Differential effects of acorn burial and litter cover on *Quercus rubra* recruitment at the limit of its range in eastern North America

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Abstract: Primary predators or dispersers such as birds and rodents cache acorns of northern red oak (*Quercus rubra* L.). A proportion of these acorns are not retrieved, and thus, animals may favour oak regeneration by placing acorns in microsites suitable for recruitment. We experimentally investigated the effects of acorn burial and litter cover on red oak recruitment at two sites at the northern limit of the species' range in North America. Laboratory experiments also tested the effects of acorn burial and litter cover on desiccation and germinability and the influence of soil moisture on germination. Burial and litter protected acorns against predation by deer in the field. Germination was promoted by burial both in field and laboratory experiments. Germination was proportional to acorn water content and to soil moisture. Seedling emergence in the field was enhanced by burial but reduced by litter cover. Acorns buried but uncovered by litter had the highest probability of recruiting a seedling. A potential effect of seed predators or dispersers on red oak regeneration and expansion is suggested, as acorn caching by birds and rodents may actually enhance population recruitment, despite high mortality through acorn consumption.

Key words: acorn burial, litter, microsite effects, recruitment, northern red oak, southern Quebec.

Résumé : Certains oiseaux et rongeurs cachent les glands du chêne rouge, *Quercus rubra* L., et sont donc des prédateurs ou disséminateurs des fruits de l'espèce. En effet, une proportion de ces glands cachés n'est pas récupérée et ces animaux semblent favoriser la régénération du chêne rouge en plaçant les glands dans des microsites favorables au recrutement de l'espèce. Nous avons expérimentalement déterminé l'effet de l'enfouissement des glands et d'un couvert de litière sur le recrutement du chêne rouge sur deux sites à la limite nord de l'aire de répartition de l'espèce en Amérique. Nous avons également déterminé l'effet de l'enfouissement et d'un couvert de litière sur la dessication et la germinabilité des glands et l'influence de l'humidité du substrat sur la germination, en milieu contrôlé. L'enfouissement et un couvert de litière protègent les glands de la prédation par les cerfs en conditions naturelles. La germination des glands est favorisée par l'enfouissement, à la fois sur le terrain et en conditions contrôlées. La germination est reliée au contenu en eau des glands et à l'humidité du substrat. L'émergence des plantules est favorisée par l'enfouissement des glands, mais réduite par un couvert de litière. Les glands enfouis mais non couverts de litière ont la plus forte probabilité de produire une plantule. Nous suggérons que les prédateurs ou disséminateurs, malgré la mortalité dûe à la consommation des glands, peuvent avoir un effet positif sur la régénération et l'expansion de l'aire de répartition du chêne rouge, puisque son comportement de cache peut améliorer le recrutement de l'espèce.

Mots clés : chêne rouge, effets du microsite, enfouissement des glands, litière, recrutement, sud du Québec.

Introduction

Many oak species in North America depend on acorn-caching animals (primary predators such as birds and

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rodents) for seed dispersal (Vander Wall 1990; Farmer 1997 and references therein). Besides its role in the transport of acorns from parental plants, caching by animals is assumed to enhance oak regeneration for two reasons (Vander Wall 1990; Johnson et al. 1997): first, by providing escape from secondary predators, e.g., deer; and second, by placing them in physiologically suitable sites for both acorn germination and seedling establishment. Thus, the effectiveness of primary predators as dispersers depends on the trade-off between acorn retrieval by these or other predators and the suitability of the site where acorns are delivered (Schupp 1993; Kollmann and Schill 1996). Yet, information on how caching activity by dispersers modifies microsite conditions for oak recruitment in the field is scarce (but see Kollmann and Schill 1996; Fuchs et al. 2000). This is especially lacking for sites such as the limits of the species' ranges where

regeneration is mainly constrained by abiotic factors, and thus, the positive effect of dispersers might be more evident, favoring not only population recruitment but also species' expansion (Griffin 1971; Vander Wall 1990; Clark et al. 1998).

