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Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA[1]

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ABRAMS, M. D. AND S. E. JOHNSON (School of Forest Resources, Forest Resources Building, Penn State University, University Park, PA 16802). Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. J. Torrey Bot. Soc. 139: 167–180. 2012.—*Odocoileus virginianus* Zimmerman (white-tailed deer) populations at Valley Forge National Historical Park in southeastern Pennsylvania have ranged from 70 to 93 deer per square km over the last decade. In 2010, we surveyed 30 fenced (to exclude deer) and unfenced paired plots established in 1992 to evaluate differences in woody and herbaceous vegetation. In addition, a broader collection and analysis of overstory and understory vegetation data were conducted in the two dry *Quercus* spp. forests and one mesic *Liriodendron tulipifera* L. forest that contain the fenced and unfenced plots. The understory of the *Liriodendron* stand had 72% cover of *Microstegium vimineum,* (Trin.) A. Camus, an exotic grass. Across all three stands, sapling and seedling densities were low to moderate (500 and 10,000 stems ha^{-1}, respectively) and were primarily shade tolerant *Acer rubrum* L. and *Nyssa sylvatica* Marsh. The numbers of *Quercus* seedlings and saplings were low to nonexistent in all stands. Similarly, the unfenced plots had low densities of seedlings and saplings, especially *Quercus*. The 18 year-old fenced plots contained 33,133 seedlings ha^{-1}, but lacked tree saplings. The fenced seedlings were dominated by *A. rubrum*, *Sassafras albidum*, (Nutt.) Nees, *N. sylvatica* and *Fraxinus americana* L. in two of the stands and *Quercus montana* L. in one of the *Quercus* stands. Shrub cover averaged 51% in the fenced plots (mainly *Lindera*, *Viburnum*, *Ligustrum* and *Lonicera*) and 5% in the unfenced plots. Moreover, *Microstegium* cover was very low in all fenced plots, possibly due to the high shrub cover. Fenced plots also had higher plant species diversity (Shannon Index and richness). The results of this study suggest that the long-term exclusion of *O. virginianus* resulted in increased tree seedling number, shrub cover and diversity, and low *Microstegium* cover, but was inconsistent in stimulating *Quercus* regeneration and sapling recruitment.

Key words: Land-use history, *Microstegium vimineum*, *Odocoileus virginianus*, *Quercus*, Valley Forge National Historical Park.

Long-term studies of forest dynamics indicate that *Quercus* species dominated much of the eastern U.S. forest biome during the last 7,000–9,000 years (Fuller et al. 1998, Abrams 2002, Abrams and Nowacki 2008). It is generally believed that this forest type was sustained over thousands of years by Native American burning (Abrams 1992, Delcourt and Delcourt 1997, Nowacki and Abrams 2008). Following European settlement, the magnitude of anthropogenic disturbances in eastern U.S. forests changed dramatically. This included extensive clearcutting, often followed by catastrophic fire, then the onset of the fire control era in the early 20th century (Smokey the Bear era), and the introduction of exotic insects and diseases (Whitney 1994, Abrams 1998, Nowacki and Abrams 2008). These factors have led to unprecedented and rapid changes in forest composition (Keever 1973, Schuster et al. 2008). This is particularly true for the eastern United States that has seen the extirpation of the once dominant *Castanea dentata*, (Marsh.) Borkh. from chestnut blight, loss of vast areas of *Pinus strobus*, L. forests, a virtual cessation of *Quercus* recruitment from fire suppression, forest succession and intensive *Odocoileus virginianus*, Zimmerman (white-tailed deer) browsing, and a rapid increase in *Acer rubrum*, L. and other native and exotic invasives (Abrams 1992, 1998, Whitney 1994, Cote et al. 2004, Heckel et al. 2010).

Odocoileus virginianus are presently abundant throughout Pennsylvania, as well as most

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of the contiguous United States (Wallner and Alverson 1997, Rooney 2001, Horsley et al. 2003). At Valley Forge National Historical Park, *O. virginianus* density is extremely high, ranging from 70–93 km^{-2} (180–240 mi^{-2}) over the last decade (National Park Service 2009). In contrast, *Odocoileus* populations in the eastern U.S. were estimated at about 4 km^{-2} prior to European settlement (McCabe and McCabe 1984). Deer density remained low or even declined initially after European settlement due to unregulated harvests and the extensive logging of forests across the state in the 19th and early 20th centuries (Latham et al. 2005). After 1900, *O. virginianus* populations started to increase dramatically in much of the eastern U.S. due to the regeneration of the cut-over forests, a decline in predators (e.g., *Canis lupus* L.; gray wolf, and *Puma concolor* L.; mountain lion) and restrictive hunting laws including the protection of does (Marquis 1981).

In National Parks, *Odocoileus virginianus* populations increased as a result of low mortality rates, a lack of recreational hunting, loss of habitat in surrounding areas due to urbanization, and the availability of ideal habitat (NPS 2009). National Parks such as Valley Forge have been managed to preserve scenic and historic landscapes, such as a mixture of forest and field, which is excellent habitat for *O. virginianus*. High deer densities can have direct and indirect negative impacts on plant and animal populations, including reductions in species richness, plant density and biomass, height growth, and the development of vertical structure (Latham et al. 2005, Long et al. 2007, Kain et al. 2011, Nuttle et al. 2011). Unmanaged *Quercus* forests with high *O. virginianus* densities are not regenerating *Quercus* (and other favored browse tree species) due to intensive foliar browsing and acorn predation (Collins and Carson 2003, Haas and Heske 2005). Previous studies have indicated that understories in these forests are dominated by ferns, the exotic grass *Microstegium vimineum,* (Trin.) A. Camus, and other species that are avoided by *O. virginianus* (Horsley et al. 2003, Eschtruth and Battles 2008, Goetsch et al. 2011). These forests are also changing as a result of forest succession to more shade tolerant trees species such as *Acer rubrum*, *Nyssa sylvatica*, Marsh. and *Fagus grandifolia* Ehrh. (Glitzenstein et al. 1990, Abrams 1992, 1998). If *O. virginianus* density is very high, regeneration of most tree, shrub and native herbs species will typically fail (Horsley et al. 2003, Ruhren and Handel 2003, Rooney 2009).

