Vaccinium myrtillus* (2) and in the open area (3), in the mesic Scots pine forest.

Subplot locations were marked in the field by permanent ribbons, with different colors for each of the acorn size class. The locality of plots in the forest space was marked permanently with a white number painted on the nearest Scots pine tree, or on wide ribbons tied to the trunk of a shrub, which allowed us to find every acorn/seedling in June and September, in the subsequent three sequential years. This also allowed us to avoid the inclusion in the study of other seedlings which germinated nearby from acorns dispersed in the meantime by birds or rodents. Unfortunately, during the summer of 2020, the shrub layer was cleared in the whole area of the Scots pine monoculture, not allowing us to collect September 2020 data for this microsite type.

***2.3. Trait measurements***

***2.3.1. The fate of acorns and seedlings***

Acorn germination and survival was checked for the first time in June 2018. In the case of a lack of seedling or an invisible sprout, the top layer of the moss or soil was gently removed to determine whether the acorn was dead, stolen or ungerminated, a then acorns were re-covered immediately, since ungerminated acorns might germinate later. Acorns were classified as: 1) dead, when the acorn was ungerminated and overgrown by black mycelium of fungi, 2) stolen, when the space was empty, 3) ungerminated – for acorns without signs of destruction, 4) sprouting acorns – for acorns germinated to a leafless short sprout, and 5) successfully germinated and developed into a seedling with a leafy stem.

Sprouting acorns and seedlings were monitored to the end of experiment, i.e. to September 2020, except seedlings under shrubs which were monitored to June 2020. In the latter case, however, we assumed that seedlings noted in June 2020 could survive to September 2020, and they were classified for the last stage of study as ‘seedlings (unsure)’. During the experiment, mortality of sprouting acorns and seedlings as well as seedling resprouting, i.e. the development of a new leafy stem, were noted.

***2.3.2. Effects of microsite and acorn size on seedling growth and survival***

Seedling survival and growth were inventoried twice a year in 2018, 2019 and 2020. The winter survival and spring growth was analyzed in June (VI), and the summer survival and growth was analyzed in September (IX) before natural abscission of leaves in the autumn. Each time each seedling was measured for the stem height (=length) from the root collar – i.e. from transition zone between the above and below-ground portion, to the stem top, and for the basal diameter (with use of the caliper). The leaf number was counted, and the blade length and width of the biggest leaf was measured. The other characteristics of leaves were also considered, such as their damage by large herbivores (leaf blade eaten, only the leaf petiole remained), or by insects (i.e. perforation or skeletonization of the blade, and/or damage of the leaf margin), and infection by fungi (visible leaf discoloration).

The complete loss of leaves, i.e. total seedling defoliation in the early (in June) or late (in September) summer, the decrease (partial defoliation) or increase of the leaf number during the summer, as well as the development of new leaves (noted in September) during summer on a stem that was leafless in June, were also noted to analyze their effects on seedling growth and survival.

***2.3.3. Quality of 3-year-old seedlings (growing in the open space and within bilberry clumps)***

After the last inventory in September 2020, all living seedlings were dug up with roots, cleared of soil, and collected for final measures. The length of seedling root – from the root collar to the end of the longest root, was measured before dividing the seedling into biomass components. Leaves, stems and roots were labeled and transported to the laboratory. Leaves were scanned and their total area for each seedling was measured using the Image\_J program. Next, all biomass components were dried at 60°C for 24 hours and weighed with an accuracy of 0.001 g to analyze the below- and aboveground accumulation of biomass.

***2.4. Data analyses***

We conducted all analyses using R software (R Core Team, 2023). We assessed acorn fate after germination using generalized linear mixed-effects models (GLMMs) for successful germination, seed theft, and acorn death, assuming binomial distributions of dependent variables. In these models we used microsite and seed size as fixed effects and subplot as a random intercept. We presented results as both probabilities and odds ratios, to show effect sizes. Odds ratio is a quotient of event probabilities between two groups of interest, showing how much higher/lower the probability of a particular event is. For GLMMs we used the *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017) packages. To assess survival probability over the whole study period we used Cox proportional hazard model, accounting for seed size and microsite, implemented in the *survival* package (Therneau and Grambsch, 2000). We used linear mixed effects models (LMMs) to assess seedling growth characteristics (i.e. stem diameter, length, leaf width, area, and number) over study dates, microsites, seed sizes, and accounting for leaf and stem damage categories. In such models we used subplot as a random intercept. We also used LMMs to assess seedling characteristics at the end of the study (biomass, its allocation, root length, and leaf traits), accounting for seed size and microsite as fixed effects and subplot as a random intercept. For all LMMs we selected best fit models using Akaike’s Information Criterion, corrected for small sample size (AICc), and we reported AICc of the null (intercept and random effects only) model (AICc0). We also provided conditional and marginal coefficients of determination (R2c and R2m, respectively). R2m indicates the amount of variance explained by fixed effects only, while R2c indicates the amount of variance explained by both random and fixed effects (Nakagawa and Schielzeth, 2013). These two coefficients and AICc were calculated using the *MuMIn* package (Bartoń, 2017). For models we reported results using ANOVA design. We presented marginal effects (i.e. estimates assuming mean values of other predictors and excluding random effects) obtained using the *ggeffects* package (Lüdecke, 2018). While interpreting results we followed the American Statisticians Association statement (Wasserstein and Lazar, 2016) and we relied on effect sizes rather than on p-values only, as this latter statistic is highly sample size dependent and can lead to misinterpretation of some significant findings.

