Soil texture, land-use intensity, and vegetation of Fort Benning upland forest sites[1]

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DILUSTRO, J. J., B. S. COLLINS, L. K. DUNCAN, AND R. R. SHARITZ. (Savannah River Ecology Laboratory, P. O. Drawer E, Aiken, S. C. 29802). Soil texture, land-use intensity, and vegetation of Fort Benning upland forest sites. J. Torrey Bot. Soc. 129(4):289-297. 2002. — Federal lands may harbor much of the diversity of upland pine-oak-hickory forests in the southeastern USA Fall Line Sandhills region. These forests are managed throughout the region; species composition is influenced by topography, soil composition, periodic natural and prescribed fires, and forest harvesting practices. Our objective was to describe the canopy and ground layer vegetation of upland sites at Fort Benning, Georgia that are managed primarily for longleaf pine (thinned, burned at 3 year intervals) and differ in soil texture (from sandy to clayey) and intensity of military training (lighter dismounted infantry vs. heavier mechanized training). We characterized surface soil texture and land-use disturbance of 32 sites, each 400 m x 400 m, and asked if canopy and ground layer community measures (species composition and richness, basal area, abundance) differed among sites on the basis of soil texture or land-use. There was significant interaction between land-use and soil texture, with a gradient of soil texture (% clay) from clayey sites within light training areas, to sandy sites in heavier training areas. Road-like features, including active and remnant trails, roads, and vehicle tracks or trails were the most frequent and abundant disturbance feature. Number of disturbance features per site did not differ among land-use/surface soil texture categories. Differences in ground layer and canopy composition among sites reflected disturbance intensity; differences in canopy composition also reflected the proportion of pine. Species richness of ground layer vegetation differed among surface soil texture/land-use categories. There was a richness gradient from heavily disturbed sites with clayey soil, through lightly disturbed sites, to heavily disturbed sites with sandy soil. Our results suggest upland pine-oak-hickory forests at Fort Benning range from sandhills scrub oak-pine to pine-hardwood to oak-hickory dominated forests, with greater species diversity in the ground layer of clayey sites. Forestry practices and disturbances associated with mechanized military training favor pine dominance, and maintain open-site, successional or fire-tolerant species in the ground layer. Although intense management toward pine monocultures can reduce within-stand diversity, federal installations such as Fort Benning may help conserve pine-oak-hickory forests in the rapidly developing Sandhills region.

Key words: pine-oak-hickory forests, sandhills, Fort Benning, soil texture, disturbance

[1]This research was supported by the Strategic Environmental Research and Development Program (SERDP), funded by the Department of Defense, as part of the SERDP Ecosystem Management Project (SEMP) CS-1114E-00. Manuscript preparation was supported by Financial Assistance Award Number DE-FC09-96SR18546 between the U.S. Department of Energy and the University of Georgia.

Received for publication December 12, 2001, and in revised form May 11, 2002.

Vegetation of the Fall Line Sandhills region is influenced by topography, drainage, soil composition and fertility, and periodic fires (Wells and Shunk 1931; Weaver 1969; Skeen et al. 1993). This region extends along the southeastern side of the Coastal Plain-Piedmont Fall Line from southern North Carolina through Georgia and parts of Alabama (Christensen 1988). Dominant potential vegetation of the region is the pine-oak-hickory forest (Küchler 1964; Skeen et al. 1993). The sandhills, remnants of ancient beach dunes, are deep, fluvial sands. On the dry ridgetops, native vegetation is a mixture of scrub oaks (especially turkey oak- *Quercus laevis* Walter) and longleaf pine- *Pinus palustris* Miller (Peet and Allard 1993; Skeen et al. 1993; Stout and Marion 1993). Very deep sands, or sites where pine was removed, may be almost pure stands of scrub oaks (Christensen 1988; Workman and McLeod 1990). More fertile, less droughty sites, and slopes grade into upland hardwood forests dominated by oak and hickory species (Workman and McLeod 1990; Skeen et al. 1993). Natural fires, a long history of burning by Native Americans, and later agriculture following European settlement may have encouraged open communities and pine establishment, and favored oaks over other hardwood species (Skeen et al. 1993). Upland forests of the southeast are usually managed for forestry production. More recently, fire exclusion and partial rather than clear-cut timber harvest have led to an increase in hardwood establishment on both sandhill ridges and more mesic sites (Christensen 1988; Skeen et al. 1993).