This research investigated the overstory and understory composition of *Quercus* and *Liriodendron tulipifera*, L. forests, which included fenced (to exclude *Odocoileus virginianus* since 1992) and unfenced plots in the Valley Forge National Historical Park, Pennsylvania (hereafter referred to as Valley Forge). This study is unique in that it is one of the longest running *O. virginianus* exclusion studies in *Quercus* forests in the eastern U.S. and it compares the impacts of *O. virginianus* exclusion in two different forest types. Other long-running *O. virginianus* exclusion studies were established in northern hardwood or mixed-mesophytic forests (Marquis 1974, Tilghman 1989, Horsley et al. 2003, Royo et al. 2010, Goetsch et al. 2011, Collins and Carson 2003). The objectives of this study are to characterize overstory and understory forest composition and vegetation differences in fenced and unfenced plots, in relation to deer browsing, in *Quercus* versus *Liriodendron tulipifera* forests at Valley Forge.

STUDY AREA DESCRIPTION. Valley Forge is located 20 km northwest of Philadelphia, PA in Chester and Montgomery counties, within the Upland Piedmont Plateau ecological region in southeastern Pennsylvania. The park consists of 1,403 ha (3,466 acres) and is located just south of the boundary between the Glaciated and Piedmont sections of the *Quercus-Castenea* Forest Region. The area has a long history of human impacts from forest clearing for encampment during the Revolutionary War (1777–1778), agriculture, industrial use, and development. All of these factors, in addition to the bedrock geology, soil composition, and site specific characteristics, such as slope, aspect, and moisture regime, influence the current-day vegetation patterns at Valley Forge (Podniesinski et al. 2005). Within Valley Forge, Mount Misery borders Valley Creek to the west and encompasses approximately 93 ha. Mount Joy borders Valley Creek to the east and encompasses approximately 94 ha (Fig. 1). Mount Misery is dominated by dry *Quercus* forests, with lesser amounts of *Liriodendron tulipifera* forests. In contrast, Mount Joy is dominated by dry *Quercus* forest in the higher elevation (west half) and *L. tulipifera* in the lower elevation

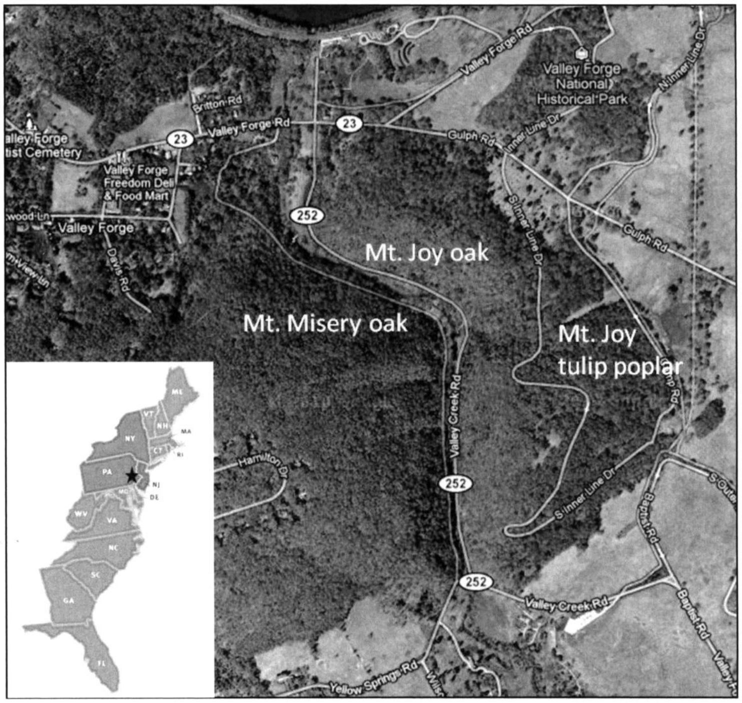

FIG. 1. Map showing the location of Valley Forge in southeastern Pennsylvania, U.S. (star indicates location on inset map), and a Google Earth image of the three study sites on Mount Misery and Mount Joy at Valley Forge.

(east half). Mount Misery consists of the Cambrian Age Chickies Formation, a very hard, erosion-resistant rock composed of quartzite and quartz schist that forms the acidic, well-drained, rocky Edgemont soils (Diefenbach et al. 2008). The forests on Mount Misery were historically used as woodlots for charcoal production associated with the charcoal iron industry; practices that helped perpetuate and reinforce *Quercus* species (Rhoads et al. 1989, Mikan et al. 1994, Abrams 2003). However, they suffered the loss of *Castanea dentata* from the chestnut blight in the early 1900s.

Mount Joy occurs on the slightly younger Cambrian Age Antietam and Harpers (undivided) formations. These rock types are composed of quartzite, schist, and phyllite, and are fairly erosion resistant. Edgemont stony loam soils derived from these formations can be somewhat calcareous and are slightly more mesic than soils that occur on the Chickies Quartzite Formation (Pennsylvania Geological Survey 1981, Podniesinski et al. 2005). These moderate slopes may have been better suited for farming historically than the steeper slopes and rockier soils of Mount Misery (Rhoads et al. 1989). The existing *Liriodendron tulipifera* forest on the lower elevation, more mesic eastern section of Mount Joy is thought to have developed following agricultural abandonment in the first quarter of the 20th century (Rhoads et al. 1989).