**3. Results**

***3.1. Fate of acorns and seedlings***

From the pool of 900 acorns sown in October 2017, in June 2018 we found 461 acorns (51.2%) successfully germinated: 237 of them were sprouted to leafless stems, and 224 were developed to leafy seedlings. A total of 195 acorns (21.7%) were ungerminated (and they all turned out to be non-viable), 41 (4.6%) were dead due to fungi infection, and 203 (22.6%) were not found (**Fig. 3**). In total, almost half (48.8%) of acorns were lost after the first winter and spring. During the second control after summer (in September 2018), the total acorn losses increased to 74.2%, and at the end of the experiment (September 2020) they amounted to 79.1%, i.e. one fifth (20.9%) of sown acorns successfully developed into seedlings which survived to the end of the experiment.

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**Fig. 3.** Overview of acorn and seedling fates during the whole study. Acorn size: L – large, M – medium, S – small.

A total of 82 leafy seedlings died during the experiment, and their mortality was the highest at the end of the first year (41.5% of all of dead seedlings were noted in September 2018), and then after winter seasons of 2019 and 2020 (23.2% and 31.7%, respectively). Sporadically, after the suspected death of a seedling, a new stem regrew (10 cases), and 60% of these resprouted seedlings survived to the end of experiment. Most (83.1%) of the acorns with delayed germination, i.e. noted as sprouting acorns in June 2018, died during the experiment. The survival rate of seedlings which developed later (from acorns with delayed germination) was 13.1%, while the survival of leafy seedlings which were noted during the first control (in June 2018) was 70.1%.

Acorn and seedling survival differed both for acorns in different size classes sown within the same specific type of microsite, as well as for acorns from the same size class sown in different microsites (**Fig. 3**). However, after the first year 72.3%, 44%, and 30% of acorns sown under shrubs, in bilberry and in the open space (respectively) were lost, and after three years the losses were 91%, 72.7%, and 73.7%, respectively.

***3.1.1. Models of acorn fate***

The probability of successful germination differed among microsites and seed sizes, with the highest under *Vaccinium* and for medium seeds (**Fig. 4, Table 1**). The odds ratio between *Vaccinium* and shrub microsites was 1.895±0.187, *Vaccinium* and bryophytes 0.635±0.176, and between shrubs and bryophytes 1.260±0.179. The odds ratio between medium and small acorn sizes was 0.461±0.179, between medium and large 0.271±0.179, and between large and small 0.190±0.178. The probability of finding an empty space (places where the acorn was stolen) differed among microsites and seed sizes, with the highest under shrubs and for large seeds. The odds ratio between *Vaccinium* and shrub microsites was 2.600±0.277, *Vaccinium* and bryophytes 1.350±0.286, and between shrubs and bryophytes 1.250±0.200. The odds ratio between medium and small acorn sizes was 0.488±0.234, between medium and large 0.640±0.212, and between large and small 1.128±0.227. The probability of acorn death was low, and only seed size revealed differences higher than 0.01 (**Fig. 4,** **Table 1**).

**Fig. 4.** Marginal mean (+SE) probabilities of acorn fates among microsites and seed size categories, assessed using generalized linear mixed-effects models.

**Table 1.** Analysis of variance for probabilities of acorn fates among microsites and seed size categories, assessed using generalized linear mixed-effects models (with acorn block as a random intercept).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Response** | **Variable** | **df** | **Sum of squares** | **Mean square** | **χ2** | **Pr (>χ2)** | **Random effect SD** |
| Germination | Microsite | 2 | 106.151 | 53.075 | 106.543 | <0.001 | 0.345 |
| R2m=0.136, R2c=0.172 | Seed size | 2 | 6.748 | 3.374 | 6.677 | 0.035 | - |
| Empty space | Microsite | 2 | 89.268 | 44.634 | 99.842 | <0.001 | 0.719 |
| R2m=0.177, R2c=0.245 | Seed size | 2 | 25.841 | 12.921 | 25.575 | <0.001 | - |
| Dead acorn | Microsite | 2 | 0.049 | 0.024 | 0.052 | 0.974 | 0.421 |
| R2m=0.007, R2c=0.013 | Seed size | 2 | 6.286 | 3.143 | 6.508 | 0.039 | - |

***3.1.2. Fate of seedlings***

The best fit Cox proportional hazard model accounted for both microsite and seed size (AICc=8789.4, AICc0=8853.0) and revealed that both factors significantly affected survival of acorns (**Table 2, Fig. 5**). Survival of large seeds after sewing was similar to medium seeds (0.77 and 0.78, respectively), but higher than of small seeds (0.73), with similar differences at the end of the study (0.26, 0.28, and 0.20, respectively). Bryophytes and *Vaccinium* provided higher survival than shrubs both at the beginning (0.77, 0.80, and 0.64, respectively) and end of the study (0.26, 0.31, and 0.10, respectively).

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**Fig. 5.** Mean (±SE) survival probability for sown acorns across whole study period and among seed sizes (L – large, M – medium, S – small) and microsites, assessed using Cox proportional hazard model (**Table 2**).

**Table 2.** Cox proportional hazard model for acorns across whole study period and among seed sizes and microsites (microsite=bryophytes and seed size=large are used as default levels).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Variable** | **estimate** | **SE** | **z** | **p** |
| microsite=shrubs | 0.541 | 0.091 | 5.959 | <0.001 |
| microsite=*Vaccinium* | -0.147 | 0.096 | -1.537 | 0.124 |
| seed size=medium | -0.041 | 0.094 | -0.439 | 0.660 |
| seed size=small | 0.183 | 0.091 | 2.010 | 0.044 |

***3.2. Seedling growth***

The best model of stem length over time comprised all of the hypothesized predictors, and the leaf damage categories had neither statistically nor ecologically significant effects (**Fig. 6,** **Table 3**). On average, stem damage decreased stem length by 13.7±1.8 mm. Across study dates, we found the tallest seedlings in *Vaccinium* (average 92.2±2.4 mm) while the lowest were in the open area in bryophytes (73.2.±2.7 mm), and there was a significant advantage of large and medium acorns (average 93.0±2.5 and 81.0±2.6 mm, respectively) over small seeds (73.6±3.2 mm). The model of stem diameter revealed the impact of three predictors – seed size, microsite, and study date. Across study dates, we found the highest diameter in the open site in bryophytes while the lowest was in *Vaccinium*, however, the average difference was <0.2 mm. For seed size we found a significant advantage of large and medium acorns (average seedling diameter amounted 2.38±0.03 and 2.19±0.02 mm, respectively) over small seeds (1.93±0.03 mm). The model of leaf number did not account for microsite effects, but accounted for study date, leaf damage categories, and seed size; the predicted leaf number dropped in all variants in Sept 2019. The predicted leaf number was higher for large and medium seeds (average 2.9±0.1 and 2.7±0.1 leaves, respectively) over small seeds (2.3±0.1). Fungi and insects decreased leaf number on average by 0.5±0.1 leaves, while herbivores by 1.3±0.1. Models of leaf width and length revealed the same trends.