The Southeastern Atlantic Coastal Plain-Piedmont Fall Line region is becoming increasingly fragmented by expanding urban areas, from Columbus, GA through Raleigh, NC. Large tracts in the Sandhill region are federally owned, including Department of Defense military installations and the Department of Energy’s Savannah River Site. With increased population growth in the Southeast, and agricultural and urban expansion, these federal lands ultimately may harbor much of the diversity of upland pine-oak-hickory forests. We investigated the vegetation of pine-oak-hickory forests and sandhills sites at Fort Benning, GA, which is used for military training activities. The objective of our research was to describe the canopy and ground layer vegetation among sites that are managed primarily for longleaf pine (thinned at 9-10 year intervals, burned at 3 year intervals) and differ in soil texture (from sandy to clayey) and intensity of land-use disturbances (from lightly used for military training; i.e., closed to tracked vehicles, to heavily used; i.e., open to tracked vehicles). We characterized soil texture and land-use disturbance among sites, and asked if canopy and ground layer community measures (species composition and richness, basal area, abundance) differ among sites on the basis of soil texture or land-use categories.

Methods. STUDY SITE DESCRIPTION AND HISTORY. Fort Benning, the U. S. Army Infantry Center, is located in the Sandhills region (Keys 1995) on the Coastal Plain-Piedmont Fall Line in west-central Georgia and eastern Alabama. The installation, which now covers 73,533 ha, was acquired in phases beginning in 1918. Prior land-use was mainly farming and grazing land. The climate is temperate, with maximum summer temperatures averaging 32˚ C (USDA 1983). Precipitation averages 132 cm per year; 50% falls from April to September (USDA 1983). The terrain of the base is characteristic Fall Line topography, with level ridge tops and gentle slopes. Soils include Troup sandy loams, Lakeland sands, Siley loamy sands, and Nankin sandy loams (Johnson 1983).

Mature longleaf pine-dominated forests cover 2800-3200 ha (4%) of Fort Benning; 3200 ha of longleaf pine plantation have been planted since 1988 and the restoration goal is 36,400 ha (50%; USAIC 2001), which may require several decades. Restoration and maintenance of the longleaf pine system on the base is driven by the conservation mandate for the protection of the federally endangered red-cockaded woodpecker (*Picoides borealis* Vieillot), and longleaf pine ecosystem is a desired future condition in the Integrated Natural Resources Management Plan (INRMP) for Fort Benning (USAIC 2001).

The research reported here was conducted on sites that are part of a larger study of the ecological effects of disturbances imposed by land-use and management practices on upland forests at Fort Benning. Military use varies within the base from heavy (tracked vehicle) traffic, to light vehicle traffic, to foot traffic during training exercises. Forests are thinned on a nine-year cycle and burned on a three-year cycle to promote a longleaf pine ecosystem. We compared vegetation and soil characteristics among 32 sites with sandy (S) vs. clayey (C) soils and heavier (H) vs. lighter (L) training. Heavier military use sites were in land compartments open to mechanized training (tracked vehicles). Lighter use sites were in compartments with dismounted infantry training (foot traffic). Sandy and clayey sites were distinguished using soil survey maps. All sites are in forest management and were burned in early 2000.

