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Deer Browsing Creates Rock Refugia Gardens on Large Boulders in the Allegheny National Forest, Pennsylvania

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Abstract.—We surveyed the vegetation growing on the surface of tall boulders (>1.5 m), on the surface of short boulders (<0.5 m) and in areas adjacent to these boulders on the soil surface in the Allegheny National Forest, Pennsylvania. Our purpose was to test the hypothesis that tall boulders serve as refugia from deer browsing for both woody plant species as well as understory herbs. We conducted our surveys during spring when many of these herbs reproduce sexually and their inflorescences are vulnerable to browsing. Deer cannot gain access and browse on these tall boulders, whereas they can easily browse plant species on shorter boulders and on the forest floor. We predicted that the tall boulders would have the highest plant diversity, woody species density and the density of reproductive individuals of understory herbs. We found a total of more than 1300 reproductive individuals of flowering herbs of more than 10 species growing on tall boulders and only 6 reproductive individuals of only a few species growing on the soil surface. Overall, there was a much greater density and diversity of woody species and sexually reproducing herbs on tall boulders or Rock Refugia Gardens than either on short boulders or the soil surface. Because the diversity and abundance of vegetation on the short boulders was nearly identical to that on the forest floor, our findings are unlikely to be explained by tall boulders providing a superior edaphic or abiotic habitat relative to habitats on the forest floor. Species accumulation curves showed that plant species continued to accrue with area on tall boulders, but did not increase with area on the forest floor or on the short boulders. These Rock Refugia Gardens demonstrate the pervasive and deleterious impact that deer are having on plant species diversity and forest regeneration in the Allegheny National Forest and likely elsewhere in the eastern US where these vertebrates are abundant.

Introduction

Large populations of white-tailed deer (*Odocoileus virginianus*) have caused extensive damage throughout large portions of the eastern deciduous forest (Rooney and Dress, 1997; Miller *et al.*, 1992; Waller and Alverson, 1997; Balgooyen and Waller, 1995; Augustine and Frelich, 1998; Webster *et al.*, 2001; Russell *et al.*, 2001; Horsley *et al.*, 2003). Overbrowsing by deer can dramatically reduce woody species diversity and abundance, thereby altering patterns of forest regeneration and succession for decades. Forest herbs may be even more vulnerable to browsing than many tree species because they cannot grow tall enough to reach a size refuge. There is evidence that some plant species may only become abundant in the Allegheny National Forest in Pennsylvania in locations that provide an effective refuge from browsers (*e.g.*, tall boulders, tree tip-up mounds, slash piles; Grisez, 1960; Rooney, 1997; Long *et al.*, 1998; Banta *et al.*, 2005).

In northern Pennsylvania, deer have been over abundant for more than 60 y and directly threaten the diversity, sustainability and conservation of forested habitats (Horsley *et al.*, 2003). Here we test the hypothesis that tall boulders serve as refugia from browsing for

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numerous woody and herbaceous species. Our previous work (Banta *et al.*, 2005) has shown that tall boulders have a higher diversity and abundance of both woody and herbaceous taxa during the mid-summer. Here we expand upon our past work in four ways. First, we now compare the vegetation on tall boulders with not only the forest floor but also with vegetation on smaller boulders that were too short to serve as refuge from deer. By surveying the vegetation on shorter boulders, we eliminate the potential that boulders could provide a more favorable edaphic or abiotic habitat to herbs and woody species. For example, below-ground competition between herbs and adult trees may be substantially reduced on the surface of boulders (Banta *et al.*, 2005). If so, then plant abundance and diversity may be higher on boulders not because boulders serve as a refugia from deer but rather they serve as a refugia from root competition. Secondly, we conducted our vegetation surveys during the early spring (vs. midsummer) when many forest herb species are typically reproductive. Thus, we could test whether boulders provide a habitat that can support sexual reproduction. Third, by surveying new boulders that were more than 30 kilometers from boulders surveyed in past work (Banta *et al.*, 2005), we can determine whether boulders may typically act as suitable refugia. Finally, we construct species accumulation curves that unequivocally demonstrate the pervasive suppression of browsing on forest biodiversity.