Obraz zawierający tekst, diagram, linia, Wykres

Opis wygenerowany automatycznie

**Fig. 6.** Marginal mean (±SE) of seedling characteristics among microsites and seed size categories over study dates, assessed using linear mixed-effects models (**Table 3**).

**Table 3.** Linear mixed-effects models of seedling growth characteristics over study dates.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Response** | **Variable** | **Sum of squares** | **Mean square** | **Numerator df** | **Denominator df** | **F** | **P** | **Random effects SD** |
| Length | Microsite | 6573.6 | 3286.8 | 2 | 256.4 | 15.6 | <0.001 | Acorn id |
| AICc=10671.6 | Seed size | 5583.4 | 2791.7 | 2 | 256.0 | 13.3 | <0.001 | 23.00 |
| AICc0=10982.8 | Leaf fungi | 585.8 | 585.8 | 1 | 1082.7 | 2.8 | 0.095 | Residual |
| R2m=0.220 | Leaf herbivory | 208.0 | 208.0 | 1 | 992.6 | 1.0 | 0.320 | 14.49 |
| R2c=0.778 | Leaf insects | 183.9 | 183.9 | 1 | 1036.7 | 0.9 | 0.350 |  |
|  | Stem damage | 25450.9 | 25450.9 | 1 | 990.4 | 121.2 | <0.001 |  |
|  | Date | 36600.0 | 7320.0 | 5 | 985.3 | 34.8 | <0.001 |  |
| Diameter | Microsite | 0.7 | 0.4 | 2 | 254.3 | 12.5 | <0.001 | Acorn id |
| AICc=-161.1 | Seed size | 3.0 | 1.5 | 2 | 256.8 | 50.7 | <0.001 | 0.26 |
| AICc0=1035.3 | Date | 63.0 | 12.6 | 5 | 976.2 | 431.8 | <0.001 | Residual |
| R2m=0.495 |  |  |  |  |  |  |  | 0.17 |
| R2c =0.848 |  |  |  |  |  |  |  |  |
| Leaf number | Seed size | 31.4 | 15.7 | 2 | 244.7 | 9.1 | <0.001 | Acorn id |
| AICc=4388.6 | Leaf fungi | 22.8 | 22.8 | 1 | 1212.2 | 13.2 | <0.001 | 0.63 |
| AICc0=4678.4 | Leaf herbivory | 214.2 | 214.2 | 1 | 1181.0 | 123.9 | <0.001 | Residual |
| R2m=0.222 | Leaf insects | 38.9 | 38.9 | 1 | 1188.4 | 22.5 | <0.001 | 1.32 |
| R2c=0.369 | Date | 137.1 | 27.4 | 5 | 1038.3 | 15.9 | <0.001 |  |
| Leaf length | Microsite | 259.1 | 129.5 | 2 | 237.1 | 0.3 | 0.773 | Acorn id |
| AICc=11304.1 | Seed size | 12018.5 | 6009.3 | 2 | 220.0 | 12.0 | <0.001 | 11.65 |
| AICc0=11733.0 | Leaf fungi | 1129.7 | 1129.7 | 1 | 1212.2 | 2.2 | 0.134 | Residual |
| R2m=0.271 | Leaf herbivory | 140228.0 | 140228.0 | 1 | 1106.4 | 279.1 | <0.001 | 22.41 |
| R2c=0.426 | Leaf insects | 2357.2 | 2357.2 | 1 | 1169.6 | 4.7 | 0.031 |  |
|  | Stem damage | 7214.2 | 7214.2 | 1 | 1123.3 | 14.4 | <0.001 |  |
|  | Date | 9127.2 | 1825.4 | 5 | 1013.6 | 3.6 | 0.003 |  |
| Leaf width | Microsite | 102.5 | 51.2 | 2 | 251.0 | 0.3 | 0.710 | Acorn id |
| AICc=9852.8 | Seed size | 2922.1 | 1461.1 | 2 | 235.0 | 9.8 | <0.001 | 6.81 |
| AICc0=10270.3 | Leaf fungi | 243.5 | 243.5 | 1 | 1213.9 | 1.6 | 0.202 | Residual |
| R2m =0.268 | Leaf herbivory | 39863.4 | 39863.4 | 1 | 1104.0 | 266.4 | <0.001 | 12.23 |
| R2c=0.441 | Leaf insects | 684.5 | 684.5 | 1 | 1165.4 | 4.6 | 0.033 |  |
|  | Stem damage | 3756.3 | 3756.3 | 1 | 1118.7 | 25.1 | <0.001 |  |
|  | Date | 12547.6 | 2509.5 | 5 | 1023.1 | 16.8 | <0.001 |  |

***3.3. Seedling characteristics***

Comparison of seedling characteristics at the end of the study revealed that those originating from large acorns had higher root and stem mass, total, mean, and specific leaf area, root length, and total biomass (**Fig. 7,** **Table 4**). We found the highest effect sizes for leaf characteristics and total biomass, where seedlings from large acorns had twice higher biomass. However, biomass allocation was lower to leaves and higher to roots, and it was similar to seedlings originating from medium acorns. For microsites we observed differences in root length and biomass allocation into leaves and roots: seedlings growing in bryophytes had longer roots and allocated more biomass into roots than into leaves.