In this paper, we experimentally analyze microsite requirements for seedling recruitment of northern red oak (*Quercus rubra* L.) in the southern part of Quebec to understand how caching may influence the species' regeneration at the northern limit of its range in eastern North America. We considered two microsite features, burial and litter cover, both of which may differ dramatically between cached and uncached acorns after primary dispersal (on soil surface, under parental trees, and covered by litter; Barnett 1977; Crow 1988; Kollmann and Schill 1996; Johnson et al. 1997). We hypothesized that burial and litter might affect oak establishment by influencing humidity in the nearby environment around the acorns, which may be relevant to recruitment since acorns lose their viability under dessication (Watt 1919; Shaw 1968; Griffin 1971). Moreover, we studied the effect of caching on different regeneration stages (e.g., post-dispersal survival, germination, and emergence) to evaluate the importance of each stage on final recruitment as well as how different stages might be differentially affected by the same microsite conditions (Schupp 1995; Kollmann and Schill 1996). More specifically, we addressed the following questions:

(1) Do burial and litter cover affect acorn germination, seedling emergence, and recruitment in the field?

(2) Is germination influenced by acorn water status under burial or litter cover conditions?

(3) Does soil moisture level affect germination?

Materials and methods

Study sites

Two sites were used for the field experiments: the first one was on Île-aux-Grues (47°02′N, 70°33′W), an island in the Montmagny archipelago in the St. Lawrence River, Quebec, and the other was in the Réserve Léon-Provancher (46°18′N, 72°31′W) on the south shore of the St. Lawrence River near Trois-Rivières, Que. Both sites are characterized by mixed hardwood stands in which red oak is associated with sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), and red maple (*Acer rubrum* L.). These forests are typical of the middle St. Lawrence section of the Great Lakes – St. Lawrence Forest Region of Rowe (1972). Both stands represent red oak populations at the northern limit of the species' distribution (Sander 1990). Potential hoarding animals such as red squirrels (*Tamiasciurus hudsonicus* L.) and blue jays (*Cyanocitta cristata* L.), and evidence of acorn caching were found at both sites. In fact, most first-year oak seedlings located in the stands apparently emerged from caches (D. García, data not shown). Mean annual temperature at nearby weather stations is ca. 5°C, and annual precipitation totals ca. 1000 mm of which ca. 24% falls as snow (Atmospheric Environmental Service 1981). The frost-free season is ca. 150 days (Atmospheric Environmental Service 1982).

Field experiment: effect of acorn burial and litter cover on acorn germination, seedling emergence, and recruitment

The experiment was simultaneously set up at both study sites in fall 2000. At each site, we collected acorns during the peak time of dispersal from at least six different trees. Acorns were tested for soundness by water floatation and removal of those defective or infested by weevil larvae (Dey and Buchanan 1995). At each site, 800 sound acorns were then placed in the field in groups of 10, each group homogeneously distributed on a surface of 20×20 cm and covered by a wire cage of $25 \times 25 \times 5$ cm (1-cm mesh). Acorns were placed with the micropyle horizontal, their longitudinal axis being equally oriented. Treatments were established in a completely randomized block design, in which each of 20 blocks had a group of acorns assigned to one of four combinations of two factors (burial and litter cover): (*i*) buried and covered by litter, where acorns were buried in the soil at 1-cm depth above the acorn and covered by litter (B^+L^+); (*ii*) buried and uncovered by litter (B^+L^-); (*iii*) unburied and covered by litter (B^-L^+); and (*iv*) unburied and uncovered by litter (B^-L^-). Blocks were separated by 2 m and arranged in four transects of five blocks per transect. Litter was taken directly from the surroundings and was composed of a mixture of leaves freshly fallen from different species, mainly red oak, sugar maple, yellow birch, and beech. Litter cover was homogeneously distributed within the cage, representing a cover of three to five layers of leaves (the number of leaf layers at the study site was 2.80 ± 0.11 (mean $\pm$ SE)). Litter that fell on the cages during the fall was systematically removed until snowfall to make sure that the only litter covering the acorns was that added experimentally. Plots were surveyed in late spring 2001 by removing the cage and carefully searching for the acorns, checking for germination (acorn split, radicle protrusion), seedling emergence (epicotyl development on germinated acorns), and recruitment (seedlings from sown acorns).

