OAK DISPERSAL SYNDROMES: DO RED AND WHITE OAKS EXHIBIT DIFFERENT DISPERSAL STRATEGIES?

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Abstract—We provide an overview of the ecological and evolutionary interactions between oaks and several of their dispersal agents, and review a series of studies that demonstrate how various acorn characteristics affect feeding and caching decisions of these animals, which in turn may influence oak dispersal and establishment. We demonstrate that acorns of red oak species show a marked dispersal advantage over those of various white oak species. From this, we predict that red oaks are likely to establish in a wider range of micro-environments and at greater distances from maternal sources, whereas white oaks should be limited to establishment closer to maternal sources. This in turn should influence the spatial pattern of oak recruitment and seedling physiological traits. We discuss current efforts to test this Differential Dispersal Hypothesis (DDH) and its implications for various aspects of oak ecology including masting, seedling physiology, and regeneration.

INTRODUCTION

Although oaks dominate many forest ecosystems worldwide (Barnes and others 1998), several aspects of oak ecology remain poorly understood including oak regeneration and masting (McShea and Healy 2001). Animals that eat and disperse acorns, such as squirrels, mice, and jays may play a pivotal role in oak forest dynamics (Jones and others 1998, Ostfeld and others 1996), influencing regeneration both positively and negatively through their roles as seed dispersers and predators. The ecology and evolution of oaks is likely to be strongly dictated by the behavioral decisions of these animals. Understanding oak forest ecosystems may therefore require multidisciplinary approaches that determine how the behavioral ecology of animals affects oak forest characteristics including levels and patterning of seedling recruitment and plant physiological traits. Our research attempts to examine such linkages by focusing on behavioral responses to various acorn characteristics as a starting point.

MECHANISMS OF OAK DISPERSAL

Acorn Characteristics and Oak Dispersal

The behavior of most acorn consumers and dispersers follows directly from several key characteristics of the two major subgenera of oaks in North America (Kaul 1985): the white oak group (hereafter WO, subgenus *Quercus*, formerly *Leucobalanus*) and the red oak group (RO, subgenus Erythrobalanus). Acorns of WO species contain low levels of both tannins (2 percent by mass) and lipids (5-10 percent) and usually germinate in the autumn, during or shortly after seed fall. Acorns of RO, in contrast, possess more tannins (6-10 percent) and lipids (18-25 percent) and usually require cold stratification to break dormancy, at least in temperate regions. In the following sections we review several lines of investigation that collectively demonstrate the influence of these acorn characteristics on the feeding and caching behavior of acorn consumers, and ultimately, the reciprocal effect of such behavioral decisions on oak dispersal and establishment.

Acorn Food Preferences

The differences in lipid and tannin levels between WO and RO acorns have long been considered primary determinants of feeding preferences of many avian and mammalian acorn consumers. Lipid levels represent the primary source of digestible energy in acorn cotyledon and are thus the reason that acorns are so highly sought for food by >150 species of wildlife (Van Dersel 1940). However tannins, a group of water soluble phenolic compounds common in acorns, readily bind to salivary and digestive enzymes reducing both their palatability and their digestibility (Robbins and others 1987, Chung-MacCoubrey and others 1997). Thus when selecting between acorn types for food, most species are faced with a trade-off between RO acorns that are high in energy but unpalatable and others (WO) that contain significantly less energy but are far more palatable and digestible (Smith and Follmer 1972).

Attempts to determine whether mammals prefer RO or WO acorns have produced varying results depending on study conditions (Lewis 1980, Smith and Follmer 1972). This controversy was largely resolved in 1986 by Smallwood and Peters who examined the feeding response of eastern gray squirrels to artificial acorns made from ground cotyledon of *Q. alba* acorns to which varying amounts of tannin and lipid were added. By presenting free-ranging gray squirrels with these artificial acorns, they found that gray squirrels selected acorns low in tannin levels in autumn when energy

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Citation for proceedings: Spetich, Martin A., ed. 2004. Upland oak ecology symposium: history, current conditions, and sustainability. Gen. Tech. Rep. SRS–73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 311 p.

requirements were low and food was relatively abundant. In contrast, in the winter when energy requirements were high, squirrels selected artificial acorns with higher lipid levels even when they contained higher amounts of tannin (Smallwood and Peters 1986).

