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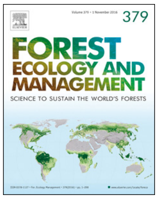

Tamm reviews

Tamm Review: Direct seeding to restore oak (Quercus spp.) forests and woodlands

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A R T I C L E I N F O

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A B S T R A C T

The scale of opportunity to implement forest restoration exceeds billions of ha worldwide, and a part of this area in northern temperate regions includes formerly oak (*Quercus* spp.)-dominated ecosystems. The cost of achieving restoration is often high, and tends to increase with severity of ecosystem degradation. Therefore, it is important to develop cost-efficient regeneration practices to support forest restoration. Direct seeding of acorns, one of the earliest artificial forest regeneration techniques developed, offers several benefits including costs that can be about a third of planting oak seedlings. However, direct seeding is presently a more uncertain practice for establishing oak forests and woodlands than is planting seedlings. Much of this uncertainty can be a result of acorn depredation by rodents even though other factors may also limit oak establishment. This review provides a synthesis of foundational knowledge, particularly from Europe and North America, pertaining to the biology and ecology of acorn production, acorn germination, early seedling growth, and acorn depredation by granivorous rodents. We build on this knowledge to review research on operational direct seeding practices and four basic strategies for acorn depredation control (chemical, ecological, physical and silvicultural). We suggest that environmentally sound approaches to minimize acorn depredation and increase seedling establishment currently exists. For example, seeding operations probably hold higher chances for success if scheduled during years of high masting, if applied on open sites (areas with little shrub and tree cover), and if acorn lots are sized and sown at an appropriate depth. Several gaps in our knowledge limit the development of improved operational practices for broader success. We lack information on basic acorn biology and proper handling and storage practices for many of the oaks around the world. And, we need research to support development of new techniques or combinations of strategies and techniques that minimize acorn depredation under a wide range of site conditions. Nevertheless, our synthesis suggests that direct seeding will remain a cost-effective and environmentally sound practice for oak forest and woodland establishment, and it will likely gain expanded use as future research informs innovation that increases seed availability, decreases acorn depredation, and raises predictability of oak seedling establishment.

1. Introduction

Forested biomes harbor a significant amount of the Earth's biodiversity and provide a wealth of other ecosystem services valued by human societies (Reid et al., 2005). However, land-use practices around the globe have resulted in widespread deforestation and forest degradation. It is estimated that more than 50% of the original forested area has been claimed by other land uses, and forest loss continues with an annual rate of loss that has averaged 0.13% since 1990 (FAO 2016). Forest restoration (Box 1) has become an important goal to mitigate the

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Box 1
Definitions and descriptions of terms and concepts used in the text (Helms, 1998; Johnson et al., 2019; Bellarosa et al., 2005; Stanturf et al., 2014).

Afforestation: establishment of forests or stands of trees on sites where "the preceding vegetation or land use was not forest" or woodland (Helms, 1998), e.g. arable fields, pasture lands or mined areas.

Reforestation: establishment of forests or stands of trees to regenerate existing forests or stands felled by natural, e.g., wind, or anthropogenic causes, e.g., wood harvesting.

Forest restoration: the process of renewing destroyed forest ecosystems and habitats (often towards a predefined historical state) by active human intervention, e.g., afforestation or conversion of tree species composition. Passive forest restoration is the managerial decision to allow natural succession for renewing forest ecosystems and habitats.

Mast seeding/masting: the copious production of fruit or seed by a tree (or other plants) with regional synchrony every two or more years.

Acorn: botanically defined as the fruit (nut) and partially encasing cap (cupule) of oaks (see Section 2.1). Practitioners conventionally apply the term "acorn" to the nut, and this manuscript carries that usage except where defined in Section 2.1.

Red oaks: species in the Section *Lobatae*, e.g. *Q. rubra*. Red oaks referenced in this text are native to North America. Acorn maturation is considered biennial as it typically occurs over 18 months.

White oaks: species in the Section *Quercus*, e.g. *Q. robur*. White oaks referenced in this text are native to Europe and North America. Acorn maturation is considered annual, as it is typically completed in one growing season.

Intermediate oaks: species in the Section *Protobalanus*, e.g., *Q. chrysolepis*. Species referenced in this text are native to western North America, and acorn maturation is typically biennial.

Ilex oaks: species in group *Ilex*, e.g., *Q. ilex*. Species referenced in this text are native to Mediterranean regions of Europe. Acorn maturation can be either annual or biennial with some species exhibiting both pathways on the same tree.

Cerris oaks: species in the group *Cerris*, e.g., *Q. suber*. Species referenced in this text are native to Mediterranean regions of Europe. Acorn maturation can be either annual or biennial with some species exhibiting both pathways on the same tree.

negative impacts of human activity on these ecosystems (Chazdon, 2008; Stanturf et al., 2014; Palma and Laurence, 2015). The scale of opportunity to implement forest restoration exceeds two billion ha worldwide (Minnemayer et al., 2011; Cernansky, 2018), and a part of this area includes formerly oak (*Quercus* spp.)-dominated ecosystems in the temperate, subtropical, and Mediterranean regions of Europe, Africa, Asia, and the Americas (Johnson et al. 2019).

Instituting practices to facilitate the natural regeneration process or to artificially establish regeneration are foundational aspects of forest restoration. Such practices are an expensive component of the forest restoration plan, and restoration costs increase with the degree of ecosystem degradation (Stanturf et al., 2001; Chazdon, 2008). This issue is ever present where restoration efforts target oak-dominated systems. In these systems, the defining oak component is usually established by planting nursery-grown seedlings (bare-root or containerized seedlings) (Dey et al., 2008). Planted seedlings normally exhibit satisfactory survival and growth following out-planting, and managers consider plantations reliable for quick establishment of forest cover (Palma and Laurence, 2015; Ceccon et al., 2016; Grossnickle and Ivetić, 2017). Plantation establishment is, however, relatively expensive and labor intensive (Löf et al., 2004). These factors reduce the cost-efficiency of implementing forest restoration, and can ultimately limit the area receiving treatment.

Facilitating the natural regeneration process can sometimes be a more cost-effective option than artificial means of forest establishment, but successful natural regeneration depends on several conditions and processes including the availability and fecundity of seed trees, the activity of seed dispersal, the quality of microsites for germination and seedling establishment, and the magnitudes of seed depredation and seedling herbivory (e.g., Leverkus et al., 2016). These conditions and processes are often missing or impaired on deforested or degraded restoration sites, and problems with oak natural regeneration, therefore, have been documented for decades in many different regions around the world (e.g., Watt, 1919; Crow, 1988; Bobiec et al., 2018).

Direct seeding (sowing seeds into soil) of acorns was an ancient technique used to artificially regenerate oak forests (Abrams and Nowacki, 2008), and it persisted in forestry in many areas through the early 20th Century as the most common practice for this purpose (Thirgood, 1971; Willoughby et al., 2004; Ammer and Mosandl, 2007). Development of seedling technologies in the 20th Century provided alternatives that reduced or eliminated issues associated with direct seeding. Issues such as poor seed quality, acorn depredation by granivorous (seed eating) rodents (e.g. Birkedal et al., 2009; Leverkus et al., 2015), competing vegetation, and browsing damage (Dey et al., 2008) cumulatively contribute to reduced seedling establishment that leads to the unreliability of direct seeding as a practice for establishing oaks. Nevertheless, direct seeding is usually the least costly approach for artificially establishing oak-dominated cover, and therefore has maintained the interest of managers through the decades (e.g. Bullard et al., 1992; Willoughby et al., 2011; Cole et al., 2011; Grossnickle and Ivetić 2017). Additionally, we contend that many of the issues associated with direct seeding operations can be anticipated and reduced or prevented given the manager has sufficient knowledge and understanding of the relevant biology, ecology, and silviculture.

There is a large body of literature relevant to direct seeding of acorns, and some contributions were published more than 190 years ago. The current paper provides a review and synthesis of knowledge made available from existing literature. We address the biology and ecology of acorn production, acorn germination, early seedling growth, and acorn depredation by rodents. We highlight acorn depredation by rodents because they are arguably the most prolific threat to sown acorns throughout temperate regions. We follow by addressing the practice of direct seeding and techniques developed to increase its effectiveness in oak regeneration and restoration. Topics presented in this section include harvesting and handling acorns, sowing practices, strategies to protect sown acorns, and economic considerations of direct seeding. We limit the scope of this review to temperate and Mediterranean Europe and North America because the literature base in these regions has grown greatly in recent decades. In our synthesis we also identify critical knowledge gaps, and we offer recommendations for future research, development and management. Accordingly, this work should support the application of direct seeding practices where forest restoration is aimed to promote oak-dominated cover, and it should also inform the development and advancement of direct seeding-based restoration practices involving other nut-producing trees comparable to oaks in temperate and tropical regions of the world.