Methods. A fixed-plot monitoring system (Storm and Ross 1992) was implemented in 1992 to evaluate vegetative communities in two large wooded areas at Valley Forge. Thirty vegetation sample sites were randomly located on Mount Misery and Mount Joy (15 in each area). At each sample site, paired plots were established where one plot was fenced to exclude *Odocoileus virginianus* but no other herbivores. The unfenced control plots were located 36.5 m from the center of the fenced plots in a random direction. Each plot was 2 × 2 m in size. The integrity of *O. virginianus* exclosure fences has been maintained over the last 18 years by the NPS. In 2010, vegetation surveys were conducted during the spring (April 10–19; for spring ephemeral flora only) and mid-summer (July 10–16) in the 30 paired 2 × 2 m fenced and unfenced understory

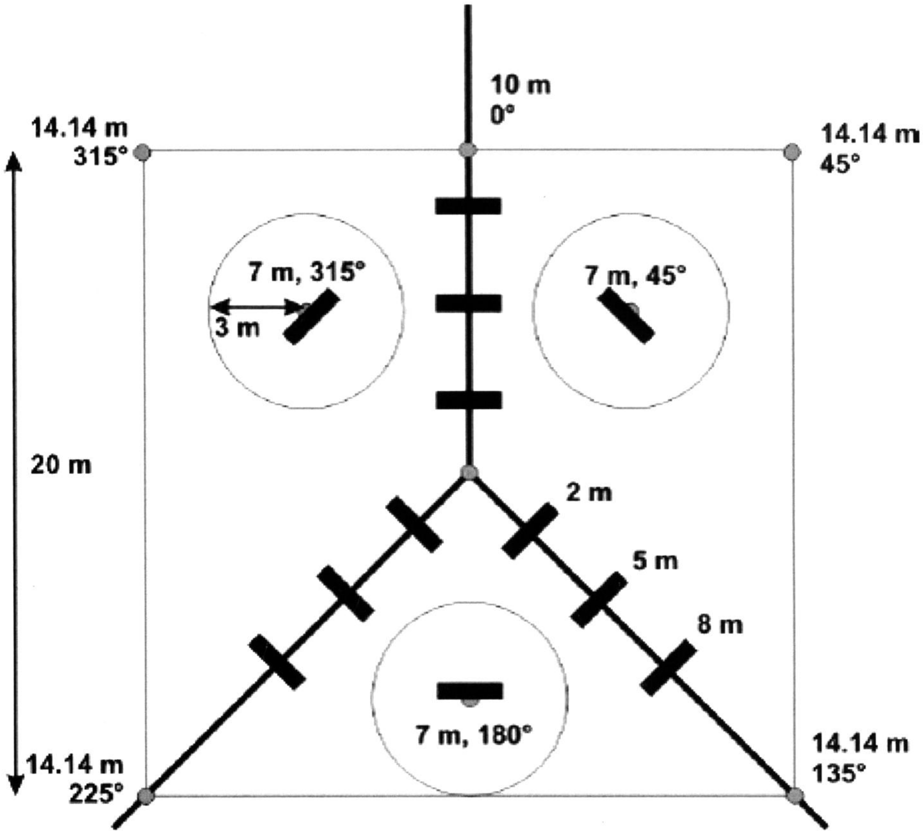

FIG. 2. Plot layout showing square tree plot with three nested 3-m radius regeneration microplots, twelve 1 m^2 vegetation quadrats along the central triad (Comiskey et al. 2009).

monitoring plots. In addition, sixty, 20 × 20 m overstory and understory plots were established and monitored in spring and summer in the three study forests: the *Quercus* forest on Mount Misery and the *Quercus* and *Liriodendron tulipifera* forests on Mount Joy (a total of 20 overstory plots per stand). The newly established 20 × 20 m plots (those that were not co-located with the existing unfenced understory plots) were randomly established along transects through the middle of the three forest stands (avoiding edge effects). The plot design of Comiskey et al. (2009) was used to inventory all overstory tree species and understory woody and herbaceous vegetation (Fig. 2).

Within the 20 × 20 m plots, species and diameter were recorded for all trees ≥ 10.0 cm dbh (diameter at breast height). Tree saplings ≥ 1.5 m in height and >1 cm dbh were measured in three permanently marked 3 m radius circular micro-plots embedded at each of the 20 overstory sample points. Tree seedlings > 5 cm tall and < 1 cm in dbh were identified in twelve 1 m^2 quadrats (in each of the 20 overstory plots), counted and assigned into height classes of 5–15 cm, 15.1–30 cm, 30.1–100 cm, 1–1.5 m, and > 1.5 m. Shrub and herbaceous species and were monitored within twelve 1 m^2 quadrats and cover was estimated into cover classes (0–4%, 5–25%, 26–50%, 51–75%, 76–95%, and 96–100%). The 30 paired, 2×2 m plots, fenced and unfenced plots (15 in each area of Mount Joy and Mount Misery) established in 1992 were surveyed for understory vegetation using the same general methodology. The Shannon-Wiener Index of diversity was calculated as $-\sum p_i \log p_i$, where p_i = relative cover for shrub, vine and herb species. In the case of tree seedlings, p_i = relative density. Species richness was calculated as the average frequency in plots. Plant nomenclature follows Gleason and Cronquist (1991). Statistical analyses were conducted using general linear models and two-sample *t*-tests at $P < 0.05$.

Table 1. The relative importance values (%) for each tree species and total tree density and basal area recorded in 20 overstory plots for the tulip poplar (*Liriodendron tulipifera*) forest on Mount Joy and oak (*Quercus*) forests on Mount Joy and Mount Misery, Valley Forge National Historical Park, PA. Relative importance value is the sum of the relative dominance, frequency, and density divided by three for each species. When noted, values in a row followed with different letters are significantly different at $P < 0.05$.