Early Germination in WOs and Embryo Excision

The behavior of early germination in WO acorns presents a second problem for acorn consumers. Rapid autumn germination in many WOs, occurring in some species while acorns are still attached to the tree (Steele pers. obs.), involves the rapid transfer of energy into a taproot that is high in cellulose and indigestible for most granivores (Fox 1974). Early germination in WO species likely represents an adaptation to prevent seed predation by granivorous mammals and birds (Barnett 1977, Steele and Smallwood 2001), and perhaps larval insect predators (e.g., *Curculio*) that begin feeding on acorns before they mature. For mammals, birds, and even some insects early germination greatly limits the availability of WO acorns as food in the autumn. Early germination means that if not eaten soon after seed fall, much of the energy of the WO crop will no longer be available to seed consumers. Moreover, if whole intact WO acorns are stored, it is likely that such energy stores would be lost as these acorns continue to produce taproots during periods of warmer weather.

At least one group of mammals—the tree squirrels (*Sciurus*) —appear to have overcome this problem with the behavior of embryo excision (Fox 1974, 1982; Pigott and others 1991). Eastern gray squirrels, for example, are known to carefully remove the radicle and excise the embryo from the apical end of WO acorns with their incisors prior to caching these acorns (Fox 1982, Pigott and others 1991). Recently we reported that this behavior is quite common, and that WO acorns with excised embryos remain in tact in the scatter hoards of squirrels for up to six months (Steele and others 2001b). Several observations also suggest that this behavior may be an adaptation unique to the genus *Sciurus*. We have observed the behavior in at least two other species of tree squirrels (*S. niger* in the midwestern U.S. and *S. aueregaster* in central Mexico), but have failed to observe any such behavior in at least four other species of small mammals, all of whom otherwise show similar feeding and caching responses to acorns (see below). Recently we presented acorns to naïve captive raised eastern gray squirrels that possessed no previous experience with acorns. The animals cached dormant RO acorns over those of WO, removed the radicles of germinating WO acorns, and on occasion excised or attempted to excise the embryos of WO acorns (Steele and others, unpublished data). We argue that this behavior is likely unique to the tree squirrels and that there is a strong innate basis for the behavior.

Caching Responses and Acorn Perishability

Both the behavior of embryo excision and the selective consumption of WO acorns in autumn suggest that some acorn consumers may be sensitive to acorn perishability due to germination. In fact, Smallwood and Peters (1986), in their analysis of acorn preferences of gray squirrels, predicted that squirrels might selectively cache RO acorns over those of WO, and that they may use tannin as a cue to identify less perishable RO acorns. Over the last decade, we have fully verified this first prediction with two series of experiments in which we have presented small mammals with RO and WO acorns. In the first, we directly observed free-ranging gray squirrels and recorded their feeding and caching decisions. The second experiment, repeated many times under a variety of conditions, involved selective provisioning of granivorous mammals with metal-tagged acorns (e.g., Steele and others 2001b). Following their dispersal, metal detectors were used to relocate the tags and determine those acorns cached and those eaten, as evidenced by discarded tags. In all such experiments we found that small mammals selectively dispersed and cached RO acorns and consistently ate those of WO species. These experiments, coupled with several others conducted on captive mammals (e.g., southern flying squirrels, white-footed mice) lead us to conclude that selective dispersal and caching of RO is a behavior common to most scatter-hoarding mammals in Eastern deciduous forests. (Although bluejays (*Cyanocitta cristata*) are also important dispersal agents of oak, especially over long distances (>1 km), most studies conclude that they selectively disperse primarily RO species with smaller acorns (Darley-Hill and Johnson 1981, Johnson and Webb 1989, but see Bossema 1979, Monsandl and Kleinert 1988 for dispersal by European jays)).

