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Experimental study of the effects of mammalian hard mast predators on acorn survival and germination

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Introduction

Oaks (*Quercus* sp.) have been a significant component of forests in the Midwestern and Eastern United States for the last 10,000 years (Abrams 1992); however, recent studies have found reason to be concerned about the future of oaks as a dominant canopy species (Beck 1992, Lorimer 1992, McCune 1985, Pallardry 1988, Reich 1990). Despite oaks remaining a prominent canopy species and no evidence that acorn production has decreased, the proportion of oak seedlings and saplings in the understory and midstory of many hardwood forests does not seem adequate to maintain oaks as a dominant canopy species (Abrams 2003, Abrams 1992, Christensen 1977). Oak-regeneration seems to be least successful on mesic sites where fast-growing, shade-tolerant species such as maples (*Acer* sp.) dominate the understory (Abrams 1998).

Some researchers predict that slow-growing, mast-producing trees such as oaks and hickories (*Carya* sp.) will, in large part, be replaced in the canopy by mesophytes within the next 50 years (Fralish 1997, Shotola 1992). Research supporting these predictions has focused mainly on the recruitment of saplings into the canopy. These studies have produced considerable evidence that fire suppression and increased herbivory by white-tailed deer (*Odocoileus virginianus*) can play major roles in decreasing the abundance of oak seedlings and saplings in the understory (Abrams 1992, Healy 1997).

Fire suppression allows forest canopies to close, which confers an advantage on shade-tolerant species such as maples (Lorimer 1989, McCune et al 1985 and Reich et al 1990). In addition, oaks invest more in the establishment of a large root system early in development compared to a greater investment in vertical growth by maples and other

mesophytes (Hodges 1992, Crow 1994 and Reich 1990). Thus, oaks can resprout following fires, but maples and other mesophytic tree species that grow vertically at a more rapid rate are able to escape the detrimental impacts of deer herbivory earlier (Lorimer 1992).

Fire suppression and deer herbivory have received more attention as factors influencing oak regeneration failure than have the earlier stages of oak recruitment (acorn survival and establishment of oak seedlings). However, both early and late stage factors potentially limiting oak regeneration must be examined if we are to appropriately manage oak forests, particularly because some acorn consumers such as deer have increased greatly in abundance in recent decades (Russell 2001).

Oak trees are much longer-lived than their seed predators (200-400 years versus 1 to a few years); therefore, the density of seed predators is driven by fluctuations in acorn production rather than trees and mast consumers coexisting in a predator-prey mediated balance. The short-term fluctuations of many mast consumers in response to pulses of acorn production, and the cascading effects throughout the forest ecosystem, are becoming better known (e.g., Wolf 1996, Ostfeld et al. 1996). However, sustained increases in the populations of important mast consumers such as deer and small mammals could result in low rates of acorn survival even during years of abundant mast production. It has been suggested that high mast production by oaks is a strategy to swamp acorn consumers and allow higher rates of acorn survival (McShea 2000 and Schnurr et al 2002). If the number of oaks in the canopy decreases while acorn consumers increase in abundance then mast years will not be as effective at increasing acorn survival.

A decrease in the abundance of oaks in the canopy of North American deciduous forests is of great concern to wildlife ecologists because acorns are one of the most important foods to wildlife in the deciduous forest during fall and winter (Rodewald 2002). Martin et al. (1951) listed 96 North American vertebrate species that consume acorns. Large mammals (e.g. deer), sciurid rodents (e.g. tree squirrels, *Sciurus sp.* and eastern chipmunks, *Tamias striatus)*, and insects (e.g., acorn weevils, *Curculio* sp.) are important acorn predators in many Midwestern oak forests. Deer, chipmunks, and mice consume acorns on the ground, while tree squirrels may harvest them both on the ground and before they fall. Estimates of the amount of the acorn crop consumed by these species are few, coarse, and varied. McShea and Schwede (1993) noted that deer moved into acorn production areas during acorn fall, and consumed 70% of the marked acorns set out by these researchers at that time. After leaf fall, consumption of acorns by deer decreased, but 61% of the marked acorns set out by McShea and Schwede (1993) was consumed by sciurid rodents. About 90% of the acorns not consumed by mammals were infested by weevils. Steiner (1996) estimated that 49% of the crop of northern red oak acorns on the ground was consumed by deer. Infestation rates of acorns by weevils may reach 100% in some years, but is often about 50% (Beck 1992). Thus, in most years, almost the entire acorn crop may be consumed; about a 90% loss may be typical (Lorimer 1992). Seed availability clearly could limit seedling establishment under some conditions.

The replacement of oaks by mesophytes is geographically widespread with many reports coming from Illinois (e.g. Ebinger 1986, Edgington 1991, Shotola et al. 1992, Strole and Anderson 1992). Therefore, hardwood forests of Illinois present a good

opportunity for research on this subject. Our study is the first to use four different types of experimental treatments to determine the effect of three different groups of mammals on acorn survival over winter and oak seedling establishment. Our study was specifically designed to determine if deer, tree squirrels, and mice have additive or compensatory effects on acorn survival and if the burial of acorns by squirrels increases acorn survival and germination.