METHODS

We conducted our survey within the Allegheny National Forest (ANF) in northwestern Pennsylvania. These forests are part of the hemlock-northern hardwoods association and experience a cool and humid climate with an average annual temperature and precipitation of 7.8 C and 106.7 cm, respectively. Our study site was located near where the Tanbark Trail crosses U.S. Route 62 about 12 miles south of Warren, Pennsylvania. The elevation of the site is ~400 m with a North-Northeast aspect. This site is located on a Venango bedrock formation and contains numerous large boulders (large sections of cross-bedded sandstone) that have broken off the top of the ridge-top and slid down the steep hillsides over geologic time. Abundant canopy tree species include Hemlock (*Tsuga canadensis*), Sugar Maple, (*Acer saccharum*), Red Maple (*A. rubrum*), White Ash (*Fraxinus americana*), Black Cherry (*Prunus serotina*) and Yellow Birch (*Betula allegheniensis*). Further descriptions of the flora, climate, and geology can be found in Hough and Forbes (1943) and Bjorkbom and Larson (1977).

In midMay 2003, we haphazardly selected and sampled the vegetation on 12 large boulders that were greater than 1.5 m in height. All boulders were at least 20 m apart and usually much further. We never observed scat or signs of browsing on boulders greater than 1.5 m tall. For eight of the twelve tall boulders we were able to locate and sample the vegetation on nearby shorter boulders (<1 m tall). We typically found both scat and evidence of deer browsing on these smaller boulders. In all cases, we avoided strongly sloping boulders because they did not develop a layer of organic matter that would allow for vegetation establishment. Finally, we sampled the vegetation on the forest floor in randomly selected adjacent control plots that were located 3–5 m away from each large boulder.

The total surface area that we sampled varied with the size of each of the tall boulders but remained constant within a grouping (*i.e.*, large boulder, small boulder if present and adjacent plot on the forest floor). In each location within the sampling area, we identified and determined the total density of all woody species and the density of herbaceous individuals that had an inflorescence. Finally, we censused all plant species within our sample areas on the boulders and forest floor to determine total species richness and to construct species area curves. Because the data did not satisfy assumptions for parametric analysis, we used the Kruskal-Wallis procedure to test for differences among species richness and the density of trees, shrubs and reproductive herbs among the three sampling locations.

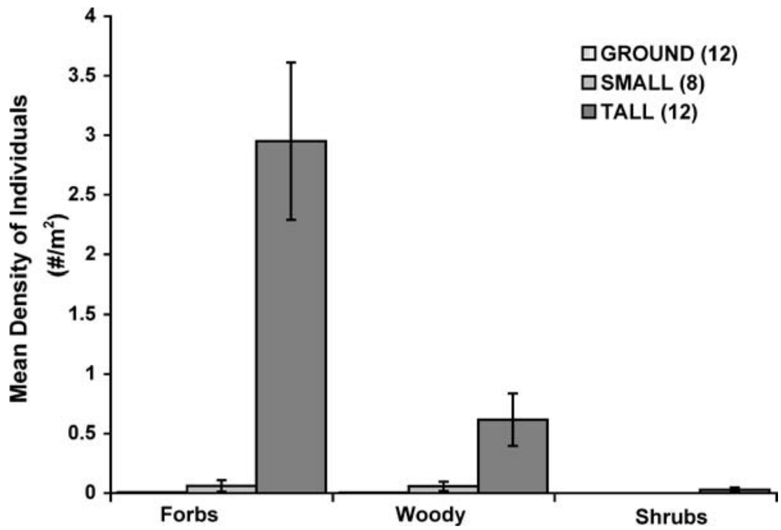

FIG. 1.—Mean plant densities (per $m^2 \pm 1$ SE) on the surface of tall boulders, small boulders and on the forest floor

The Kruskal-Wallis procedure is the non-parametric analog to the one-way ANOVA and compares between the medians of two or more samples to determine if the samples have come from different populations (Sokal and Rohlf, 1995).

