Grapevine (*Vitis* spp.) dynamics in association with manual tending, physiography, and host tree associations in temperate deciduous forests

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A B S T R A C T

The role of lianas (woody vines) in the development and diversity of both tropical and temperate forests under differing management scenarios has not been thoroughly explored. We examined changes in grapevine (*Vitis* spp.) densities over time in clearcut stands as influenced by manual tending, physiography, and host tree associations. We used data from long-term studies on 66 clearcut stands dominated by temperate deciduous forest tree species on the Hoosier National Forest in south-central Indiana, USA. Fourteen of the stands had grapevines removed manually, approximately during the stem exclusion stage of development. Grapevine densities steadily increased from age 5 until age 15, which coincides with the period of stem exclusion of these stands. Subsequent grapevine mortality may have been related to light competition. Manually treated stands had similar grapevine densities as untreated stands after 20 years across sites, and it appeared that only on the most xeric area was the grapevine treatment effective in reducing grapevine densities. During early stand development, ranging from ages 5 to 17, grapevine density was strongly related to slope position, but as stands developed through the stem exclusion stage, aspect emerged as a stronger factor influencing grapevine density. Black cherry (*Prunus serotina* Ehrh.), walnut (*Juglans* spp.), and elm (*Ulmus* spp.) were the most common grapevine host trees under both treated and untreated scenarios, which may be associated with the crown architecture of these species. Results suggest lianas play a critical role in the early development of disturbed forest sites in temperate deciduous forests. With concerns that lianas are increasing in abundance and distribution in these forest types, understanding their role in forest dynamics, such as host tree associations at different stages of development, competition dynamics on different sites and corresponding influences on tree growth, species composition, and diversity, will be critical to decision-making processes in achieving desired management goals in the future.

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1. Introduction

Interest in the study of lianas (woody vines) and their ecology has increased over the last few decades in recognition of the integral role they play in forest dynamics and development of forest communities. Lianas of tropical forests have received some attention recently; however, structure and dynamics of liana communities in temperate forests has not been well documented (Carter and Teramura, 1988; Collins and Wein, 1993; Putz, 1995;

Talley et al., 1996; Allen et al., 1997, 2005, 2007; McNab and Loftis, 2002). Concerns have been raised about increased growth and abundance of lianas in tropical forests (Wright et al., 2004), possibly due to elevated levels of atmospheric CO_2 (Condon et al., 1992; Granados and Körner, 2002; Phillips et al., 2002; Mohan et al., 2006; Zotz et al., 2006), disturbances, and fragmentation (Schnitzer and Bongers, 2002). Bragg (2004) observed increases in liana abundance of upland old-growth forests in Arkansas, USA using photographic evidence and attributed increases over the 20th century to the exclusion of fire, and Schnitzer (2005) proposed increasing minimum winter temperature trends may also result in increased liana abundance and their expansion to higher latitudes.

Historically, research on lianas of temperate forests of the Central Hardwood Forest region, USA, most notably grapevines

(*Vitis* spp.), was centered on controlling them to promote timber production in cove hardwood forest types in the Appalachian region (Trimble and Tryon, 1974, 1979; Smith, 1984), and, more recently, the role of grapevines in even-aged management of oak-hickory forests (Fischer, 1987). Grapevines are a source of great concern for forest and wildlife managers in temperate hardwood forests. They are an important forest community species because they produce food and cover for many species of birds and mammals (Martin et al., 1951). Other benefits such as increased species diversity and structural diversity may also be related to liana abundance (Pérez-Salicrup et al., 2004). However, forest managers often view grapevines as problematic because of the threat they pose to growth and quality of developing timber, especially on high quality sites where grapevines tend to proliferate (Trimble and Tryon, 1979). They are direct competitors with trees for sunlight, soil moisture, and nutrients, which may reduce tree growth rates (Dillenburg et al., 1995). Grapevines also increase host tree susceptibility to wind damage (Allen et al., 1997) and may result in greater ice damage to tree tops and limbs (Smith, 1984). In a competition experiment, Dillenburg et al. (1993, 1995) reported that photosynthesis, leaf nitrogen status, and biomass allocation of sweetgum (*Liquidambar styraciflua* L.) were reduced by above- and below-ground competition with Japanese honeysuckle (*Lonicera japonica* Thunb.) and Virginia creeper (*Parthenocissus quinquefolia* (L.) Planchon).

Even-aged management of forest stands and stand-replacing disturbances, as well as minor disturbances, often increase opportunities for growth and proliferation of grapevines. Grapevines respond positively to forest disturbances that increase light, water, and nutrient resources, trellises (downed woody debris and developing seedlings), and establishment opportunities. Grapevines are intolerant of shade and when exposed to sunlight, stems may produce epicormic branches (Smith, 1984). Grapevines root or layer easily when they come into contact with soil, and they sprout prolifically when cut or damaged (Smith, 1984). Shutts (1968) reports that shoot growth is rapid; Trimble and Tryon (1979) observed that young grapevine stump sprouts grew 4.6 m in a single season. Grapevines are supported by tendrils that allow vines to attach and grow on vegetation, and Trimble and Tryon (1979) suggest that tendrils attach to tree crowns when trees are young, thus developing and proliferating in developing tree crowns. Putz (1995) however, suggests that even non-adhesive tendrils limit the size of grapevine hosts.

