



Effects of interspecific competition from surrounding vegetation on mortality, growth and stem development in young oaks (*Quercus robur*)



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ABSTRACT

Facilitation by a neighboring woody understory has been suggested as a cost-effective and sustainable way to regenerate oaks. However, concerns about reduced plant growth and quality due to competing neighboring vegetation have hindered implementation. Here we studied competitive effects from herbaceous and woody vegetation on survival, growth, canopy development and stem quality in pedunculate oak (*Quercus robur*) in an open-field experiment in southern Sweden. Oaks were grown for eight years in four different competition treatments: no competing vegetation, with herbaceous vegetation (mainly grasses), with woody vegetation, and with both herbaceous and woody vegetation. During the first four years, competition had little effect on oak survival. However, after eight growing seasons, survival rates decreased to about 20% for oaks surrounded by woody vegetation, in contrast to oaks grown with only herbaceous vegetation that had a survival rate of near 100%. Competition from herbaceous and woody vegetation both reduced oak stem diameter and height growth, but they affected height growth differently. During the first growing seasons, oaks in the treatment with woody vegetation were able to keep up with the height growth of the surrounding vegetation. Thereafter, height growth stagnated, and after eight growing seasons heights of oaks in the treatment with woody competitors were only 30–39% that of oaks in the treatment without competing vegetation. In contrast, competition from herbaceous vegetation only restricted oak height development marginally. Interspecific competition not only restricted growth and survival but also shifted shoot architecture, resulting in a greater frequency of oaks with straight monopodial stems. Although competition from both herbaceous- and woody vegetation positively affected stem straightness, plots with woody vegetation had a greater proportion (0.42) of oaks with a single straight monopodial stem. Our results demonstrate that the facilitative competitive effects from herbaceous and woody vegetation could be used to control allocation patterns in young oaks, promoting development of tall straight monopodial stems. Considering the observed trade-off between high stem quality and survival, we recommend long-term assessment of this trade-off prior to application in practical forestry.

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1. Introduction

Oak trees (*Quercus* spp.) are important components of many temperate forests throughout America and Eurasia, where they provide a great number of ecosystem services (Johnson et al., 2009). In Sweden for example, more than 50% of all red listed species (The 2015 Red List of Swedish Species, is based on the international IUCN criteria (ArtDatabanken, 2015)) on forest land depend on valuable broadleaved trees such as oaks (Berg et al., 1994). Oak forests provide not only high value timber and

bio-energy products, but these forests are also valued environments for recreation and other cultural services, and oak is often a preferred species for climate change adaptation of forest management (Bolte et al., 2009; Löf et al., 2016).

Despite the species' ecological and societal values, decreasing oak dominance is occurring worldwide and oak natural regeneration problems in high quality broadleaf sites have been documented for decades in many different regions around the world (Watt, 1919; Crow, 1988; Dey et al., 2012; Jensen et al., 2012a). Natural and silvicultural disturbances, especially historical land-use systems (e.g. grazing), are considered to promote oak regeneration (Vera, 2000). However, much knowledge about the factors that drive oak regeneration is missing (Götmark et al., 2011; Annighöfer et al., 2016). This

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causes serious problems for sustainable management of oak forests and when using oaks during forest restoration.

In addition, insufficient knowledge is available concerning the response of oaks in mixtures with other tree species. Mixed-species plantations have been identified as representing an important tool for forest restoration since such plantations may meet a wider variety of social, economic, and environmental objectives in comparison with monocultures (Paquette and Messier, 2010). Planted mixtures with oak and other broadleaves are often used in afforestation programs (Gauthier et al., 2013), and mixtures with planted oak and naturally regenerated pioneer broadleaved tree species such as birch (*Betula* spp.) and aspen (*Populus tremula*) are increasingly being established in clear-cut areas following conifers or in areas where conifers have been storm-felled (Löf et al., 2010). While tree mixtures may help meet multiple objectives, the greater complexity associated with interspecific interactions requires more knowledge for effective management.

Competitive interaction is a major factor structuring plant communities (Harper, 1977; Grime, 1977). During the past 50 years, numerous studies have attributed poor tree seedling survival and growth to competition from herbaceous and woody vegetation (e.g. Götmark et al., 2011). Oaks are not as shade-tolerant as many other trees and shrubs, and light is considered to be a major limiting factor for oak regeneration (Ligot et al., 2013). Both herbaceous vegetation and various woody plant species are well known to compete for below- and above-ground resources and reduce performance in oaks (Jensen et al., 2011; Jensen et al., 2012a). Low light in combination with repeated browsing or grazing is considered an especially harmful situation for young oaks (Kelly, 2002; Jensen et al., 2012b). However, little is known regarding mortality rates in oaks when growing amongst other woody vegetation.

