LITTERFALL: AN OVERLOOKED FOOD SOURCE FOR WINTERING WHITE-TAILED DEER

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Abstract: Litterfall in mature forest stands may be a significant food resource for white-tailed deer (*Odocoileus virginianus*) wintering in northern regions, but has received little study. To determine forage production, we measured biomass of litterfall in unharvested stands of 3 wintering areas, and biomass of browse from deciduous trees and shrubs in unharvested stands and harvested patches of the same wintering areas during January–March 1994. Mean biomass of northern white-cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*), arboreal lichens (*Usnea* spp. and *Evernia* spp.), and hardwood leaves in unharvested stands was 18.4 kg/ha (SE = 4.80). At mean digestible energy (DE) levels of 1.5 and 1.7 kcal/g dry matter (DM), biomass of hardwood browse and litter biomass did not differ ($P > 0.15$) between harvested patches and unharvested stands. At greater mean levels of digestible energy (1.9 and 2.1 kcal/g DM), biomass was greater ($P < 0.05$) in unharvested stands than harvested patches because of the relatively high DE content of litterfall. We concluded that litterfall in unharvested stands was high relative to the availability of more commonly measured browses (e.g., understory trees and shrubs), and may be more palatable and of greater nutritional value. However, availability of hardwood browse during winter may be more predictable than litterfall.

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Wintering areas are critical habitat for white-tailed deer in northern regions because of reduced snow depths and enhanced thermal cover on these conifer-dominated sites (Telfer 1967, Ozoga 1968). However, the mature conifer canopy also reduces production of hardwood browse in the understory (Blouch 1984), and preferred browses such as northern white-cedar and eastern hemlock are typically unavailable because of overbrowsing (Frelich and Lorimer 1985, Verme and Johnston 1986). In addition, most browse species readily available in wintering areas are relatively low in nutritional value (Robbins and Moen 1975, Mautz et al. 1976).

There is some evidence that litterfall may be an important winter food for white-tailed deer, but litterfall has rarely been included in studies of food availability. Crawford (1982) and Shively (1989) reported that tame white-tailed deer ate eastern hemlock shoots that collected on the snow surface following periods of strong winds. Stevenson and Rochelle (1984) and Hodgman and Bowyer (1985) found that black-tailed deer (*O. hemionus columbianus*) and white-tailed deer consume considerable amounts of arboreal lichens during winter. Arboreal lichens have a substantially greater digestibility than other common winter foods (Robbins 1987) and may be an important winter food resource.

We quantified litterfall deposited during winter in forest stands typically used by deer in Maine wintering areas. To evaluate the potential significance of litterfall to wintering deer, we also compared biomass and nutritional quality

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of litterfall in unharvested forest stands to production of woody browse in harvested and unharvested areas.

STUDY AREA

We conducted our study in 3 deer wintering areas in central Maine (Sebec, Macwahoc Plt, and T1 R5 WELS Townships) from 1 January to 31 March, 1994. This region has severe winters, with mean January temperatures of −15°C and mean annual snowfall of 180–250 cm (McMahon 1990). During the winter of 1994, biweekly snow depths ranged from 0 to 77 cm in the open and 0 to 61 cm under the softwood canopy; total snowfall was 234 cm. Forests of the region have been classified as northern hardwood-hemlock-white pine (*Pinus strobus*; Westveld et al. 1956). Common canopy species in our study sites were eastern hemlock, spruce (*Picea* spp.), balsam fir (*Abies balsamea*), northern white-cedar, white pine, yellow birch (*Betula alleghaniensis*), and red maple (*Acer rubrum*). Understory species included American beech (*Fagus grandifolia*), beaked hazelnut (*Corylus cornuta*), yellow birch, paper birch (*B. papyrifera*), gray birch (*B. populifolia*), red maple, sugar maple (*A. saccharum*), mountain maple (*A. spicatum*), striped maple (*A. pensylvanicum*), pin cherry (*Prunus pensylvanica*), red oak (*Quercus rubra*), aspen (*Populus* spp.), white ash (*Fraxinus americana*), willows (*Salix* spp.), balsam fir, and spruce. Trees were relatively large; the mean diameter at breast height for mature species on our study sites was 58–76 cm for northern white-cedar, 48–56 cm for balsam fir, 46–66 cm for spruce, 64–84 cm for eastern hemlock, and 89–136 cm for white pine.