	Relative importance value (%)		
Species	Mt. Joy tulip poplar	Mt. Joy oak	Mt. Misery oak
Liriodendron tulipifera	50.55 **a**	9.726 **b**	10.44 **b**
Acer rubrum	7.47	12.42	13.92
Fraxinus americana	6.48	1.38	*
Carya tomentosa	3.48	0.88	0.89
Nyssa sylvatica	3.43 **a**	15.77 **b**	14.45
Quercus velutina	3.41	10.90	7.43
Quercus montana	3.26 **a**	9.92 **b**	19.08 **c**
Cornus florida	2.92	0.41	0.38
Prunus avium	2.42	*	*
Quercus alba	2.13	2.55	3.57
Acer platanoides	2.11	0.96	*
Pinus strobus	1.91	2.01	*
Acer saccharum	1.74	*	*
Prunus serotina	1.62	1.97	*
Carya glabra	1.61	0.41	*
Cercis canadensis	1.09	0.55	*
Quercus coccinea	1.03 **a**	11.71 **b**	19.31 **b**
Ailanthus altissima	0.91	*	*
Quercus rubra	0.88	4.55	1.54
Robinia pseudoacacia	0.82	*	*
Celtis occidentalis	0.71	0.49	*
Betula lenta	*	6.55	0.82
Sassafras albidum	*	4.36	5.42
Fagus grandifolia	*	1.66	2.38
Ulmus rubra	*	0.83	*
Castanea dentata	*	*	0.38
Density (Trees ha^{-1})	227.5 **a**	422.5 **b**	475.0 **b**
Basal area (m^2 ha^{-1})	33.69	27.71	31.34

Results. A total of 21 tree species were recorded in the overstory plots in the *Liriodendron tulipifera* forest on Mount Joy (Table 1). *Liriodendron* had a relative importance value (RIV) of 50%, the highest ($P = 0.032$ and 0.033) among the three stands, followed by *Acer rubrum* and *Fraxinus americana* with a combined RIV of 14%. Five *Quercus* species, each with a RIV of 1–3%, were recorded on the site. The *Quercus* forest on Mount Joy also contained 21 tree species and was dominated by five *Quercus* species that represented nearly 40% of the RIV. The RIV of *Q. coccinea*, *Q. velutina* and *Q. montana* was higher than those of *Q. rubra* and *Q. alba*. Other common trees in the stand included *Nyssa sylvatica*, *A. rubrum*, *L. tulipifera* and *B. lenta*, L. A total of 14 tree species were recorded in the *Quercus* forest on Mount Misery (Table 1). Five *Quercus* species represented 51% RIV and *Q. coccinea* and *Q. montana* represented most of this total. Other important trees in the stand included *N. sylvatica*, *A. rubrum* and *L. tulipifera*. *Quercus montana, Q. coccinea, N. sylvatica* RIV were significantly lower ($P = 0.0001$ to 0.05) in the Mount Joy tulip poplar stand versus the two oak stands (Table 1). Total tree density was higher ($P = 0.0001$ and 0.0001) and basal area was lower in the two oaks stands versus the tulip poplar stand (Table 1).

A total of 13 tree species were recorded as seedlings in the three forests with a density ranging from 3000 ha^{-1} (in the tulip poplar forest) to 7667 ha^{-1} (in the oak forest on Mount Misery; Table 2). The two oak forests contained a higher ($P = 0.044$ and 0.012) total density of tree seedlings than did the tulip poplar stand. In terms of individual species, *Nyssa sylvatica*, *Acer rubrum,* and *Sassafras albidum* seedling density were significantly higher ($P < 0.042$) in the oak versus tulip poplar stands. *Quercus* seedlings and saplings for all tree species were scarce in all three stands (Table 2). In the tulip poplar stand, most saplings were *Fraxinus americana* followed by

Table 2. Number of seedlings and saplings per ha surveyed for tree species recorded in the tulip poplar forest on Mount Joy and oak forests on Mount Joy and Mount Misery, Valley Forge National Historical Park, PA. Within the seedling or sapling categories, values in a row followed with different letters (when noted) are significantly different at $P < 0.05$.

	Mt. Joy tulip poplar		Mt. Joy oak		Mt. Misery oak	
Species	Seedlings	Saplings	Seedlings	Saplings	Seedlings	Saplings
Liriodendron tulipifera	1125	*	*	*	250	35
Cercis canadensis	917	24	*	*	*	*
Sassafras albidum	333 **a**	*	2542 **b**	24	2333 **b**	24
Nyssa sylvatica	250 **a**	18 **a**	2917 **b**	147 **b**	2375 **b**	177 **b**
Prunus serotina	167	*	333	18	417	*
Acer rubrum	125 **a**	12 **a**	1167 **b**	53	1333 **b**	142 **b**
Prunus virginiana	42	*	42	*	*	*
Carya glabra	42	*	*	*	*	*
Quercus montana	*	*	250	*	875	6
Quercus velutina	*	*	42	*	42	*
Quercus coccinea	*	*	*	6	*	*
Betula lenta	*	*	125	*	*	*
Fraxinus americana	*	41	42	6	*	*
Carya cordiformis	*	6	*	*	*	*
Carya tomentosa	*	6	*	*	*	12
Ostrya virginiana	*	*	*	*	42	*
Cornus florida	*	24	*	6	*	*
Pinus strobus	*	*	*	6	*	*
Acer saccharum	*	24	*	*	*	*
Acer platanoides	*	*	*	*	*	6
Viburnum prunifolium	*	18	*	*	*	*
Fagus grandifolia	*	*	*	*	*	35
TOTAL	**3001 a**	**173**	**7460 b**	**266**	**7667 b**	**437**

Acer saccharum, Marsh., *Cercis canadensis*, L., and *Cornus florida* L. in equal proportion. *Nyssa sylvatica* and *A. rubrum* were the dominant saplings in the two oak stands.