Understanding grapevine patterns of abundance and distribution under naturally developing stands and control treatment management scenarios is critical to our understanding of forest ecosystem dynamics. This study evaluates development of grapevines in silvicultural clearcuts, under both natural and manual tending of grapevines scenarios, over a period of 20 years as they relate to site and host preferences. Objectives of this study included (i) examining change in grapevine densities of untreated stands 4–35 years after clearcut harvesting using a chronosequence of stands; (ii) evaluating grapevine density, presence, and distribution across sites of two separate study periods and in response to grapevine removal; and (iii) exploring grapevine and host tree associations. A similar article was recently published (Morrissey et al., 2008a), but this study presents data from a larger number of ecological regions and provides a different and more thorough method of statistical analysis than what was presented in Morrissey et al. (2008a).

2. Methods

2.1. Study area

This study was conducted within the Hoosier National Forest (HNF), which is dominated by upland hardwood forests in the

unglaciated central portion of southern Indiana, USA. Overstory species composition of the HNF has been strongly influenced by anthropogenic disturbance in the early 1800s with the intensification of European settlement and associated land-clearing for agriculture, mining, and timber harvesting (Ponder, 2004). Many agricultural areas were later abandoned due to low productivity, but widespread burning and grazing continued until the 1930s. Since that period, fire suppression has greatly reduced understory disturbance within these forests and periodic timber harvest has been the primary disturbance mechanism (Parker and Ruffner, 2004).

The HNF is located within the Shawnee Hills and Highland Rim ecological sections of the Interior Low Plateau (Homoya et al., 1985). The Shawnee Hills section includes the Crawford Uplands and Crawford Escarpment subsections. The Crawford Uplands subsection is characterized by rugged hills of acid silt loams of the Wellston–Zanesville–Berks association formed from sandstone and loess, marked by sandstone outcrops and rock shelters. Broad ridges and flats with moderately deep to deep soils are found throughout the subsection. Oak-hickory is the dominant forest type on upland slopes with typical species such as white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Münchh.), chestnut oak (*Quercus montana* Willd.), and hickory (*Carya* spp.). Mesic species such as American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh), white ash (*Fraxinus americana* L.), yellow poplar (*Liriodendron tulipifera* L.), and black walnut (*Juglans nigra* L.) are common in coves. In the Crawford Escarpment subsection, sandstone outcrops and rock shelters are not present as in the Crawford Uplands subsection, although much of the upland sections are otherwise similar in soils and topography. In upland areas, post-oak (*Quercus stellata* Wangenh.) and black oak tend to replace chestnut oak on drier sites, while some of the cove species present on the Crawford Uplands subsection are absent in the Crawford Escarpment subsection (Homoya et al., 1985).

The Highland Rim section includes the Brown County Hills and Mitchell Karst Plain subsections (Homoya et al., 1985). The Brown County Hills subsection is composed of shallow, well-drained acid silt loams of the Berks–Gilpin–Weikert association that were formed from weathered bedrock and minor amounts of loess. Topography of the area is typically composed of deeply dissected uplands, steep slopes, and narrow hollows. Oak-hickory is the major forest association on upland sites with chestnut oak dominating the overstory of ridge tops. Lower areas are composed of more mesic species such as American beech, northern red oak (*Quercus rubra* L.), sugar maple, and white ash. The Mitchell Karst Plain subsection is characterized by irregular topography with larger portions of rolling slopes with Karst features intermixed with areas of steep hillsides, bedrock outcrops, and cliffs (Homoya et al., 1985).

Natural regions were not considered independent. Grapevine densities indicated that stands of both regions were not significantly different ($P > 0.05$). Grapevine species in the south-central Indiana region include summer grape (*Vitis aestivalis* Michx.), winter grape (*Vitis cinerea* (Engelm.) Engelm. ex Millard), fox grape (*Vitis labrusca* L.), riverbank grape (*Vitis riparia* Michx.) and frost grape (*Vitis vulpina* L.), though no distinction between species was made in recording grapevine occurrence.

2.2. Sampling and vine control

In 1986, 74 stands were located and inventoried to evaluate regeneration of clearcut upland hardwood sites in southern Indiana (Fischer, 1987). All sampled stands were selected based on the requirement that they were harvested between 1969 and 1982 and had complete management records including age, acreage, and

sawtimber volume by HNF species groups. Stands ranged in age from 5 to 17 years old at time of measurement. Sampling was conducted between July 1986 and March 1987. Measurement plots were 0.004 ha circular plots with a resulting sampling intensity of one percent (1%). All trees and woody shrubs greater than 1.37 m were tallied by species, crown class, and origin (seedling, seedling sprout, stump sprout, or residual). All wild grapevines rooted within sample areas were tallied using the same procedure as Standiford and Fischer (1980); however, host tree species was not recorded. In 2004, new plots were established in 70 stands because the 1986 plot centers could not be effectively relocated and four of the stands changed ownership during that period. Plots were arranged at a density of 2.5 plots per ha for a sampling intensity of approximately 10%. Within circular plots, 0.04 ha in size, trees with a diameter at breast height (dbh) of 2.54 cm and greater were measured. Species, dbh, and crown class (dominant, intermediate, suppressed) were recorded for each tree. The number of grapevines rooted in the plot and entangled in the canopy of a tree within the plot, and the tree it was associated with was also recorded. Aspect was recorded to the nearest 5° of azimuth, and slope position was recorded as upper, mid, and lower slopes.

Manual tending of grapevines with chainsaws was conducted in 14 stands (233 plots) within the Shawnee Hills natural region, and these were compared to 52 stands (711 plots) that received no grapevine treatment; four stands were excluded from the study because it was uncertain if those stands were treated for grapevines. HNF contract regulations required that at least 90% of all grapevine stems were to be cut within 46 cm of the ground with no chemical application to or removal of severed stems. Stands were treated between 1986 and 1989 with no specific season of treatment identified, and stands ranged in age from 7 to 15 years at the time of treatment, shortly after the beginning of the stem exclusion stage of stand development (Fischer, 1987).

