



Oaks and acorns

Organizers: **Arndt Hampe** (CSIC) and **Delphine Grivet** (CIFOR-INIA)



Oaks (*Quercus*) are foundation species in many forest systems throughout the northern hemisphere. Worldwide, more than 500 oak species interact with innumerable associated organisms, many of them dependent on their hosts. Efficient natural regeneration of oak forests is critical to their conservation. The production, dispersal and germination of acorns and the early establishment of seedlings represent key stages in that process, as they determine the abundance and spatial distribution of recruiting plants and ultimately shape the demographic and genetic structure of forest stands. Different components of oak regeneration have been intensively studied using several approaches including long-term monitoring of acorn production, observation and experimentation in the field, behavioural studies of acorn dispersers, and molecular techniques. The aim of our symposium is to assemble different perspectives on oak regeneration and to provide a platform for discussing implications of the spatiotemporal patterns observed for the conservation and management of oak forest systems.



(Photo : ripe acorns on the ground (top); pedunculate oak (*Quercus robur*) seedling (right).
 All © Arndt Hampe ; Blue jay (*Cyanocitta cristata*) carrying an acorn. © Pat Hemlepp)

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Plenary 30'

The importance of multidisciplinary approaches for understanding the seed dispersal process: An example from the North American oaks

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Although a unified theory of seed dispersal has been slow to emerge, recent studies employing an integrative approach have greatly improved our understanding of this complicated but important ecological process. Here we review (1) a series of ecological, behavioral, and genetic approaches that have been used to understand oak dispersal in temperate forests of North America, (2) the consistencies and inconsistencies that result from these varied approaches, and (3) the additional approaches needed to resolve these inconsistencies. We report on a series of recent studies that show how secondary dispersal, cache memory, predator-prey interactions, and a retriever's advantage can all influence the seed dispersal process. By simulating predation of scatter-hoarding tree squirrels immediately after caching, we demonstrate that cache owners have a retrieval advantage over conspecifics even in a high-density population. We also show how habitat structure influences the placement of various seed types and how this influences spatial variation in cache pilferage. Our recent findings suggest that scatter hoarding is a dynamic process often controlled by the cache owner but also influenced by other ecological factors. We suggest that the close integration of genetic studies with behavioral and ecological experiments is vital for reconstructing the various mechanisms that contribute to the process of seed dispersal.

Oral 15'

Contrasting patterns of seed dispersal in two red oak populations revealed by hierarchical Bayesian model integrating genetic and ecological data

Emily Moran¹, James S Clark

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Scale of seed and pollen movement has a critical influence on plant population dynamics and their response to environmental change through migration or adaptation. Oaks (*Quercus* spp.), an ecologically and economically important component of many temperate forests, are usually considered to be relatively dispersal limited, but seed trap data does not capture secondary dispersal by animals. Genetic parentage analyses, combined with ecological information, can help to overcome some of these challenges. We apply a hierarchical Bayesian parentage model to two red oak stands in North Carolina. We ask whether the scale of effective seed and pollen movement differs between these populations and, if so, this difference can be explained by site history and plant-animal interactions. Effective pollen dispersal distances were long at both sites (mean > 60 m); average mother-seedling distances were significantly higher than previous seed-trap-based estimates at the Piedmont site, but at the Appalachian site conformed more closely to the initial gravity-created seed dispersal kernel, although disperser activity levels are similar. Patterns of spatial genetic structure are consistent with the



history of each site. The relatively long dispersal distances observed at the Piedmont vs. Appalachian site suggests that in some areas dispersal may not strongly limit oaks' abilities to reach suitable recruitment sites, whereas at other sites dispersal could interact with reduced disturbance frequencies to reduce oak seedling recruitment.

Using animal foraging models to understand patterns of seed movement in oaks.

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Many plant species depend upon animals for seed dispersal, yet animals disperse seeds while pursuing their own social and behavioral agendas. Models for estimating seed dispersal patterns in plant populations typically follow various forms of more or less diffusive dispersal kernels, and through the use of such techniques broad patterns of seed dispersal have been successfully described in a variety of systems. However, in some animal-mediated systems this approach appears to be inadequate for understanding seed dispersal patterns that nonetheless arise from well-known and repetitive aspects of animal behavior. Here we describe a novel approach in which we draw upon well-established animal foraging models to incorporate important details of animal behavior into analyses of seed dispersal. We demonstrate our approach by analyzing the movement of acorns (*Quercus* spp.) by the cooperative-breeding acorn woodpecker (*Melanerpes formicivorus*) in an oak savannah in southern California, USA.