Methods and Materials

Study sites and experimental treatments:

We conducted our study in four upland hardwood forest remnants in central Illinois, USA. Four study sites were used in this project. Two study sites, Allerton Park, Piatt Co. (600 ha), and Vermillion River Observatory (VRO), Vermillion Co. (184 ha) are among the largest tracts of upland hardwood forest remaining in central Illinois. The other two study sites, Brownfield Woods (24 ha) and Hart Woods (16 ha), Champaign Co., are smaller forest remnants, although Hart Woods is set in a larger tract of forested land.

Three sets of experimental treatments (4 experimental plots per set of treatments) were constructed at each of the four sites (48 plots total). Sets of treatments were located at least 150 m apart and plots within each set of treatments were located no more than 10 m from one another. All sets of treatments were constructed in suitable areas of hardwood forest (e.g., level topography, good representation of oaks in the canopy).

Experimental plots were each 2 m x 2 m and comprised one of four treatments. Total exclosures (-mice, -squirrels, and -deer) consisted of wooden frames covered on the top

and four sides with 0.63-cm (¼") mesh galvanized steel hardware cloth. Exclosure walls were 1.5 m tall and buried 20 cm under the soil surface with an additional 10 cm of hardware cloth bent outwards to discourage small mammals from burrowing under the walls. Deer and squirrel exclosures (-squirrels and -deer) were similar to Total exclosures, but had 2.5-cm holes cut in the hardware cloth at ground level. Eight holes were cut on each side of each exclosure to allow access by white-footed mice. Deer exclosures (-deer) also were similar to Total exclosures, but the hardware cloth covering the walls began 30 cm above the soil surface to allow access by all small mammals. The final treatment was an Open plot consisting of a 2m by 2m area marked only by four steel fence posts, one at each corner.

We conducted our study from fall 2001 to fall 2003. In November of 2001 and 2002, after natural acorn fall had ended, we temporarily removed all leaf litter from each experimental plot and all acorns and tree seedlings were removed and discarded. A 1.5 m by 0.75 m sampling frame was then placed on the bare ground within each plot. The frame was aligned so that two of the length-wise corners lie along the center of the plot. The location of the centered corners were marked with small metal stakes that were left in place throughout the experiment so that the sampling frame could be replaced in the same location. Cord attached to the frame at 25 cm intervals was used to provide a grid-like spatial reference. A single northern red oak acorn (*Quercus rubra*) was buried about 2 cm deep at each intersection of the cords and where the cords intersect the centered side of the frame. The frame was then moved to the other half of the exclosure (placing two corners of the sampling frame on the centered stakes) and one northern red oak acorn was buried 2 cm deep at each intersection of the cords (total n = 25). The sampling frame was

then removed and the leaf litter was replaced. After replacing the leaf litter, the sampling frame was set back in place and a single northern red oak acorn was then dropped onto the center of each square formed by the cord. This allowed surface acorns to be mixed with the leaf litter. The frame was then moved to the other half of the plot and a single northern red oak acorn was placed in the center of each square except those squares in the row farthest from the center (n = 25). Each plot thus received 50 acorns, 25 buried to imitate caching by rodents and 25 on the surface. The acorns were obtained from a commercial distributor (F.W. Schumacher Co., Inc., Sandwich, MA) and only intact acorns free of damage and insect infestation were set out.

We used northern red oak acorns for two reasons. First, the large size of red oak acorns precludes interference by gape-limited birds such as blue jays and small woodpeckers on the control plots (Darley-Hill and Johnson 1981). Second, red oak acorns germinate in the spring after remaining dormant all winter in contrast to acorns from the white oak group that begin germination in fall shortly after they reach the ground. Our experiment was designed to evaluate over-winter survival of acorns and germination the following spring.

In late April – early May 2002 and 2003 we gently removed the leaf litter from each plot and recorded number, condition (rotten or otherwise damaged, intact but not germinating, germinating) of all acorns on the surface. We then set the sampling frame in place and gently excavated the soil beneath each intersection of the cords on the sampling frame. The number, location, and condition of all buried acorns were recorded. Germinating acorns were disturbed as little as possible and all other acorns were returned to their original locations (buried or on surface) after examination and before the leaf

litter was replaced. We visited each site the following September and recorded the number of oak seedlings in each plot. This sampling procedure allowed us to monitor acorn survival from fall to spring of each year, germination of acorns remaining in the spring, and establishment of oak seedlings.

