EFFECTS OF MARCESCENT LEAVES ON WINTER BROWSING BY LARGE HERBIVORES IN NORTHERN TEMPERATE DECIDUOUS FORESTS

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ABSTRACT: Presence of marcescent leaves during winter is a common phenomenon in northern-temperate deciduous forests across the Holarctic, but the ecological significance of marcescence on woody vegetation has received little attention. Especially, implications for browsing by cervids during winter have not been determined. Therefore, I conducted a feeding trial using free-roaming red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and sika deer (*Cervus nippon*) to evaluate effects of marcescent leaves on herbivory of European beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), and common oak (*Quercus robur*) during winter. The feeding trial was conducted in Jægersborg Dyrehave, Denmark, during February 1992. Forty small-diameter (< 6 mm) branches of each tree species with ≤ 2 years of growth and marcescent leaves present were divided into 2 groups. One group had their leaves removed (treatment) and the other group had the leaves retained (control). Branches were labeled, weighed, and randomly placed in a grid (0.5 x 0.5 m apart) in the field. After 7 days, branches were counted and weighed to determine amount of browse removed. In addition, 12 branches of each species were collected for biomass and chemical analyses. Stems and leaves were analyzed separately for crude protein, neutral-detergent fiber, acid-detergent fiber, lignin, and cellulose. Both beech and hornbeam were browsed significantly more by weight and by number of branches when the leaves were removed. Oak branches were browsed the same regardless of leaf presence. Biomass of marcescent leaves of beech and hornbeam were a significantly greater proportion of the overall branch biomass compared with oak. Chemical analyses showed that stems of hornbeam and beech, when compared with their marcescent leaves, had somewhat higher food quality when fiber and crude protein were compared, but marcescent leaves had a higher lignin content. Leaves compared with stems of common oak had a higher protein and lower lignin content compared with other species. These results indicate that marcescent leaves greatly reduced the nutritive value of winter browse, which was reflected in the lower browse preference for their leaves. Therefore, marcescent leaves may be viewed as an anti-herbivore mechanism.

ALCES VOL. 37 (2): 475-482 (2001)

Keywords: beech, Cervidae, deer, food quality, food selection, foraging ecology, hornbeam, marcescent leaves, oak, plant defenses, plant-herbivore interactions

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During winter, presence of marcescent leaves (senescent leaves still attached to the branches), on beech, hornbeam, and common oak is a striking phenomenon of hardwood forests in northern Europe. Marcescence is a juvenile trait in young trees or lower branches of larger trees (Schaffalitzky de Muckadell 1962), where leaves are retained up to a height of about 3 m during the entire winter, and not shed until spring. The ecological significance of marcescent leaves on woody vegetation has received little attention in the past century. Mostly, interest has concentrated on physiological aspects of marcescence in plants (Berkeley 1931, Hoshow and Guard

1949, Addicott 1982) or its evolutionary implications for the development of deciduousness (Wanntorp 1983). Implications for herbivory, however, have not been determined. A few explanations have been presented to explain why dead leaves may remain attached throughout the winter. Otto and Nilsson (1981) suggested that senescent leaves are retained until the start of the next growing season to delay nutrient cycling. Shedding of leaves in spring ensures release of nutrients from decomposition, benefiting the parent tree instead of being leached out during winter. Nonetheless, modeling results by Escudero and del Arco (1987) suggested that marcescence had no effect on timing of return of soil nutrient from marcescent leaves. In contrast, Baagöe and Bræstrup (1986) reported that retained leaves may help accumulate windblown snow, which provides more water during spring and, presumably, increased survival of young trees. Schaffalitzky de Muckadell (1959) suggested that presence of marcescent leaves was a juvenile trait more pronounced in shaded plants, which could be indicative of important, but unknown, silvicultural properties. Neither Baagöe and Bræstrup (1986) nor Schaffalitzky de Muckadell (1959) offered empirical evidence to support their views. Several studies have investigated the physiological mechanisms behind marcescence (Berkeley 1931, Hoshow and Guard 1949, Addicott 1982), but none have offered an ecological explanation of the phenomenon.