There were eight 400 m x 400 m sites in each soil type/land-use category (HS, HC, LS, LC). In each site, we established a 100 x 100 m vegetation sampling plot with five 100 m transects spaced every 20 m along one edge of the plot. Sampling points were established at 20 m intervals on each transect, to yield 5 points per transect and 25 points in each site. Trees were surveyed at each point using the point quarter method. Ground layer vegetation, defined as vegetation < 1.4 m height, was surveyed by line-intercept along a 6 m transect at each sampling point. Vegetation that intercepted the vertical plane of the transect was included. Nomenclature follows Radford et al. (1968).

Surface soil texture of each site was determined from soil core samples 2 cm wide by 28 cm deep. Cores were taken from nine uniformly spaced points in each of the 32 sites and texture was determined using a micropipette method (Miller and Miller 1987).

Land-use intensity in each site was assessed by a disturbance survey. Two 300 m transects that bisected the center of the vegetation plot were established in each 400 m x 400 m site. The transects ran North-South and East-West from the plot centers. Features associated with forestry, military use, and natural disturbance, including roads, tank trails, gullies, and canopy openings, were assessed by line-intercept along each transect.

DATA ANALYSES. Non-metric multidimensional scaling (NMDS; SAS 2000), based on Lance-Williams dissimilarity, was used to summarize trends in canopy and ground layer vegetation among sites. We compared stress (badness of fit) of one-, two-, and three-dimensional analyses to determine when adding dimensions did not substantially improve the fit. Analysis of variance (ANOVA) was used to determine if vegetation measures, disturbance features, or soil textures differ among sites in the four surface soil texture/land-use categories: HS, HC, LS, and LC. Pairwise differences among categories were tested by bonferroni t-tests (SAS 2000).

Results. SOIL TEXTURE AND DISTURBANCE AMONG SITES. Soil clay content ranged from 2 % in a sandy site to 48 % in a clayey site; sand content ranged from 32 % in a clayey site to 91 % in a sandy site. Two sites, C1A and I5B, were misclassified *a priori* (Fig. 1a) and were switched for the data analyses reported below. Clayey sites generally had greater variation in percent clay and sand among and within sites. In addition, there was significant interaction between military land-use and soil texture (ANOVA; df=1; ms=3732; F=22.45; p<0.0001), with a gradient of soil texture (% clay) from sites classified as clayey and light land-use, to sandy sites with heavy use (Fig. 1a).

Among sites, land-use (forestry or military training-generated) or natural disturbance features occupied from 7% to 50% of sample transect length; half of the sites were at least 30% disturbed. Sites within soil texture/land-use categories differed in amount of disturbance (ANOVA df=3; ms=19822; F=6.19; p=0.002; Fig. 1). Clayey sites in heavy military use areas (HC sites) had greater length of sampling transects in disturbance features (Fig. 1b).

Disturbance features included those due to natural disturbance (e.g., treefalls), forestry practices (e.g., skidders), and military use (e.g., tank tracks), or some combination of these (e.g., mounds that could have been left by treefalls, harvesting, or military use) (Fig. 2). Over all sites, gullies were the most frequently encountered disturbance feature, and clearcuts were the most abundant (Fig. 2). However, road-like features, including active and remnant trails, roads, and vehicle tracks or trails, were, collectively, the most frequent and abundant disturbance (Fig. 2). The number of disturbance features in each site ranged from 4 to 13, and disturbance feature richness did not differ among land-use/soil texture categories (ANOVA df=3; ms=0.548; F=0.08; p = 0.97).

VEGETATION AMONG SITES. Common in the ground layer vegetation of all sites were *Liquidambar styraciflua* L. sprouts/seedlings, Poaceae (grasses other than identifiable *Andropogon* spp.), *Andropogon* spp., and *Heterotheca graminifolia* (Michaux) Shinners (Table 1). Pines, including *P. taeda* L., *P. echinata* Mill., and *P. palustris* Mill., dominated the canopy of most sites (Table 1). The proportion of pine in the canopy varied among sites from 12% to 99.9%. Four of the 32 sites (B2A, B2B, B2C, D16E), with < 30% pine in the canopy were considered hardwood sites dominated by oaks (*Quercus falcata* Michx., *Q. alba* L., and *Q. nigra* L.; Table 1).