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**Fig. 7.** Marginal mean (+SE) seedling characteristics among microsites and seed size categories, assessed using linear mixed-effects models (**Table 4**).

**Table 4.** Linear mixed-effects models of seedling characteristics over study dates.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Response** | **Variable** | **Sum of squares** | **Mean square** | **Nume-**  **rator df** | **Deno-**  **minator df** | **F** | **P** | **R2** |  | **Random effects** | **SD** |
| Leaf mass | microsite | 0.033 | 0.033 | 1 | 77.449 | 1.533 | 0.219 | R2m | 0.060 | Acorns block | 0.111 |
|  | seed size | 0.118 | 0.059 | 2 | 83.022 | 2.769 | 0.069 | R2c | 0.403 | Residual | 0.146 |
| Root mass | microsite | 0.145 | 0.145 | 1 | 76.073 | 1.623 | 0.207 | R2m | 0.117 | Acorns block | 0.241 |
|  | seed size | 1.401 | 0.701 | 2 | 81.723 | 7.842 | 0.001 | R2c | 0.465 | Residual | 0.299 |
| Stem mass | microsite | 0.006 | 0.006 | 1 | 81.132 | 0.567 | 0.454 | R2m | 0.137 | Acorns block | 0.110 |
|  | seed size | 0.161 | 0.081 | 2 | 84.689 | 8.217 | 0.001 | R2c | 0.612 | Residual | 0.099 |
| Leaf mass fraction | microsite | 0.088 | 0.088 | 1 | 153.000 | 13.770 | <0.001 | R2m | 0.090 | Acorns block | 0.000 |
|  | seed size | 0.017 | 0.008 | 2 | 153.000 | 1.294 | 0.277 | R2c | 0.090 | Residual | 0.080 |
| Root mass fraction | microsite | 0.260 | 0.260 | 1 | 55.963 | 18.127 | <0.001 | R2m | 0.117 | Acorns block | 0.024 |
|  | seed size | 0.044 | 0.022 | 2 | 69.630 | 1.553 | 0.219 | R2c | 0.151 | Residual | 0.120 |
| Stem mass fraction | microsite | 0.017 | 0.017 | 1 | 60.516 | 2.711 | 0.105 | R2m | 0.027 | Acorns block | 0.064 |
|  | seed size | 0.003 | 0.002 | 2 | 66.049 | 0.244 | 0.784 | R2c | 0.404 | Residual | 0.080 |
| Total leaf area | microsite | 793.503 | 793.503 | 1 | 74.391 | 0.477 | 0.492 | R2m | 0.127 | Acorns block | 16.597 |
|  | seed size | 32226.962 | 16113.481 | 2 | 84.535 | 9.695 | <0.001 | R2c | 0.251 | Residual | 40.767 |
| Mean leaf area | microsite | 0.737 | 0.737 | 1 | 86.045 | 0.009 | 0.926 | R2m | 0.117 | Acorns block | 2.659 |
|  | seed size | 1613.010 | 806.505 | 2 | 97.644 | 9.560 | <0.001 | R2c | 0.186 | Residual | 9.185 |
| Specific leaf area | microsite | 15648.817 | 15648.817 | 1 | 84.655 | 1.471 | 0.229 | R2m | 0.133 | Acorns block | 77.587 |
|  | seed size | 171594.322 | 85797.161 | 2 | 90.174 | 8.064 | 0.001 | R2c | 0.446 | Residual | 103.146 |
| Root length | microsite | 22863.573 | 22863.573 | 1 | 70.646 | 11.519 | 0.001 | R2m | 0.167 | Acorns block | 28.716 |
|  | seed size | 29877.254 | 14938.627 | 2 | 78.006 | 7.526 | 0.001 | R2c | 0.411 | Residual | 44.552 |
| Total biomass | microsite | 0.010 | 0.010 | 1 | 79.257 | 0.050 | 0.824 | R2m | 0.114 | Acorns block | 0.451 |
|  | seed size | 2.933 | 1.467 | 2 | 83.292 | 7.517 | 0.001 | R2c | 0.566 | Residual | 0.442 |

**4. Discussion**

Our experimental study revealed that the majority (79.1%) of red oak acorns sown in the Scots pine forest did not survive. However, overall survival rate was twice higher than reported by Dyderski and Jagodziński (2019), who found average survival of 12.5±2.2% (after one year) in various types of temperate forests. The difference can result from the fact that the behavior of acorn hoarders – i.e. searching for acorns formerly cached and their consumption (Wang et al., 2014, and references therein) was excluded in our study (otherwise the final losses could have been even higher). On the other hand, acorns for sowing were randomly selected, while animals choose seeds for hoarding (Pesendorfer et al., 2016). Some rodents and birds prefer larger acorns (rich in food reserves) and are less likely to eat them *in situ* than to remove and hoard them (Forget et al. 1998; Vander Wall 2001; Xiao et al. 2006), while others prefer smaller acorns as they are easier to carry (Muñoz and Bonal, 2008; Muñoz et al., 2012). In the first scenario, larger acorns would dominate among those dispersed outside the area of cultivation which facilitates higher acorn survival and seedling establishment and recruitment. In the second scenario preferences for small acorns would result in red oak regeneration failure—as we showed in this study, a majority of small seeds are lost. However, use of red oak acorns by animals is very complex and context dependent, and relies, among others, on the composition and size of animal guilds in a specific forest area, on acorns crop abundance in a specific year, or availability of other food resources (Wróbel et al., 2022).

Nevertheless, this study revealed that the very large losses in the pool of sown acorns were caused by acorn pilferage (28.5% of lost acorns), the death of sprouting acorns (27.7%) and the lack of acorn germination (27.4%). Leafy seedling death (10.7%) and the acorn death caused by contamination by fungi (5.8% of lost acorns), were less important when we analyzed the whole pool, however, the study indicated that the fate of acorns depended significantly on the acorn size and was different for each of the three microsite types.