Along with the experimental manipulations described above, we monitored acorn fall and background densities of acorns at each study site. Beginning in early September of each year, we counted the number of acorns of each species in 12 1-m^2 plots at each set of experimental treatments within each site. The acorn sampling plots were located at 10-m intervals along two 50-m transects, one transect on each side of the set of experimental plots. A random direction and distance (1-5 m) from each 10-m interval determined the location of each plot. The number of acorns at each experimental plot was sampled bi-monthly during peak acorn fall (mid-September to mid-November) and monthly thereafter through April 2003. These data provide information on the density of acorns in the areas around each set of experimental plots, as well as spatial variation in acorn abundance at each site. These data also describe rates of accumulation and depletion of acorns at each site over the years in which the study was conducted.

Small mammals were live trapped for two consecutive nights in the autumn and spring of each year. Twenty-four Sherman live traps (HB Sherman Co., Tallahassee, FL) were placed at 10-m intervals around each set of experimental plots. Three additional Sherman live traps also were set around the deer and sciurid exclosures. Live trapping was not extensive enough to estimate population densities, but provided confirmation of the occurrence of small mammals at each site. Sherman traps were baited with mixed birdseed and the number and species of all small mammals captured at each site was

recorded. To confirm the presence of squirrels at each set of experimental plots, at least one squirrel nest was located within 30 m of each set of plots. Deer activity was noted near each set of treatments by identifying deer browse along our 50-m transects.

We used analysis of variance (ANOVA) blocking for site (study site), placement (buried or surface), and treatment (exclosure type) to compare effects of our experimental treatments on acorn survival. The site variable was entered into the model as a random variable to examine differences among our four study sites on acorn fate (depredated, intact but not germinated, germinated). In addition, we used a chi-squared test to compare germination rates of surface acorns and buried acorns that remained to spring.

Results

Background acorn counts and presence of mammals

Acorns typically began appearing on the ground at our study sites in late September, but almost all acorns except rotten or damaged ones were gone by February. In the fall of 2001, acorns were least abundant at Brownfield Woods and most abundant at the two larger sites (Allerton Park and VRO, Fig. 1). In the fall of 2002, few acorns were detected during our sampling at any site (Fig. 2). Qualitatively, we would characterize fall 2001 as a season of moderate acorn production and fall 2002 as a season of poor acorn production.

White-footed mice were the only small mammals captured. We captured 1-6 white-footed mice near each set of treatments in each trapping survey. Because of extensive disturbance of traps by raccoons and squirrels at many sites, especially Brownfield

Woods and Hart Woods, trap success could not be compared among sites. Browsing of saplings or shrubs by deer was recorded each spring at each site, and deer and tree squirrels were regularly seen during visits to all sites.

Survival of acorns

Acorn survival (surface and buried acorns pooled) differed among treatments for both spring of 2002 and 2003 ($P < 0.0001$). A posteriori pairwise comparisons using the LSD procedure indicated that Total exclosures differed significantly from all other treatments, Deer and squirrel exclosures differed significantly from all other treatments, but Deer exclosures and Open plots did not differ significantly from each other in both 2002 and 2003.

No surface acorns were detected on the Open plots or on the Deer exclosures in spring of either year. In spring 2002, only four of 12 deer and sciurid exclosures had acorns remaining on the surface, and ≤ 4 acorns were detected per plot (Fig. 3). In spring 2003, Brownfield Woods was the only site with any acorns detected on the surface in Deer and squirrel exclosures. One of these plots had 1 surviving acorn, another had 4 surviving acorns, and the third had 22 surviving acorns (Fig. 4). In contrast, we recovered 22-25 intact or germinating acorns from each Total exclusion plot except one plot in VRO in 2002 (Fig. 3 and 4).

Buried acorns had significantly higher survival rates than acorns on the surface in both 2002 ($P < 0.0001$) and 2003 ($P < 0.01$). In spring 2002, few buried acorns were recovered from plots that allowed access by squirrels at our smaller sites (Brownfield Woods and

Hart Woods). The number of acorns recovered from Deer exclosures and Open plots at the two larger sites (Allerton Park and VRO) ranged from 5 – 23 (Fig. 5). The number of buried acorns recovered from plots where squirrels were excluded varied from 14 - 23 in spring 2002. The loss of buried acorns from several Total exclusion plots was puzzling, particularly where most acorns were recovered on the surface. These plots invariably had extensive tunneling by eastern moles (*Scalopus aquaticus*). Moles do not eat acorns but as they burrowed under our exclosures it is likely that buried acorns fell into their burrows and were displaced. In spring 2003, we recovered few if any buried acorns from plots where squirrels had access at all four study sites (Fig. 6). In contrast to 2002, only 3 - 10 buried acorns were recovered from Deer and squirrel exclosures, except for one plot at Brownfield Woods where 25 were recovered. Mole activity was not as apparent in 2003 and 20 - 25 buried acorns were recovered from Total exclusion plots (Fig. 6).