2. Biological and ecological background

2.1. Acorn development and morphology

An important aspect of oak reproductive biology that imparts practical implications is flower ontogeny and the subsequent fruit maturation period. An annual pattern of flowering and fruit maturation is shared among the many white oak (section *Quercus*) species which are distributed throughout North America and Europe (Nixon, 1993) (Box

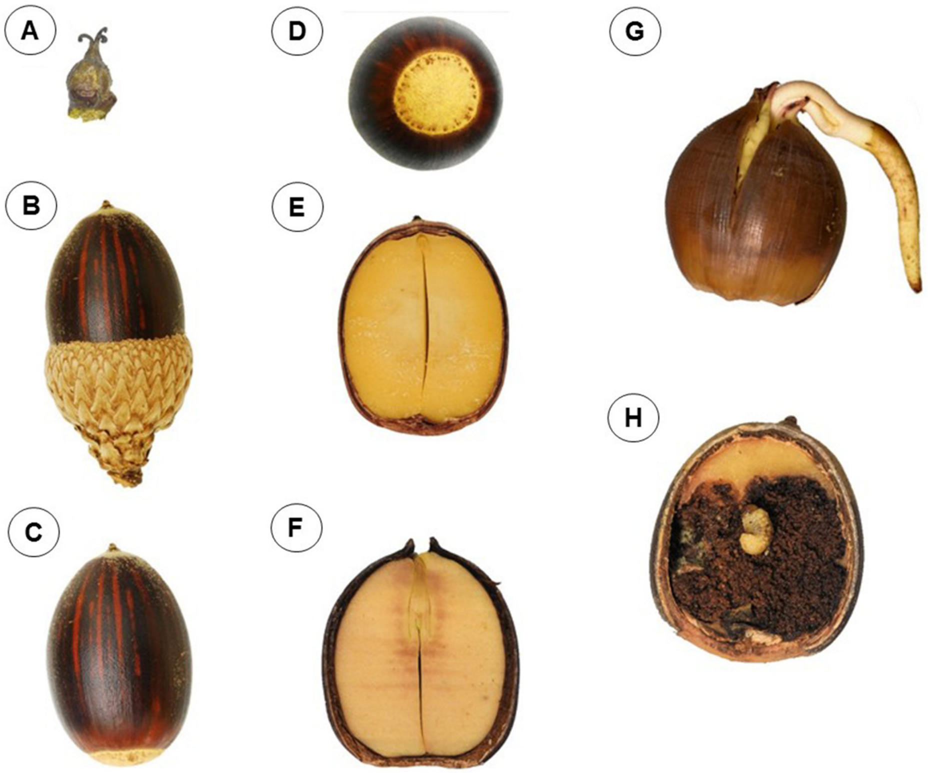

Fig. 1. Images of relevant aspects of acorn morphology and condition. Pistillate flower of *Q. nigra* (section *Lobatae*) in the dormant season following the first season of growth—note the persistent styles (A). Nut (calybium) and acorn cap of mature *Q. texana* acorn (B). Nut of mature *Q. texana* acorn after shedding from the cap (C). Abscission scar at the base of a mature *Q. texana* nut (D). Longi-section of mature *Q. texana* (section *Lobatae*) acorn illustrating the two cotyledons and the embryo axis—note the lack of radicle extension (E). Longi-section of mature *Q. michauxii* (section *Quercus*) nut—note the radicle has begun to elongate and the pericarp has begun to open (F). *Q. michauxii* nut that has initiated partial germination upon shedding from the tree—note radicle extension and the dormant epicotyl (plumule) between the cotyledonary petioles (G). Acorn weevil (*Curculio* sp.) and feeding damage that has reduced soundness of a mature *Q. texana* acorn (H). Photos by S. Griffin and E. Gardiner.

1). For the white oaks, female flowers are pollinated, an ovule is fertilized and the fruit matures within the same year (Fig. 1) (Kaul, 1985; Nixon, 1993). In contrast, the red oaks (section *Lobatae*), which are endemic to North America, produce female flowers that are pollinated in the first year, but ovule fertilization and fruit maturation are typically delayed into the second year (Fig. 1) (Nixon, 1993; Kaul, 1985). A similar biennial pattern of flower ontogeny and fruit maturation is found for the intermediate oaks (section *Protobalanus*) that are endemic to western North America (Nixon, 1993). Oaks prevalent in the Mediterranean region of Europe do not necessarily exhibit a singular pathway of flower ontogeny and fruit maturation. In particular, species in the groups *Cerris* and *Ilex* exhibit either an annual or biennial pattern, with some species even exhibiting both pathways to fruit maturation (Borgardt and Nixon, 2003; Díaz-Fernández et al., 2004). Thus, flowering ontogeny and fruit maturation can draw practical implications of importance to the practitioner or seed orchard manager tasked with planning for seed procurement.

Flowering and fruiting for all oaks results in production of the acorn. The acorn consists of the fruit, recognized as a nut (calybium), and the partially encasing cap (cupule) (Fig. 1) (Kaul, 1985; Borgardt and Nixon, 2003). The nut typically contains one seed (single embryo) of which the embryo axis and two fleshy cotyledons are encased by the seed coat and pericarp (Bonner and Vozzo, 1987). Upon maturation, the nut, for most species, is released from the cap revealing a distinct abscission scar at its base (Fig. 1).

In temperate regions of the northern hemisphere, acorn maturation coincides with waning of the growing season so that nut drop begins in the early fall (see Díaz-Fernández et al. (2004) for variation in some Mediterranean species). Shedding of the nut is preceded by chlorophyll loss in the pericarp and a subsequent change in color from green to tan, brown, or black (Bonner, 1976; Gordon, 1992). At this time, relative compositions of carbohydrates and lipids in the seed differ among sections and species, and this reveals contrasting strategies of energy storage that also suggests implications relative to dormancy. In general, white oaks develop seeds that mature to compositions of about 35–55% carbohydrates and 1–8% lipids, while red oaks develop seeds that mature to compositions of about 25–45% carbohydrates and 10–20% lipids (Bonner, 1971, 1974, 1976).

2.2. Seed dormancy and germination

Germination, the process by which the embryo develops into an independent seedling, follows a hypogeal pattern in oaks (Bonner et al., 1994). In this pattern, the cotyledons remain encased in the pericarp, while the radicle (early root) and then the epicotyl (early stem) elongate into their respective soil and air environments (Fig. 2) (Bonner et al., 1994). Seed dormancy exhibited by oaks is generally considered slight, but considerable variation is observed among and within species. The greatest level of seed dormancy has been observed for some of the red oaks, for which several weeks of exposure to a moist, cold environment is necessary before germination (Bonner and Vozzo, 1987; Bonner, 2008) (Box 1). The white oaks typically exhibit a lesser degree of seed dormancy, and radicle extension may begin as soon as the nut is shed from the tree (Bonner and Vozzo, 1987; Gordon, 1992). Complete germination, though, is inhibited by epicotyl dormancy in several species. Initiation of epicotyl elongation may trail radicle development by several months because their stratification requirements differ (Farmer, 1977). For some red oaks and white oaks with relatively large ranges, strength of seed dormancy appears positively correlated with latitude of origin (Farmer, 1974; Özbingöl and O'Reilly, 2005). As a result, the requirements for stratification during seeding operations may differ locally for a given species.

In natural forests and woodlands, seed viability retention and germination success are highly influenced by the seedbed environment (Harmer, 1995). Viability is maintained when the acorn avoids desiccation, exposure to extreme temperatures, and hypoxia (Guo et al., 1998; Connor, 2004; Greenberg et al., 2012). If seed viability is retained through dormancy, germination will proceed given environmental conditions of sufficient moisture, appropriate temperature, and available oxygen (Korstian 1927) (Fig. 2). Seed tissue moisture contents range between 30 and 55% when the nut is shed from the tree (Bonner, 1998; Bonner and Vozzo, 1987), but germination is improved if the nut

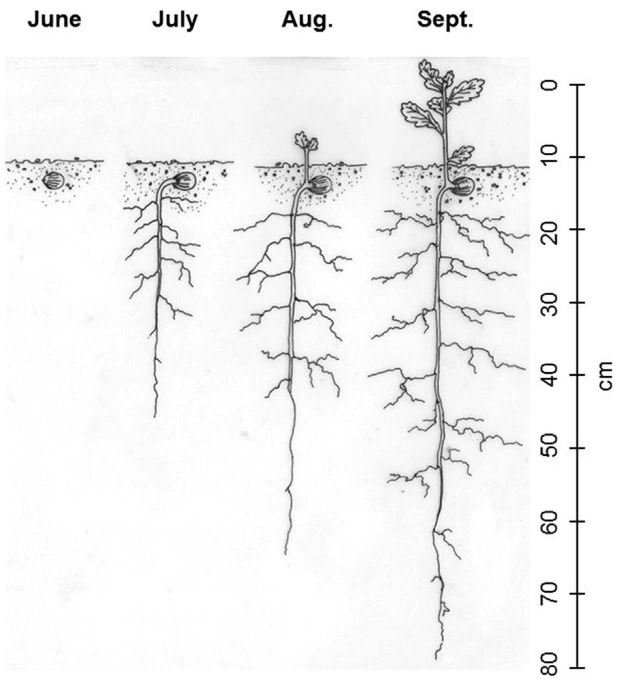

Fig. 2. Illustrated germination and seedling development for *Q. robur* (section *Quercus*) direct seeding in May on an old field in Sweden that received competition control. Scale above- and belowground in cm. Data from Löf and Welander (2004) and drawing by T. Vollbrecht.

imbibes water from the seed bed to raise tissue moisture content (Bonner 1998). Temperature requirements for germination vary greatly by species (Matsuda and McBride, 1989). Given sufficient moisture, germination is initiated and advances when seedbed temperatures meet species-specific metabolic requirements—freezing temperatures suspend the process and can damage radicles and epicotyls (Aizen and Woodcock, 1996). Oxygen availability is generally not limiting to germination in natural environments, except where seedbeds are water-logged or submerged by floodwater (Guo et al., 1998; Urbieta et al., 2008). Other factors in the environment can also impact germination (Lombardo and McCarthy, 2009). Branco et al., (2002), for example, illustrated that *Q. suber* acorns severely damaged by insects showed a reduced germination capacity and subsequent seedling mass.

As alluded to above, the timing, rate and progression of germination is inherently different among the oaks and sometimes even within the range of a given species. White oaks endemic to eastern North America and northern Europe typically initiate germination in the fall of the seed drop year, but epicotyl dormancy delays complete germination until the following spring (Farmer, 1977; Harmer, 1995). Most red oaks from eastern North America initiate germination in the spring that follows autumnal seed drop (Korstian, 1927). Germination for an intermediate oak species studied in California began in the winter and progressed as favorable temperatures permitted (Matsuda and McBride, 1989). Germination for Cerris and Ilex groups start once again as soon as there are appropriate conditions of moisture and temperature after seed drop. This may span from autumn to late winter, with seedling emergence occurring in the spring following seed maturation (Pemán et al. 2012). These phenological patterns are not universal within the respective oak sections. Several white oaks in western North America, for example, do not exhibit epicotyl dormancy or the associated delay in progression to complete germination shown by white oaks in eastern North America and Europe (Matsuda and McBride, 1989).