In another series of experiments we sought to determine specific cues that small mammals use to determine which acorns to eat and which to disperse and cache. Hadj-Chikh and others (1996) addressed this question by presenting free ranging gray squirrels with pairs of acorns that varied with respect to several characteristics (i.e., size, perishability due to germination schedules, fat and tannin levels). They produced overwhelming support that the animals were responding to acorn perishability over any other factor, including tannins. Likewise, in a related experiment, Steele and others (1996) found that tree squirrels selectively cache sound acorns over those infested with insect larvae, which the animals instead consume along with the larvae. Together these results indicate that tree squirrels, and perhaps other acorn consumers, rely on acorn perishability to make caching decisions.

More recently we also have found that tree squirrels can distinguish between dormant and non-dormant RO acorns even when the non-dormant acorns exhibit no physical signs of germination (Smallwood and others 2001, Steele and others 2001a). Moreover, by manipulating acorn chemistry and creating artificial acorns with one type of pericarp (WO or RO) that contain ground RO or WO cotyledon (with varying concentrations of fat and tannin), Steele and others (2001a) showed that squirrels only cache those artificial acorns constructed of RO pericarps, regardless of their contents. However, when these RO pericarps are first soaked in acetone (to potentially control for chemical cues in the pericarp), gray squirrels consistently consume these acorns. These results point to a chemical cue (or the absence of one) in the pericarp that may be used by the animals to identify dormant, non-perishable seeds (Steele and others 2001a). Future efforts are directed at comparing the chemical profiles of dormant and non-dormant acorns and determining whether squirrels detect a dormancy cue or simply respond to damaged packaging (i.e., the pericarp).

Partial Consumption of Acorns

In addition to selectively caching RO acorns, small mammals and several other acorn consumers, selectively consume portions of individual acorns in a manner that may also influence dispersal and establishment of the oaks. Steele and others (1993) found that several vertebrates as well as weevil larvae (genus *Curculio*) selectively feed on the basal portion (proximal end) of several species of RO acorns, especially when acorns and other food are abundant (Steele and others 1993). Each vertebrate species uses a markedly different technique for opening acorns, but each frequently consumes only 10-40 percent of the basal portion of the cotyledon.

Because the acorn embryo (< 1 percent of the biomass of the acorn) is located in the extreme apical end of the fruit, many of these partially eaten acorns can still germinate. In greenhouse experiments, for example, germination rates are as high or higher for partially eaten acorns as they are for intact seeds (Steele and others 1993). In behavioral experiments, Steele and others (1998) also found that gray squirrels often dispersed and cached the potentially viable apical fragments. And, although germination and establishment rates of partially eaten acorns in the field are substantially lower than those of whole acorns, these observations suggest that the ability to survive partial predation may represent a means by which several RO species sometimes escape seed predation. We suggest that in the life of an oak (150 or more years) infrequent establishment as a result of partial acorn consumption need only occur rarely for this to represent a successful reproductive strategy.

Tests of alternative hypotheses to explain the underlying causes of the behavior point to a suite of chemical and physical traits that may collectively promote partial consumption and subsequent survival of RO seeds. Steele and others (1993) found that tannin levels (as measured by protein binding capacity) are significantly higher in the apical half of the acorns of two RO species, where the embryo is located. More recently, several of us also found that both lipid levels and Na levels are significantly higher in the basal half than the apical half of three additional species of acorns (Steele and others, unpublished data). Consequently, the top of the acorn may not only be more palatable and digestible because of lower tannin levels but may also contain more energy (lipid), and an important nutrient (Na), often limiting for herbivorous mammals such as tree squirrels (Steele and Koprowski, 2001 and references therein). In other experiments, Steele and others (1998) have shown that although partial acorn consumption is not influenced by the thickness or presence of the pericarp, the shape of the acorn can affect the behavior. When acorns are shelled and the cotyledon is carved so the basal and apical ends of the acorn are reversed, tree squirrels begin eating from the true apical end of the seed (which looks like the basal end). Thus it appears several physical and chemical characteristics may act synergistically to promote partial consumption of the basal half of acorns and subsequent survival of these damaged fruits.