2.3. Data preparation

Grapevine density of individual plots was stratified by a combination of age group, transformed aspect code (hereinafter, referred to as aspect code), and slope position. Age groups were classified by 3-year interval, each of which consisted of more than 100 plots, with the exception of the 19–21-year age group that had only 30 plots. Aspect code was determined based on Beers et al. (1966) aspect transformation procedure, which was reduced to two aspect codes. Xeric aspects (135–315°) range from southeast to northwest sites, while mesic aspects (315–135°) range from northwest to southeast sites. Slope position was grouped according to lower, mid, and upper slope; an approach adopted from Bowersox and Ward (1972). Plot distribution for the two sample periods by aspect code and slope position is shown in Table 1. A total of 1624 plots were established in 1986 and 1252 plots were established in 2004. Species selection for host tree association was based on number of trees tallied (>100) and species of interest. American beech, ironwood (Ostrya virginiana (Mill.) K. Koch), and blackgum (Nyssa sylvatica Marsh) had more than 100 trees tallied, but were excluded from analysis based on the low number of vines found in them. Some species were grouped according to genus: elm (Ulmus spp.), aspen (Populus spp.), ash, hickory, and walnut. White oak, chestnut oak, swamp white oak (Quercus bicolor Willd.), chinkapin oak (Quercus muehlenbergii Engelm.), and bur oak (Quercus macrocarpa Michx.) were classified as the white oak group. Northern red oak, black oak, and scarlet oak were classified as the red oak group. Sugar maple, red maple (Acer rubrum L.), black cherry (Prunus serotina Ehrh.), sassafras (Sassafras albidum (Nutt.) Nees), and yellow poplar were analyzed as individual species.

Table 1

Number of plots for 1986 and 2004 sampling periods according to grapevine treatment, aspect code, and slope position in hardwood stands of the Hoosier National Forest, south-central Indiana, USA.

Vine control	1986		2004	
	Xeric	Mesic	Xeric	Mesic
Treated				
Upper	55	58	51	43
Middle	128	114	76	80
Lower	36	28	35	35
Treated totals	219	200	162	158
Untreated				
Upper	137	144	112	98
Middle	321	442	241	327
Lower	62	99	82	72
Untreated totals	520	685	435	497
Grand totals	739	885	597	655

2.4. Data analysis

Density measures of grapevine across plots did not meet assumptions of parametric statistics; thus, we used JMP version 5.1 (SAS Institute, Inc., Cary, NC, USA) to analyze the data using regression tree analysis to evaluate factors that contributed to grapevine density in the 2004 dataset (Fan et al., 2006). Regression trees use an iterative process to split data into partitions called binary recursive partitioning. The algorithm selects the factor to split that partitions data into two groups such that it takes magnitude of an effect on the continuous variable, grapevine density, into account, rather than residual variance. Partitioning is then applied to each of the new branches and continues until each node reaches a user-specified minimum node size (20 plots) and becomes a terminal node, or further splits do not justify complexity of the tree relative to increased explanation of variance of the variable of interest. Assuming grapevine density is an indicator of its competitiveness, explanatory site-related variables yielded from the regression tree were then used to frame further exploration of competitive success of grapevines in relation to site. Grapevine occurrence in relation to host species was examined using chi-square (χ^2) analysis on the presence or absence of grapevines for each dominant or co-dominant tree tallied in non-treated plots for the 2004 data set. Statistical differences were based on $\alpha = 0.05$.

3. Results

3.1. Grapevine density change over time

Grapevine density appeared to have steadily increased over time until 13–15 years after silvicultural clearcutting (Fig. 1). After approximately 15 years of age, grapevine densities appeared to have steadily decreased until age 35; stands treated for grapevines after the 1986 sample period were not included in the data for age groups beyond age 18. In terms of vine control, plots targeted for manual tending (n = 419) in 1986 had more vines than untreated plots (n = 1205). Treated plots (n = 320) had similar vine density as untreated plots (n = 932) in 2004 (Fig. 2).