During the experiment, some cages at Réserve Léon-Provancher evidenced attack and acorn predation by white-tailed deer (*Odocoileus virginianus* Zimmermann). Thus, we recorded the treatment of those cages damaged by deer and collected the data on germination, emergence, and recruitment for the surviving acorns (number of acorns: B^+L^+, 180; B^+L^-, 197; B^-L^+, 156; B^-L^-, 19). Deer were not present at Île-aux-Grues, and no cage removal or acorn predation was detected at this site.

Laboratory experiment 1: effect of burial and litter on acorn germination

In November 2000, one hundred sound acorns from Île-aux-Grues were individually weighed and placed in 250-mL plastic pots filled with 150 g of sterilized sand, which were then watered to saturation level (ca. 19% moisture content) by adding 35 mL of distilled water per pot. Two factors considered were acorn burial and litter cover, with 25 pots assigned to each of the four combinations of burial and litter as above. Buried acorns were placed in the sand with the micropyle horizontal at 1-cm depth above the acorn. Litter was applied by covering the sand surface with three to five layers of leaves collected from Île-aux-Grues. Acorn weights did not differ between treatments at the be-

ginning of the experiment ($F_{3, 96} = 0.79$, $p = 0.49$, one-way ANOVA). Initial acorn water content was $45.37 \pm 1.17\%$ (calculated from the difference between wet and dry weights for a subsample of 20 acorns from the initial pool, by oven-drying at 80°C for 24 h). Pots were placed in a germination chamber for acorn stratification, at 4°C, in darkness, for 3 months (see Dey and Buchanan 1995). Pots were not watered during stratification, thus suffering progressive desiccation. After that period, acorn germination (acorn split, radicle protrusion) was checked, and wet weight was recorded. The temperature regime was then changed to 25:15°C (day:night) with a 16 h light : 8 h dark photoperiod, and pots were watered to saturation level (35 mL). After 1.5 months, germination was checked again, and dry weight was determined for all acorns.

Acorn water loss during stratification was followed on 10 additional acorns in the combination no burial – no litter, following the procedure described above. We assumed that acorn water loss in the remaining combinations should be lower or similar to those of no burial – no litter, since this combination represents the lowest level of acorn protection against desiccation. These control acorns were individually weighed every 2 weeks, and dry weight was determined at the end of the stratification period. Acorn water content was then calculated for each date, showing a progressive decrease and passing the threshold value for acorn viability (20% water content; Watt 1919; Dey and Buchanan 1995) after 60 days stratification.

Laboratory experiment 2: effect of decreasing soil moisture levels on acorn germination

In November 2000, one hundred sound acorns from Île-aux-Grues were individually weighed and placed in 250-mL plastic pots filled with 150 g of sterilized dry sand. Acorns were partially buried (half of the acorn) with the micropyle horizontal. Four groups of 25 pots were assigned to each one of four treatments representing a decreasing gradient of soil moisture from saturation: 19, 14, 6, and 3%. These values were established by adding, respectively, 35, 25, 10 and 5 mL of distilled water to the pots. No differences in acorn weight were found between treatments at the beginning of the experiment ($F_{3,96} = 0.07$, $p = 0.97$, one-way ANOVA). The initial acorn moisture content was $50.55 \pm 0.56\%$ (calculated from a subsample of 10 acorns from the initial pool, by oven-drying at 80°C for 24 h). All pots were sealed with plastic wrap and vaseline, to preclude soil water loss, and stratified in darkness in a chamber at 4°C, for 3 months. After that, acorn germination (acorn split, radicle protrusion) was checked and temperature regime was changed to 25:15°C (day:night) with a 16 h light : 8 h dark photoperiod. Germination was checked again after 1.5 months.