Individual oaks may reach very old ages (>900 years) and intraspecific differences in tree mortality play a crucial role in determining plant community structure, successional dynamics as well as in the maintenance of species diversity (Larsen and Johnson, 1998; Emborg et al., 2010). Thus, quantifying and predicting tree mortality is important for better understanding of the species' ecological characteristics as a foundation for forest management. Traditional oak regeneration is either based on a single cohort (artificial regeneration; direct seeding, container or bare-root plants) or multiple cohorts (natural regeneration over several mast-years). Our current understanding of how cohort dynamics (sapling survival, growth and development) are affected by interspecific competition is limited, making it difficult to identify and use potentially critical physiological thresholds in practical forestry. For example, how much interspecific competition (strength and duration) can oak regeneration endure before reaching an unfavorable status or tipping-point at population level? And how do we identify these physiological thresholds?

Nevertheless, interference from surrounding vegetation is not necessarily negative for oaks (Jensen et al., 2012a,b; Muhamed et al., 2013). The importance of facilitative processes (positive species interactions) for plant community structure and dynamics has been increasingly recognized especially in stress-exposed and low productivity habitats (Brooker et al., 2008; Gómez-Aparicio, 2009; Le Bagousse-Pinguet et al., 2012), whereas the importance of indirect facilitation under temperate and more productive conditions appears to be more ambiguous. Facilitation may be important, for instance, in situations where browsing animals impose severe constraints on oak establishment. Even though browsing animals prefer oaks, species in the woody understory may act as facilitators of oak seedling establishment by providing some protection (Jensen et al., 2012b). In addition, young oaks may exhibit weak apical dominance and apical control in open conditions with little competition for light, which may result in poor stem form and thick lateral branches near the ground – thus reducing future

timber value (Collet et al., 1998; Skrzyszewski and Pach, 2015). Few experiments have been carried out exploring such possible positive effects (i.e. indirect facilitation) of surrounding vegetation on oak regeneration. Understanding such effects is essential baseline knowledge for the development of much needed new regeneration methods.

In this paper, we report on the results of an experiment in southern Sweden that ran for eight growing seasons following establishment. The experiment evaluated the effects of four different herbaceous- and woody-vegetation competition treatments on survival, growth and stem form in young oaks (*Quercus robur* L.). We tested the hypotheses that: (1) interspecific competition from herbaceous- and woody-vegetation reduces oak growth and survival; (2) aboveground competition will shift the shoot architecture of the oaks, optimizing light capture in a dense mixed species canopy, resulting in greater stem height to diameter ratios and lower living crown ratios; (3) this trade-off between height- and diameter growth is more pronounced when oaks are exposed to strong aboveground competition (i.e. competition from woody vegetation); and (4) aboveground competition from herbaceous- and woody vegetation facilitates the development of tall straight monopodial oaks by strengthening the inherent apical dominance/control and promoting height growth. The results are discussed with the aim of providing information and guidance for practical forest management, leading to improved regeneration of oaks.

2. Material and methods

2.1. Study site and experimental design

Our study was conducted in an open-field experiment established in 2007 at the Swedish University of Agricultural Sciences in Alnarp, Sweden (55°39'40"N, 13°05'04"E).

The climate is coastal temperate with mild winters. During this experiment (2007–2015) the mean air temperature (T_{air}) for January and July varied from -4.0 to 4.2 °C and from 16.7 to 20.9 °C, respectively (Table 1). Annual precipitation varied between 592 and 1201 mm. Most years had relatively normal temperature and rainfall levels compared to the 30-year mean, although more dry and wet periods occurred. On the 7th of September 2008, 2009, 2010 and 2015, light availability was measured in each treatment. Between 2008 and 2010 we used Minikin quantum sensors (EMS, Brno, Czech Republic) to measure light levels 85 cm above ground, whereas an LI-190R quantum sensor (LI-COR, Lincoln, Nebraska, USA) were used 2015 to measure light levels at 130 cm above ground. Relative light was calculated for each treatment by comparison with measurements taken under full light conditions. Canopy closure occurred 2009 and 2013 in treatments with (W and HW) and without (C and H) woody vegetation, respectively.

Prior to establishment, vegetation occupying the field was mainly comprised various species of *Sorbus* sp. and grasses. To prepare the site for the experiment, it was cleared in early spring 2007 and planted with honey clover (*Melilotus albus*), a nitrogen-fixing legume. In October 2007, the field was sprayed with glyphosate (Roundup®, Monsanto, USA) and plowed in preparation for planting. The soil at the site is a sandy loam with a pH of 6.3 (soil water) and increased clay content below 60 cm.

The experiment was designed in randomized blocks, consisting of four blocks with four competition treatments. Four 6×6 m plots, with 1 m spacing and 0.5 m buffer zones, were established in each of four separate blocks. In December 2007, 25 two-year-old bare-root oak seedlings were planted at a spacing of 1×1 m in each plot (a total of 400 seedlings). Planting stock (seedlings)

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