2.3. Initial seedling growth and survival

Most of the discussion in this section is focused on initial growth and survival of the new germinant, i.e., aspects of growth and survival between germination and exhaustion of cotyledonary reserves. We describe ontogeny during initial growth and also provide review of key environmental factors that can impact seedling growth and survival during this period. A comprehensive review of environmental factors that impact oak seedling growth and survival after cotyledonary reserves are depleted is beyond the scope of this manuscript. The reader is referred to Johnson et al. (2019) for a broader synthesis of this topic through the regeneration phase.

In all oaks, growth of the new germinant is characterized by the development of a large taproot followed by the shoot (Johnson et al., 2019) (Fig. 2). Root growth progresses rapidly with increasing soil temperatures of spring and summer months. For oaks studied in northerly regions, soil temperatures optimal for root growth range around 25 °C, which is somewhat higher than optimum for other tree species (Larson, 1970; Lyr and Garbe, 1995; Lyr, 1996). Under ideal conditions, some oak seedlings can develop a taproot that penetrates more than 100 cm into the soil during the first growing season, but soil that is dry, water-logged, compacted, shallow, or presenting physical impedances can restrict or obstruct root growth (Riedacker et al., 1981; Teskey and Hinckley, 1981; Riedacker and Belgrand, 1983; Löf and Welander, 2004; Cambi et al., 2018). This root development during the first year is primarily supported by energy and nutrient reserves of the cotyledons, and these reserves are exhausted quicker when conditions are unfavorable for seedling growth (Richardson, 1956; Brookes et al., 1980; Frost and Rydin, 1997). Upon development in the first year, the taproot appears to function mostly as a storage organ—water and nutrient uptake are conducted by lateral and fine roots (Johnson et al., 2019). Root cutting is conventionally practiced on bare-root seedlings in the nursery or at out-planting (Andersen, 2004), but the natural development of a taproot may be advantageous during periods of drought. There are some indications that cutting the taproot can lead to long-term negative consequences for root development and subsequent drought avoidance of the tree (Zadworny et al., 2014).

Development of the oak shoot is sequentially initiated after partial establishment of the taproot (Fig. 2), but the interval in this phenology can vary substantially among species due to environment, inherent ontogeny, and the previously discussed epicotyl dormancy (Johnson et al., 2019). The initial shoot (epicotyl) can appear determinate in growth, such that elongation ceases and a terminal bud forms at the apex during the early growing season. Additional shoot elongation typically does not occur in the first growing season where seedlings experience limiting light, water, or nutrients (Reich et al., 1980; Crow, 1988; Buckley et al., 1998). However, episodic shoot flushing advances shoot elongation of the oak seedling when resource availability is not limiting (Longman and Coutts, 1974; Reich et al., 1980). Under favorable conditions, multiple shoot flushes may be produced during the same growing season, each flush being preceded by a distinct quiescent period in shoot elongation during which a terminal bud develops (Hanson et al., 1986; Thomas and Gausling, 2000; Löf and Welander, 2004). Observations on some oak seedlings (e.g., *Q. alba*, *Q. marilandica*, and *Q. pubescens*) indicate a prioritization of shoot and root growth such that most root growth, including that of lateral and fine roots, is minimized during periods of shoot flush (Reich et al., 1980, Willaume and Pagès, 2006). However, research on other species (e.g., *Q. robur*) did not find evidence of this phenomenon (Harmer, 1990). Regardless, the characteristic growth pattern of periodic shoot flushing enables the manager to evaluate the status and progress of the regenerating oak cohort, and may serve as decision-support for informing needed action. For example, a cohort lacking multiple flushes may indicate the need for control of competing vegetation.

Though not ubiquitous, reports on several European and North American oaks demonstrate a positive relationship between acorn mass and germination under field conditions as well as various indices of early growth in oak seedlings (Tecklin and McCreary, 1991; Aizen and Woodcock, 1996; Gómez, 2004; Karrfalt 2004; Navarro et al., 2006;

Laliberté et al. 2008; González-Rodrígues et al., 2011; St-Denis et al., 2013). A few different mechanisms may be responsible for this relationship (Quero et al., 2007). For some species, it is suggested that relatively large acorns provide appreciably bigger pools of energy and nutrient reserves that support seedling growth and survival by buffering against environmental stress (Jarvis, 1963; Aizen and Woodcock, 1996; Kormanik et al., 1998). Aizen and Woodcock (1996), for example, found that relatively large *Q. rubra* acorns produced seedlings that survived spring frosts more readily than seedlings produced from small acorns. For other oaks, relatively large acorns produce relatively large seedlings, and bigger seedlings are thought to have a higher competitive ability than smaller seedlings (Quero et al., 2007). Irrespective of the mechanism driving the positive seed mass-seedling growth and survival relationships, sizing acorn lots could prove advantageous for improving establishment and growth in direct seeding operations (Kormanik et al., 1998; St-Denis et al., 2013).

Under most field conditions, initial growth and survival appear primarily determined by cotyledonary reserves, but resource availability, i.e. light, water, and nutrients, as for example influenced by competing vegetation, can also impact vigor and fate of the oak germinant. Light availability, owing to the fact that oaks are only intermediate shade tolerant (Röhrig, 1967; Johnson et al., 2019), has often been related to poor seedling growth or survival in temperate forests (Ashton and Larson, 1996; Buckley et al., 1998). Welander and Ottosson (1998) showed that *Q. robur* seedlings can survive under 2% of full light during the first growing season, but more light is needed to sustain survival in subsequent growing seasons. Results from field studies confirm the ability of many species to establish and persist for a few years in low-light understories (Buckley et al., 1998; Puerta-Piñero et al., 2007; Brose and Rebbeck, 2017). Crow (1992) observed a 5-year “half-life” for a cohort of *Q. rubra* seedlings established in the understory of a mixed broadleaf and conifer forest in northern Wisconsin, USA. Field studies have also shown that initial growth or, more specifically, carbon gain during initial growth is typically not greatly limited nor enhanced by light availability (Ziegenhagen and Kausch, 1995; Gardiner and Hodges, 1998). Rather, the new germinant exhibits plasticity in proportional shoot and root growth that initiates acclimation to its light environment. Stem and leaf growth are favoured proportionately in low light environments, while root growth is favoured in high light environments (Ziegenhagen and Kausch, 1995; Gardiner and Hodges, 1998). Beyond the first flush (development of the epicotyl), competition for light can be significant in understory environments of mature forests (Ashton and Larson, 1996; Buckley et al., 1998, Brose and Rebbeck, 2017), and in relatively large openings where herbaceous or shrubby vegetation overtops the oak seedling (Jensen et al., 2011). Thus, light availability appears most limiting to oak seedling growth and survival after cotyledonary reserves are depleted (Crow, 1988; García-Cebrián et al., 2003), or when other interacting factors stress the seedlings, as described later in this section (McGraw et al., 1990; Küßner, 2003).

On sites targeted for forest restoration or rehabilitation, growth and survival of new oak germinants can potentially be impaired by competitive herbaceous and woody vegetation (Kolb and Steiner, 1990; Frost and Rydin, 1997). Experimental investigations on this issue have linked decreased growth or survival to below-ground mechanism of competition (Kolb and Steiner, 1990; Frost and Rydin, 1997). Kolb and Steiner (1990) observed a marked reduction in the initial growth rate of *Q. rubra* established in competition with grass (*Poa pratensis*), and suggested that the effect was likely due to competition for soil water. Indeed, root and shoot growth of *Q. rubra* has been shown to decrease with decreasing soil osmotic potential (Larson and Whitmore, 1970). Nevertheless, negative impacts of competition on the oak seedling are generally more pronounced after cotyledonary reserves are depleted (Becker and Levý, 1983; Löf et al., 2004; Valkonen, 2008). For example, Löf and Welander (2004) reported an 80% growth reduction in *Q. robur* three years after establishment amongst herbaceous vegetation that significantly reduced soil water availability. Because of the widely observed detriments to oak seedling growth, control of competing vegetation is conventionally accepted to be key to successful direct seeding (e.g. Willoughby et al., 2004). Still, particularly in Mediterranean climates, some shrubs may facilitate oak seedling establishment and growth through shading that reduces water stress (Crow, 1992; Puerta-Piñero et al., 2007; Smit et al., 2008; Leverkus et al., 2016).

In contrast to the evidence that illustrates competition for soil water during initial growth, research has not demonstrated a soil nutrient availability impact to the oak germinant (Kolb et al., 1990). Newnham and Carlisle (1969), who studied mineral nutrition of *Q. robur* and *Q. petraea*, observed symptoms of nitrogen deficiency 85 days after establishment in nitrogen poor sand culture. Based on their description, the onset of deficiency symptoms occurred presumably after seedlings had initiated a second flush of growth. It is conventionally accepted that the cotyledons supply sufficient mineral nutrition to support seedling growth through the first flush, and published work on numerous oaks supports this assertion (Villar-Salvador et al., 2009; Yi and Wang, 2016).

In addition to availability of cotyledonary reserves, young oak seedlings possess inherent characteristics that bolster survival and resilience in responding to environmental stress or disturbance such as frost, herbivory or fire (Johnson et al., 2019). Their characteristic growth pattern of periodic shoot flushing, the ability to sprout above the root-collar, and, in some species, sprouting from lignotubers and rhizomes, enables the plant to respond to a change in resource availability or tissue damage (Crow, 1988; Molinas and Verdaguer, 1993). Interestingly, sprouting is not dependent on seedling establishment, but can be initiated at the earliest stages of epicotyl elongation. Gelviz-Gelvez et al. (2017) demonstrated increased sprouting and survival if the seedling retained functional cotyledons. However, the ability of the oak seedling to tolerate or respond to disturbance can be linked to resource availability, even prior to depletion of cotyledonary reserves (Frost and Rydin, 1997). For example, McGraw et al. (1990), who defoliated first-year *Q. rubra* seedlings, noted higher mortality among seedlings in shaded environments as compared to those in full sun. Additionally, sprouting is dependent upon survival of tissue holding pre-formed shoot buds and a supporting root system—below-ground mortality resulting from stress such as root hypoxia, for example, prevents sprouting (Gardiner and Hodges, 1996).