Germination rates

Of all the acorns recovered in 2002 and 2003, a greater proportion of buried acorns were germinating than surface acorns (years pooled: $X^2 = 793$; $df = 3$; $P < 0.001$). In 2002, 53 out of 281 (18.9%) acorns surviving on the surface were germinating by early May. In contrast, 514 out of 670 (76.7%) surviving buried acorns, were germinating. In 2003, only 1 out of 324 (0.3%) acorns surviving on the surface were germinating, whereas 349 out of 405 surviving buried acorns were germinating by early May (Fig. 7).

Seedling establishment

In September 2002, 6 – 17 oak seedlings were present on plots from which deer and squirrels were excluded, whereas 0 – 6 seedlings were present on Open plots and Deer exclosures (Fig. 8). In September 2003, no oak seedlings were present on any Open plots or Deer exclosures , whereas the number of oak seedlings present on Total exclosures and Deer and squirrel exclosures varied from 1 – 33 (Fig. 9).

Discussion

This study has demonstrated that the primary Midwestern mammalian mast consumers (White-tailed deer, sciurids, and white-footed mice) have a compensatory effect on the survival of surface acorns. Even in plots that deer and squirrels were excluded from mice consumed 98% of all surface acorns in 2002 and 92% of all surface acorns in 2003. It has been well documented that deer consume a high proportion of the acorn crop produced each year in the Midwest (McShea 1993, Steiner 1996); however, previous to this study there had been little documentation on the impact that acorn consumption by mice and sciurids has on over-winter survival of acorns. While it is clear that sciurids and mice play an important role in acorn survival on a small scale (2m x 2m) exclosures, future studies done on a larger scale would help to determine if these small mammals can impact acorn survival in a larger area.

It is well known to ecologists that squirrels not only consume acorns upon finding them, but they also cache acorns for later consumption. It has been shown that caching of acorns by squirrels increases the survival of acorns (Barnett 1977). Our data showed a similar increased survival of buried acorns in comparison to surface acorns. No surface acorns survived in plots that squirrels had access to in 2002 or 2003. In contrast, in 2002

squirrels consumed about ¾ of the buried acorns in they had access to (Fig. 5) and in 2003 they consumed nearly all buried acorns accessible to them (Fig. 6). A similar year to year trend was seen with mice and buried acorn consumption. On average, mice consumed fewer than 10 buried acorns per plot in 2002 and consumed more than 15 buried acorns per plot in 2003. When considering the much higher natural production of acorns in the fall of 2001 in comparison to fall 2002 it seems that both mice and squirrels are more likely to forage for buried acorns when fewer surface acorns are available. These data support the idea that buried acorns have higher survival rates then surface acorns, and the concept that several years of low mast production followed by a year of very high mast production is a strategy used by oaks to swamp acorn consumers and increase acorn survival.

While our data on buried acorn survival agreed with Barnett (1977), we found different results for germination rates between buried and surface acorns. Barnett did not find an increased rate of germination for buried acorns in comparison to surface acorns. The data we collected using buried and surface acorns suggests that buried acorns experience greatly increased rates of germination (Fig. 7). Given the much higher rate of germination that we recorded for buried acorns compared to acorns on the surface, the importance of a mast year may not only be directly due to the high number of acorns produced, but also due to more cached acorns not being rediscovered by squirrels.

The number of oak seedlings that we observed the following fall at each plot reflected the number of buried acorns we had recorded the previous spring. These data further exemplify the important role that caching of acorns by squirrels plays in the early stages of oak regeneration. However, it remains to be determined how great an impact this

behavior has in a completely natural setting. Steele et al (2001) found that only 18.2% of 286 acorns cached by squirrels were not recovered. Further studies showing the survival and germination rate of acorns naturally cached by squirrels will help to confirm the importance squirrels and their caching behavior have on early stages of oak regeneration.

The replacement of oaks by maple in Midwestern hardwood forests will be detrimental to wildlife in many ways. The most significant impact will be the loss of acorns as a major part of many wildlife species diets in the fall and winter months. Acorns have many beneficial characteristics that maple seeds do not. First of all, acorns are very digestible and much larger than maple seeds; therefore, acorns can provide more energy than maple seeds (Kirkpatrik and Penkins 2002). In addition, acorns have a hard outer coat that allows them to exist for longer periods of time without decomposing. This allows animals such as squirrels to cache acorns and consume them at a later date. Other wildlife species that don't cache acorns also benefit from this characteristic because during years of high mast production acorns may remain available in winter months when food is scarce. In addition to the advantages acorns provide over maple seeds, it has been suggested that the leaves and bark of oaks provide many benefits to wildlife that maples are not able to compensate for (Rodewald 2003).

In addition to the many mammal species that will be negatively affected by the transition of oak dominated to maple dominated forests many bird species will also suffer as this transition takes place. These species include, but are far from limited to, the red-bellied woodpecker (Melanerpes gallopavo), blue jay (Cyanocitta cristata), and wild turkey (Meleagris gallopavo) (McShea and Healy 2002, McShea and Schwede 1993). The large number of bird and mammal species that will be affected by the transition from

oak dominated to maple dominated forests is reason for concern that cascading effects may bring about major shifts in wildlife communities. This could have dramatic impacts on the Midwestern forests as we know them today and have for the last several centuries.