***4.1. Ungerminated acorns***

Acorns for sowing were randomly selected and their viability was not tested (e.g. in the floating test; Gribko and Jones, 1996), thus some of them were naturally unable to germinate (De Groote et al., 2018). The proportion of ungerminated acorns, likely damaged by insects, destroyed by fungi, or with malformed embryos, was relatively high, as it constituted over one fifth (21.7%) of the total pool of sown acorns. The proportion of nonviable seeds in the seed crop produced by the adjacent red oak trees, however, can vary significantly in sequential years, e.g. in 2018 it amounted to only 7%, while in 2019 it was 75% (Woziwoda et al., 2023). The high ‘initial’ nonviability of acorns produced by *Q. rubra* can significantly impact its regeneration in the mesic Scots pine forest.

The lack of acorn germination could also result from seed destruction after sowing, e.g. due to seed desiccation (Goodman et al., 2005) or over-freezing, post-dispersal predation by insects or infection by fungi (Dey and Parker, 1996). Among ungerminated acorns with visible signs of fungal pathogens (4.6% of the total pool), the highest mortality rate was noted for the small acorns, indicating that they are the most susceptible to fungal infestation. We suppose that all acorns could have been at risk of fungal infection even before sowing, as numerous acorns from the previous year and overgrown with black mycelium were found in the litter under *Q. rubra* canopy (personal observations). However, acorns could also be infected after sowing (Washington, 2003; and references therein), and it is likely that the high humidity among dense bilberry shoots most favored the development of pathogenic fungi. To confirm that observation we encourage further, specialized myco-ecological studies.

***4.2. Acorn pilferage***

We found that the acorn pilferage was positively corelated with the acorn size, regardless of the type of microsite, as larger acorns are more easily found by acorn consumers/pilferers (Vander Wall, 1990). The large acorns smell more intensively (Luft et al., 1994), and this factor could be responsible for a loss of 35% of seeds from the pool of acorns sown in the open space. In a few cases acorns were stolen in mass and the range of theft covered a few adjacent subplots, with the highest number of 28 large acorns stolen from six consecutive subplots (placed in a row at one-meter intervals). This indicates a concentration of searches by acorn pilferers after finding a single acorn and confirms the assumption that pilferers are more likely to find and pilfer seeds that are closer together (Stapanian and Smith, 1984; Vander Wall, 1990). Searching for acorns among dense bilberry stems (Woziwoda et al., 2019a) was more difficult, thus the five-acorn sets sown in sublots within bilberry clumps were least often pilfered (9.4% of all pilfered acorns). It is also worth noting that large acorns were most frequently missing.

High acorn losses due to acorn theft could be partially explained by the long-time exposure of seeds sown in the fall season to predators (Bonner, 2008; Birkedal et al., 2010). In the native range of *Q. rubra*,post-dispersal acorn theft and predation is indicated as one of the most important factors decreasing the natural regeneration of red oak populations (Crow, 1992; Dey and Parker, 1996). However, the post-dispersal acorn losses due to acorn theft are context dependent (Buckley et al., 2006; González-Rodríguez and Villar, 2012; Lichti et al., 2017; Bartlow et al., 2018; Löf et al., 2019) and differ significantly among sites (Buckley et al., 1998; Smallwood et al., 2001; Pèrez-Ramos and Marañón, 2008; Birkedal et al. 2009, 2010; Martelletti et al., 2018; Schupp et al., 2019). The highest rates of acorn disappearance occurred under shrubs – where the acorn loss amounted from one third for the pool of small seeds to almost half of the large and medium ones, however, it was surprising that, as in previous field studies, the highest seedling frequency was noted in just this type of microsite (Woziwoda et al., 2018b).

***4.3. Weather impacts***

The changeable weather in autumn 2017 and winter 2017/2018 with alternating snow cover occurrence and melting surely enhanced activity of rodents searching for food (Pucek et al., 1993; Orrock and Danielson, 2009), which could increase acorn losses (Pereira and Koprowski, 2019). However, *Q. rubra* seeds and seedlings are highly susceptible to the soil/air temperature and moisture (Suszka and Krawiarz, 1971; Crow, 1988; Dey and Parker, 1996; Noland et al., 2013), so this changeable weather also impacted them directly. A few frosty days in the rainy autumn could initiate natural stratification of oak seeds, and the post-frost weather warming favored fast acorn germination (so-called *cold-followed-by-warm stratification*, Suszka and Krawiarz, 1971). Cool (0-5°C) and moist conditions for 30-45 days is enough to break the dormancy in red oak seeds (Schopmeyer, 1974), and acorns can germinate after 10 days when the ambient temperature is above 4.5°C (Korstian, 1927). During colder winters with prolonged below-zero temperatures acorns are subjected to cold stratification and their dormancy lasts much longer (92-144 days), i.e. up to spring of the next year (Suszka and Krawiarz, 1971; Johnson et al., 2002). However, insufficiently protected acorns – i.e. those deposited in the bare soil under shrubs, could die when the temperature decreased below -8oC, as it is lethal for oak seeds (Suszka and Krawiarz, 1971; Suszka and Tylkowski, 1981). The extreme low temperatures below -20oC noted in the early spring of 2018 could have killed some of the still dormant acorns and damaged some of the growing sprouts, which increased the pool of ‘ungerminated’ acorns. Spring frosts recorded at the ground level every year during the experiment, also threatened sprouting acorns (in the first season) and leafy seedlings (each year), as their exposure to -3oC for several hours causes partial to complete necrosis of the aerial shoot and expanding leaves (Aizen and Woodcock, 1996). Late spring frost is the primary factor limiting the northern distribution of *Q. rubra* in its native range (Neilson and Wullstein, 1983). Thus, climate fluctuations with periodic warming in winter, like the weather observed in December 2019, or the snowless winters like in 2019/2020, followed by drastic cooling in the late winter or spring, can be devastating for *Q. rubra* regeneration.