2.4. Acorn depredation by rodents

Because of their high energy and nutrient contents, acorns are an important food source for a wide range of animals including insects, birds, and mammals such as rodents, suids, and cervids (Johnson et al., 2019). Compared to other temperate tree seeds, acorns are often preferred by granivorous rodents (Jinks et al., 2012). Many animals, such as the wild boar (*Sus scrofa* L.) and the white-tailed deer (*Odocoileus virginianus* L.), opportunistically feed on acorns when available, and fluctuations in their population densities often indicate benefits of available oak mast (Wentworth et al. 1992; Melis et al., 2006). Other animals, particularly rodents that scatter-hoard or cache acorns like the yellow-necked mouse (*Apodemus flavicollis* Melch.) and the white-footed mouse (*Peromyscus leucopus* Raf.), may exhibit population cycles that are even more strongly dependent on mast crops (Wolff, 1996; Šipoš et al., 2017). Regardless of population dependence, acorns shed to the ground in natural forests are rapidly removed by animals and either consumed, or hoarded for later consumption (Crawley and Long, 1995; den Ouden et al., 2005). Animals that cache or disperse acorns for later consumption may act as both acorn predator and facilitator of natural regeneration because some acorns are dispersed to micro-sites suitable for seedling growth and survival (Gómez et al., 2018). This is the case for some forest-dwelling rodents including mice, rats and squirrels (Gómez et al., 2018). However, their strong dependence on mast can lead to seed depredation issues on restoration sites. Rodents can remove

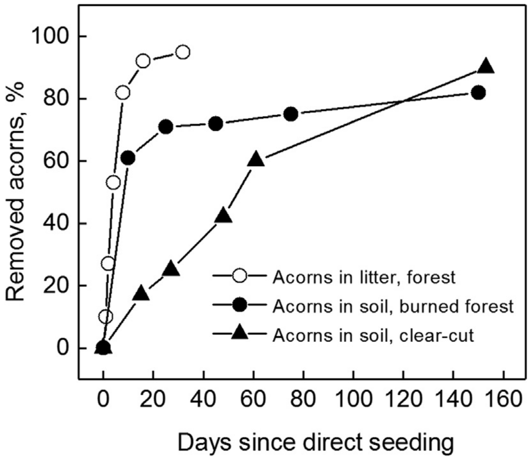

Fig. 3. Acorn removal over time when sown in litter in a forest, in soil of a burned forest, and in soil of a clearcut. Redrawn from den Ouden et al. (2005), Puerta-Piñero et al. (2010), and Birkedal et al. (2009), respectively.

acorns from forest restoration sites within weeks of sowing, even if acorns are buried (Fig. 3). Thus, an understanding of granivorous rodent behavior can inform oak direct seeding operations and the need to protect sown acorns (see Section 3.3).

Granivorous rodents use their sensitive olfactory sense to locate buried seeds (Howard et al., 1968), and acorns emit many compounds that may act as odors (Colville et al., 2012). But their use of smell in seed detection has not been studied in detail (Yi et al., 2013), and compounds rodents perceive during foraging for buried acorns have not been identified. Studies on other seeds indicate that attraction increases when seeds imbibe water and germination begins, at least in drier climates (Vander Wall, 1998). Additionally, few studies have examined other acorn preference factors of rodents (Muñoz et al., 2012; Rosalino et al., 2013). There are some indications that rodents prefer to consume and disperse relatively large acorns over small ones (Muñoz and Bonal, 2008a; Zhang et al., 2008). Conflicting results have been found regarding rodent preference for acorn tannin levels (Zhang et al. 2013).

A sizable volume of research has been published on how rodents forage for food in the field (Lichti et al., 2017). An established observation is that predator avoidance activities reduce rodent foraging efficiency (Krijger et al., 2017). Thus, rodents prefer to forage for acorns in low-risk patches such as under and near shelterwoods, shrubs, slash piles and stone walls (Fuchs et al., 2000; Buckley and Sharik, 2002; Orrock et al., 2004; den Ouden et al., 2005; Birkedal et al., 2009; Perea et al., 2011a; Van Ginkel et al., 2013; Leverkus et al., 2015). Seed preferences may also be altered depending on the risk level perceived by the foraging animal. For example, Perea et al. (2011a) found that the wood mouse (*A. sylvaticus* L.) made more selective choices when foraging under shelter versus foraging in open habitats. And, light changed foraging behavior such that foraging activity and acorn predation decreased with increasing illumination from the moon (Perea et al., 2011b).

As the main prey of several terrestrial predators, forest-living granivorous rodents exhibit various anti-predator behaviors including a sensitivity to predator odors (Apfelbach et al., 2005; Hegab et al, 2015). Field tests indicated that voles (*Microtus* spp. Schrank) avoided food mixed with stoat or weasel odors (Sullivan et al., 1988a; Sullivan et al., 1988b). Similar research conducted with acorns and acorn predators is scant, but Sunyer et al. (2013) observed increased vigilance and freezing behavior by the wood mouse when foraging acorns in the presence of predator scents. Thus, predator odors may have application for reducing post-sowing acorn depredation by rodents (see Section 3.3).

The cyclic dynamics of many forest-dwelling, granivorous rodent populations have been documented in several regions within the temperate zone. Population cycles, as mentioned above, can be closely tied to the periodic nature of oak masting and therefore will exhibit spatial and temporal variability (Wolff, 1996; Šipoš et al., 2017). Šipoš et al. (2017) postulated that intraspecific competition for food in some granivorous rodent populations is most acute in years that follow a heavy mast year. Likewise, there is evidence that population densities within a year are greatest during the summer and lowest in the early spring (Ostfeld et al., 1996; Stenseth et al., 2002). Managers could make informed decisions regarding the timing of direct seeding operations, and could project acorn depredation control needs if restoration sites are evaluated for depredation risks prior to direct seeding. However, much still needs to be learned about the temporal and spatial dynamics of granivorous rodent populations, and relationships between population densities and acorn depredation rates.

3. Implementing direct seeding

3.1. Harvesting and handling acorns

Acorn collection has been traditionally conducted in seed orchards or in natural forests. Established seed orchards produce acorn crops of known genetic source, but there are few oak seed orchards and they have historically produced limited amounts of seed (Savill and Kanowski, 1993). Some European countries regulate transfer of seed between regions, and typically select and register particular forest stands for the purpose of acorn collection (Gordon, 1992; Savill and Kanowski, 1993). This same level of quality control regarding genetic or geographic source is absent in the United States where protocols for seed transfer have not been developed (Gardiner et al. 2002). Failure to consider the genetic or geographic source of acorn stocks could result in poor establishment success (Dicke and Toliver, 1987), and reduced stand productivity (Greene et al., 1991). Dicke and Toliver (1987), who worked in Louisiana, USA, found that age 5 seedling survival ranged 30% among 24 open-pollinated *Q. pagoda* families.

Regardless of whether the tree is growing in a seed orchards or forest, acorn production is dependent in part on the periodicity of mast years (Box 1). Significant masting occurs no more than every 2- to 4-years for many species (Gordon, 1992; Bonner, 2008), and this leads to considerable variation in annual yield. Natural stands targeted for acorn production can be managed to maximize yield and for improved acorn collection. Selecting genetically superior mast producers (Greenberg, 2000), thinning the stand with consideration for balance between crown development and retaining a high density of acorn producers (Healy, 1997), and cleaning to remove understory trees and shrubs can boost acorn production and facilitate acorn collection. A study conducted by Healy (1997) in Massachusetts, USA illustrated that the effect of thinning on stand-level acorn production was most evident in years of relatively small acorn crops.

Techniques used to collect acorns beneath masting oaks have included hand-gleaning, vacuuming, sweeping or raking from the forest floor; placing seed traps or collection sheets beneath the crown; or employing a tractor-pulled mechanical nut harvester (Bonner and Vozzo, 1987; Gordon, 1992). Loss of acorn viability has not been attributed to any of the various collection techniques, but many reports substantiate risks associated with natural factors. Desiccation (Joët et al., 2013), fungal pathogens (Andersson, 1992) freezing (Barrett, 1931), fire (Greenberg et al., 2012), and insects (Lombardo and McCarthy, 2009) can impair acorn viability, birds and mammals can quickly consume a majority of the crop (Shaw, 1968; Gómez et al., 2003), and acorns can be swept-away by floodwater (Bespalov and Os'kina, 2006). These reports imply that acorn collection should proceed during the period of acorn shedding when availability of viable seed is maximal.