RESULTS

We sampled boulder areas ranging from 11.96 m^2 to 83.07 m^2 with an average surface area of 30.34 m^2 (± 1 SE 5.5 m^2). We found significantly higher densities of reproductive herbaceous species on the tall boulders than on either the short boulders or forest floor ($X^2 = 25.5$, df = 2, $P < 0.001$; Fig. 1). There were a total of 1338 flowering herbs on the tall boulders and only 6 on the forest floor. The most abundant flowering herb species observed on the tall boulders were flowering herbs including Canada Mayflower (*Maianthemum canadense*; Tall Boulders: = x = 61), Solomon's Seal (*Polygonum biflorum*; Tall Boulders: x = 13.5) and Red Trillium (*Trillium erectum*; Tall Boulders: x = 3). Similarly, tree species density was greatest on tall boulders ($X^2 = 17.2$, df = 2, $P = 0.0002$; Fig. 1). Abundant woody species included Hemlock, Striped Maple, Red Maple and Black Birch (*Betula lenta*). The most commonly observed species on the forest floor were Violets (*Viola* spp.) and Black Birch.

Overall species richness was greatest on tall boulders ($X^2 = 22.7$, df = 2, $P < 0.001$; Fig. 2). There was a mean species richness of 4.58 species on tall boulders compared to 0.5 and 0.17 species on the short boulders and forest floor, respectively. The number of species sampled increased with area only on the tall boulders (Fig. 3) reaching a total of 25 species.

DISCUSSION

The goal of this work was to test the hypothesis that tall boulders would serve as a sanctuary for numerous plant species that are vulnerable to heavy browsing in the Allegheny National Forest in Pennsylvania. Our results unequivocally confirm the predictions of this hypothesis: the abundance of woody and sexually reproducing herbaceous species as well as overall species richness were dramatically higher on tall boulders than on the forest floor or

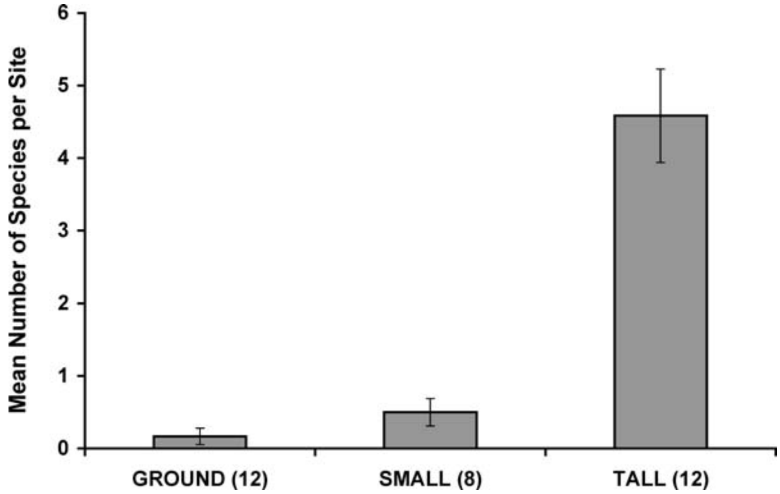

FIG. 2.—Mean plant species richness per sampling location (±1 SE) on the surface of tall boulders, small boulders and on the forest floor

on smaller boulders. Deer browsing led to a situation where species richness did not increase with an increase in area. This, more so than other response variables, signals the pervasive and deleterious influence that browsing is having on plant biodiversity in the region.