Approximately three times as many sprouting acorns were recorded after the first winter/spring season in the open space and within bilberry clumps than under shrubs (91, 113, and 33, respectively), and the higher seedling survival noted in microsites with than without a moss layer (77 and 97 seedlings *versus* 50, respectively), indicated that acorn burial under a dense moss cover was protective from frosts for red oak acorns; therefore the results obtained confirmed the hypothesis on the ‘burial effect’. Such protection was especially important for survival of seedlings growing from large acorns, which are characterized by rapid germination (Pritchard, 1991), which -in turn- is explained by their lesser sensitivity to dehydration (Pritchard, 1991; Goodman et al. 2005; Ramírez-Valiente et al., 2009; Ganatsas and Tsakaldimi, 2013).

An interesting finding was that small acorns buried in the moss remained in the dormancy stage longer and sprouted later – in the early summer. Being more sensitive to low temperatures, they could be likely subjected to ‘cold stratification’ (Suszka and Krawiarz, 1971) and remained in the dormant stage during winter warming spells. Their slow and erratic germination in spring could also result from too much desiccation and decreased seed viability (Goodman et al., 2005). Paradoxically, protection of acorns from frost that was too good, by being buried under moss cover during the mild winter of 2017/2018, could also result in not completely satisfying the stratification requirements of *Q. rubra* seeds (Bonner, 1973). Without prior cold stratification, these acorns were able to germinate in humid conditions only when the temperature exceeded 20°C (Suszka and Krawiarz, 1971). Delayed germination and slow seedling growth allowed avoidance of the negative impacts of spring frosts (Aizen and Woodcock, 1996), however, long acorn dormancy and rapid seedling development in hot and dry summer days resulted in extremely high mortality of germinating seeds and early seedlings. Our study revealed that nearly 90% of sprouting acorns with delayed germination sown in the open space as well as under shrubs, and over 75% of such acorns in bilberry clumps, died during the summer 2018. The higher acorn/seedling survival noted in bilberry microhabitats resulted from the higher moisture and lower summer temperatures which likely occurred within bilberry clumps. However, neither the shade of bilberries or shrubs nor the moss cover sufficiently protected the rising sprouts and seedlings from the summer drought, due to desiccation of cotyledons in acorns, or leaves on seedlings (Weber and Gates, 1990; Bonner, 2008; Walters et al., 2023). Admittedly seedlings are able to compensate for losses connected with foliage reduction by delayed autumnal leaf senescence together with a delayed bud burst in the subsequent spring, however, it has to be corelated with the re-watering of soil after summer drought (Vander Mijnsbrugge et al., 2016) and also with the lack of early autumnal frosts, and such conditions did not occur in the study area. However, the most effective drought avoidance mechanisms of oak seedlings, i.e. reduction of the leaf area (Jacobs et al., 2009) was observed in our experiment, and was clearly noticed for all seedlings – regardless of acorn size category and type of microsite, in September 2019, i.e. after a dry spring and extremely dry and hot summer. The rate of height growth of shoots also slowed down then, while the growth in thickness of shoots was undisturbed, which indicated allocation of resources into more permanent parts of the seedlings, i.e. in stems and roots (Jacobs et al., 2009).

***4.4. Seedling growth and survival***

Our study showed that acorn size strongly affected *Q. rubra* seedlings by increasing seedling emergence, growth and survival in the first three years. The positive correlations (with some exceptions) between acorn size and acorn germination and survival percentage of seedlings was also described in the *Q. rubra* native range (Kormanik et al., 1998b; but see: Auchmoody et al., 1994).

Oaks growing from large acorns were taller and more vital than those growing from small acorns, however, differences between specimens from large and medium acorns were not significant. It suggests the presence of an acorn mass and size threshold, above which *Q. rubra* seedlings develop successfully. This threshold can potentially serve as an indicator of successful regeneration. In this experimental study delayed germination meant the longer duration of leaf emergence and consequently – shorter leaf longevity, i.e. limited time for effective photosynthesis for seedling growth, especially important for early seedling survival (De Groote et al., 2018). Seedlings growing from larger acorns completed their leaf production in spring (before June 2018), while those growing from small acorns unfolded their leaves later, over the summer (up to September 2018). The fast depletion of nutrient resources insufficient for initial root growth and development of aboveground biomass to sustain the individuals via photosynthesis resulted in the highest mortality of seedlings growing from small acorns (De Groote et al., 2018). In accordance with Seiwa and Kikuzawa (1996), the simultaneous expansion and development of leaves in the beginning of the vegetative season allows the reduction of environmental stress and decreases mortality rate after seedling emergence. The noted intraspecific differences in seedling dimensions resulted from acorn size, but they were also modified by the environmental conditions of microsites (Long and Jones, 1996; Koch et al., 2004; Tozer et al., 2015). Despite relatively homogeneous light conditions prevailing under the pine canopy, oak seedlings growing within bilberry clumps were protected at the initial phase of growth from direct sunlight by relatively tall bilberry stems (Woziwoda et al., 2019a), and light deficiency forced development of bigger leaves (Kuehne et al., 2014; Dyderski and Jagodziński 2019). It also resulted in larger seedling dimensions noted in bilberry than in the other two types of microsites studied. Seedlings competing with bilberry for light grew taller, but their diameter was smaller, while seedlings growing in the open area – without competition of herbaceous plants, invested more resources in roots and stem diameter, compared to the height. Results were in accordance with other studies showing positive relationships between oak regeneration biomass and understory species richness and diversity (Kolb and Steiner, 1990; Jensen et al., 2011; Dyderski and Jagodziński, 2018; but see Löf et al., 2021). The differences found, however, could also result from forest site fertility (De Groote et al., 2018).