Statistical analysis

Multivariate contingency models (nominal logistic model (NLM) procedure of JMP statistical package; SAS Institute Inc. 2001) were used to analyse simultaneously the effects of (*i*) burial, litter, their interaction, and block on germination, emergence, and recruitment for individual acorns in the field experiments; (*ii*) burial, litter, and their interaction on predator attack for individual cages at Réserve

Léon-Provancher; (*iii*) burial, litter, their interaction, and initial seed weight on germination for individual acorns in the laboratory experiment 1; and (*iv*) soil moisture level and initial seed weight on germination for individual acorns in the laboratory experiment 2. Pairwise comparisons between treatments were made by partial χ^2.

A two-way ANOVA with interaction was used to analyse the effect of burial and litter on acorn moisture content after stratification, in laboratory experiment 1. This model was performed by standard least squares procedure of JMP (SAS Institute Inc. 2001), including initial seed weight as a covariable and after arcsine transformation of the dependent variable. Pairwise comparisons between treatments were made by a posteriori contrast (differences in the minimum square mean).

Results

Field experiment: effect of burial and litter cover on germination, seedling emergence, and seedling recruitment

Germination percentages were 80.5% at Île-aux-Grues and 94.9% at Réserve Léon-Provancher. Burial significantly affected germination probability (Tables 1 and 2), being higher for buried acorns. Total emergence for germinated acorns was 31.7% at Île-aux-Grues and 48.8% at Réserve Léon-Provancher. Emergence was significantly higher when acorns were buried but uncovered by litter (Tables 1 and 2). The percentage of initially sown acorns recruiting seedlings was 25.9% at Île-aux-Grues and 46.4% at Réserve Léon-Provancher. Recruitment was positively affected by burial but negatively affected by litter at both sites, with no interaction between factors (Table 2). As a result, the highest probability to recruit a seedling appeared for acorns buried and uncovered by litter (Tables 1 and 2). A significant block effect was detected at both study sites for most analysed variables (Table 2).

Deer attacked 36.3% of acorn cages at Réserve Léon-Provancher. Cages with acorns unburied and uncovered by litter had the highest probability of attack (Fig. 1). Both burial ($\chi^2 = 19.4$, $p < 0.0001$) and litter cover ($\chi^2 = 6.5$, $p = 0.011$) significantly reduced the probability of attack by deer. The interaction between these factors was not significant (B × L, $p = 0.10$; NLM).

Laboratory experiment 1: effect of burial and litter on acorn germination

Total acorn germination was 27.0%, mostly occuring during the stratification period. Acorns buried and covered by litter showed the highest germination percentage (Table 3). Both burial and litter had significant and independent effect on germination (burial: Wald $\chi^2 = 14.2$, $p < 0.0001$, df = 1; litter: Wald $\chi^2 = 5.9$, $p < 0.05$, df = 1; B × L: Wald $\chi^2 = 1.5$, $p > 0.05$, df = 1), while initial acorn weight did not affect germination (Wald $\chi^2 = 2.7$, $p > 0.05$, df = 1; NLM).
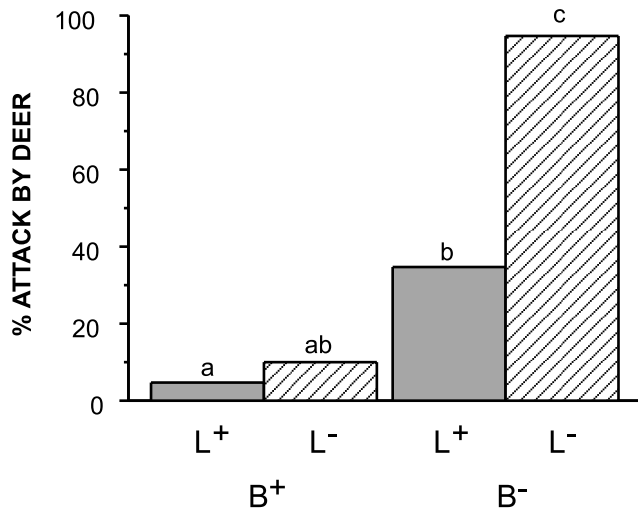
Acorn moisture content after stratification was significantly higher for acorns buried and covered by litter than for the other treatments (Table 3). Burial and litter were significant factors on acorn water content (burial: $F_{1,95} = 196.1$, $p < 0.0001$, df = 1; litter: $F_{1,95} = 89.0$, $p < 0.0001$, df = 1), but litter effect was only evident for buried acorns (B × L:

Table 1. Percentage of *Quercus rubra* germination, emergence (seedlings from germinated acorns) and recruitment (seedlings from sown acorns) at two sites, in relation to burial and litter cover.