The oak stand on Mount Joy contained 13 of the 14 recorded shrub and vine species, whereas the other two stands contained eight and nine of these species (Table 3). Shrub and vine cover was greater ($P = 0.017$) in the Mount Misery oak stand due to the higher cover of *Kalmia latifolia* L. A total of 24 herbaceous species with a total cover ranging from 0.2% to 74.0% were recorded in the spring and summer surveys in three forests (Table 4). The highest cover ($P = 0.0001$) was recorded in the *Liriodendron tulipifera* forest due to the overwhelming dominance (72% cover) by *Microstegium vimineum*. This species also represents nearly all of the 10% herbaceous cover in the *Quercus* forest on Mount Joy (Table 4; Fig. 3). The oak stand on Mount Misery had the lowest cover of herbs ($P = 0.0001$).

Across all three stands, fifteen species were recorded as tree seedlings in the thirty fenced plots, compared with only six species in the unfenced plots (Table 5). The fenced plots in the three surveyed forests contained an average of 33,133 tree seedlings ha^{-1} compared with 6257 seedlings ha^{-1} in the unfenced plots. Seedling density in the fenced plots was higher ($P = 0.021$) in the two oak stands versus the tulip poplar stand (Table 5). *Quercus montana, Acer rubrum, Sassafras albidum, Nyssa sylvatica* and *Fraxinus americana* represented the majority of seedlings in fenced plots in the oak stands. In the unfenced plots, *N. sylvatica, A. rubrum* and *S. albidum* were the dominant seedlings in all three stands. Seedling density of *Q. montana* in the fenced plots on Mount Misery oak was the highest density of any species in all three stands, whereas *Acer rubrum* seedling density in the Mount Joy oak stands was second highest. The density of seedlings is low for the other four *Quercus* species present in the forest overstory, and there are no *Q. alba* seedlings present in fenced or unfenced plots throughout the three forests. Only 18 saplings, representing a density of 750 ha^{-1}, were recorded in the 30 fenced and unfenced plots (data not shown). The majority of saplings were *N. sylvatica* in the oak forest on Mount Misery. Fencing and stand type had a significant effect on number of tree seedlings ($P = 0.005$ and 0.002, respectively). Most

Table 3. Percent cover of woody shrub and vine species recorded in the tulip poplar forest on Mount Joy and oak forests on Mount Joy and Mount Misery, Valley Forge National Historical Park, PA. When noted, values in a row followed with different letters are significantly different at $P \leq 0.05$.

Species	Cover (%)		
	Mt. Joy tulip poplar	Mt. Joy oak	Mt. Misery oak
Parthenocissus quinquefolia	0.25	0.18	0.04
Toxicodendron radicans	0.19	0.24	0.05
Berberis thunbergii	0.13	0.01	*
Lindera benzoin	0.08	0.16	*
Viburnum prunifolium	0.08	0.05	0.12
Euonymus alata	0.06	0.03	0.01
Hamamelis virginiana	0.01	0.42	0.06
Vitis sp.	0.01	0.01	*
Kalmia latifolia	*	2.43 a	8.70 b
Lonicera japonica	*	0.02	*
Viburnum acerifolium	*	0.02	*
Vaccinium angustifolium	*	0.01	0.23
Smilax glauca	*	0.01	0.04
Gaylussacia sp.	*	*	0.02
TOTAL	**0.80**	**3.58 a**	**9.26 b**

individual species numbers were not significantly different due to high plot-to-plot variation.

A total of 29 species were recorded as shrubs and vines in the fenced plots, compared with 11 such species in the unfenced plots (Table 6). Fenced plots had higher (P = 0.0001) total cover (mean = 60%) of these species than did the unfenced plots (mean = 6.5%) in each and all of the three stands. Total cover of shrubs and vines was higher ($P = 0.021$) in the Mount Joy tulip poplar stand compared with the two oak stands due to the dominance of *Lindera, Ligustrum, Lonicera* and *Viburnum*

Table 4. Percent cover of herbaceous species in the tulip poplar forest on Mount Joy and oak forests on Mount Joy and Mount Misery, Valley Forge National Historical Park, PA. When noted, values in a row followed with different letters are significantly different at $P < 0.05$.

Species	Cover (%)		
	Mt. Joy tulip poplar	Mt. Joy oak	Mt. Misery oak
Microstegium vimineum	72.17 **a**	9.97 **b**	0.03 **c**
Arisaema triphyllum	0.64	0.03	*
Cardamine impatiens	0.35	0.12	*
Allium sp.	0.24	*	*
Polygonum caespitosum	0.21	*	*
Viola sp.	0.09	*	0.01
Claytonia virginica	0.05	*	*
Circaea alpina	0.04	*	*
Alliaria petiolata	0.03	*	*
Boehmeria cylindrica	0.03	*	*
Carex sp.	0.01	0.13	*
Carex pensylvanica	0.01	0.03	0.01
Duchesnea indica	0.01	*	*
Geranium carolinianum	0.01	*	*
Oxalis stricta	0.01	*	*
Podophyllum peltatum	0.01	*	*
Sanguinaria canadensis	0.01	*	*
Sanicula sp.	0.01	*	*
Veronica hederifolia	0.01	*	*
Bartonia virginica	*	0.02	*
Prenanthes altissima	*	0.01	*
Chimaphila maculata	*	*	0.12
Gaultheria procumbens	*	*	0.01
Thelypteris noveboracensis	*	0.07	0.07
TOTAL	**73.92 a**	**10.38 b**	**0.25 c**