3.2. Regression tree analysis

The most obvious difference between the 1986 and 2004 grapevine densities was the initial split of the regression trees (Fig. 3). In 1986, slope position was the single strongest factor (52% of total sum of squares (SS)) influencing grapevine densities, with
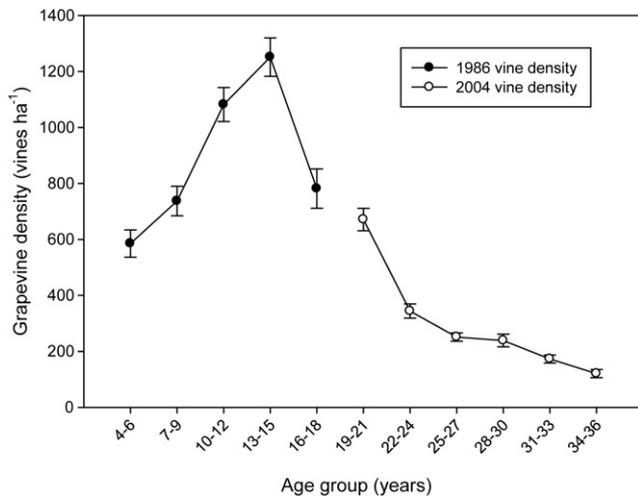
Fig. 1. Chronosequence of grapevine (*Vitis* spp.) density (± standard error) by age group after silvicultural clearcutting of stands on the Hoosier National Forest in south-central Indiana, USA. Figure is based on plot data from the same stands, but different plot centers, during two different sample periods. All age groups had a minimum of 100 plots with the exception of the 19–21-year old group that had 30 plots.
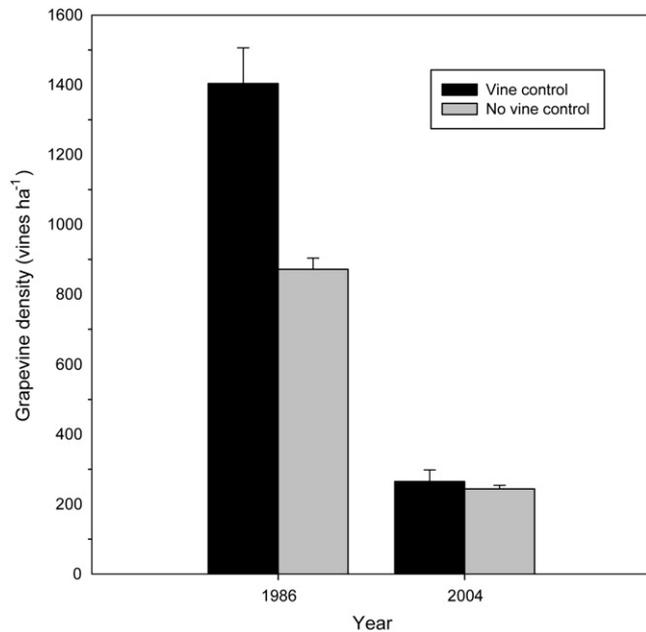

Fig. 2. Change in grapevine density from 1986 to 2004 as influenced by manual tending of grapevines in hardwood stands of the Hoosier National Forest, south-central Indiana, USA.

lower slope positions producing more grapevines. In 2004, aspect was the first split of the regression trees of both treated and untreated plots, with north- to east-facing mesic slopes having higher grapevine densities. A comparison of regression trees of treated and untreated stands of 2004 indicated few differences in terms of grapevine density across most sites. Grapevine densities on south- to west-facing upper slope positions were much lower than all other slope and aspect combinations.

3.3. Grapevine presence by site

In the 1986 sample period, grapevine presence showed an increasing, yet weak trend moving from upper slope positions to lower slope positions, with only slightly more plots with grape-vines on more mesic aspects (Table 2). In 2004, stands that

received no manual tending to control grapevines showed similar percentages of plots with grapevines across all slope positions, yet on mesic aspects, 91% of plots had one or more grapevines compared to 82% on xeric aspects. Treated stands showed a lower percentage of plots with grapevines on upper slope positions relative to middle and lower slope positions regardless of aspect. A total of 78% of plots in treated stands also had one or more grapevines compared to 87% of plots in untreated stands.

3.4. Host species association

Chi-square analysis indicated that not all species groups had the same probability of having grapevines ($P < 0.0001$, Table 3). Black cherry had more than twice as many grapevines than expected ($X = 674.1 > 31.26^2{}_{\times 11[0.001]}$). Walnut and elm species also had more grapevines than expected. Some species groups had fewer grapevines than expected, including the red and white oak groups, aspen species, and yellow poplar. Sassafras, sugar maple, red maple, as well as ash and hickory species did not have more or less grapevines than expected.

4. Discussion

4.1. Grapevine dynamics

Grapevines compete for light, water, and nutrients in developing forests, and their success is related to their ability to acquire resources. It is thus not surprising that over time, grapevine density, presence, and distribution varied in response to site, species association, and treatment. It is well documented that vines are opportunistic organisms that proliferate in fragmented forest edges (Londré and Schnitzer, 2006), including canopy gaps (Schnitzer and Carson, 2001), and larger natural (Allen et al., 2005) and harvest openings (Trimble and Tryon, 1974, 1979; Schnitzer et al., 2004). Grapevines use tendrils to climb other woody plants, and early successional habitats provide abundant trellis opportunities. On a high quality mixed-hardwood site in the Appalachian region, USA, Trimble and Tryon (1979) observed 172,900 grapevine seedlings ha^{-1} 1 year after clearcutting, and after 5 years the density was a mere fraction of that at 4878 grapevines ha^{-1}. At a similar age, we observed lower grapevine densities (525 ± 63 grapevines ha^{-1}), but older stands showed increasingly higher densities up until about age 15; Beck and Hooper (1986) noted a similarly high increase in grapevine coverage in developing clearcuts between ages 5 and 10 in a high quality mixed-hardwood stand in North Carolina, USA. Fischer (1987) estimated that complete canopy closure occurred about age 11 on these sites, as indicated by high tree mortality rates, and we see a similar pattern in grapevine stems in stands greater than 15 years of age until approximately age 24 when grapevine mortality rates appear to diminish. As developing clearcuts enter the stem exclusion stage, competition for resources greatly intensifies, and density-dependent mortality increases.