In northern-temperate deciduous forests, woody browse for ungulates may be limited to low tree branches or young trees because of extensive snow cover. Ungulates generally are unable to browse selectively for stems and buds by avoiding dead leaves (Kay 1987). Consequently, these large herbivores must ingest marcescent leaves when browsing woody vegetation. This behavior may greatly influence the overall quality of winter food for ungulates, and indicates that marcescent leaves should be considered in the context of ungulate herbivory. I tested 2 hypotheses concerning effects of marcescent leaves on winter browsing by cervids. First, presence of marcescent leaves decreases browsing on juvenile winter twigs of oak, beech, and hornbeam. Second, marcescent leaves function as a defense against herbivory by lowering winter browse quality.

STUDY AREA

Jægersborg Dyrehave, located within the northern suburbs of Copenhagen, Denmark, was utilized for an open-field feeding trial (Fig. 1). The study site was located within the northernmost extent of the temperate deciduous forest zone in Europe (Dahl 1998). These forests are dominated

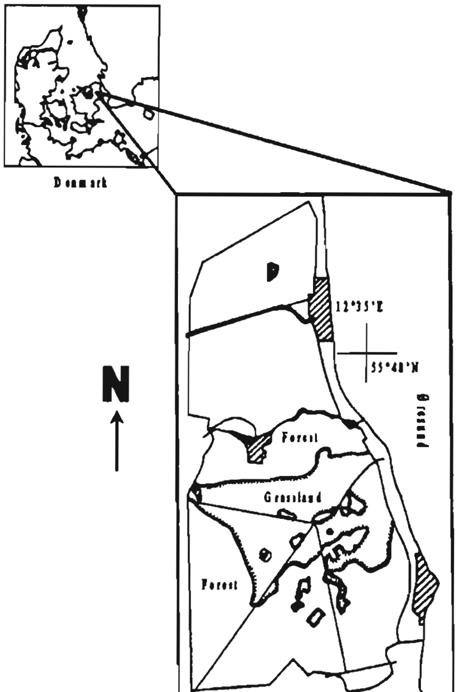

Fig. 1. Geographic location of open-field feeding trial (✱) with free-roaming red deer, fallow deer, and sika deer during winter at Jægersborg Dyrehave, Denmark, 1992.

by beech, oak species, and hornbeam, generally with a limited shrub layer. A prolific herbaceous layer, however, dominates the forest floor in early spring before leafout. Forest and grassland habitats of Jægersborg Dyrehave are managed primarily for recreational day use by the general public by providing a parkland landscape. The area also is managed for high-density populations of free roaming red deer (*Cervus elaphus*), sika deer (*Cervus nippon*), and fallow deer (*Dama dama*), which provide recreation for royal hunting parties. Consequently, supplemental feeding with hay, straw, and beets is conducted during winter.

METHODS

An open-field feeding trial with free-roaming red deer, sika deer, and fallow deer was conducted during February 1992. Forty small-diameter (< 6 mm) canopy branches of each of the 3 dominant tree species with ≤ 2 years of growth and marcescent leaves present were divided into 2 groups. One group had the leaves removed (treatment) and the other group had the leaves retained (control). Branches were labeled, weighed to the nearest 1 g, and randomly placed in a grid (0.5 x 0.5 m apart) in the field. Ungulate species had access to the feeding site; however, red deer and fallow deer predominantly used the area. After 1 week all branches were weighed again. Because of temperatures < 0° C, the reduction in weight reflected amount of browsing rather than desiccation, and for each individual branch, percent browsing was calculated. In addition, 12 branches of each species were collected for biomass and chemical analyses. Stems and leaves were analyzed separately for crude protein (micro-Kjeldahl), neutral detergent-fiber (NDF), acid-detergent fiber (ADF), lignin, and cellulose (Goering and Van Soest 1970; Mould and Robbins 1981, 1982; Hanley et al. 1992).

Statistical analyses included ANOVA, *t*-test, and regression analysis (Zar 1984). Percentage values were corrected for lack of normality with arcsine transformations.

RESULTS

Within each species, a comparison of initial biomass of branches between weights of control and treatment groups indicated that there was no significant difference ($t_{118} = 0.184$, $P = 0.854$). Unbrowsed branches did not experience any change in weight. I therefore concluded that only undetectable changes in moisture content of the branches may have occurred.