Tests that provide screening of acorns or gauge viability during collection, storage, or sowing are indispensable to the success of direct seeding operations. But, research has yet to forward a practical and

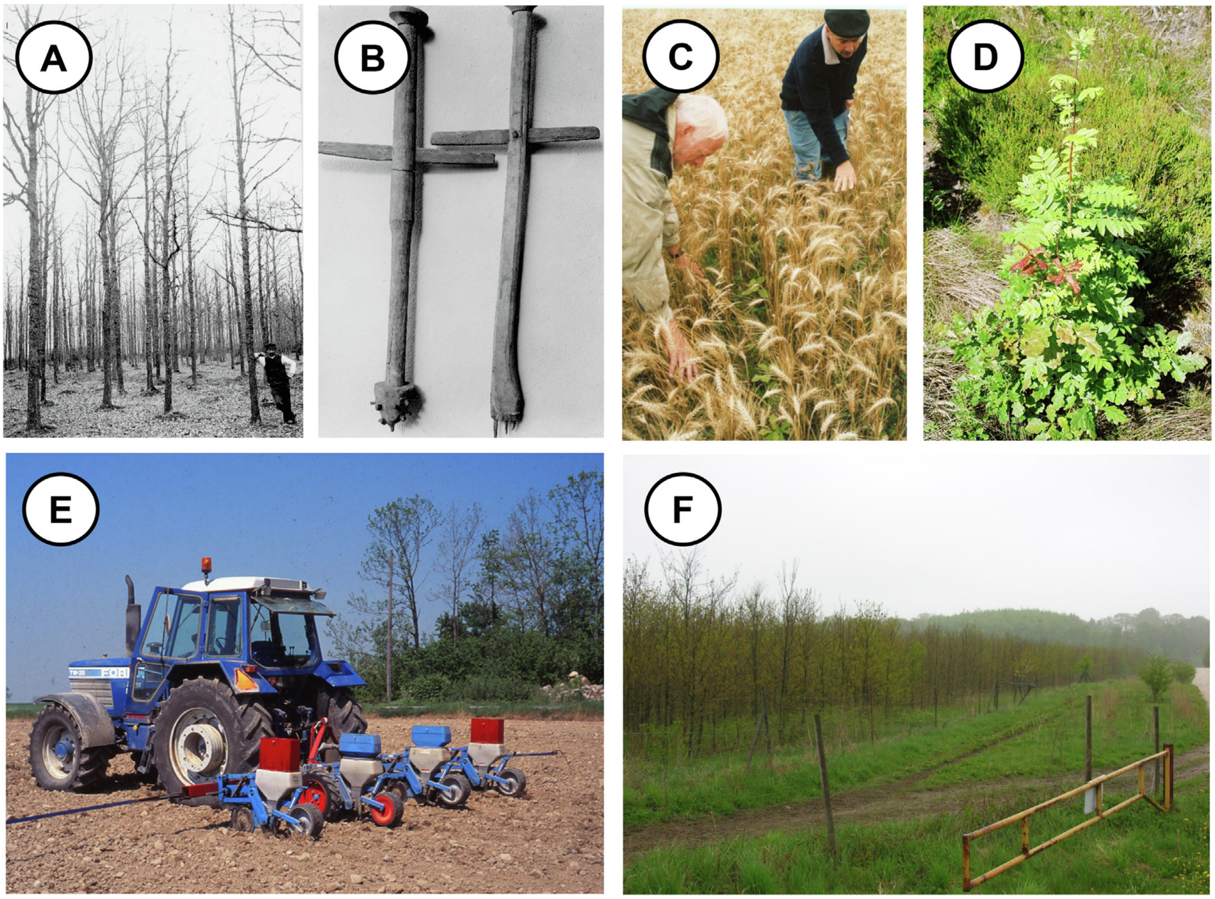

Fig. 4. Various stands and sowing practices including a 64-year-old oak (Quercus sp.) stand originated from direct seeding in 1858, in Sweden (A), two versions of Gren's acorn sowing tool invented around 1830 in Sweden (B), a young cohort of *Q. robur* that originated from acorns sown with a cover crop of wheat (*Triticum aestivum*) (C), a young cohort of *Q. robur* originated from acorns sown in mixture with rowan (*Sorbus aucuparia*) (D), a tractor with Egedal's pea (*Pisum sativum)* sowing equipment adapted for sowing acorns in large-scale afforestation projects (E), and a 13-year-old, dense *Q. robur* stand seeded with the aforementioned sowing equipment (F). Photo A by G. Schotte; B by C.F. Eklöf (Forest Library Archive in Umeå, Sweden); C and D by P. Madsen; E by E. Møller-Madsen; and F by M. Löf.

non-destructive technique that provides a completely accurate index of acorn viability. A simple cutting test is often used to obtain a quick visual assessment of acorn soundness during collection operations (Gordon, 1992; Bonner 2008). Immersing acorns in water or "float-testing" is a common practice used to separate desiccated and insect damaged acorns from the lot (Bonner and Vozzo, 1987). The principle is that sound acorns of appropriate moisture content will sink while dehydrated acorns and those with internal air pockets produced by feeding insect larvae will be buoyant (Fig. 1). Bonner (2008) noted that this practice is also important for priming acorn moisture content prior to storage. But, there are some shortfalls with using the float test as a viability screen—Gardiner (2001) noted that the acorn of *Q. lyrata* naturally floats, and other workers have described over-estimation of damage in acorns that have been mildly desiccated (Gribko and Jones, 1995; Miller and Schlarbaum, 2005). Viability of acorn lots has also been sampled with metabolic staining (Bonner, 2008). These stains, such as used in the tetrazolium test and the indigo carmine test, provide contrast between enzymatically active tissues and inactive or dead tissues, particularly in the embryo (Gordon, 1992). Other experimental techniques, including x-ray imaging and Fourier transform infrared spectrometry (Connor and Sowa, 2003; Goodman et al., 2005), show promise for accurately gauging acorn viability, but these techniques have yet to be developed for applied use.

Methods to calculate an index of acorn vigor that strongly correlates to either storability or field performance have not been developed (Bonner, 1998). Germination capacity, which is important for calculating sowing density prescriptions, can be estimated with a well-designed and properly monitored germination test. The International Seed Testing Association (ISTA) has established a standardized germination test used for purposes of issuing an ISTA certificate of seed quality. This test follows a strict protocol for preparing acorns, maintaining environmental conditions, and observation over a 4-week period to quantify germination capacity. In practice, many managers procure acorns outside of the ISTA purview and devise simple testing procedures to accommodate their purposes. Germination capacity, for example, has been determined by sowing acorns in trays of vermiculite, sand, or peat which are maintained under a temperature and moisture regime conducive to germination (Matsuda and McBride, 1989; Finch-Savage and Clay, 1994; Bonner, 2008; Greenberg et al., 2012).

Acorn viability degrades rapidly after shedding from the tree, and this has been primarily attributed to desiccation (Pritchard, 1991; Gosling, 1989; Connor and Sowa, 2003). Acorn moisture content, depending on species, generally ranges between 30 and 55% at the time of shedding, but it quickly falls in low humidity environments (Bonner, 1974; Gosling, 1989; Sobrino-Vesperinas and Viviana, 2000; Joët et al., 2013). As examples, viability was lost when moisture content dropped below 26% in *Q. coccifera* and Q. *pubescens*, 22% in *Q. alba*, 19% in *Q. robur*, and 15% in *Q. nigra* (Finch-Savage, 1992; Bonner, 1996; Connor et al., 1996; Ganatsas and Tsakaldimi, 2013). Owing in part to their desiccation sensitivity, acorns have a recalcitrant storage behavior that necessitates they be stored with a relatively high moisture content under temperatures near freezing (Bonner, 1990). Acorns for most oak species can be stored up to six months without losing viability when storage temperatures range from −3 up to 4 °C (Bonner and Vozzo, 1987; Gordon, 1992). Soaking acorns in water for up to 48 h prior to storage eliminates uncertainty about seed moisture status and ensures sufficient hydration for storage (Gordon, 1992). Storage trials indicate that packing hydrated acorns in polyethylene bags is an effective method to hold moisture status while allowing for some gas exchange that supports respiration (Gosling, 1989; Bonner and Vozzo, 1987; Pasquini et al., 2011). But, the moist storage requirement also provides a favorable environment for fungal pathogens deleterious to acorn viability, and pre-storage treatment of acorns with hot-water thermotherapy and/or fungicides may be necessary to limit such pathogens (Delatour, 1978; Finch-Savage et al., 2003; Knudsen et al., 2004; Schröder et al., 2004). Storage practices for extending acorn viability beyond the collection year have not been developed for most oak species. However, some red oaks and European white oaks have demonstrated viability retention for up to 18 months when stored at −2 °C (Bonner, 1990; Connor, 2004; Noland et al., 2013).

3.2. Site preparation, sowing practices, and maintenance

Direct seeding has been practiced to establish oaks at least since the 15th Century, and it remained the primary practice for oak artificial regeneration, or for supplementing natural regeneration, through the early 20th Century (Willoughby et al., 2004; Abrams and Nowacki, 2008) (Fig. 4). Early operations saw acorns in monoculture or in mixture with other tree species, and sometimes together with an annual cereal cover crop. These operations, practiced for afforestation and reforestation, were very labor intensive as they employed manual or horse-driven site preparation, manual weeding, and relatively high acorn sowing rates (e.g., 7–8 acorns per sowing spot with sowing spots on a 1.8 × 1.8 m spacing). However, seed and salary costs were low and alternatives were seldom available (Cotta, 1828; Burckhardt, 1870; Krahl-Urban, 1959; Carbonnier, 1975).

Direct seeding may be best suited for application on afforestation sites because site preparation can often be used to create near-ideal conditions for acorn germination and seedling establishment (e.g., Møller-Madsen and Honoré, 1992; Grossnickle and Ivetić, 2017). Soils can be prepared to create large areas with minimal competing vegetation and rodent habitat—standard agricultural machinery such as tractors and tool attachments add efficiencies to soil cultivation, seeding, covering acorns with soil, and herbicide application (Fig. 4). Afforestation operations today typically call for seeding rates of ca 3000–10,000 high-quality acorns per ha to produce ca 1000–3500 seedlings per ha a few years after seeding (Møller-Madsen and Honoré, 1992; Lockhart et al., 2003; Dey et al., 2008). Broadcast seeding typically requires a higher seeding rate because this type of operation does not protect sown acorns from desiccation and depredation as effectively as operations that bury the acorn (Lockhart et al., 2003). There are no clear benefits of cover crop usage when direct seeding acorns on afforestation sites, but results probably depend on the site and type of cover crop (Willoughby et al., 2004; Balandier et al., 2009).