Negative effects of lianas on host tree growth and development have been documented in both temperate and tropical forests. Damage ranges from infrequent stand level events, such as ice storm damage (Siccama et al., 1976) or large-scale wind events (Allen et al., 1997), to individual tree events or more subtle growth and development inhibition. Featherly (1941) and Whigham (1984) observed slower stem growth rates of liana host trees. Reduced growth of host trees may be associated with reduced photosynthetic carbon assimilation due to limitations in water, nutrient, and light availability. Lianas compete with other plants for below-ground resources (Whigham, 1984; Pérez-Salicrup and Barker, 2000; Schnitzer et al., 2005), and they can reduce available solar radiation to host plants (Lutz, 1943; Hegarty, 1991; Dillenburg et al., 1995). Mechanical damage caused by vines
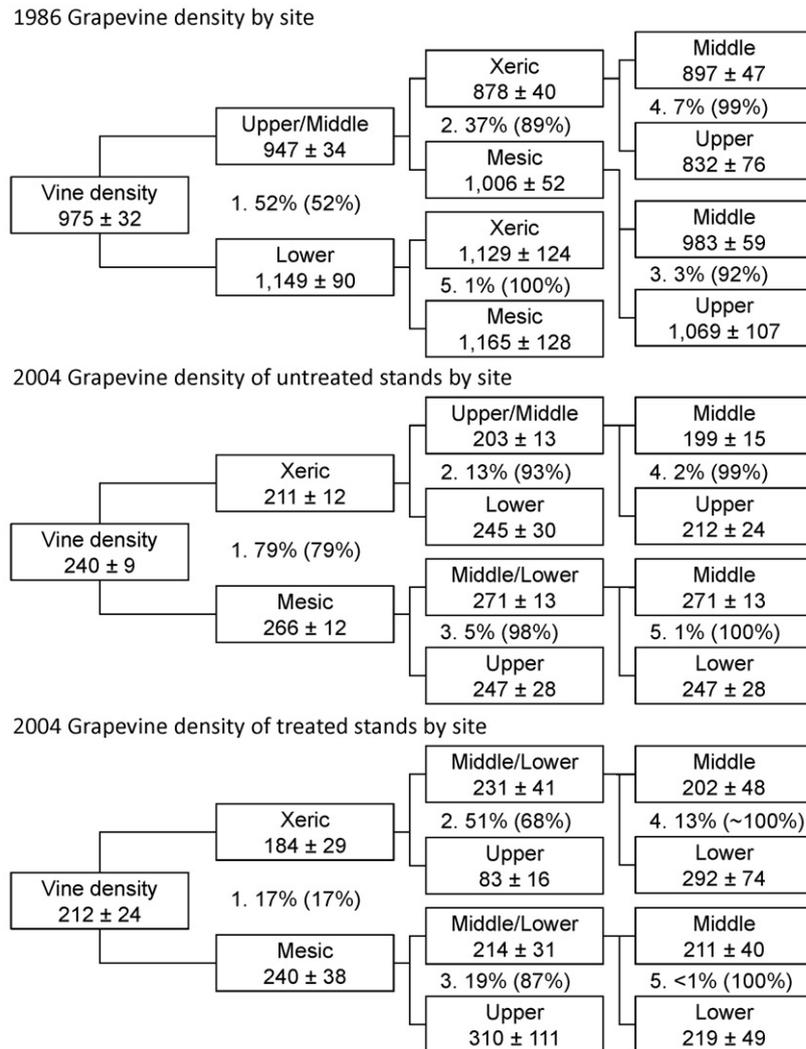
Fig. 3. Regression tree analysis of plot grapevine densities (± standard error) for the 1986 sampling period, and the treated and non-treated 2004 sampling period of clearcut stands on the Hoosier National Forest, south-central Indiana, USA. At each split, the order number of the split is indicated along with each percentage of total sums of squares, followed by the cumulative percentage of total sum of squares.

may also result in loss of branches and leaves (Smith, 1984), or photosynthetic conducting tissue due to stem constriction (Lutz, 1943). To the degree that lianas decrease host tree fitness, trees without lianas have an advantage, thus, influencing the competitive stage and future development of the stand (Schnitzer and Bongers, 2002). Putz (1980, 1984) contended that host tree competition with lianas has exerted strong selective pressure on tropical trees. Because grapevine host trees of the earlier sample were not identified, we could not speculate on possible selection pressures as a result of grapevine occurrence.

Our initial hypothesis was that grapevines would be more strongly associated with seedlings that quickly invade clearcut sites and exhibit rapid growth, such as yellow poplar and black cherry. Hegarty (1991) noted that tendril climbers, such as grapevines, tend to be associated with early successional and pioneer species groups. Observations of Trimble and Tryon (1979) indicated that in clearcut sites grapevines became attached to tree crowns and boles by tendrils when they were very young, thus, providing grapevines with an early competitive advantage as indicated by their higher densities as young stands develop. Species groups such as black cherry, walnut, and elm, where grapevines were found to be more prevalent, tend to have crowns that provide increased light penetration due to their branch

architecture and leaf morphologies in contrast to species such as yellow poplar and oak (USDA Natural Resources Conservation Service, 2008). We cannot, however, speculate as to whether yellow poplar or any other species were common host species for grapevines at earlier stages of development. On these same sites, Morrissey et al. (2008b) determined that neither yellow poplar nor black cherry showed significant reductions in relative density of dominant and co-dominant trees between the two sample periods, indicating that they remained competitive during that period despite grapevine competition. We speculate that as competition for light resources increased in developing canopies, grapevine densities decreased, perhaps as a result of their shade intolerance. Although no data was collected with regard to mechanical damage to crowns of host trees, it was observed that black cherry crowns were often thin and malformed, although this may also be attributed to abrasion with neighboring trees during wind events, site characteristics, or environmental circumstances.

4.2. Grapevine control efforts

Trimble and Tryon (1979) recommended control measures for young even-aged stands on high quality sites that included manually cutting all grapevine stems that extended into the

Table 2
Breakdown of percentage of plots with one or more grapevines present (GV $\geq$ 1) per plot by sample period, treatment, aspect, and slope position of silvicultural clearcuts on the Hoosier National Forest in south-central Indiana, USA. Because plot sizes of the 1986 and 2004 sample periods are different, it is not appropriate to directly compare results.