METHODS

Within each wintering area, we selected 2 pairs of harvested and unharvested stands that ranged in size from 2.5 to 5.0 ha. Harvested stands had received patch cuts between 1985 and 1987 that covered 20–50% (1.0–2.5 ha) of the area; individual patches ranged in size from 400 to 2,000 m^2. In harvested stands, we only conducted sampling within cut patches. We measured biomass of hardwood browse from 1 to 15 January in harvested and unharvested stands, and litterfall from 1 January to 31 March in unharvested stands only. We did not measure litterfall in harvested stands, because the canopy had been removed within patches; thus, any litter collected on these sites would have been from surrounding areas. We measured biomass of hardwood browse using 14–25 systematically located 2- × 5-m plots and counted all hardwood twigs, browsed and unbrowsed, within 0.5–2.0 m of ground level using a twig-count method (Shafer 1963). We measured the diameter of each twig at the proximal end of current annual growth and used diameter-based regression equations to estimate twig biomass. Browse availability is expressed as biomass available to deer (kg/ha) at the start of the experimental period. We did not measure biomass of conifer browse because balsam fir is a low-quality forage (Ullrey et al. 1968), and northern white-cedar and eastern hemlock were rare in the understory.

We measured litterfall using 20 litter traps arranged in a 4 × 5 grid with 20-m spacing. Litter traps were circular containers with a diameter of 50.8 cm and depth of 68.6 cm. Every 30 days, litter was sorted by species, dried, and weighed. Potential forages from litterfall were arboreal lichens, conifer foliage (northern white-cedar, eastern hemlock, balsam fir, spruce, white pine), and hardwood leaves (Crawford 1982, Hodgman and Bowyer 1985); individual conifer needles were excluded. We also estimated biomass of lichens on fallen limbs too large for collection in litter traps by systematically searching unharvested stands for branches with lichens. We searched sites 2–4 days after snowfalls of ≥5 cm (n = 9) to avoid counting branches located in previous searches. We measured branch length and subjectively categorized lichen abundance (low, medium, high) to estimate lichen biomass on each branch. We estimated mean biomass of lichens for each category of abundance by cutting 30 branches of each category and determining dry mass of lichens per centimeter of branch length. Litterfall measurements are expressed as biomass available to deer (kg/ha) from 1 January to 31 March.

To assess potential importance of high-use litterfall from an energetic perspective, we estimated forage biomass available in harvested patches and unharvested stands at DE levels of 1.5, 1.7, 1.9, and 2.1 kcal/g of DM (Hobbs and Swift 1985). For analyses, we defined high-use litter as northern white-cedar, eastern hemlock, arboreal lichens, and hardwood leaves. We excluded balsam fir, spruce, and white pine from analyses of forage availability because balsam fir is considered a poor forage (Ullrey et al. 1968), and spruce and white pine are not commonly

Table 1. Mean biomass (kg/ha) of litterfall available to white-tailed deer in 6 unharvested softwood stands in 3 deer wintering areas in central Maine, Jan–Mar 1994.

	n	$\bar{x}$	SE
High quality litter			
Northern white cedar	6	1.95	1.07
Eastern hemlock	6	9.15	5.08
Lichen	6	4.13	0.79
Hardwood leaves	6	3.16	1.16
Balsam fir	6	13.10	6.70
High-use litter[a]	6	18.39	4.80
Other litter[b]			
Spruce	6	35.58	16.07
White pine	6	0.94	0.67
Total litter	6	68.00	11.64

[a] High-use litter includes northern white cedar, eastern hemlock, lichen, and hardwood leaves.
[b] Spruce and white pine are not considered potential foods for white-tailed deer in Maine.

consumed by deer in Maine (Crawford 1982, Shively 1989). We estimated energetic content of litterfall and hardwood species with DE values from Hobbs et al. (1981), Gray (1993), and Raymond (1994). We used t-tests to compare forage biomass between harvested patches and unharvested stands at mean levels of diet quality. We used nested analysis of variance to compare biomass of total hardwood browse, individual species of browse, and litter between harvested patches and unharvested stands.