Recruitment of *Quercus robur* at its southern range limit: lessons for the conservation of marginal populations

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A better understanding of how relict populations perform under environmental conditions close to their tolerance limits would allow developing efficient strategies for their conservation and management in a changing climate. Here, we evaluate whether tree fecundity and recruitment success show consistent relationships with population size and degree of spatial isolation in a set of 19 *Quercus robur* relict stands located in central Spain, the southern range margin. We showed that flower production occurred in all trees studied regardless of stand size, internal fragmentation, and degree of isolation. Acorn production also occurred in all stand studied (but not in all trees), and it was positively related to stand size and tree density. Seedling emergence was low and mostly concentrated beneath tree canopies. However, seedling survival after summer drought was relatively high (above 50% and 20% after first and second summer). Survival was higher in canopy gaps, where emergence was very low because of limited acorn dispersal. Overall, sapling recruitment was very low, and again independent of stand size and isolation. Our results suggest that past and recent limitations for *Q. robur* regeneration seem to be more associated to anthropogenic disturbance than to climatic constraints or population structure.



Exploring the mechanisms that determine oak regeneration at regional scale: the interplay between interacting organisms and landscape structure

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We used several models to examine the direct and indirect effects of landscape traits and plant-animal interactions on three life-cycle stages of the Mediterranean oak tree, *Quercus ilex*. Models were built combining field and GIS-based information on habitat patches and considering the connectivity of each patch, as the ability of an acorn of reaching each patch, realistically computed using observed dispersal patterns of the main acorn dispersers. Biotic interactions as well as landscape traits controlled *Q. ilex* regeneration. Jay acorn dispersal was highly positive for *Q. ilex* establishment being relevant for all stages and connectivity values while wild boars negatively affected establishment by seed and seedling predation. The connectivity of each patch entailed direct and indirect effects on biotic interactions. Our results advocate that regeneration at a regional scale strongly depends on a complex relationship between landscape and the interacting organisms that move throughout it.

Effects of seed characteristics on the individual seed fates of a deciduous oak species *Quercus serrata*

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To examine effects of seed characteristics, including tannin content and size, on their seed fates in the individual seed scale, extent of intraspecific variations in seed characteristics was examined in *Q. serrata*. Then we conducted the field experiment, analyzing the relationships between seed traits (size and tannin content) of individual acorns and their seed fates (seed dispersal and survival) using a nondestructive method of estimating the chemical contents of individual seeds. This method was developed by near infrared spectroscopy (NIRS) to solve a problem: a conflict between obtaining the information of seed chemical traits and pursuing seed fate. In the field experiment, I obtained the following results: tannin content (0.1-31.5%, $n = 8988$) and seed size (0.1-5.0g, $n = 8940$) varied largely among individual acorns of *Q. serrata*; on one hand, large and low-tannin seeds tended to be dispersed well; and on the other hand, small and high-tannin ones tended to survive well. These results have indicated that individual seeds may not survive in even probability due to selective consumption by seed consumers according to tannin content and seed size. It was also revealed that advantageous seed traits to dispersal and survival were opposite to each other. Studies examining the effects of seed traits on seed fates in the field were quite limited (e. g. Sork, 1984; Gómez, 2004; Xiao *et al.*, 2004). None of the studies focused on variation in chemical traits among individual seeds.



Evolutionary interactions between rodents and nuts : A review in China

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We will review our recent advances in seed-rodent interactions performed at several field sites across China. Our long-term research on seed-rodent interactions is aimed to fully understand how scatter-hoarding rodents as both seed predators and seed dispersers select plant seeds based on seed traits (e.g. seed size, seed chemistry, seed germination/dormancy and hull hardness), and how such behavioral preferences by these animals in turn influence dispersal and establishment of related plants, including the evolution of seed traits under selection. In this talk, we will focus on feeding and hoarding preferences among different rodent species and its impacts on seed dispersal and seedling establishment. In particular, we will also show some new findings about the squirrel-oak interactions in China. According to these recent advances, we suggest that behavioral preferences of scatter-hoarding animals can have a substantial impact on plant demography and vegetation diversity, including the evolution of related seed traits.