	Xeric aspect			Aspect summary	Mesic aspect			Aspect summary	Total
	Upper	Middle	Lower		Upper	Middle	Lower		
1986									
No GV	31%	23%	19%	25%	28%	20%	18%	21%	23%
GV $\geq$ 1	69%	77%	81%	75%	72%	80%	82%	79%	77%
2004 non-treated									
No GV	20%	18%	16%	18%	13%	9%	1%	9%	13%
GV $\geq$ 1	80%	82%	84%	82%	87%	91%	99%	91%	87%
2004 treated									
No GV	31%	22%	20%	25%	30%	15%	17%	20%	22%
GV $\geq$ 1	69%	78%	80%	75%	70%	85%	83%	80%	78%

Table 3
Grapevine occurrence distribution based on presence/absence data of dominant or co-dominant trees in untreated hardwood stands of the Hoosier National Forest, south-central Indiana, USA.

Species groups	No. of trees tallied	No. of vines observed	No. of vines expected	χ^2	P-value
More than expected					
Black cherry (Prunus serotina)	2,968	1081	500	674.1	<0.001
Elm (Ulmus spp.)	1,046	262	176	41.6	<0.001
Walnut (Juglans spp.)	114	39	19	20.4	<0.05
Less than expected					
White oak (Quercus spp.)	2,408	224	406	81.5	<0.001
Aspen (Populus spp.)	1,283	91	216	72.5	<0.001
Yellow poplar (Liriodendron tulipifera)	4,458	549	751	54.5	<0.001
Red oak (Quercus spp.)	2,612	311	440	38.0	<0.001
Not significant					
Sassafras (Sassafras albidum)	1,617	210	273	14.4	NS
Red maple (Acer rubrum)	1,787	242	301	11.6	NS
Ash (Fraxinus spp.)	1,281	263	216	10.3	NS
Sugar maple (A. saccharum)	1,579	304	266	5.4	NS
Hickory (Carya spp.)	389	55	66	1.7	NS
Total	21,542	3631			

canopy near ground level. In terms of grapevine densities, stands that were treated with manual tending to control grapevines were not significantly different than untreated stands almost 20 years later (Fig. 2). Based on a required reduction of at least 90% of grapevine densities in all treated stands, which was later verified through sampling (Tormoehlen, USDA Forest Service, pers. comm.), it was expected that post-treatment densities would have been significantly lower than the untreated stands; in fact, grapevine densities of treated stands likely increased slightly over that same period after the tending treatment. Grapevine density increases may be related to canopy height. Trimble and Tryon (1976) recommended a minimum height of 7.6 m with a closed canopy for vine control intervention and the average height of treated stands was approximately 8.7 $\pm$ 0.5 m; thus, if no herbicides are to be used in the manual tending operation, it may be prudent to do so at a slightly higher minimum height than generally recommended.

There were no differences across slope position and aspect combinations with the exception of upper slope positions of xeric sites where it appears grapevine densities remained low (Fig. 3). Upper slope positions of xeric sites, the least productive of all sites surveyed, may have been too dry to support the vigorous sprout growth of cut grapevine stems needed to ascend to the upper canopy, thus, providing the trees with a competitive advantage over the grapevines. Large vessel diameters of Vitis spp. tend to make them more susceptible to cavitation or embolism, and may limit their success on drier sites (Bell et al., 1988). Alternatively, on more mesic sites, cut grapevine stems likely resulted in some vigorous sprouts that were able to grow quickly enough and

exploit minor canopy gaps to attain a prominent canopy position. Trimble and Tryon (1979) observed annual growth rates of 4.6 m for young grapevine stump sprouts, and Boring et al. (1981) noted even higher growth rates. Many grapevine sprouts could have reached the canopy within 2–3 growing seasons if sufficiently able to compete for available resources, notably light and water, to sustain growth.

A key aspect of manual tending that cannot be addressed is the effect on the dynamics of those stands compared to untreated stands. In terms of species associations, stands that had grapevine removal treatments showed no differences compared to treated stands with black cherry, walnut, and elm species. Bruner (1967) removed Japanese honeysuckle vines from yellow poplar saplings with four herbicide applications over a 5-year period on a mesic early successional site in South Carolina, USA. Although the herbicide treatment did not reduce the number of saplings with heavy vine infestations (100%), it did lower mortality compared to non-treated saplings.

Understanding these subtle dynamics of grapevine populations and relationships with site and host preferences is an important aspect of early developmental stages of regenerating temperate forests. This study provides insight into changes in grapevine populations over time under both natural stand development and grapevine control scenarios in disturbed temperate forests. Our results contribute new supporting evidence as to the prominent influence of grapevines during the regeneration phase in temperate deciduous forests and suggest that more intensive research in this area appears warranted.

5. Conclusions

Lianas are fast-growing, successional woody species that must rely on competing vegetation for structural support, and are therefore able to allocate more resources to leaf production, stem and root elongation, and reproduction, and act as a source of competition for certain desirable forest species. Lianas play an important role in forest dynamics by contributing to tree mortality, differentially affecting growth rates of competing species, and providing valuable wildlife habitat components. The pervasive nature of lianas in tropical forests has promoted some studies examining their various ecosystem functions, but in temperate forests, where lianas are less abundant, there has been even less research, presumably because it is assumed their role is diminished in accordance with their abundance.