	B+		B⁻	
	L+	L⁻	L+	L⁻
Germination				
Île-aux-Grues	86.50*a*	92.46*a*	70.50*b*	72.50*b*
Réserve Léon-Provancher	96.67*a*	97.46*a*	89.74*b*	94.74*ab*
Emergence				
Île-aux-Grues	32.37*a*	70.65*b*	2.13*c*	10.34*d*
Réserve Léon-Provancher	56.32*a*	75.52*b*	7.86*c*	11.11*c*
Recruitment				
Île-aux-Grues	28.00*a*	66.83*b*	1.50*c*	7.50*d*
Réserve Léon-Provancher	54.44*a*	73.60*b*	7.05*c*	10.53*c*

Note: Values with different letters are significantly different ($p < 0.05$) after partial χ^2. B⁺, buried, B⁻, unburied; L⁺, covered by litter; L⁻, uncovered by litter.

Fig. 1. Percentage of *Quercus rubra* acorn cages attacked by deer at Réserve Léon-Provancher ($n = 20$ cages/treatment), in relation to burial (B⁺, buried; B⁻, unburied) and litter cover (L⁺, covered by litter; L⁻, uncovered by litter). Bars with different letters are significantly different ($p < 0.05$) after partial χ^2.

F = 113.6, *p* < 0.0001, df = 1). Initial acorn weight, however, did not affect water content ($F_{1,95} = 0.01$, $p > 0.05$, df = 1; two-way ANOVA).

Laboratory experiment 2: effect of decreasing soil moisture levels on acorn germination

Total acorn germination was 65.0%, mostly occurring during the stratification period. Soil moisture affected germination, which sharply decreased at low soil moisture levels, independently of initial seed weight (soil moisture content: Wald $\chi^2 = 23.9$, $p < 0.0001$, df = 3; seed weight: Wald $\chi^2 = 1.5$, $p > 0.05$, df = 1; NLM; Fig. 2).

Discussion

Results from both field and laboratory experiments show

Table 2. Summary of nominal logistic models for the probability of germination, emergence, and recruitment for *Quercus rubra* at two study sites, considering burial (B) and litter cover (L) as main factors (df: B = 1, L = 1, B × L = 1, block = 19).

	Île-aux-Grues	Réserve Léon-Provancher
Germination		
Burial (B)	41.39***	5.21*
Litter (L)	3.56ns	0.02ns
B × L	1.87ns	0.19ns
Block	47.08**	13.48ns
Emergence		
B	89.02***	41.33***
L	29.30***	4.28*
B × L	0.01ns	0.02ns
Block	75.24***	45.36***
Recruitment		
B	102.33***	43.11***
L	28.80***	3.84*
B × L	0.15ns	0.01ns
Block	68.89***	51.88***

Note: Wald χ^2 and *p* values are shown. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, $p > 0.05$.