Non-metric multi-dimensional scaling (NMDS) was used to evaluate vegetation patterns among the sites. The NMDS revealed differences in ground layer and canopy composition among sites related to disturbance intensity (Fig. 3a,b). In general, both sandy and clayey sites in the light disturbance category grouped in the upper left quadrant of the canopy tree plot (Fig. 3a) and to the left of the y-axis in the ground layer vegetation plot (Fig. 3b). Differences in canopy composition among sites also reflected the proportion of combined pine species (results not shown). One site in the light military use category, A15B, appears compositionally more related to sites with heavier military use (Fig. 3a,b). This site tends to burn more frequently than the 3-year cycle of the other sites, and the canopy is > 90% longleaf pine.

Species richness and basal area of canopy trees did not differ among sites categorized by military disturbance and soil texture (ANOVA, $p = 0.42$ for richness, 0.13 for basal area). Tree density (stems per ha) tended to be greatest on LC and least on HC sites (ANOVA df=3, ms=0.0062, $F=2.61$, $p=0.06$; Fig. 4).

Species richness of ground layer vegetation differed among soil texture/land-use categories (ANOVA, df=3, ms=149.9, $F=8.48$, $p<0.0001$). There was a decreasing richness gradient from heavily disturbed sites with clayey soil, through lightly disturbed sites, to heavily disturbed sites with sandy soil (Fig. 4).

Discussion. Land at Fort Benning is used primarily to support the military mission, and land compartments are designated for infantry or mechanized training. Upland forests in training compartments are managed toward a longleaf pine ecosystem through thinning and prescribed burning. Disturbance features at 32 upland forest sites at Fort Benning reflected military land-use patterns, forestry practices, and natural disturbances. The amount of disturbance (length of sample transect classified as disturbed/total transect length) ranged among sites from <10% to 50%, with half of the sites having at least 30%. Some disturbance features, such as tank trails, were clearly related to military training. Others, such as skidder marks, were related to forestry practices. Some disturbances, however, could not be classified unambiguously by land-use origin. These included road-like features, which were the most frequent and abundant disturbance features. All the 32 upland forest sites at Fort Benning had at least one remnant or active trail or road.

The patterns of natural disturbance, combined with military and forestry-associated land-use, likely have resulted in a range of disturbance effects among upland sites at Fort Benning. Mechanized training, with tracked and wheeled vehicles, compacts soil and crushes or uproots vegetation (Demarais et al. 1999). Dismounted infantry training can result in vegetation being cut or trampled (Demarais et al. 1999). Forestry practices such as thinning open the canopy and, especially if skidders are used, disturb the soil. Prescribed burning reduces understory vegetation and promotes fire-tolerant species in the ground cover (e.g., Masters et al. 1998; Sparks et al. 1998).

Over time, land-use effects on ecosystems accumulate. Accumulation of forest management effects depends on the frequency and intensity of practices such as thinning and burning. Disturbances from military activities also are cumulative, especially if the same training sites are used repeatedly (Demarais et al 1999). Both frequency and severity (e.g., mechanized vs. infantry training) of military training can influence the degree of soil compaction and rate of vegetation loss or retrogression to early or midsuccessional communities (Demarais et al. 1999). At Fort Benning, land-use effects may be more persistent on heavily used, clayey (HC) sites. These sites had significantly greater length of transect classified as disturbed than other land-use/soil texture categories.

Land-use effects also can be concentrated or diffuse. At Fort Benning, mechanized training creates large roadways along ridgetops; erosion from these areas results in gullies and deposition lower on slopes. Infantry training can have more diffuse effects as troops move over the landscape (Demarais et al. 1999). The significant interaction between military land-use and percent clay among the 32 sites, with heavier use (H) sites having less clay than lighter use (L) sites, could be due to sand deposited from disturbed ridgetops in the land compartments open to mechanized training.