The risks of failure for direct seeding are much greater when practiced in small fields (ca < 1–2 ha) or on forest lands (e.g., Bullard et al., 1992). Rodent populations are characteristically high, leading to acorn depredation in these situations—but, acorn depredation decreases with increasing size of forest openings and clearcuts (Dey et al., 2008). Prescribed burning, herbicide application, and mechanical site preparation can effectively reduce competing vegetation and rodent habitat, especially if rather heavy disturbance is applied (Johnson, 1981) (Fig. 4) (see Section 3.3). However, many restoration sites cannot receive prescribed fire, herbicide use is restricted on forest land in many countries, and soil cultivation is difficult and expensive when stumps, stones, and other obstacles are present on the site (Löf et al., 2016). Thus, options for vegetation control that protect seeds and seedlings can be unavailable or prohibitively expensive. Madsen (2005) described several horse- or tractor-driven techniques for direct seeding and reforestation, and reported establishment rates from 1% to 84% when trials were evaluated 1–4 years after seeding in Denmark. However, steps to protect sown acorns were not undertaken in these trials. Thus, compared to direct seeding on afforestation sites, higher sowing rates are typically needed, and managers should expect variable results. This can be acceptable in some restoration situations where forest practitioners are not concerned with achieving high stocking levels, such as where acorn seeding is used to supplement natural mixed-species regeneration (Stanturf et al. 2009).

In temperate regions, there is no clear indication of the best season (fall, winter, or spring) for direct seeding, though it may be preferable to seed white oak acorns in the fall because of their propensity to germinate upon shedding (Madsen, 2005; Dey et al., 2008). In Mediterranean climates, direct seeding is practiced in fall to allow seedlings maximum root development before the characteristic summer drought (Leiva and Díaz-Maqueda, 2016). Seedling counts are typically greatest immediately after the first growing season, then establishment percentages usually decrease over time before stabilizing (Madsen and Löf, 2005). Patience and keen observation are needed when evaluating direct seeding operations. New germinants are usually smaller than transplanted seedlings, and they can be suppressed by browsing damage and competing vegetation (Grossnickle and Ivetić, 2017). Therefore, evaluating success and stand stocking may not be possible until 3–5 years after seeding.

New oak germinants sometimes need protection from wild or domestic ungulates. Their selective browsing of palatable foliage can severely limit establishment and growth of oaks (Kuijper et al., 2009). The impact of wild ungulates on plantation establishment can be reduced by culling populations (hunting) and/or increasing animal carrying capacity of the forest landscape (Rooney et al., 2015). Fencing is used to physically protect regenerating stands, while a variety of shelter types have been developed to protect individual seedlings. High costs associated with installation and maintenance are major constraints to the extensive use of physical protection. Furthermore, rodent abundance and activity often increases inside fenced areas, because of reduced competition with ungulates, protection from ungulate trampling, and refuge from wild boar predation (Muñoz and Bonal, 2007; Pérez-Ramos and Marañón, 2008). Direct seeding acorns in combination with encouraging natural regeneration of other tree species could potentially reduce ungulate herbivory on oak germinants through associational resistance (Cook-Patton et al., 2014). However, this will probably not serve as complete protection as Jensen et al. (2012) showed oak seedlings grown together with other woody species received only about 20% less browsing damage.

3.3. Protecting sown acorns from rodents

In recent decades, much research has focused on techniques to protect sown acorns from rodent depredation (Fig. 5). Treating acorns with poisons that kill or repel rodents (Anonymous, 1947) is largely prohibited today, and practitioners search for environmentally friendly approaches to protect sown seed. An ideal protection technique would effectively reduce acorn depredation, not impair germination, not hinder plant development, maintain cost advantages of direct seeding over planting seedlings, and be environmentally benign.

Table 1 provides a summary of published information concerning various strategies and techniques used to protect acorns from depredation by granivorous rodents. Strategies to reduce acorn depredation can be classified as chemical, ecological, physical, or silvicultural, but all have ecological basis as described in Section 2.4. Non-lethal chemical approaches to reduce seed depredation, such as repellents and masking scents, have been studied mainly in agricultural settings (Hansen et al., 2016). Application of chemical approaches in forest restoration has shown inconsistent results in reducing acorn depredation (Dey et al., 2008; Willoughby et al., 2011). Plant-based chemicals that have shown effectiveness in reducing rodent depredation on sown acorns, such as capsaicin, neem, citronella and other oils, typically

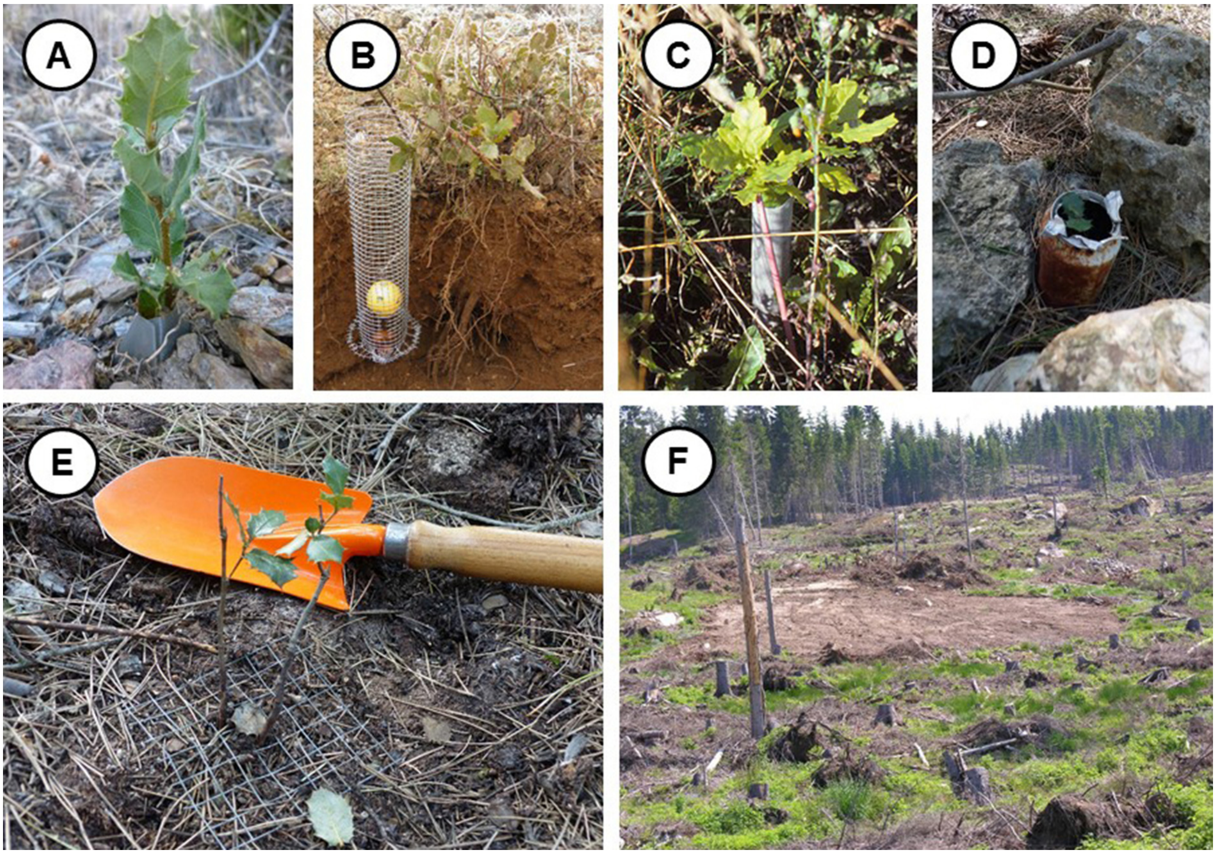

Fig. 5. Various devices and techniques for protecting sown acorns from depredation by granivorous rodents at forest restoration sites. These include a seed shelter from which a *Q. ilex* seedling emerged (A), a wire mesh cylinder used to protect a *Q. ilex* seedling (B), small degradable tube from which a *Q. robur* seedling emerged (C), a perforated beverage can and *Q. ilex* seedling (D), a square wire mesh screen from below which a *Q. ilex* seedling emerged—note the multiple sprouts and browsing damage on the sprouts (E), and mechanical site preparation to expose mineral soil on a ca 0.33 ha plot) (F). Photo A by A. Leverkus; B, D and E by J. Reque; and C and F by M. Löf.

reduce acorn germination (Bäumler et al., 1990; Leverkus et al., 2013; Villalobos et al., 2019). Relatively few studies have addressed the use of predator odors to repel rodents and reduce seed depredation. Villalobos et al. (2019) in a laboratory study, showed that mink (*Mustela vision*) excrement held potential for reducing acorn depredation by rodents. Because rodent behaviour is altered when they detect predators (see section 2.4), chemical techniques based on this knowledge may warrant further development. While rodents increase vigilance behavior in the presence of predator odors, studies show little evidence of reduced foraging (Verdolin, 2006). This may be because natural repellents can quickly lose their potency as odors can dissipate within one day (Bytheway et al., 2013). Sullivan et al. (1988a) described a repelling effect of dithiolanes on the pocket gopher (*Thomomys talpoides* Richardson), but observed these compounds to rapidly polymerize when exposed to ambient conditions. Additionally, repellent formulations have often relied on a single compound while natural odors consist of a bouquet of compounds (Apfelbach et al., 2015). Research efforts should be made to produce more complex mixtures that are delivered with a steady release rate to increase repellency.

Some authors have proposed that soaking acorns in diesel for a few hours before sowing would provide effective repellency (Bäumler et al., 1990). However, a recent field experiment noted increased depredation and reduced seedling emergence when acorns were treated with diesel (Leverkus et al., 2017). Farlee (2013) suggested that placing cow manure on top of sown seed was a broadly available, inexpensive and potentially useful protection technique. However, acorns were not among the seed included in that work, so we are not aware of data supporting its effectiveness. Other substances that may have repulsive smells or tastes to rodents, such as dog faeces, ox bile, or human hair, have been used by practitioners in hopes of protecting sown acorns (Zadocs, 2013), but we could find no published data to support their effectiveness.