Table 3. Percentage of *Quercus rubra* germination and mean values (± SE) of the acorn moisture content after stratification, in relation to burial (B⁺, buried; B⁻, unburied) and litter cover (L⁺, covered by litter; L⁻, uncovered by litter), in laboratory experiment 1.
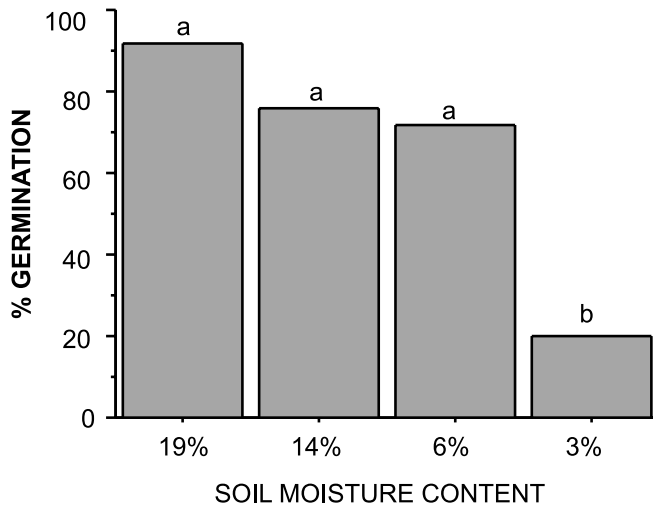
Burial	Litter	Germination (%)	Acorn moisture (%)
B+	L+	76.00*a*	41.24±2.38*a*
B+	L⁻	20.00*b*	13.33±0.93*b*
B⁻	L+	8.00*b*	7.05±0.79*c*
B⁻	L⁻	4.00*b*	8.84±0.67*c*

Note: Germination percentages and mean moisture percentages with different letters are significantly different ($p < 0.05$) after, respectively, partial χ^2 and minimum square means contrasts.

that red oak recruitment is affected by acorn burial and by the presence of a litter cover. However, the effect of these two factors differs depending on the regeneration stage. Our field experiment suggests a significant role for deer as acorn predators (see also Griffin 1971; Barnett 1977; Vander Wall 1990; Dey and Parker 1996) and shows that burial and litter cover protected acorns against secondary predators, perhaps by decreasing the encounter probability (Ovington and McRae 1960; Kikuzawa 1988; Myster and Pickett 1993; Kollmann and Schill 1996). Thus, acorns benefit from burial and litter by escaping post-dispersal secondary predators.

For those acorns surviving predation, both field and laboratory data showed that burial also promotes germination. Related to this, our laboratory experiments also showed that a reduction in acorn water content is associated with a decrease in germination ability. On the other hand, germination was strongly prevented at low soil water contents. These re-

Fig. 2. Percentage of *Quercus rubra* germination in relation to soil water content in the laboratory experiment 2. Bars with different letters are significantly different ($p < 0.05$) after partial χ^2.

sults support the idea that the positive effect of acorn burial depends on the provision of a moist environment preventing seed desiccation. By holding the environment at a higher humidity level and by permitting good seed–soil contact, burial enhances acorn moisture and, therefore, contributes to maintaining acorn viability through the dormancy period (Watt 1919; Shaw 1968; Griffin 1971; Nyandiga and McPherson 1992; Kollmann and Schill 1996; Germaine and McPherson 1998). Conversely, no litter effect on germination was shown by our field data. It is possible that litter presence in our study site did not impose differences in substrate humidity strong enough to affect germination. This was indirectly suggested by our laboratory experiment, where, under conditions of poor watering and strong dessication, acorns covered by a protective layer of leaves suffered lower water losses and had a higher percent germination (see also Barrett 1931; Shaw 1968; Sander 1990; Dey and Parker 1996). In addition, the existence of snow cover during the entire winter might modify the role of litter in the field by altering the humidity gradients at ground surface (see also Shimano and Masuzawa 1998).

Emergence was positively affected by burial at both study sites, as shown for other *Quercus* species (Barrett 1931; Tripathi and Khan 1990; Kollmann and Schill 1996; Fuchs et al. 2000). Lower emergence from unburied acorns was apparently caused by drying out and freezing of the growing radicle (Watt 1919; Ovington and McRae 1960; Kollmann and Schill 1996; Germaine and McPherson 1998, 1999). Conversely, emergence was consistently reduced by litter cover, for both buried and unburied acorns. This reduction in emergence may be due to allelopathic effects on radicle growth (Farmer 1997; and references therein), physical barrier and anomalous epicotyl development leading to withering (Barrett 1931), or damage by litter animals or pathogens (Barrett 1931; Facelli and Pickett 1991).