Ungulates strongly selected against branches with marcescent leaves of beech and hornbeam, but showed no preference in common oak (ANOVA: leaves: $F_{1,120} = 18.981$, $P < 0.0001$; species: $F_{2,120} = 19.803$, $P < 0.0001$; leaves x species interaction: $F_{2,120} = 7.924$, $P = 0.001$) (Fig. 2). For beach and hornbeam, all branches without leaves were browsed, while 5 branches of each of the species were unbrowsed. Oak branches were browsed evenly with 1 branch

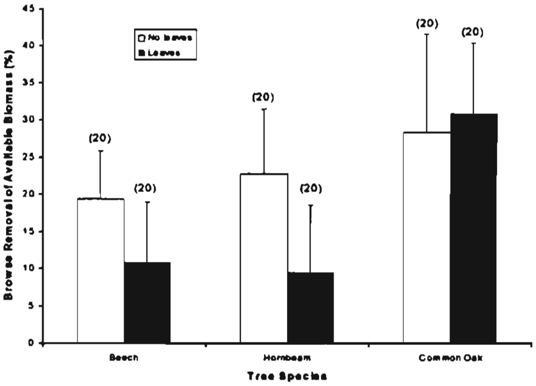

Fig. 2. Browse preference for branches with and without marcescent leaves by ungulates in northern temperate deciduous forests during winter 1992. Three species were compared: beech, hornbeam, and common oak. Bars are SD; $n = 20$. A significantly (ANOVA) lower preference occurred for beech ($P < 0.0008$) and hornbeam ($P < 0.0001$) twigs with marcescent leaves compared with twigs without leaves. Common oak showed no difference ($P = 0.5531$).

in each treatment unbrowsed. In contrast to oak, marcescent leaves constituted a significantly ($P = 0.0002$) greater proportion of the branch biomass in both beech and hornbeam (Fig. 3). Ungulates showed no selection for branch size during the feeding trial (beech: $r^2 = 0.05$, hornbeam: $r^2 = 0.06$, oak: $r^2 = 0.006$).

Chemical analyses indicated that beech and hornbeam had roughly 6% crude protein in both leaves and stems (Table 1). In contrast, common oak had almost 10% in stems, but < 4% in leaves. Beech and hornbeam also showed similar contents of NDF, ADF, and hemicellulose, whereas oak had somewhat lower levels of NDF and ADF, but higher levels of hemicellulose. The most noticeable difference in fiber was higher levels of lignin in the marcescent leaves of beech and hornbeam compared with stems. In contrast, stems of oak had a higher lignin content than leaves, but were lower in lignin than leaves of hornbeam and beech. Cellulose levels were highest in beech and hornbeam ranging from 33-35% in leaves to 39-42% in stems. Levels of cellulose in oak ranged from 33% in stems to 25% in leaves. Ash content was not important, and was < 1% in all species.

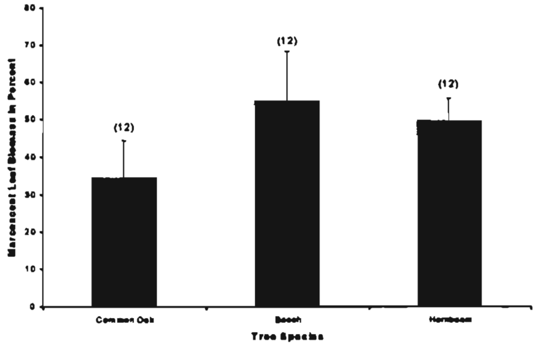

Fig. 3. Marcescent leaf biomass as percentage of total 2-year branch biomass of common oak, beech, and hornbeam during winter. Beech and hornbeam had a significantly ($n = 12$, $P = 0.0001$) higher amount of marcescent biomass compared with common oak.

DISCUSSION

Plants are not passive participants in herbivory (Klein 1977, Bryant et al. 1985, Rhoades 1985, Bryant et al. 1991). Secondary chemicals, hairs, and thorns (Schaffalitzky de Muckadell 1962, Crawley 1983) are typical characteristics acquired to render tissues less suitable to herbivores, and occur to a greater extent in juvenile and

Table 1. Mean percentage of crude protein and fiber components in marcescent leaves and stems of 3 deciduous trees from temperate forests of Denmark during winter, 1992. Standard deviation in parenthesis; $n = 4$.