Because granivorous rodents find buried seeds mainly through olfactory signals, future research should identify the chemical cues to which they react. An understanding of the chemical cues that lead rodents to acorns would potentially allow for development of masking agents. Indeed, investigators studying shrub facilitation of oak regeneration suggested that the Scotch broom (*Cytisus scoparius* L.) may mask the smell of sown acorns and thereby offer protection from rodent depredation (Martelletti et al., 2018). However, developing chemical techniques to confuse and/or deter rodents may be complicated because the agent would have to retain integrity under field conditions.

Ecological strategies are based on rodent-predator interactions or other behavioural traits that can influence acorn depredation (Table 1). For example, adding perches to a forest restoration site can attract birds of prey that could reduce rodent populations, or restrict rodent activity to areas perceived as secure (Farlee, 2013). Effectiveness of this technique is not guaranteed as it relies on the assumption that avian predators would hunt near raised perches (Birkedal et al., 2009). Another technique yet to be tested for direct seeded acorns involves food satiation (Sullivan, 1979). Some studies have found that acorn survival is relatively higher during high masting years or at high acorn abundance (Crawley and Long, 1995; Pérez-Ramos and Marañón, 2008; Kellner et al., 2014). We have not found work that establishes this connection with sown acorns, but an alternative technique might be to satiate depredating rodents on the restoration site with other foods such as cereal grains (Sullivan, 1979).

Physical strategies involve devices that reduce or prevent rodent

Table 1

Summary of strategies and techniques to control acorn depredation during direct seeding operations for oak forest and woodland restoration. Relative values for protection and use efficiency were estimated qualitatively by the authors with a maximum positive effect scoring "+ + +".

Strategy	Technique	Description	Protection efficiency	Use efficiency	Effect on seeds or seedlings	References
Chemical	Capsaicin/Chilli	Acorn imbibed	+	+ + +	Reduced establishment	Leverkus et al. (2013) and Villalobos et al. (2019)
	Diesel, Neem	Acorn imbibed	+	+ + +	Reduced germination	Bäumler et al. (1990) and Leverkus et al. (2017)
	Predator scent/excrement	Near acorns / acorn imbibed	+	+ +	None	Sunyer et al. (2013) and Villalobos et al. (2019)
	Aluminum ammonium sulphate	Mixed with acorns	+	+ + +	None	Willoughby et al. (2011)
Ecological	Predator-prey interactions	Raptor perches	+	+	None	Birkedal et al. (2009)
	Food satiation	Provisioning alternative food	?	+ +	None	
Physical	Mesh cage	Cage inserted in soil	+ + +	+	Restricts seedlings if not removed	Weitkamp et al. (2001)
	Seed shelter	Capsule buried in soil	+ + +	+ +	Restricts seedlings if not degradable	Castro et al. (2015) and Leverkus et al. (2015)
	Seed/seedling protector	Mesh cylinder inserted in soil	+ + +	+	Strangles larger seedlings	Reque and Martin (2015)
	Sowing tubes	Narrow tubes inserted in soil	+ +	+ +	Delayed frost hardening	Bowersox (1993), Löf et al. (2004) and Madsen and Löf (2005)
	Wire mesh plate	Buried in soil (6 mm mesh size)	+ + +	+ +	Strangles seedlings	Prévosto et al. (2011a, 2011b)
Silvicultural	Site selection	Forest type/adjacent habitats	+ +	+ + +	None	Johnson (1981), Madsen and Löf (2005) and Birkedal et al. (2009)
	Timing of seeding	Different seasons	+	+ +	Depends on acorn storage	Birkedal et al. (2009, 2010) and Leiva and Díaz-Maqueda (2016)
	Sowing depth	Increased soil depth	+ +	+ + +	Delayed emergence and growth	Nilsson et al. (1996) and Leverkus et al. (2013
	Herbicides	Vegetation control	+ +	+ +	Seedling damage	Willoughby et al. (2004) and Balandier et al. (2009)
	Leaving woody debris	Wild boar damage control	+	+ + +	Higher rodent depredation	Puerta-Piñero et al. (2010) and van Ginkel et al. (2013)
	Mechanical site preparation	Different soil disturbances	+	+ + +	Improved seedling growth	Nilsson et al. (1996), Birkedal et al. (2010) and Martelletti et al. (2018)

access to the acorn (Table 1) (Fig. 5). Various devices have shown to be very effective in protecting sown acorns, but they tend to significantly increase regeneration costs (Prévosto et al., 2015). Several styles of mesh cages have been successfully used to thwart acorn depredation, but they require being subsequently removed to avoid restricting seedling development (Weitkamp et al., 2001). Castro et al. (2015) recently designed a "seed shelter", composed of two truncated cones joined at their larger openings. This shelter, which is moderately easy to use in the field, allows for natural root and stem growth by the oak germinant. It was also designed with a vertical suture to allow its opening with stem growth. This shelter effectively eliminates acorn depredation by rodents, but it could be improved by constructing it from a degradable material (Castro et al., 2015; Leverkus et al., 2015). Reque and Martin (2015) developed a device that protects the acorn from depredation and the new germinant from browsing. It consists of a wire mesh cylinder with a circular crown and conical frustum on the bottom into which the acorn is placed, and a degradable sphere is placed in the cylinder to discourage depredation from above. This device has shown to be effective against rodent and wild boar acorn depredation, but its effects on seedling and sapling development need further study. Small and narrow (< 26 cm length and < 30 mm diameter) degradable tubes have been extensively tested and it was found that rodents often gnawed through the tube or dug underneath to access the acorn. Additionally, this technique may increase seedling frost damage (Bowersox, 1993; Löf et al., 2004; Madsen and Löf, 2005). Another commonly tested and practiced technique involves burying wire mesh screen (10–20 cm square) above the sown acorn (Dey et al., 2008; McCreary, 2009; Prévosto et al., 2011a; Prévosto et al., 2011b). The screen is effective in limiting acorn depredation, but the wire mesh could damage the developing seedling. Farlee (2013) suggested that a perforated beverage can placed over sown seed might provide an effective depredation barrier. This simple and inexpensive technique has not been evaluated for handling efficiency or protection efficacy with sown acorns.

Silvicultural strategies to limit acorn depredation may employ cultural treatments to the restoration site, and/or may implement an appropriate direct seeding operation (Table 1). They are frequently the only consideration given to acorn depredation control during operational forest and woodland restoration. Some site preparation practices have proven beneficial for reducing acorn depredation, particularly on afforestation sites. Site preparation with herbicides can create areas temporarily void of vegetation—rodents avoid these areas and emerging seedlings also benefit from the reduced competition (Willoughby et al., 2004; Balandier et al., 2009). This can be a very efficient treatment on some afforestation sites, but herbicides are prohibited at forest sites in some countries. Mechanical site preparation has also been tested with the idea that cultivation could remove or degrade rodent habitat. Efficacy of mechanical treatments for reducing rodent damage has been variable, but seedling growth appears to benefit (Johnson, 1981; Nilsson et al., 1996; Birkedal et al., 2010) (Fig. 5). Several authors have reported on the importance of removing slash piles on forest sites because they provide rodent habitat and typically lead to increased acorn depredation (Johnson, 1981; Birkedal et al., 2010; Puerta-Piñero et al., 2010; van Ginkel et al., 2013). It should be noted, however, that slash piles and shrubs can also limit acorn depredation and seedling herbivory by wild boar and domestic ungulates where these animals are more of a concern than rodents.

There is compelling evidence that site selection can impact the degree of acorn depredation by rodents. Several authors advise against direct seeding acorns near forest edges or in small openings—lowest acorn depredation has been observed in forest openings larger than 1–2 ha, and in old fields that do not have adjacent rodent habitats (Johnson, 1981; Bullard et al., 1992; Dey et al., 2008). Others suggest that managers concentrate direct seeding operations at sites of low productivity with adjacent conifer forests, and avoid sites with adjacent broadleaved forests and their associated high rodent populations

(Madsen and Löf, 2005; Birkedal et al., 2009).

As described in Section 2.4, rodent populations are dynamic. Population cycles can be observed over the course of a year and across several years. We noted previously that rodent populations tend to peak in the summer and decrease through the seasons to early spring (Ostfeld et al., 1996; Stenseth et al., 2002). There are indications that acorn depredation increases when rodent populations are high. Diverging results have been reported in respect to acorn depredation and seedling establishment relative to sowing season, but this appears to be linked to region. Several authors working in northerly temperate climates observed that lowest seed depredation and greatest seedling establishment is achieved with spring sowing rather than fall or summer sowing (Madsen and Löf, 2005; Dey et al., 2008; Birkedal et al., 2009; Birkedal et al., 2010). Leiva and Díaz-Maqueda, 2016, who studied the Mediterranean *Q. ilex* subsp. *ballota* L., observed lower seed depredation and greatest seedling establishment in the fall during the peak of seed availability. Additional study of acorn depredation in relation to timing of rodent population cycles, and manipulation of sowing rates relative to population dynamics are needed.

Selecting an appropriate sowing depth is a practical silvicultural technique that can provide some protection during direct seeding operations. Sowing depths around 7–10 cm may effectively thwart some depredation by rodents (Nilsson et al., 1996; Fuchs et al., 2000). Greater depths could certainly be used for species with relatively large acorns such as *Q. texana,* which demonstrated acceptable emergence when seeded 15 cm deep (Johnson and Krinard, 1987). However, Leverkus et al. (2013) cautioned that the effectiveness of this technique can be low, and there may be other trade-offs such as reduced seedling emergence rates (Johnson, 1981; Johnson and Krinard, 1987). Practitioners are encouraged to gain an understanding of the local site and species variables, like acorn size, soil texture, and availability of rodent habitat, which could inform selection of appropriate sowing depths on their forest and woodland restoration sites.