Forest management practices and recent land-use at Fort Benning are reflected in the species composition of canopy vegetation. Most of the 32 upland forest sites were dominated by pines, including *Pinus taeda* (22 sites), *P. palustris* (5 sites) and *P. echinata* (2 sites). Five sites had a significant hardwood component in the canopy, and four sites, with < 30% pine, were considered hardwood-dominated. The proportion of pine in the canopy was greater in sites with more intense land-use, including heavier military use (H) sites and the most frequently burned site (A15). The relative proportion of pines and hardwoods in other southern mixed forests that are less intensively managed also may be related to the disturbance regime. Brockway and Outcalt (1998) suggest that gap size has an important influence in the regeneration of longleaf pine ecosystems. Dynamics of southeastern Arkansas pine-oak forests left relatively undisturbed for decades suggest shade-intolerant pines are replaced by more shade-tolerant hardwoods (Shelton and Cain 1999; Cain and Shelton 2000).

Composition of ground layer vegetation also reflects forest management practices and recent land-use at Fort Benning. Ground layer species such as *Heterotheca graminifolia, Andropogon* spp, *Rhus copallina* L., and *Pteridium aquilinum* (L.) Kuhn are typical on sandhills in the region (e.g., Workman and McLeod 1990; Harper et al. 1997), but may also be associated with managed or disturbed sites such as pine plantations and old fields (Workman and McLeod 1990). The most abundant woody species in the ground layer of the Fort Benning sites, *Liquidambar styraciflua,* occurs frequently in old fields, pine plantations, and hardwood forests throughout the southeastern coastal plain (Workman and McLeod 1990). Differences in ground layer composition among sites appear related to response of the suite of subordinate species to land-use intensity, with a richer assemblage of species on clayey sites. Other research has shown species composition responses to land management. In shortleaf and loblolly pine stands subjected to winter burn cycles from 0 to 9 years, burning tended to increase the cover of composites and graminoids, and ground layer cover was less with more frequent burning (Cain et al. 1998). Simkin et al. (2001) suggest that historical fire regimes select for a generalized sprouting response to disturbance.

Land-use at Fort Benning occurs over a patchwork of soil types, and variation in soil texture influenced species richness in the ground layer of the 32 upland forest sites. Both heavily and lightly disturbed clayey sites had significantly greater species richness in the ground layer than sandy sites. Rodgers and Provencher (1999) also found greater species richness in areas with finer soil texture in Florida longleaf pine sandhill sites. The greater species richness could reflect better soil quality, i.e., less nutrient and water stress, or more patchy soil texture in clayey compared to sandy sites at Fort Benning. It might also represent a more diverse or longer successional pathway that allows a greater temporal response to land management practices on clayey sites. Shelton and Cain (2000) suggest that pine regeneration on higher quality sites is impeded by intense non-pine competition, which implies greater species richness on these sites. Historic land-use practices also may have affected soil quality and subsequent vegetation response at Fort Benning. Soil degradation by agriculture reduced the rate of secondary succession and diversity of later successional hardwood species in east Tennessee forests (Lafon et al. 2000).

Results from the 32 sites suggest undisturbed upland forests at Fort Benning are most likely part of the southern pine-oak-hickory forest. They would naturally grade from sandhills scrub oak-pine vegetation toward pine-hardwood or oak-hickory dominated forests, with greater species diversity in the ground layer of clayey sites. On the installation, forestry practices, including pine planting and frequent burning, and disturbances associated with mechanized military training favor pine dominance, and maintain open-site, successional or fire-tolerant species in the ground layer. As noted by Skeen et al. (1993) for southern pine-oak-hickory forest generally, land management at Fort Benning mimics historical land-use effects, from burning by Native Americans, through intensive agriculture that followed European settlement, to large-scale clearing for pine production (Skeen et al. 1993). Although intense management toward pine monocultures reduces within-stand canopy diversity (Skeen et al. 1993), the oak-hickory-pine forest appears resilient to intensive land-use (Skeen et al. 1993), including intensive management and military training activities. As urban and industrial development continue to expand in the southeastern Fall Line region, federal installations such as Fort Benning may help conserve the biological diversity of the region (Leslie et al. 1996). Identification of disturbance thresholds is needed to guide the managers of such military bases in sustainable forest management practices that can support the military mission and maintain biological diversity (Hedman et al. 2000).