Sample	Protein	NDF[1]	ADF[2]	Hemicellulose	Lignin	Cellulose
Beech						
Stems	6.7(0.91)	72.5(3.55)	58.0(3.57)	14.5(0.35)	16.0(2.70)	42.0(5.79)
Marcescent leaves	6.0(0.27)	69.9(4.04)	58.8(2.79)	11.1(1.29)	23.9(1.76)	35.2(1.72)
Hornbeam						
Stems	6.4(0.32)	71.6(4.53)	57.5(5.75)	14.1(1.75)	18.8(1.99)	38.7(7.58)
Marcescent leaves	5.9(0.39)	66.9(2.51)	54.6(0.69)	12.3(2.14)	22.7(3.05)	33.0(3.21)
Common Oak						
Stems	9.7(0.39)	68.9(2.96)	53.0(3.52)	15.8(1.66)	20.3(3.77)	32.7(3.00)
Marcescent leaves	3.8(0.71)	58.6(4.13)	42.6(2.75)	16.0(2.77)	17.8(1.52)	25.1(3.49)

[1] Neutral-detergent fiber.

[2] Acid-detergent fiber.

adventitious shoots than in adult plants (Bryant and Kuropat 1980). Young trees within reach of browsing ungulates are especially vulnerable to herbivory and would require more protection from browsing than out-of-reach stems and branches.

The feeding trial I conducted clearly demonstrated that ungulates avoided branches of beech and hornbeam with marcescent leaves, but not branches of common oak (Fig. 2). This avoidance can be attributed to the lower composite forage quality of branches (Table 1) rather than branch size.

Marcescent leaves of beech and hornbeam likely reduced overall digestibility (Table 1) of available forage for ungulate herbivores because of their high lignin and low protein content (Van Soest 1994). The low nitrogen values of marcescent leaves in this study were comparable to values from regular abscised senescent leaves (Killingbeck 1996). Furthermore, leaves constituted almost 50% of the available biomass on stems (Fig. 3). In contrast, marcescent leaves of oak only provided about 30% of the available biomass. Also, protein content of oak was higher than in beech and hornbeam. This outcome was clearly reflected in the results from browsing of stems (Fig. 2). Therefore, marcescent leaves may act as a defense mechanism against large herbivores, in a manner similar to thorns and secondary chemicals.

Accessibility to low-hanging branches and juvenile trees may become critical to ruminant herbivores during winter when snow accumulations cover the herbaceous layer and limit availability of shrubs. Browsing woody vegetation provides the only source of food during that season. When marcescent leaves constitute most of the diet, ungulates spend more time processing food, especially increased rumination time because of lower food quality (Robbins 1993). When leaves finally are shed in spring, the herbaceous layer of the forest floor is usually well established (Vedel 1975), and browsing pressure on woody vegetation is diminished (Strandgaard 1972).

My results probably should be viewed as conservative, because ungulates in this study received supplemental high-quality food during winter. As a consequence, they would not require large amounts of low-quality browse, which may explain why common oak with marcescent leaves was not avoided. Overall, common oak had a better forage quality compared with beech and hornbeam (Table 1).

Marcescence also occurs in species outside northern Europe. In the deciduous forests of North America, pin oak (*Quercus palustris*) and American beech (*Fagus grandifolia*) retain their leaves (Brockman 1979). In addition, *Salix pulchra* in arctic environments of Alaska and eastern Siberia has marcescent leaves (Hultén 1968). Given that marcescent leaves occur in woody vegetation in several taxonomic groups within the Holarctic, where winter browsing by large ungulates is a major component of the ecosystem (Franzmann 1978, Wallmo 1981, Bryant and Maser 1982, Clutton-Brock et al. 1982, Baker 1984, Putman 1996), leaves likely are retained throughout winter as an energetically inexpensive way of reducing herbivory. Furthermore, the European species only retain their leaves within the reach of large herbivores such as red deer.

In conclusion, I propose that marcescent leaves should be viewed as a defense mechanism against browsing by large herbivores. Herbivores most affected by decreased food digestibility and quality would be the concentrated selectors with relatively low to medium rumino-reticular volume to body-weight ratios, such as roe deer (*Capreolus capreolus*), white-tailed deer (*Odocoileus virginianus*), black-tailed deer (*O. hemionus*), and moose (*Alces alces*) (Klein 1985, Hofmann 1988).

ACKNOWLEDGEMENTS

I thank K. Waage Sørensen for logistical support in the field. Foremost, I thank D. R. Klein for being a mentor and providing me with a great beginning. Appreciation is extended to F. S. Chapin and R. W. Ruess for their helpful reviews of an earlier draft of the manuscript.

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