Seedling recruitment in the field was mainly affected by processes acting between germination and emergence, as this regeneration stage decreased the recruitment probability more than the germination stage itself. More importantly, the cumulative effects of burial and litter on germination and emergence determined a strong microsite effect on red oak recruitment in the field, with acorns buried but uncovered by litter having the highest recruitment probability. This forest-microsite specificity contrasts with the common assumption of low site sensitivity for larger-seeded trees like oaks (Seiwa and Kikuzawa 1996; Farmer 1997). On the other hand, considering germination and emergence separately as stages leading to recruitment enabled us to determine a differential effect of burial and litter depending on the stage. In fact, litter may be beneficial to seeds by reducing predation and increasing germination under water stress conditions but detrimental to seedlings by inhibiting emergence. This can be interpreted as a seed–seedling conflict determining the final outcome of recruitment, as safe sites for seeds are not necessarily safe sites for emerging seedlings (Lamont et al. 1993; Schupp 1995; see also Kollmann and Schill 1996 for *Quercus petraea*; Weltzin and McPherson 1999 for *Quercus emoryii*).

Our results suggest a potential beneficial effect of seed dispersers on red oak recruitment, by determining where acorns are delivered. In this sense, dispersers such as blue jays are known to selectively cache acorns in patches such as regenerating forest, forest gaps, and forest edges (Harrison and Werner 1984; Johnson and Adkisson 1985; Johnson et al. 1997). Caching in these open environments would match red oak requirements for germination and, more importantly, emergence (i.e., burial and no litter cover) and might be considered as "directed dispersal", since seeds are dispersed nonrandomly into more suitable patches (Vander Wall 1990; Johnson et al. 1997, Wenny 2001). In addition, this effect of directed dispersal may be even more significant at the northern limit of the species' range, where germination and emergence are more constrained by abiotic factors like frost and desiccation (Griffin 1971; Barnett 1977; Crow 1988; Germaine and McPherson 1999). By demonstrating a microsite effect on red oak recruitment, our study provides empirical support to the role of animal dispersers in the northwards expansion of red oak in North America (Johnson and Webb 1989; Vander Wall 1990). This role would be related both to the long dispersal distance provided by animals (Johnson and Webb 1989; Clark et al. 1998) and to the quality of caches as microsites where acorns escape abiotic (desiccation, frost) as well as biotic (seed predators, litter) mortality factors.

Acknowledgements

References

Atmospheric Environmental Service. 1981. Canadian climate normals. Temperature and precipitation. 1951–1980. Environment Canada, Atmospheric Environment Service, Downsview, Ont.

Atmospheric Environmental Service. 1982. Canadian climate normals. Frost. 1951–1980. Environment Canada, Atmospheric Environment Service, Downsview, Ont.

Barnett, R.J. 1977. The effect of burial by squirrels on germination and survival of oak and hickory nuts. Am. Midl. Nat. **98**: 319–330.

Barrett, L.I. 1931. Influence of forest litter on the germination and early survival of chestnut oak, *Quercus montana* Willd. Ecology, **12**: 476–484.

Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb, T., and Wyckoff, P. 1998. Reid's paradox of rapid plant migration. BioScience, **48**: 13–24.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*): a review. For. Sci. **34**: 19–40.

Dey, D., and Buchanan, M. 1995. Red oak (*Quercus rubra* L.) acorn collection, nursery culture and direct seeding: a literature review. Ontario Forest Research Institute, Toronto, Ont. For. Res. Inf. Pap. No. 112.

Dey, D., and Parker, W.C. 1996. Regeneration of red oak (*Quercus rubra* L.) using shelterwood systems: Ecophysiology, silviculture and management recommendations. Ontario Forest Research Institute, Toronto, Ont. For. Res. Inf. Pap. No. 126.

Facelli, J.M., and Pickett, S.T.A. 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. **57**: 1–32.

Farmer, R.E., Jr. 1997. Seed ecophysiology of temperate and boreal zone forest trees. St. Lucie Press, Delray Beach, Fla.