While fire suppression and deer herbivory currently seem to be the most important factors in oak regeneration failure, as oaks become less abundant in the canopy and acorns consequently become more rare, the early stages of oak regeneration (acorn survival and germination) will become increasingly limiting factors.

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Fig.1 – Background acorn counts at our four sites in the winter of 2001 to 2002

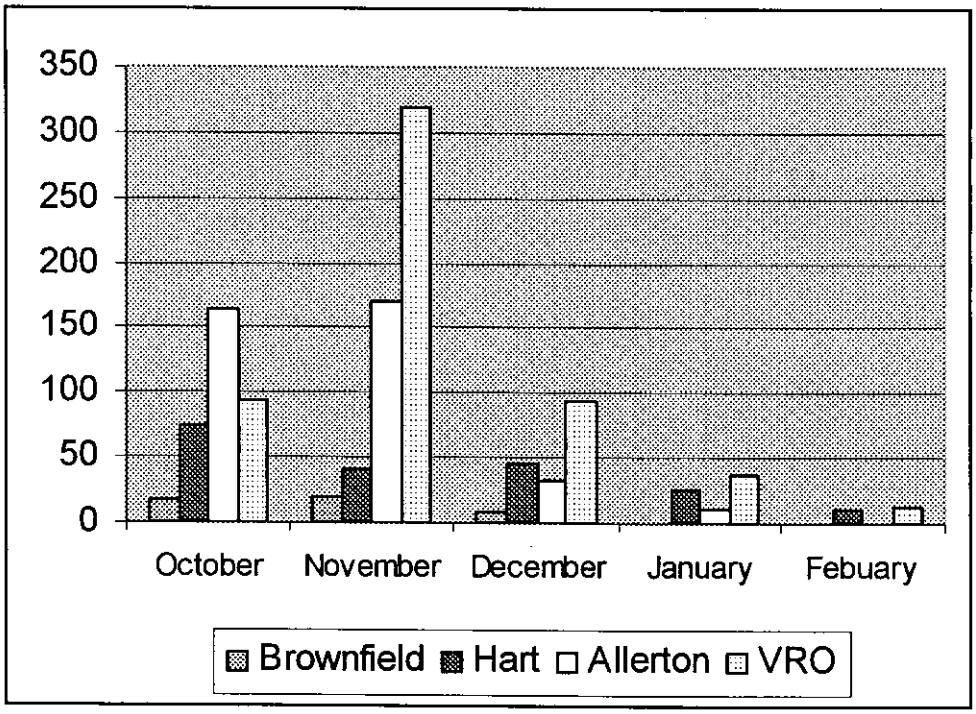

Fig.2 – Background acorn counts at our four sites in the winter of 2002 to 2003

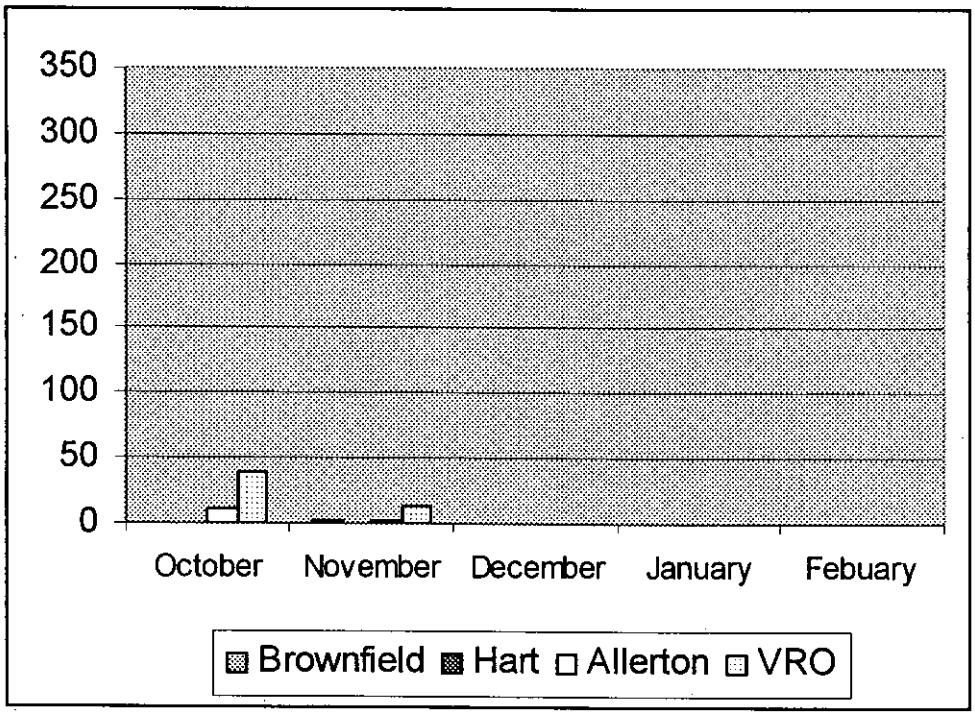

Fig. 3 – The average number of acorns recovered on the surface in each experimental treatment plot during spring 2002