Our study indicated that after clearcutting grapevines tended to increase in density early in the stand initiation stage through to the stem exclusion stage, at which time grapevine populations declined quickly, presumably related to competition-induced mortality. It was evident that site also played an important role at differing stages of stand development, and may have contributed to increased effectiveness of manual tending treatments on some sites. Preferred grapevine and host tree associations were evident, which alludes to their importance in temperate forest dynamics as stands develop and mature. Boring et al. (1981) reported that grapevines in a 1-year old clearcut in North Carolina, USA accounted for only 5.2% of vegetative biomass, but they played an important role in conserving site nutrients and recovery of nutrient cycling processes, further evidence of their influence on early stand development. Thus, past studies examining lianas in temperate forests, though relatively limited in number, indicate that lianas do indeed play a critical role in the early development of disturbed forest sites.

Concerns regarding increases in mean winter temperatures, atmospheric CO_2, and forest fragmentation have also lead to speculation that such conditions may result in increasing abundance of lianas and a wider distribution in temperate forests (Londré and Schnitzer, 2006), thus, recognizing the role of lianas in temperate forests will become increasingly important. Enhancing knowledge of lianas in relation to factors such as treatment costs and efficacy, host tree associations at different stages of development, competition dynamics on different sites and effects on growth, species composition, and diversity may favor certain management goals. For example, grapevines on currently less desirable host trees, such as yellow poplar in many parts of the Central Hardwood Forest region of the USA (Morrissey et al., 2008b), may in fact be an advantageous scenario that limits growth of yellow poplar through above- and below-ground competition from grapevines, which in turn favors more desirable intolerant species, such as oaks.

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References

Allen, B.P., Pauley, E.F., Sharitz, R.R., 1997. Hurricane impacts on liana populations in an old growth southeastern bottomland forest. Journal of the Torrey Botanical Society 124, 34–42.

Allen, B.P., Sharitz, R.R., Goebel, P.C., 2005. Twelve years post-hurricane liana dynamics in an old-growth southeastern floodplain forest. Forest Ecology and Management 218, 259–269.

Allen, B.P., Sharitz, R.R., Goebel, P.C., 2007. Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? Forest Ecology and Management 242, 17–23.

Beck, D.E., Hooper, R.M., 1986. Development of a southern Appalachian hardwood stand after clearcutting. Southern Journal of Applied Forestry 10, 168–172.

Beers, T.W., Dress, P.E., Wenzel, L.C., 1966. Aspect transformation in site productivity research. Journal of Forestry 64, 691–692.

Bell, D.J., Forseth, I.N., Teramura, A.H., 1988. Field water relations of three temperate vines. Oecologia 74, 537–545.

Boring, L.R., Monk, C.D., Swank, W.T., 1981. Early regeneration of a clear-cut southern Appalachian forest. Ecology 62 (5), 1244–1253.

Bowersox, T.W., Ward, W.W., 1972. Prediction of oak site index in the ridge and valley region of Pennsylvania. Forest Science 18, 192–195.

Bragg, D.C., 2004. Composition, structure, and dynamics of a pine-hardwood old-growth remnant in southern Arkansas. Journal of the Torrey Botanical Society 131, 320–336.

Bruner, M.H., 1967. Honeysuckle—a bold competitor on bottomland hardwood sites. Forest Farmer 26, 9–17.

Carter, G.A., Teramura, A.H., 1988. Vine photosynthesis and relationships to climbing mechanics in a forest understory. American Journal of Botany 75, 1011–1018.

Collins, B.S., Wein, G.R., 1993. Understory vines: distribution and relation to environment on a southern mixed hardwood site. Bulletin of the Torrey Botanical Club 120, 38–44.

Condon, M.A., Sasek, T.W., Strain, B.R., 1992. Allocation patterns in two tropical vines in response to increased atmospheric CO_2. Functional Ecology 6, 680–685.

Dillenburg, L.R., Whigham, D.F., Teramura, A.H., Forseth, I.N., 1993. Effects of vine competition on availability of light, water, and nitrogen to a tree host (Liquidambar styraciflua). American Journal of Botany 80 (3), 244–252.

Dillenburg, L.R., Teramura, A.H., Forseth, I.N., Whigham, D.F., 1995. Photosynthetic and biomass allocation responses of Liquidambar styraciflua (Hamamelidaceae) to vine competition. American Journal of Botany 82, 454–461.

Fan, Z., Kabrick, J.M., Shifley, S.R., 2006. Classification and regression tree based survival analysis in oak-dominated forests of Missouri's Ozark highlands. Canadian Journal of Forest Research 36, 1740–1748.

Featherly, H.I., 1941. The effect of grapevines on trees. Oklahoma Academy of Science Proceedings 21, 61–62.

Fischer, B.C., 1987. The regeneration response to clearcutting on the U.S. Forest Service Hoosier National Forest. Purdue University Report submitted to the Hoosier National Forest. USDA Forest Service, p. 84.

Granados, J., Körner, C., 2002. In deep shade, elevated CO_2 increases the vigor of tropical climbing plants. Global Change Biology 8, 1109–1117.

Hegarty, E.E., 1991. Vine–host interactions. In: Putz, F.E., Mooney, H.A. (Eds.), The Biology of Vines. Cambridge University Press, Cambridge, England, pp. 357–376.

Homoya, M.A., Abrell, D.B., Aldrich, J.D., Post, T.W., 1985. The natural regions of Indiana. Proceedings Indiana Academy Science 94, 245–268.

Londré, R.A., Schnitzer, S.A., 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. Ecology 87, 2973–2978.

Lutz, H.J., 1943. Injuries to trees caused by Celastrus and Vitis. Bulletin of the Torrey Botanical Club 70, 436–439.

Martin, A.C., Zim, H.S., Nelson, A.L., 1951. American Wildlife and Plants: A Guide to Wildlife Food Habitats. Dover Publications, New York, 499 p.