Table 1—Overview of characteristics of RO and WO acorns, behavioral responses to these characteristics by acorn consumers, and the influence of these responses on the oaks

Acorn characteristics	Acorn type	Response and influence on oaks	References
Low tannin, low fat	WO	Selective consumption of WO in autumn	Smallwood and Peters 1986
High tannin, high fat	RO	Selective consumption of RO in winter Selective caching of RO for winter	Smallwood and Peters 1986 Smallwood and Peters 1986
Early germination	WO	Consumption of acorns	Hadj-Chikh and others 1996 Steele and others 2001a
		Embryo excision by tree squirrels	Fox 1982, Pigott and others 1996 Steele and others 2001a
Delayed germination	RO	Selective scatter hoarding of RO Potential for far greater dispersal in RO	Hadj-Chikh and others 1996 Smallwood and others 1998
Insect Infestation	RO and WO	Selective consumption of infested acorns Selective scatter hoarding of RO only	Steele and others 1996
Chemical gradients in acorns	RO and WO	Partial consumption of RO only and subsequent survival of damaged seeds	Steele and others 1993 Steele and others 1998
Acorn shape	RO	Partial consumption of RO	Steele and others 1998
Acorn size	RO	Selective long distance dispersal of Smaller-seeded RO by jays Selective scatter hoarding of Larger-seeded RO by tree squirrels	Darley-Hill and Johnson 1981 Steele and others unpub. data