FIG. 3. Top left – Fenced plot dominated by *Lonicera* species and *Lindera benzoin* in tulip poplar forest with *Microstegium vimineum*-dominated understory on Mount Joy; bottom left – forest overstory (large *Q. montana* in left foreground) and *M. vimineum*-dominated understory in the *Quercus* forest on Mount Joy; top right - *Quercus* forest on Mount Misery with very sparse forest understory and apparent deer browse line; bottom right - high density of *Q. montana* seedlings in fenced plot in *Quercus* forest on Mount Misery.

species (Table 6). *Parthenocissus quinquefolia* (L.) Planch and *Rubus pensilvanicus* Poir. were the dominant shrub and vine species in Mount Joy oak fenced plots (Table 6). A total of nine exotic species occur as shrubs and vines, including three of the five most dominant in the fenced plots. Across all 30 plots, fencing and stand type had a significant effect on cover of shrub species (P = 0.0001 and 0.058, respectively)

A total of 34 herbaceous species (including five exotics) were recorded in the 30 fenced plots versus 14 species in the unfenced plots (Table 7). Total herb cover in the fenced plots and unfenced plots was fairly similar in all three stands. However, herb cover was significantly higher (P = 0.003) in the Mount Joy tulip poplar stand versus the two oak stands. This was due to the high cover of *Podophyllum* (a spring ephemeral), *Osmorhiza, Polygonatum* and *Cimicifuga* in the fenced plots and *Microstegium* in the unfenced plots in that stand. Indeed, the very low cover of *Microstegium* in all of the fenced plots is notable (Table 7; Fig. 3).

The total number of species (tree, shrubs, vines, and herbs) in the 30 fenced plots (78 species) is higher than that in the unfenced plots (31 species; Tables 5, 6 and 7). Most of this difference is due to the high number of shrubs and herbs in the fenced plots in the Mount Joy tulip poplar forest (a total of 38 species). Shannon-Wiener Index of diversity measurements were significantly higher (P = 0.001) across all fenced versus unfenced plots in two stands (Table 8). However, Shannon diversity was not significantly different (P = 0.246) between the fenced and unfenced plots in the *Quercus* forest on Mount Misery. Species richness measurements (average frequency of a species) were significantly different (P = 0.006) across all fenced versus unfenced plots in the three stands (Table 8). Species richness was significantly higher between

Table 5. Number of seedlings per hectare surveyed for all tree species recorded in 30 fenced and unfenced paired plots for the tulip poplar forest on Mount Joy (n = 8 paired plots) and oak forests on Mount Joy and Mount Misery (n = 7 and 15 paired plots, respectively), Valley Forge National Historical Park, PA. When noted, values in a row followed with different letters are significantly different at $P < 0.05$.

	Mt. Joy tulip poplar		Mt. Joy oak		Mt. Misery oak	
Species	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
Acer rubrum	1562	312	13214 **a**	357 **b**	6167	1167
Sassafras albidum	1562	625	2500	*	9166	3500
Ulmus rubra	1250	*	*	*	*	*
Liriodendron tulipifera	937	937	*	357	*	*
Quercus montana	937	*	714	*	19833	1833
Acer platanoides	937	*	1071	*	*	*
Quercus rubra	312	*	714	*	167	*
Prunus serotina	312	*	2500	*	1000	333
Nyssa sylvatica	312	*	6429	2500	6167	2667
Cercis canadensis	312	*		*	*	*
Fraxinus americana	*	*	8214	*	*	*
Quercus velutina	*	*	357	*	1167	*
Carya glabra	*	*	357	*	*	*
Betula lenta	*	*	357	*	*	*
Carya tomentosa	*	*		*	166	*
TOTAL	**8437 c**	**1875 c**	**36428 a**	**3214 b**	**43833 a**	**9500 b**

Table 6. Percent cover of woody shrub and vine species recorded in 30 fenced and unfenced paired plots for the tulip poplar forest on Mount Joy (n = 8 paired plots) and oak forests on Mount Joy and Mount Misery (n= 7 and 15 paired plots, respectively), Valley Forge National Historical Park, PA. When noted, values in a row followed with different letters are significantly different at $P < 0.05$.

	Mt. Joy tulip poplar		Mt. Joy oak		Mt. Misery oak	
Species	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
Lindera benzoin	37.75 **a**	0.50 **b**	*	*	*	*
†*Ligustrum vulgare*	17.63	*	*	*	*	*
†*Lonicera maackii*	17.25	*	*	*	*	*
†*Lonicera japonica*	14.75	*	*	*	*	*
Viburnum prunifolium	9.50	5.00	2.14	*	*	0.53
†*Rosa multiflora*	7.88	*	*	*	*	*
Viburnum acerifolium	4.75	*	5.71	*	5.93	*
†*Rhodotypos scandens*	4.75	*	*	*	*	*
†*Celastrus orbiculatus*	2.38	0.25	0.29	*	*	*
†*Lonicera morrowii*	1.88	*	*	*	*	*
Parthenocissus quinquefolia	1.25	8.00	11.71	0.29	0.13	0.40
†*Rubus phoenicolasius*	0.75	*	*	*	*	*
†*Euonymus alata*	0.50	0.25	*	*	*	*
Toxicodendron radicans	0.25	0.25	3.00	0.57	0.13	0.13
Vitis vulpina	0.25	*	*	*	*	*
Rubus pensilvanicus	*	*	8.57	*	0.13	*
Rhododendron periclymenoides	*	*	2.43	*	3.13	*
Vaccinium angustifolium	*	*	0.29	*	3.93	0.67
Kalmia latifolia	*	*	*	*	3.13	0.13
Kalmia angustifolia	*	*	*	*	2.67	*
Gaylussacia frondosa	*	*	*	*	1.27	*
Gaylussacia baccata	*	*	*	*	1.00	*
Viburnum dentatum	*	*	*	*	1.00	*
Smilax glauca	*	0.25	0.29	*	0.40	0.13
Gaylussacia spp	*	*	*	*	0.27	*
Hamamelis virginiana	*	*	*	*	0.27	0.13
Phytolacca americana	*	*	0.29	*	*	*
Vitis aestivalis	*	*	*	2.14	0.13	*
Vaccinium stamineum	*	*	*	*	0.13	*
TOTAL	**121.52 a**	**14.50 b**	**34.72 c**	**3.00 b**	**23.65 c**	**2.12 b**