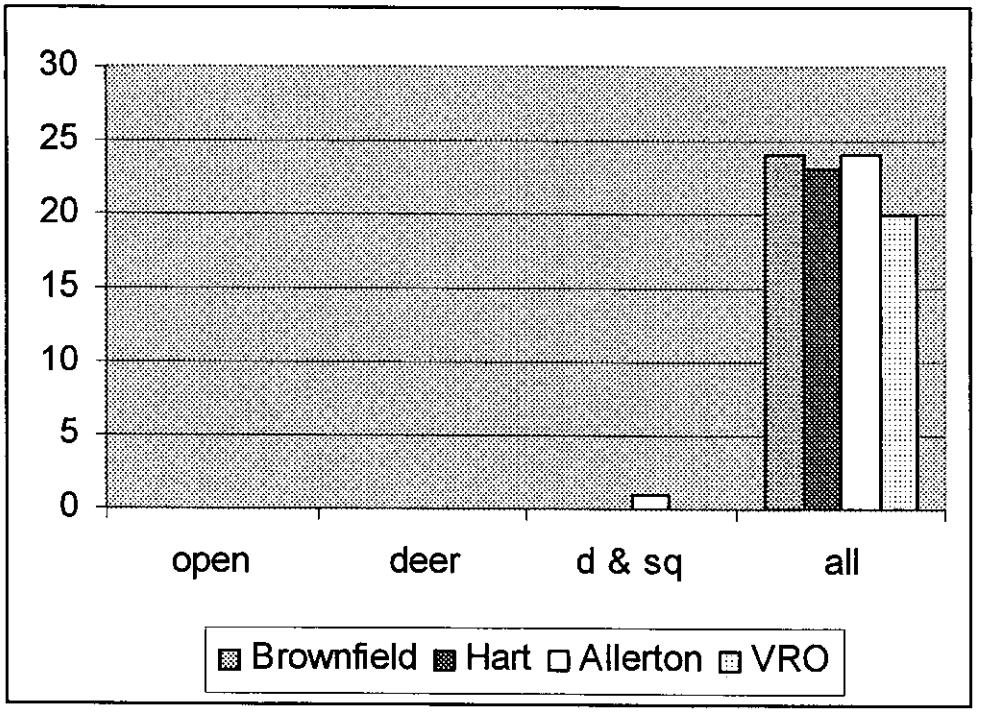

Fig. 4 – The average number of acorns recovered on the surface in each experimental treatment plot during spring 2003

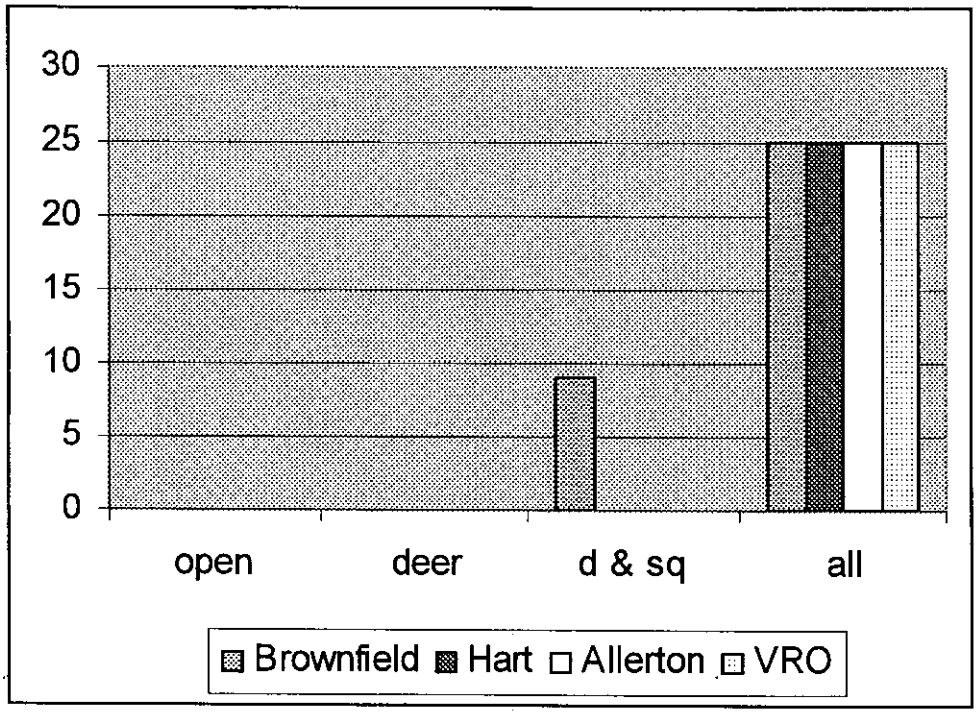

Fig.5 – The average number of buried acorns recovered in each experimental treatment plot during spring 2002