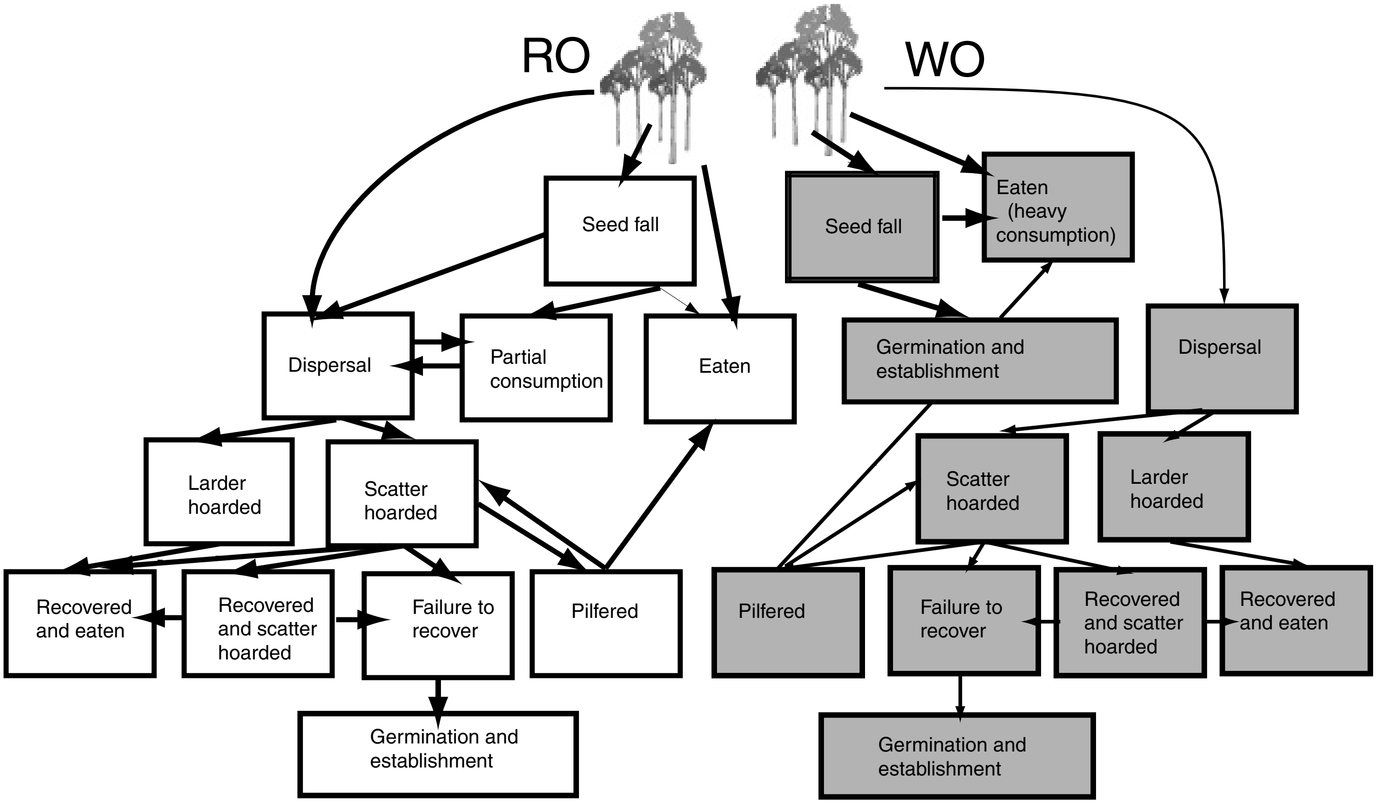

Figure 1—Acorn fate diagram for species of red oak (open rectangles) and white oak (shaded rectangles). The width of arrows is proportional to the probability of the corresponding event.

SYNTHESIS, IMPLICATIONS, AND FUTURE DIRECTIONS

Acorn Fates and The Differential Dispersal Hypothesis (DDH)

The studies reviewed above collectively point to a marked contrast in dispersal strategies of the two primary groups of oaks in North America. Table 1 summarizes the major behavioral responses of avian and mammalian agents of oak dispersal to the different characteristics of RO and WO acorns. Figure 1 is a seed fate diagram that integrates these various responses.

The obvious conclusion to follow from these summaries is that acorns of RO have a significant dispersal advantage. RO acorns are dispersed greater distances from their sources, cached more often in a wide variety of environments, and even show the ability, under some circumstances, to escape partial predation. Acorns of WO, in contrast, should show short dispersal distances and may be in fact adapted for rapid germination near or under parent trees. Although most of our studies have been conducted in eastern deciduous forests, we predict that because of the consistent differences between RO and WO acorns across North America, this phenomenon of differential dispersal is likely to occur throughout temperate forests of North America. If in fact RO and WO species exhibit contrasting dispersal syndromes, several important implications may follow.

Differential Dispersal and the Spatial Arrangement of Oaks

One likely outcome of these contrasting dispersal strategies is a significant difference in the spacing of RO and WO seedlings (Smallwood and others 1998, Steele and Smallwood 2001). RO seedlings are likely to establish at greater distances from parents and thus become more widely spaced; WO seedlings should be clumped near or under parent trees. In an initial test of this hypothesis, Smallwood and others (1998) measured the distribution of seedlings and adult trees of several oak species in the same forest plot to construct best-fit, putative seedling shadows using the computer models of Ribbens and others (1994). The two WO species studied (*Q. alba* and *Q. prinus*) had short truncated seedling distributions and extensive clumping of seedlings within a few meters of the parent. In contrast, the two RO species (*Q. rubra* and *Q. velutina*) showed no clumping and seedling shadows of RO extended much farther than those of WO.