The reader should note that combined effectiveness of multiple strategies, chemical, ecological, physical and silvicultural, is largely unknown, but it can be reasoned that use of multiple techniques may offer greater effectiveness than any single technique. For example, Leverkus et al. (2015), who worked with *Q. ilex* subsp. *ballota* L. on a site damaged by wildfire, illustrated substantially lower acorn depredation by rodents on portions of the site where trees were salvaged and slash was masticated. However, in these salvaged sites acorn predation by wild boars was greatest. The solution to this habitat trade-off was the use of individual, physical acorn protectors (the "seed shelter") in areas with abundant coarse woody debris where rodent population was higher, but that hampered the foraging by wild boars; despite the seed shelter was not effective against the wild boars, the combination of an effective protector against rodents and habitat characteristics against larger predators reduced acorn losses considerably. In any case, development of new techniques to protect sown acorns should consider the ability of rodents to learn how to overcome obstacles while searching for food (Muñoz and Bonal, 2008b).

3.4. Economic considerations of direct seeding

Though direct seeding is generally considered a low-cost practice for establishing oak stands, there is little information available on actual operational costs, especially for reforestation operations. For afforestation, a few studies provide costs information. Bullard et al. (1992) calculated the cost for direct seeding on old fields without fencing was about one-third the cost of planting seedlings. Similar estimates were suggested by several other studies (Møller-Madsen and Honoré, 1992; Madsen, 2005; Leverkus, 2016; Grossnickle and Ivetić, 2017). Møller-Madsen and Honoré (1992), who included the cost of fencing in their study, reported that cost varied with size of the restoration area. On former farmland, it is possible to use agricultural equipment for site preparation, vegetation control, and seeding. So, fixed costs decrease as size of the restoration area increases. Costs can be further reduced by incorporating other "economies of scale", such as using implements with several acorn seeding units (Fig. 4). But, the cost advantages of direct seeding can diminish if pre-commercial thinning is accounted for in the establishment costs. Oak stands established through direct seeding can sometimes develop into denser stands than those that were established by planting seedlings, and they may require more release treatments and pre-commercial thinning to reduce intra- and interspecific competition. Furthermore, the risks of plantation failure can be higher for direct seeding operations than for seedling planting operations, especially on reforestation sites. Therefore, a meaningful cost comparison between seeding and planting operations would perhaps be to determine the cost per "free-to-grow" tree, i.e., including all costs up to when a tree requires no further management to maintain dominance in the young stand (Dey et al., 2008). Such analyses have yet to be conducted, but could be performed where data on stand development through the regeneration phase is available.

4. Conclusions and future direction

In many ways acorns are ideally suited for direct seeding. The high energy and nutrient reserves stored support rapid development of relatively large and robust seedlings, and the cotyledonary reserves, strong taproot, and ability to sprout enable new germinants to survive periods of various stresses such as drought, herbivory, fire, frost, and low light availability.

There are also several advantages of direct seeding as compared to planting seedlings for restoration of oak forests and woodlands. Key advantages, along with disadvantages, are summarized in Table 2. The potential for low costs and operation flexibility are perhaps the most attractive advantages, particularly for large-scale restoration efforts. Regeneration cost can sometimes be reduced to about a third of the cost of planting seedlings (Palma and Laurence, 2015; Ceccon et al., 2016; Grossnickle and Ivetić, 2017). There are also some indications that mature oak stands originated from direct seeding may avoid drought more so than stands that originated from planted seedlings (Zadworny et al., 2014), because of the naturally developed taproot on seedlings that develop in place. Additionally, direct seeding operations, as compared to seedling planting operations, minimize the risk of spreading soil-borne pathogens such as the insidious *Phytophthora* species involved in tree declines (Grünwald et al., 2012). Importantly, direct seeding operations are also compatible with promotion of other restoration goals. For example, forest restoration plans often include goals associated with recovery of many ecosystem functions like supporting biodiversity. Direct seeding is, in this respect, well suited to establishment of relatively more diverse vegetation communities of herbaceous and woody species (Twedt and Wilson, 2002). And, mixed-species forests can be managed to meet a greater variety of social, economic, and environmental objectives (Gamfeldt et al., 2013).

At present, however, direct seeding must be viewed as a more uncertain practice for establishing oak forests and woodlands than is seedling planting (Table 2), and patience and keen observation are needed when evaluating direct seeding operations. This is particularly the case for restoration sites that are relatively small fields or forest openings. There is overwhelming evidence that depredation of sown acorns by granivorous rodents accounts for a significant portion of the reported direct seeding failures, especially those occurring during the establishment year (e.g., Bullard et al., 1992; Madsen, 2005; Dey et al., 2008; Leverkus et al., 2013). Research synthesized in this review suggest that environmentally sound solutions to minimize acorn depredation and increase seedling establishment are beginning to emerge. For example, direct seeding operations probably have higher chances for success during years of high masting because rodent populations are likely to quench their feeding and hoarding where mast is most abundant and easy to obtain. In these years, sowing planned during the autumnal seed drop can reduce acorn collection and storage costs, and

Table 2

Summary of advantages and disadvantages relative to direct seeding acorns versus planting seedlings for restoring oak forests and woodlands.

Advantage/disadvantage	Direct seeding	Planting
Root system development	Normal development of the tap root	Destruction of the tap root. Potential negative consequences in the short and long term
Production cost	Low. Reduction in costs as only acorn storage and some preparation is needed	High. Need to cultivate plants in nurseries for ≥1–2 years
Restoration cost	Low. Easier transportation to sowing site; more propagules can be mobilized per worker. Smaller sowing holes	High. Need to handle seedlings with certain weight and volume. Need bigger holes for plantation
Flexibility for restoration operation	High. Sowing date not so constrained by local climatic conditions. Very versatile at any spatial scale, including remote areas	Low. Planting date constrained by climatic conditions. Higher need for adequate infrastructures such as gravel roads to reach planting points
Biodiversity	Better since regenerations will become more structurally diverse	Result in more homogenous structure of regenerations
Plant disease transmission	Low risk. Acorns are easier to keep in aseptic conditions	High risk. Plants and/or soil may be contaminated in nurseries
Predictability of reforestation success	Low; failure of sowing points will be more stochastic, but this can be compensated with higher sowing density	High; More planting points will end up with living seedlings, generating a more homogeneous plant distribution
Risk of losses by seed predators	High. Acorns should be protected against predators	Null
Sensibility to competing vegetation	Higher since seedlings initially are smaller	Lower since seedlings initially are bigger
Dependence on years with available acorns	Higher since heavy acorn crops occur irregularly	Lower since seedlings can grow and be stored longer times in nurseries

perhaps even reduce the risks of losing acorn viability during storage. Concentrating direct seeding operations on restoration sites with low rodent populations can also improve success. Sites with significant tree or shrub cover, forest edges, and those that are smaller than 1–2 ha should raise concern for high acorn depredation.

Acorn germination and initial seedling growth can typically occur across a range of field conditions given appropriate soil moisture and temperature. Several studies for a range of oaks demonstrate that acorn size can impact early survival, growth and tolerance to environmental stress. Relatively large acorns hold higher probabilities of seedling establishment, so sizing acorn lots can be a simple practice for improving direct seeding success. After the first flush of stem and leaf growth, relatively open restoration sites are best suited for continued development, especially if herbaceous competitors are controlled. Several site preparation practices can reduce such competition, and also curtail rodent activity and their depredation on sown acorns. Herbicides, prescribed burning, or mechanical site preparation can minimize rodent habitats such as dense herbaceous and woody vegetation, woody debris, and slash piles.

Most information synthesized in this text was collected on relatively few species of major importance in Europe and North America. We still lack a thorough understanding of the reproductive biology and ecology of many important oak species, and we lack information on their acorn biology and appropriate handling and storage practices. This restricts global application of our current knowledge, and requires managers to consider the literature in the context of local species and conditions. Seed availability can also be an issue because of the scarcity of seed-tree stands, the large annual variability in masting, and the relatively short-lived viability of acorns in storage. Restoration practitioners seeking to utilize direct seeding need to account for unpredictable availability of seed in their planning. It remains that we need more basic research that supports development of alternative acorn storage practices and reveals the impact of acorn storage on field performance.

As a primary cause of failure when direct seeding acorns to restore oak forest and woodlands, we need research to support development of innovative techniques that effectively minimize acorn depredation under a wide range of site conditions. Various depredation control techniques based on chemical, ecological, physical or silvicultural strategies have shown encouraging results, but their application is typically limited in scope. Because rodent foraging is dependent on their olfactory system, and rodent foraging behavior is altered by predator scent, there appears to be great potential to explore techniques that can mask acorn scent, repel rodents, or otherwise disrupt their foraging on sown acorns (Sunyer et al., 2013; Yi et al., 2013, Villalobos et al., 2019). But, development of techniques to deliver long-term effectiveness of olfactory agents under field conditions provides additional obstacle to achieving success with chemical strategies for acorn depredation control. Techniques based on ecological strategies have likewise not been well developed. For example, it is suggested that providing alternative food could satiate rodents on small-scale operations, but this remains to be demonstrated. Physical impedances to acorn depredation have demonstrated very acceptable performance in depredation control. Yet, shelters developed for this purpose have associated materials and labour costs that can prohibit large-scale application, and their durability under field conditions can have detrimental consequences to the developing oak or the restoration site. Acorn depredation control based on silvicultural strategy includes perhaps the most widely practiced approaches, particularly for large-scale restoration operations. The manager can address potential acorn depredation prior to direct seeding by writing a well-designed forest restoration plan that addresses proper site selection, appropriate site preparation, and suitable sowing depths and densities. And, techniques from chemical, ecological or physical strategies can be layered with silvicultural techniques to potentially increase depredation control on difficult sites. But, additional research is needed to gain a better understanding of efficacy when techniques based on silvicultural strategy are applied with techniques based on chemical, ecological, or physical strategies.

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