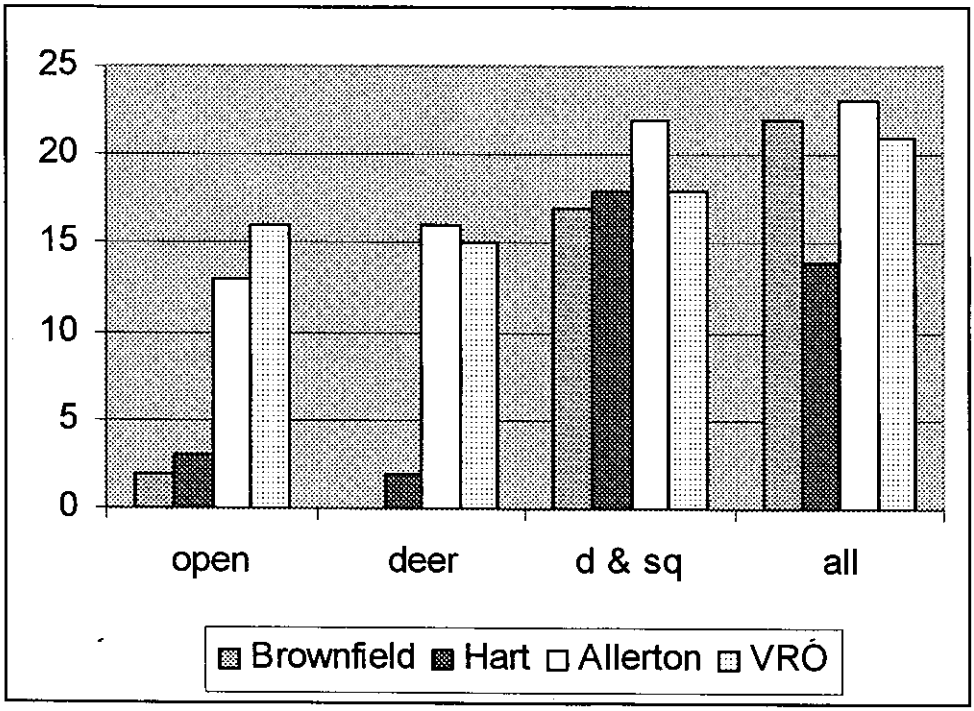

Fig.6 – The average number of buried acorns recovered in each experimental treatment plot during spring 2003

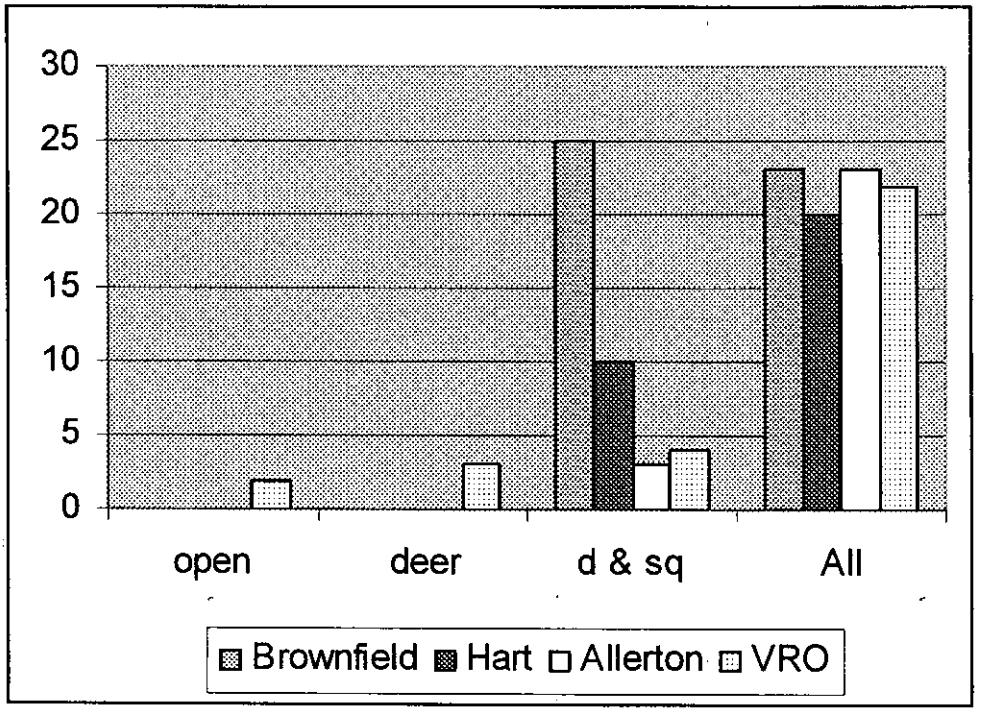

Fig. 7 – Germination rates of surface and buried acorns recovered in 2002 and 2003