Although results of Smallwood and others (1998) support the DDH, they demonstrate the expected pattern of seedling distribution for only one site. We are currently examining seedling distributions for six additional oak forests throughout eastern North America to determine the consistency of these findings. In addition Smallwood's results are derived from computer models that generate expected distributions in relation to putative, not definitive, parents. To more definitively determine seedling-parent distances, we are currently conducting parentage analysis of seedlings (via microsatellite DNA fingerprinting) in several managed and old-growth stands of oak in the central and eastern U.S. Although the final outcome of these genetic analyses is not yet available one of two general conclusions is likely.

If the molecular analyses ultimately show greater dispersal of RO seedlings than WO as predicted, these contrasting dispersion patterns are likely to result in two sets of alternative cascading effects for the two subgenera of oaks. Assuming the microenvironment beneath parent trees is both more shaded and exhibits less variability in microsite conditions, white oak seedlings would then be expected to be more shade tolerant, less capable of colonizing new micro-environments, and more competitive than RO seedlings (reviewed by Steele and Smallwood 2001). Currently we are testing several of these predictions.

If, on the other hand, the molecular results fail to support the hypothesis by showing white oak seedlings to be widely dispersed, as preliminary results suggest, the most obvious question to follow will be how are white oaks dispersed? Perhaps seedlings exhibit different distributions than seeds because of strong differential survival of rarely dispersed seeds. White oaks may therefore be more dependent than ROs on such rare events, the occasional acorn that is carried and dropped, or the exceedingly rare occasions when whole WO acorns are scatter-hoarded and subsequently forgotten. Perhaps in the life of an oak such rare events are, simply, the rule.

Differential Dispersal and Masting in Oaks

A second implication to follow from our behavioral studies, regardless of the molecular findings, concerns the masting patterns in RO and WO species. Masting is the synchronized, episodic production of seeds by one or more tree species in one year, followed by widespread crop failure in others. Masting is common in oaks and considered by many as a genetically influenced factor affecting their dispersal and establishment (Crawley and Long 1995, Koenig and Knops 2001, Sork and others 1993). In a recent review Koenig and Knops (2001) concluded that masting in oaks is an adaptive response that is best explained by the predator satiation hypothesis. This hypothesis argues that mast failures serve to decrease seed predators, while good crop years result in satiation of seed predators and seedling establishment.

Koenig and Knops (2001) also note, however, that the most significant evidence against the predator satiation hypothesis for oaks "…is the lack of synchronization in masting behavior among species within a community, in particular between species requiring different numbers of years to mature acorns" [e.g., RO and WO species]. We argue that such asynchrony between RO and WO species (especially within a community) is expected because of differential treatment of WO and RO acorns by acorn consumers. Although ROs clearly would benefit from synchronized masting with WOs, since WO acorns could then satiate predators while RO acorns were dispersed, WOs may have no advantage in masting with ROs and may potentially be at a disadvantage of synchronizing its mast with species that are preferred for caching. This could potentially explain some asynchrony in acorn masting as WOs evolve to "escape" masting with RO. We have tested this prediction by simulating RO and WO acorn abundance and found that significant scatter hoarding of WO acorns only occurs when these acorns are abundant and ROs are not (Steele and others, unpublished data). Because of the extreme susceptibility of WO acorns to predation, we also expect seed fall patterns within a season to differ between the two oak groups, with WO species showing rapid seed fall and RO species extending their release of acorns over longer periods. We are currently testing these hypotheses by conducting a meta-analysis of acorn production studies.

In conclusion, seed consumers have the potential to affect such wide-reaching factors as plant spatial patterns, physiological traits, and degree and timing of acorn masting. Understanding the degree to which these behaviors influence oak dynamics may prove critical for effectively managing oak ecosystems in the face of such threats as forest fragmentation and climate change.

ACKNOWLEDGMENTS

We thank Wilkes University, The University of Richmond, and The School of Forest Resources, PSU for support during preparation of this manuscript. Financial support of our research is provided by the National Science Foundation (DBI-9978807).

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