Table 7. Percent cover of herbaceous species recorded in 30 fenced and 30 unfenced paired plots for the tulip poplar forest on Mount Joy (n = 8 paired plots) and oak forests on Mount Joy and Mount Misery (n = 7 and 15 paired plots, respectively), Valley Forge National Historical Park, PA. When noted, values in a row followed with different letters are significantly different at $P < 0.05$.

	Mt. Joy tulip poplar		Mt. Joy oak		Mt. Misery oak	
Species	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
Podophyllum peltatum	22.63	*	*	*	*	*
Osmorhiza claytoni	6.63	*	*	*	*	*
Polygonatum biflorum	5.25	*	5.43	*	0.13	*
Cimicifuga racemosa	4.00	*	*	*	*	*
Circaea alpina	3.13	*	*	*	*	*
Arisaema triphyllum	2.38	1.00	*	*	*	*
Sanguinaria canadensis	2.38	*	*	*	*	*
Claytonia virginica	2.13	*	*	*	*	*
Polygonum virginianum	1.88	*	*	*	*	*
Viola sp.	1.88	0.75	*	*	*	*
Maianthemum racemosum	0.75	*	2.14	*	1.13	*
Geranium carolinianum	0.50	*	*	*	*	*
Uvularia perfoliata	0.50	*	*	*	0.13	*
†*Alliaria petiolata*	0.25	0.25	7.86	*	*	*
Allium sp.	0.25	0.25	*	*	*	*
†*Cardamine impatiens*	0.25	3.75	*	*	*	*
Eupatorium purpureum	0.25	*	*	*	*	*
Hepatica nobilis	0.25	*	*	*	*	*
Geum canadense	0.25	*	*	*	*	*
†*Microstegium vimineum*	0.25 **a**	63.38 **b**	0.29	2.71	*	*
Pteridium aquilinum	0.25	*	*	*	0.13	*
Sanicula sp.	0.25	*	*	*	*	*
Symphyotrichum divaricatum	0.25	*	*	*	2.53	*
Dennstaedtia punctilobula	*	*	*	*	6.93	2.53
Maianthemum canadense	*	*	*	*	1.00	0.13
Desmodium nudiflorum	*	*	*	*	1.00	*
Thelypteris noveboracensis	*	*	*	*	0.27	1.00
Chimaphila maculata	*	*	*	*	0.27	0.27
Aralia nudicaulis	*	*	*	*	0.27	*
†*Polygonum caespitosum*	*	1.00	*	*	0.13	*
Isotria verticillata	*	*	*	*	0.13	*
Medeola virginiana	*	*	*	*	0.13	*
Prenanthes altissima	*	*	*	*	0.13	*
Boehmeria cylindrica	*	0.50	*	*	*	*
Carex swanii	*	*	0.29	*	*	*
†*Duchesnea indica*	*	0.25	*	*	*	*
Carex pensylvanica	*	*	*	*	*	0.13
TOTAL	**56.54 a**	**71.13 a**	**16.01 b**	**2.71 b**	**14.31 b**	**4.06 b**

fenced and unfenced plots for all vegetation classes (except herbs in two stands) and total richness within each of the three stands.

Discussion. Most sub-xeric oak forests in the eastern U.S. are a combination of the original mixed-*Quercus* canopy coupled with later successional (non-*Quercus*) species that appear to be the future stand dominants (Keever 1973, Abrams and Downs 1990, Lorimer 2001). The *Quercus* forests at Valley Forge fit this general description in that they contain about 40–50% importance of overstory *Quercus* coupled with a significant *Nyssa sylvatica* and *Acer rubrum* component. The *Quercus* forests also contain about 10% overstory *Liriodendron tulipifera*. This species is intolerant of shade, but often occurs as a gap-phase species in middle- to late-successional forests (Kasmer et al. 1984, Abrams and Downs 1990). The *Liriodendron* forest on Mount Joy differs edaphically, in land-use history and vegetation composition and structure than the *Quercus* forests. We believe the lower slope *L. tulipifera* forest developed following agricultural abandonment in the first quarter of the 20th century, in contrast to the higher elevation *Quercus* forests (Rhoads et al. 1989).

Table 8. Shannon-Wiener Index of diversity and species richness measurements for trees, woody shrubs and vines, and herbaceous species groups recorded in 30 fenced and unfenced paired plots for the tulip poplar forest on Mount Joy (n = 8 paired plots) and oak forests on Mount Joy and Mount Misery (n = 7 and 15 paired plots, respectively), Valley Forge National Historical Park, PA. When noted, values in a row followed with different letters are significantly different at $P < 0.05$.