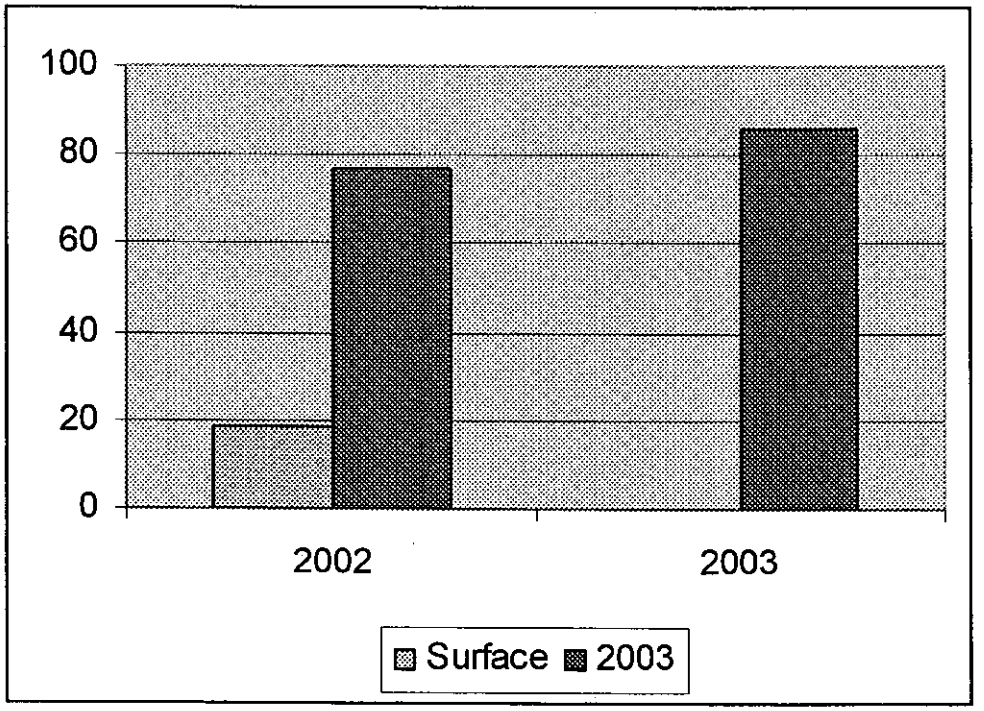

Fig. 8 – The number of oak seedlings observed in experimental treatments in September 2002

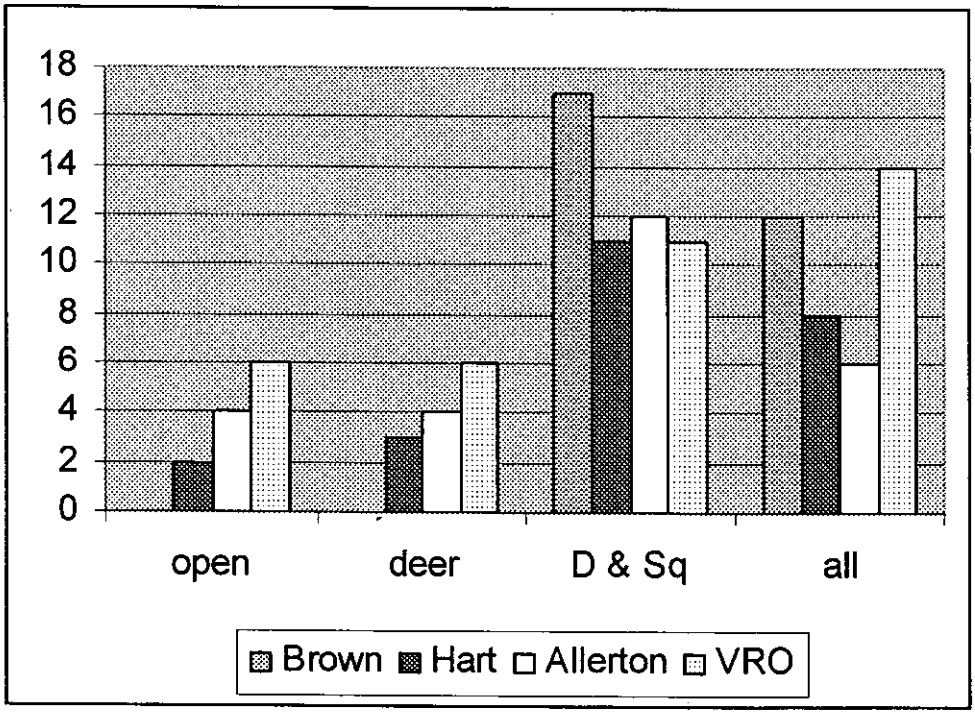

Fig. 9 – The number of oak seedlings observed in experimental treatments in September 2003