***4.5. Seedling damages – causes and consequences for their growth and survival***

In our study the total defoliation of some seedlings or complete damage of leafy stems was noted both at the early (i.e. in June) and late summer (in September). These serious seedling damages could result from heavy spring frosts or summer droughts as we showed above, or from browsing by large ungulates (Kern et al., 2012; Granger et al., 2018; Löf et al., 2021). Admittedly browsing on small (< 20 cm tall) oak seedlings is reported as low and classified as a minor mortality factor (Götmark et al., 2005), however, the pressure of ungulates on oak juveniles is context dependent, and in some cases it can be very heavy (Dey and Parker, 1996; Riepšas and Straigyté, 2008; Averill et al., 2016; Granger et al., 2018). In a mosaic of forest patches with different tree species composition, i.e. Scots pine-red oak stands with closed canopies and completely reduced herbaceous and moss layers (where animals rest in shade) and Scots pine monocultures with open canopy and a well-developed herb and moss layers (where they feed), the migration of large herbivores like red deer *Cervus elaphus* L. and European roe deer *Capreolus capreolus* L., is inevitable. The co-occurrence of bilberry clumps and numerous seedlings and saplings of the red and pedunculate oaks (Woziwoda et al., 2018b)attracts ungulates, especially in June-July, when they readily feed on bilberry leaves and fruits (Melis et al., 2006; Nestby et al., 2011) and occasionally – on juvenile oaks. The browsed leafless seedlings were found both concentrated in one space and as dispersed single individuals growing within the same subplot among (1-4) other leafy specimens. It resulted from a different browsing strategy of herbivores: some of them can forage leisurely in one place, which results in local damage to a higher number of seedlings, while others gnaw on seedlings when they wander (Götmark et al., 2005; Oswalt et al., 2006; Cushman et al., 2020, and references therein).

Seedlings that lost all of their photosynthetic capacity in June usually recovered from defoliation before September. In the first year of growth seedling recovery could depend on the availability of still unused resources stored in the cotyledons, although Aizen and Woodcock (1996) found no relationship between acorn size and survival of defoliated red oak seedlings. In the next years the regrowth of defoliated/damaged seedlings was conditioned by resources deposited in roots, where a large proportion of carbohydrates assimilated during the previous vegetative season is stored, and translocated aboveground, e.g. to the leaf buds, if necessary (Farmer, 1975; Jacobs et al., 2009; Wang et al., 2023). Johnson (1994) and Jacobs et al. (2009) indicated that enlarging the root system (high root to shoot ratio) is a natural preparation of red oak seedlings for eventual release, as their shoots are often damaged or dieback (due to diverse biotic or abiotic factors), and resprout from adventitious buds at the root collar. However, resprouted seedlings as well as those that recovered from defoliation were shorter than undamaged ones, and 30% of them died in the next season. Their weak growth and survival, similarly to seedlings growing from acorns with delayed germination, could be explained in part by a shorter leaf longevity, insufficient photosynthetic capacity, and productivity that was too low during vegetative season (Larson, 2011; Wang et al., 2023).

***4.6. Verification of the previous results***

Our experimental study revealed that acorn germination as well as seedling survival was higher within bilberry clumps and in the open space than under shrubs, while the higher number of juvenile specimens as well as higher proportion of germinated to ungerminated acorns was previously noted under shrubs than in the open areas or within clumps of *V. myrtillus* (Woziwoda et al., 2018b). This discordance could be explained by: (1) a much higher number of acorns being deposited each year under shrubs than in the open space or within bilberry clumps, or (2) by underestimated losses in the two latter habitats due to ‘unrealized’ consumption or re-caching of acorns deposited there (the natural behavior of acorn consumers was not ‘activated’, as they were excluded from the phase of acorn-hoarding).

This experiment showed that acorns buried under the compact moss wefts more often developed into seedlings, so the positive “burial effect” was confirmed. Obtained results, however, undermined the theory -previously accepted by us (Woziwoda et al., 2018b), on the “nurse effect” of native shrubs on red oak seed germination and seedling growth. Rather, shrubs were much more frequently chosen by acorn hoarders as recognizable orientation points in the pine monoculture (Smallwood et al., 2001; Pesendorfer et al., 2016). However, for the same reason, acorns deposited under shrubs were more frequently found by acorn pilferers and consumed (or re-cached), and an extremely small proportion of acorns deposited in this type of microsite finally developed into seedlings (9%). Higher theft of acorns cached beneath the tree canopy than in the open area, as well as successful recruitment of acorns cached in the latter, neither pilfered nor recovered by granivores rodents, was also shown by Muñoz and Bonal (2011) for holm oak *Q. ilex* in a savanna-like landscape. The high number of *Q. rubra* juveniles growing under native shrubs could be explained by the lesser pressure of ungulates on the few surviving red oak seedlings, as large ungulates are more interested in foraging on taller plants if they are available (González-Rodríguez and Villar, 2012; Jensen et al., 2012), and in this context – the ‘nurse effect’ of shrubs for *Q. rubra* seedlings can be confirmed. It also partially explains the less frequent occurrence of taller saplings in the mesic Scots pine forest than in mixed Scots pine-pedunculate oak forest, where a denser shrub layer occurs (Woziwoda et al., 2019b).