RESULTS

Northern white-cedar, eastern hemlock, lichens, and hardwood leaves comprised 27.0% (18.4 kg/ha) of total litterfall in unharvested stands (Table 1). Mean total biomass of hardwood browse in harvested patches (33.6 kg/ha) was greater than in unharvested stands (3.0 kg/ha; $F_{1,10} = 31.15$, $P < 0.001$; Table 2). Paper birch ($F_{1,10} = 13.06$, $P = 0.005$), red maple ($F_{1,10} = 16.53$, $P = 0.002$), willow ($F_{1,10} = 5.63$, $P = 0.039$), and yellow birch ($F_{1,10} = 9.67$, $P = 0.011$) had greater biomass in harvested patches compared to unharvested stands.

Harvested patches had greater biomass of hardwood browse than unharvested stands at the lowest mean level of DE (1.5 kcal/g DM; $t_{10} = 2.02$, $P = 0.034$; Table 3). There was no difference between biomass of hardwood browse in harvested patches and unharvested stands at levels of DE ≥1.7 kcal/g DM. Biomass of high-use litter was substantially greater than biomass of hardwood browse in harvested patches and unharvested stands at DE levels >1.5 kcal/g DM. Availability of total forage (hardwood browse and high-use litter) was greater in unharvested stands than harvested patches at DE levels of 1.9 ($t_{10} = 1.93$, $P = 0.037$) and 2.1 kcal/g DM ($t_{10} = 2.26$, $P = 0.023$).

DISCUSSION

Litterfall may be a significant dietary component of wintering deer in Maine. In the unharvested stands we studied, high-use litter accounted for >85% of the available forage during January–March. Similarly, Rochelle (1980) found that litterfall biomass during October–March was greater than browse biomass in some stands on northern Vancouver Island. Several studies suggest that this litterfall may be consumed by wintering deer. Crawford (1982) and Shively (1989)

Table 2. Biomass of hardwood browse (kg/ha) available to white-tailed deer during winter on harvested and unharvested sites in 3 deer wintering areas in central Maine during Jan–Mar 1994.

	Unharvested			Harvested			
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	P
American beech	6	0.21	0.19	6	1.06	1.04	0.404
Beaked hazelnut	6	2.00	1.98	6	2.31	1.77	0.914
Gray birch	6	0.04	0.03	6	0.42	0.21	0.092
Mountain maple	6	0	0	6	0.22	0.22	0.334
Paper birch	6	0.21	0.16	6	5.75	1.69	0.005
Pin cherry	6	0	0	6	2.02	0.86	0.088
Red maple	6	0.28	0.23	6	7.22	1.91	0.002
Red oak	6	0	0	6	2.18	1.46	0.136
Striped maple	6	0	0	6	0.14	0.14	0.329
Sugar maple	6	0	0	6	1.77	1.77	0.315
Aspen spp.	6	0.01	0.01	6	2.38	1.51	0.120
White ash	6	0.01	0.01	6	0.31	0.20	0.150
Willows spp.	6	0	0	6	0.44	0.20	0.039
Yellow birch	6	0.26	0.20	6	8.19	2.81	0.011
Total	6	3.01	2.28	6	33.64	2.25	0.001

Table 3. Hardwood and litter biomass (kg/ha) available to white-tailed deer at 4 levels of mean digestible energy on harvested and unharvested sites in 3 central Maine deer wintering areas, Jan–Mar 1994.