Because we sampled both tall boulders that deer could not gain access to and short boulders that had active signs of deer browsing and use, our results cannot be explained by

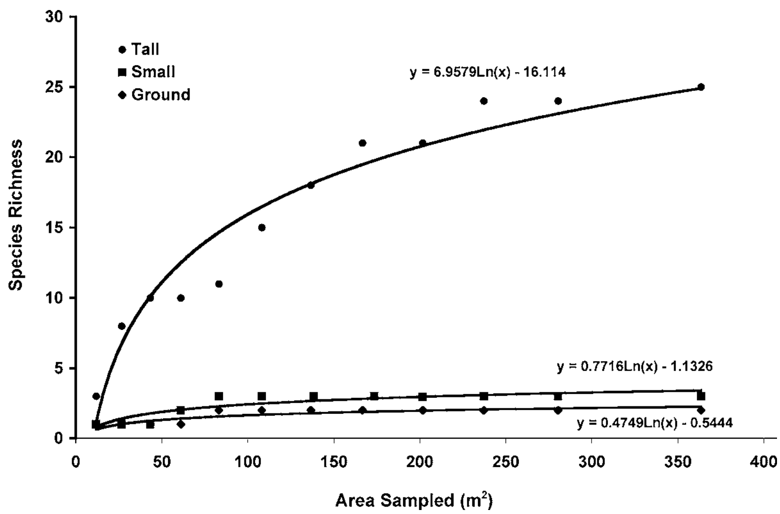

FIG. 3.—Species-area accumulation curves for both woody species and herbs growing on tall boulders, on small boulders, and on the forest floor. Note that there were only 8 short boulders but 12 tall boulders and 12 sample locations on the forest floor. Curves were fitted using a semi-log area function (*see* Rosenzweig 1995, Brown and Lomolino 1998)

arguing that the surface of boulders are a superior edaphic habitat. For example, belowground competition between herbs and adult trees might be substantially reduced on the surface of boulders because roots from adult trees cannot penetrate rock substrates (Banta *et al.*, 2005). Because we did not find and increase in the abundance of herbs or woody species on short boulders, this argument is effectively eliminated. Additionally, unlike previous work (Banta *et al.*, 2005), we demonstrate that the herb communities growing on tall boulders are provided a major sanctuary whereby their reproductive structures are protected from browsers. Other studies have also found that the sexual reproduction of herbaceous forest herbs is particularly sensitive to browsing (*e.g.*, Rooney, 1997; Knight, 2003). Overall, our results suggest that current levels of browsing may be having an impact on sexual reproduction that may further compound the deleterious impact of browsing on plant diversity and abundance. Thus, browsing may not only reduce population size by reducing plant abundance but also reduce effective population size by reducing levels of genetic diversity via a reduction in sexual reproduction and outcrossing. The role of these tall boulders as a reservoir of genetic diversity still requires much further work.

We term the vegetation on these tall boulders Rock Refugia Gardens and suggest that they may be common throughout the eastern deciduous forest wherever these boulders (or other types of refugia) occur and wherever deer are abundant. We have now documented two regions within the Allegheny National Forest where these boulders serve as refugia (Banta *et al.*, 2005) and Rooney (1997) documented a third area in the nearby Minister Creek Watershed. This suggests that these tall boulders may serve as an important reservoir of biodiversity; however, their importance may be limited because their total surface area is a small fraction of the ANF (Banta *et al.*, 2005). Nonetheless, Milchunas and Noy-Meir (2002) reviewed the impact on biodiversity of relatively small geologic refugia worldwide and concluded that they serve as important reservoirs of regional diversity and argued for their conservation. The vast majority of the refugia described by Milchunas and Noy-Meir (2002), however, were larger than the relatively small boulders we surveyed and that occur in the ANF. Overall, further research is required to elucidate the distribution, type, abundance, patch size, species diversity and importance to biodiversity conservation of these small refugia in regions where they occur and where deer or other browsers are abundant. These Rock Refugia Gardens provide an opportunity to study the colonization potential of recently isolated, dense patches of forest herbs in a landscape matrix where these herbs are now sparsely distributed. The demographics of herb populations could be quantified inside and outside of fenced exclosures leading away from dense herb patches that occupy different boulders. In this way, the importance of these refugia to biodiversity conservation and as future source populations can be assessed.

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