	Mt. Joy tulip poplar		Mt. Joy oak		Mt. Misery oak	
	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
Shannon Index						
Tree	2.13 **a**	1.01 **b**	1.77 **a**	0.68 **b**	1.46	1.42
Shrub/vine	2.07	1.02	1.74	0.78	2.17	1.71
Herb	2.18 **a**	0.52 **b**	1.13 **a**	0.00 **b**	1.75	1.04
Richness						
Tree	1.63 **a**	0.88 **b**	4.29 **a**	0.57 **b**	3.27 **a**	1.87 **b**
Shrub/vine	4.75 **a**	1.38 **b**	3.00 **a**	0.57 **b**	2.93 **a**	1.07 **b**
Herb	5.50	3.13	1.00	0.43	1.53 **a**	0.40 **b**
TOTAL	**11.88 a**	**5.38 b**	**8.29 a**	**1.57 b**	**7.73 a**	**3.33 b**

In general, *Liriodendron tulipifera* is a disturbance-oriented tree species that would normally be replaced during succession by more shade tolerant tree species (Keever 1973, Kasmer et al. 1984, Downs and Abrams 1990). In the Valley Forge *L. tulipifera* stand, however, the understory has been intensively browsed by deer and is overwhelmingly dominated by *Microstegium* (Fig. 3). This grass has become a problematic invasive in many eastern forests near urban and suburban centers with high *Odocoileus virginianus* populations, and is interfering with the regeneration of native tree species (Fryer 2011, Cheplick and Fox 2011, Beasley and McCarthy 2011). *Microstegium* is typically avoided by *O. virginianus* (Kellogg and Bridgham 2004, Baiser et al. 2008, McGrath and Binkley 2009). The reasons for this avoidance are unknown but may be due to low nutrients, toxic chemicals and/or high silica content. The cover of certain invasive species may be much higher on post-agricultural abandonment sites relative to less disturbed forest sites (Glitzenstein et al. 1990, Motzkin et al. 1996, Abrams and Hayes 2008). This may be one reason for high *Microstegium* cover in the tulip poplar versus oaks stands.

The unfenced plots at Valley Forge have much lower plant diversity, tree seedling density and shrub and vine cover when compared with the fenced plots. These impacts from intense deer browsing have been reported elsewhere in Pennsylvania and throughout much of the eastern U.S (Horsley et al. 2003, Latham et al. 2005, Long et al. 2007, Kain et al. 2011). In addition we found that *Microstegium* cover was much lower in the fenced plots, particularly in the *Liriodendron* stand. The higher cover of woody understory species in the exclosures is apparently producing high levels of low shade (personal observation) that suppressed the *M. vimineum* (Fig. 3). A recent study reported that the presence of tree regeneration and mid-story tree layer shaded out *M. vimineum* and will likely erode its dominance in forest stands over time (Beasley and McCarthy 2011).

Tree seedling numbers were higher in the fenced plots, yet few of these plots contained many *Quercus* seedlings. The reason for low *Quercus* seedling numbers in the fenced plots in the *Liriodendron tulipifera* forest is probably related to a lack of *Quercus* trees in the forest overstory. In contrast, *Quercus* trees represented 40% of the Mount Joy oak forest, yet only 5% of seedlings present in the fenced plots were *Quercus*. The fenced plots on Mount Misery contained a reasonably high number of *Q. montana* seedlings (19,833 ha^{-1}), but had few or no seedlings of the four other *Quercus* species present in the overstory. Most notable is the lack of *Q. coccinea* seedlings whose overstory importance equaled that of *Q. montana* (19% each). The reason for the success of *Q. montana* and failure of the other *Quercus* individuals to produce seedlings in the fenced plots is unknown. Even more pronounced is the lack of *Quercus* saplings in the 18 year-old exclosures (Fig. 3). The scarcity of *Quercus* seedlings and saplings in the understory of closed canopy, sub-xeric *Quercus* forests exposed to *Odocoileus virginianus* browsing is typical for much of the eastern U.S. (Abrams 1992, Abrams and Hayes 2008, Shuster et al. 2008).

Most eastern *Quercus* species are considered to have only moderate understory shade tolerance and their growth from the seedling to sapling stage is often limited by low light levels in the forest understory (Lorimer 2001, Abrams 2003). Deer exclosures do not correct this problem. Indeed, the small fenced areas used in this study may exacerbate the situation by concentrating competing plant species in a small area (Table 4, Fig. 3). This may be due, in part, to the fences providing a perch for birds and the vegetation within providing cover for small mammals (personal observation). These animal vectors most likely provide high seed inputs of plant species, including exotics in the fenced plots. In contrast, the shade tolerant *Nyssa sylvatica* and *Acer rubrum* have been much more successful in establishing seedlings and saplings in the three study sites, including both the fenced and unfenced plots. In addition to their high shade tolerance, these species are less favored browse species for *Odocoileus virginianus* compared with *Quercus* species (Horsley et al. 2003, Cote et al. 2004, Abrams 1998, 2007). Presently, *A. rubrum* and *N. sylvatica* at Valley Forge have a much higher importance than their historical level (Mikan et al. 1994, Black and Abrams 2001). *Nyssa* usually represents about 5% relative importance in most eastern forests and is considered a consummate subordinate species rather than a high ranking overstory dominant (Abrams 2007). Nonetheless, we believe the dominance of *A. rubrum* and *N. sylvatica* will continue to increase with or without a reduction in *O. virginianus* density, as will their role as *Quercus* replacement species in Valley Forge forests. The existing deer browse impacts on other aspects of the forest ecosystems will likely persist well into the future (Nuttle et al. 2011).

Based on the results of this study, we are not confident that the existing overstory *Quercus* at Valley Forge will be replaced by new *Quercus* trees at a sufficient rate over the next century or more (if the NPS decides on this desired outcome). The current ecological conditions in the forests at Valley Forge suggest significant forest management intervention is needed sooner rather than later, such as the ongoing reduction in deer populations, thinning of the forest overstory and reducing the cover of *Microstegium*. In the various fenced plots, species diversity and *Q. montana* seedling density was higher, while *Microstegium* cover was lower, by eliminating deer browse. These are positive signs and suggest that without significant intervention, the loss of *Quercus* dominance in Valley Forge forests will be one of the primary consequences of the continuation of intense *O. virginianus* browsing and unabated forest succession and spread of invasives.

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