	Unharvested			Harvested			
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	P
Hardwood biomass							
2.1 kcal/g	6	0.01	0.01	6	2.38	1.38	0.177
>1.9 kcal/g	6	0.02[a]	0.02	6	4.89	2.82	0.177
>1.7 kcal/g	6	0.05	0.03	6	9.70	5.36	0.161
>1.5 kcal/g	6	0.80	0.33	6	22.28	6.80	0.034
Hardwood and high-use litter biomass[b]							
2.1 kcal/g	6	20.13	5.04	6	2.38[c]	1.38	0.023
>1.9 kcal/g	6	20.81	4.92	6	4.89	2.82	0.037
>1.7 kcal/g	6	22.07	4.90	6	9.70	5.36	0.152
>1.5 kcal/g	6	22.54	4.97	6	22.28	6.80	0.978

[a] Means for lower levels of digestible energy are cumulative and include biomass available at greater values of digestible energy.
[b] High-use litter includes northern white cedar, eastern hemlock, lichen, and hardwood leaves.
[c] Litterfall was not measured on harvested sites.

reported high consumption of hemlock litter (33% of total intake by mass) and arboreal lichens (19% of total intake by mass) by tame deer in Maine wintering areas, and Rochelle (1980) found that lichen litterfall was 4 times greater inside deer exclosures than outside.

Litterfall also may be greater in nutritional quality than hardwood browses available to wintering deer. Digestibility values for eastern hemlock (2.41 kcal/g DM), northern white-cedar (2.46 kcal/g DM), and arboreal lichens (2.86 kcal/g DM) are greater than digestibility values for hardwood browses (Mautz et al. 1976, Hobbs et al. 1981). Balsam fir accounted for 19.3% (13.1 kg/ha) of total litterfall, but its value to deer is uncertain because of poor digestibility (Ullrey et al. 1968) and high concentrations of plant secondary compounds (Robbins et al. 1987, Thompson et al. 1989). However, foliage from the tops of mature balsam fir that falls as litter may be more palatable and have lower concentrations of plant secondary compounds than lower growing foliage, as has been observed with Douglas-fir (*Pseudotsuga menziesii*; Tucker et al. 1976, Dawson et al. 1990).

Arboreal lichens accounted for only 6.1% (4.13 kg/ha) of the total biomass of litter available to deer in unharvested stands. However, because of their high digestibility, they accounted for 30.6% of the total energy available at a mean DE level of 2.1 kcal/g DM. Selective foraging of arboreal lichens by deer could significantly raise overall diet quality and reduce overwinter loss of mass. Stevenson and Rochelle (1984) found that arboreal lichens constituted 26% by volume of black-tailed deer rumen contents, which indicated deer may consume large quantities of lichens.

Litterfall also may be an important winter forage for fawns in northern regions because of their low fat reserves and the energetic demands of extreme winter conditions. Gray and Servello (1995) estimated overwinter loss of mass to be ≥30% for fawns on diets containing >70% hardwood browse and attributed this loss to gut-fill limitations associated with low-quality diets. The inclusion of relatively small amounts of high-quality forages (e.g., litterfall) may allow deer to raise overall diet quality during winter and maintain adequate food intake on browse diets.

Total biomass of hardwood browse in harvested patches was approximately 50% greater than available forage (hardwood browse and high-use litter) in unharvested stands. However, unharvested stands had greater biomass available at mean levels of diet quality ≥1.9 kcal/g DM because of relatively high digestibility of most litter components. However, DE estimates for hardwood browses were based on current annual growth, which may not be entirely consumed by deer (Wetzel et al. 1975). Because a negative relation exists between the diameter of hardwood twigs and DE content (Gray 1993), deer could improve diet quality by selecting twigs of smaller diameter at the expense of forage biomass.

Unlike woody browse, litter is not available continuously throughout winter but is present in pulses over short time periods. Litter deposition may be influenced by strong winds and precipitation (Edwards et al. 1960, Rochelle 1980), and snow frequently covers fallen litter. Stevenson and Rochelle (1984), however, found no relations among litter deposition and wind, snow depth, or precipitation and suggested that deposition is influenced by individual storms rather than overall weather patterns. Weather conditions (precipitation, storm frequency) from 1 January to 31 March in our study area were typical for the region; there were 10 winter storms with snow accumulation ≥5 cm.

We have observed that litter periodically resurfaces during winter thaw periods. As a result, litter availability may increase substantially during spring thaw, a critical period for wintering deer. Energetic constraints on foraging may also influence use of litter. Small, widely scattered particles may not be used, especially when snow depths limit deer movement. During these periods, litter use may be limited to areas along trail systems, but this limitation likely applies to woody browse as well (Weckerly and Kennedy 1992).

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