Fuchs, M.A., Krannitz, P.G., and Harestad, A.D. 2000. Factors affecting emergence and first-year survival of seedlings of Garry oaks (*Quercus garryana*) in British Columbia, Canada. For. Ecol. Manage. **137**: 209–219.

Germaine, H.L., and McPherson, G.R. 1998. Effects of timing of precipitation and acorn harvest date on emergence of *Quercus emoryi*. J. Veg. Sci. **9**: 157–160.

Germaine, H.L., and McPherson, G.R. 1999. Effects of biotic factors on emergence and survival of *Quercus emoryi* at lower treeline, Arizona, U.S.A. Écoscience, **6**: 92–99.

Griffin, J.R. 1971. Oak regeneration in the upper Carmel Valley, California. Ecology, **52**: 862–868.

Harrison, J.S., and Werner, P.A. 1984. Colonization by oak seedlings into a heterogeneous successional habitat. Can. J. Bot. **62**: 559–563.

Johnson, W.C., and Adkisson, C.S. 1985. Dispersal of beech nuts by blue jays in fragmented landscapes. Am. Midl. Nat. **113**: 319–324.

Johnson, W.C., and Webb, T. 1989. The role of blue jays (*Cyanocitta cristata* L.) in the postglacial dispersal of fagaceous trees in eastern North America. J. Biogeogr. **16**: 561–571.

Johnson, W.C., Adkisson, C.S., Crow, T.R., and Dixon M.D. 1997. Nut caching by blue jays (*Cyanocitta cristata* L.): implications for tree demography. Am. Midl. Nat. **138**: 357–370.

Kikuzawa, K. 1988. Dispersal of *Quercus mongolica* acorns in a broadleaved deciduous forest 1. Disappearance. For. Ecol. Manage. **25**: 1–8.

Kollmann, J., and Schill, H.-P. 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio, **125**: 193–205.

Lamont, B.B., Witkoski, E.T.F., and Enright, N.J. 1993. Post-fire litter microsites: safe for seeds, unsafe for seedlings. Ecology, **74**: 501–512.

Myster, R.W., and Pickett, S.T.A. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. Oikos, **66**: 381–388.

Nyandiga, C.O., and McPherson, G.R. 1992. Germination of two warm-temperate oaks, *Quercus emoryi* and *Quercus arizonica*. Can. J. For. Res. **22**: 1395–1401.

Ovington, J.D., and McRae, C. 1960. The growth of seedlings of *Quercus petraea*. J. Ecol. **48**: 549–555.

Rowe, J.S. 1972. Les régions forestières du Canada. Can. For. Serv. Publ. No. 1300F.

Sander, I.L. 1990. *Quercus rubra* L. Northern red oak. *In* Silvics of North America. Vol. 2. Hardwoods. *Techical coordinators*: R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. No. 654. pp. 727–733.

SAS Institute Inc. 2001. JMP® statistics and graphics guide, version 4 edition. SAS Institute Inc., Cary, N.C.

Schupp, E.W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio, **107/108**: 15–29.

Schupp, E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot. **82**: 399–409.

Seiwa, K., and Kikuzawa K. 1996. Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. Vegetatio, **123**: 51–64.

Shaw, M.W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in north Wales. J. Ecol. **56**: 647–660.

Shimano, K., and Masuzawa, T. 1998. Effects of snow accumulation on survival of beech (*Fagus crenata*) seeds. Plant Ecol. **134**: 235–241.

Tripathi, R.S., and Khan, M.L. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. Oikos, **57**: 289–296.

Vander Wall, S.B. 1990. Food hoarding in animals. The University of Chicago Press, Chicago, Ill.

Watt, A.S. 1919. On the causes of failure of natural regeneration in British oakwoods. J. Ecol. **7**: 173–203.

Weltzin, J.F., and McPherson, G.R. 1999. Facilitation of cone specific seedling recruitment and shifts in temperate savanna ecotones. Ecol. Monogr. **69**: 513–534.

Wenny, D.G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. Evol. Ecol. Res. **3**: 51–74.