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Table 1. Dominant canopy and ground layer plants in each of 32 Fort Benning sites with sandy (S) or clayey (C) soil and heavier (H) or lighter (L) military use. Canopy species listed collectively comprised ≥ 50% relative dominance at the site. Ground layer plants listed comprised ≥ 10% total cover in the site. * Poaceae (grasses other than identifiable *Andropogon* spp.)

	Lighter Military Use																Heavier Military Use															
	Clayey Soil								Sandy Soil								Clayey Soil								Sandy Soil							
	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H	A	B	C	D	E	F	G	H
CANOPY																																
Carya spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Carya ovata K. Koch	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Liriodendron tulipifera L.	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pinus echinata Miller	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	X	-	-	-	X	X	-	X	-	-	-	-	-	-	-	-
Pinus palustris Miller	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	-	X	-	X	-	-	-	X	-
Pinus taeda L.	-	-	X	X	X	-	X	X	X	X	X	X	X	X	X	X	X	-	-	X	X	-	X	X	X	X	-	X	X	X	X	X
Quercus alba L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Quercus falcata Michaux	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus nigra L.	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GROUND LAYER																																
Andropogon spp.	X	-	X	-	-	-	X	-	-	-	-	-	-	-	-	-	X	-	-	X	-	-	X	-	-	-	-	-	-	X	-	-
Carya spp.	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-

Desmodium spp.	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poaceae *	X	X	-	-	-	-	-	-	-	X	-	X	-	-	X	X	-	X	X	X	X	-	-	X	-	-	X	X	X	-	-	-
Quercus spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Rubus spp.	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Simlax spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Vaccinium spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Vitis spp.	-	X	-	-	-	-	X	-	X	-	X	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	X
Clitoria mariana L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-
Cnidoscolus stimulosus (Michaux) Engelm. & Gray	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Gelsemium sempervirens (L.) Aiton f.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-
Heterotheca graminifolia (Michaux) Shinners	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	X	X	-	-	X	-	X	-	X	X	X	-	-
Ilex glabra (L.) Gray	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Liquidambar styraciflua (L.)	-	-	X	X	X	-	X	X	X	-	X	X	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Myrica cerifera L.	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteridium aquilinum (L.) Kuhn	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	X	-	-	-	X	X	-	-	-	-	-	-	-	-	-
Quercus margaretta Ashe	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus nigra L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhus aromatica Aiton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Rhus copallina L.	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Toxicodendron radicans (L.) Kuntze	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-

Figure Legends

Fig. 1. a) Clay content (%) and b) amount of disturbance (m of line “disturbed” per 600 m sampled) in sites with lighter (L) or heavier (H) land-use and sandy (S) or clayey (C) soil. Shown are the category means (■) and standard deviation (-), and mean of each site (♦) within the category. Category means with the same letter do not differ significantly.

Fig. 2. Frequency (number encountered over all sites) and relative abundance (length of transect of feature/total length of sample line over all sites) of natural and land-use disturbance features in 32 400 x 400 m sites.

Fig. 3. NMDS of canopy (a) and ground layer (b) vegetation among sandy and clayey sites with heavier or lighter military use.

Fig. 4. Canopy tree density (stems/ha) and ground layer richness (number of species per point) in sites categorized as heavy (H) or light (L) military use and clayey (C) or sandy (S) soil. Shown are the category means (■) and standard deviation (-), and mean of each site (♦) within the category. Category means with the same letter do not differ significantly.