In our former study we stated that seedlings growing under deciduous shrubs were favored by higher soil moisture (covered by the litter) and higher soil fertility resulting from the yearly supply of carbon and other elements from decomposing litter (Woziwoda et al., 2018b), however, our 3-year observations and study results contradict this. The leaves under shrubs were blown away by the wind, and soil was bare or covered with a very thin layer of pine needles, thus uncovered topsoil was not protective for acorns – they could easily over-freeze and dry out (Collins and Good, 1987; Facelli and Picket, 1991; Bonner, 2008; Launiainen et al., 2022). A different situation was found within dense clumps of the dwarf-shrub – *V. myrtillus*, where each year soil humus was supplied with bilberry leaves, rich in macro- and micronutrients (Woziwoda et al., 2019a). Admittedly *Q. rubra* is considered as a stress-tolerant tree species, able to survive highly reduced soil fertility (Zerbe and Wirth, 2006; Chmura, 2014; Miltner and Kupka, 2016), however, occurrence of deciduous leaf litter and yearly supplies of nutrients favors its growth (Major et al., 2013; Woziwoda et al., 2019b). Additionally, after rainfall the moss layer occurring among bilberry stems holds higher humidity for a longer time, while in the more open areas the moss ‘carpet’ dries out more quickly (personal observations). The higher moisture of the first microhabitat could increase the maintenance of seed viability through the dormancy period (García et al., 2002; Kang et al., 2023), which, also explains the more effective growth and higher survival rate of red oak seedlings (Dickson and Tomlinson, 1996) noted in bilberry.

The limited nutrient and water availability, characteristic for soils of coniferous forests in general (Zwydak et al., 2011), and their concentration in the near-surface layer of the soil, forces belowground competition of plants (Facelli and Pickett, 1991; Schuler and Robinson, 2010; Luo et al., 2023). Digging seedlings for biomass research (in September 2020), we revealed a highly compacted tangle of plant roots, mainly of pines (*P. sylvestris* produces a long taproot, but also a wide network of shallow lateral roots, Roberts, 1976; Čermák et al., 2008). The primary taproots of red oak seedlings were often twisted, indicating difficulties in ‘breaking through’ through this layer. This belowground pine-oak competition for nutrients and water could also limit the aboveground growth of oaks (Wang et al., 2023). As commercial forests worldwide are currently dominated by pine tree species, the interspecific pine-oak belowground competition could be one of the key-factors limiting natural regeneration of *Quercus* species(Lorimer, 1992; Konopka et al., 2005; Fei et al., 2011; Luo et al., 2023). The successful artificial regeneration of *Q. rubra* observed in European forests (Nicolescu et al., 2018) is facilitated by limiting competition from other plants, e.g. by mechanical scarification of the soil, i.e. periodic destruction of the existing root layer (Miltner and Kupka, 2016). In nature large areas with disturbed and uprooted soil are left by wild boars, *Sus scrofa* L*.*, after their active ploughing in the ground in search of food (Sütő et al., 2019). Wild boar occurrence in forest ecosystems may be an important factor favoring oak regeneration, albeit the longer presence of big ungulates limits activity of acorn hoarders in open areas, and hidden acorns are actively searched out and consumed by boars (Focardi et al., 2000; Muñoz and Bonal, 2007; Suselbeek et al., 2014).

**5. Conclusions**

The three-year-long experimental study revealed that only one fifth of *Q. rubra* acorns sown in the mesic Scots pine forest successfully developed into viable seedlings. The losses in the pool of sown acorns were caused by: acorn pilferage (28.5% of lost acorns), the death of sprouting acorns (27.7%), the lack of acorn germination (27.4%), leafy seedling death (10.7%), and acorn death due to fungal infection (5.8%). However, the fate of acorns and seedlings depended on the acorn size and differed for each of the three types of microsites studied. The final success in seedling survival was three times higher within bilberry clumps and in the open area than under shrubs (27.3%, 26.3%, and 9% of sown acorns, respectively). Acorn germination and seedling growth and survival were positively correlated with the acorn size – twice as many viable seedlings developed from large and medium acorns than from the small ones (38.8%, 40.4%, and 20.7% of seedlings, respectively). Acorn deposition in the bare soil under shrubs turned out to be the least favorable for seed germination as well as for early seedling growth, as acorns there were more easily found by seed pilferers (42% of acorns sown under shrubs ‘disappeared’) and more often died, likely due to over-freezing/desiccation during frosty spring days or summer droughts, than acorns buried under dense moss layers in the open area or among dense bilberry stems. It resulted in the highest proportion of ungerminated acorns (26%) and the lowest proportion of acorns germinated into seedlings (16.7%) found there among the three microhabitat types.

Results confirmed the positive effects of acorn burial under the dense moss layer in the open areas and within bilberry clumps, both on acorn germination and seedling growth. However, seedlings growing in these two microsites were more often damaged by large ungulates, than those growing under shrubs, and that explains the higher number of *Q. rubra* saplings noted in the latter microhabitat in our previous study (Woziwoda et al., 2018b). In this context, the ‘nurse effect’ of shrubs on red oak seedlings was confirmed. However, field observations and obtained results deny the positive effects of litter of deciduous shrubs on red oak regeneration in the mesic pine forest (because the litter was blown out from under the bushes every year).

This relatively short-lasting experiment indicated that red oak acorn germination and seedling growth was strongly impacted by the weather fluctuations. The mild (snowless) winter, heavy spring frosts, and summer droughts decreased viability of acorns and seedlings. Fast acorn germination in the spring and development of leafy seedlings in the first vegetative season was crucial for seedling survival. In turn, the longer acorn dormancy and their delayed germination in the early summer was what contributed to the greatest losses of seeds within bilberry clumps and in the open spaces (28.7% and 27.3% of acorns lost there, respectively), and this also indicates the negative consequences of burying seed under the moss cover (protection is ‘too good’).

Our study showed that the occurrence of the dense moss layer within extensive bilberry clumps, and small clusters of shrubs, together with the local (temporal) destruction of the root layer (to limit belowground competition between oaks and other species), favors *Q. rubra* regeneration in the European mesic Scots pine forests. However, predicted range shifts of native European tree species (Koch et al., 2022), and expected dramatic loss of *V. myrtillus* climatic optima (Puchałka et al., 2023b) will also impact the regeneration and distribution of introduced *Q. rubra* (Puchałka et al., 2023a, and references therein).

**Availability of data and materials**

Data uploaded as supporting information.

**Declaration of competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Funding**

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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