McNab, W.H., Loftis, D.L., 2002. Probability of occurrence and habitat features for oriental bittersweet in an oak forest in the southern Appalachian Mountains. Forest Ecology and Management 155, 45–54.

Mohan, J.E., Ziska, L.H., Schlesinger, W.H., Thomas, R.B., Sicher, R.C., George, K., Clark, J.S., 2006. Biomass and toxicity responses of poison ivy (Toxicodendron radicans) to elevated atmospheric CO_2. Proceedings of the National Academy of Sciences of the United States of America 103, 9086–9089.

Morrissey, R.C., Gauthier, M.-M., Kershaw Jr., J.A., Jacobs, D.F., Fisher, B.C., Seifert, J.R., 2008a. Grapevine dynamics after manual tending of juvenile stands on the Hoosier National Forest, Indiana. Proceedings of the 16th Central Hardwood Forest Conference, April 7–9, 2008. West Lafayette, IN. USDA Forest Service General Technical Report NRS-P-24, pp. 395–404.

Morrissey, R.C., Jacobs, D.F., Seifert, J.R., Kershaw, J.A., Fischer, B.C., 2008b. Competitive success of natural oak regeneration in clearcuts during the stem exclusion stage. Canadian Journal of Forest Research 38 (6), 1419–1430.

Parker, G.R., Ruffner, C.M., 2004. Current and historical forest conditions and disturbance regimes in the Hoosier–Shawnee ecological assessment area. In: Thompson III, F.R. (Ed.), The Hoosier–Shawnee Ecological Assessment. USDA Forest Service General Technical Report NC-244, pp. 23–59.

Pérez-Salicrup, D.R., Barker, M.G., 2000. Effect of liana cutting on water potential and growth of Senna multijuga (Caesalpinioideae) trees in a Bolivian tropical forest. Oecologia 124, 469–475.

Pérez-Salicrup, D.R., Schnitzer, S.A., Putz, F.E., 2004. Community ecology and management of lianas. Forest Ecology and Management 190, 1–2.

Phillips, O.L., Martinez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Mendoza, A.M., Neill, D., Vargas, P.N., Alexiades, M., Cerón, C., De Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M., Vinceti, B., 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418, 770–774.

Ponder Jr., F., 2004. Ecological regions and soil conditions in the Hoosier–Shawnee ecological assessment area. In: Thompson III, F.R. (Ed.), The Hoosier–Shawnee

Ecological Assessment. USDA Forest Service General Technical Report NC-244, pp. 9–22.

Putz, F.E., 1980. Lianas vs. trees. Biotropica 12, 224–225.

Putz, F.E., 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65, 1713–1724.

Putz, F.E., 1995. Relay ascension of big trees by vines in Rock Creek Park, District of Columbia. Castanea 60, 167–169.

Schnitzer, S.A., Parren, M.P.E., Bongers, F., 2004. Recruitment of lianas into logging gaps and the effects of pre-harvest liana cutting in a lowland forest in Cameroon. Forest Ecology and Management 190, 87–98.

Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166, 262–276.

Schnitzer, S.A., Carson, W.P., 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82 (4), 913–919.

Schnitzer, S.A., Bongers, F., 2002. The ecology of lianas and their role in forests. Trends in Ecology and Evolution 17, 223–230.

Schnitzer, S.A., Kuzee, M., Bongers, F., 2005. Disentangling above- and below-ground competition between lianas and tress in a tropical forest. Journal of Ecology 93, 1115–1125.

Shutts, L.M., 1968. Autoecology and Fruit Production of Summer Grape (*Vitis aestivalis*) and Silverleaf Grape (*V. aestivalis* var. argentifolia) in the Virginia Highlands. Virginia Polytechnic Institute, Blacksburg, VA, p. 55.

Siccama, T.G., Weir, G., Wallace, K., 1976. Ice damage in a mixed hardwood forest in Connecticut in relation to Vitis infestations. Bulletin of the Torrey Botanical Club 103, 180–183.

Smith, H.C., 1984. Forest management guidelines for controlling wild grapevines. In: Research Paper NE-548. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, PA, p. 15.

Standiford, R.B., Fischer, B.C., 1980. Fifteen year results of three harvesting methods on composition and development of regeneration in southern Indiana upland hardwoods. In: Garrett, H.E., Cox, G.S. (Eds.), Proceedings of the 3rd Central Hardwood Forest Conference. pp. 408–419.

Talley, S.M., Lawton, R.O., Setzer, W.N., 1996. Host preferences of *Rhus radicans* (Anacardiaceae) in a southern deciduous hardwood forest. Ecology 77, 1271–1276.

Trimble Jr., G.R., Tryon, E.H., 1974. Grapevines a serious obstacle to timber production on good hardwood sites in Appalachia. Northern Logger 23, 22–23.

Trimble Jr., G.R., Tryon, E.H., 1976. Grapevine control in young even-aged hardwood stands. Northern Logger 24 (9), 12–13.

Trimble Jr., G.R., Tryon, E.H., 1979. Silvicultural control of wild grapevines. West Virginia Agricultural Experiment Station Bulletin 667, p19.

USDA Natural Resources Conservation Service, 2008. The PLANTS database, version 3.5 [online]. Available from http://plants.usda.gov [cited October 28, 2008].

Whigham, D.F., 1984. The influence of vines on the growth of *Liquidambar styraciflua* (sweetgum). Canadian Journal of Forest Research 14, 37–39.

Wright, S.J., Calderon, O., Hernandez, A., Paton, S., 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85, 484–489.

Zotz, G., Cueni, N., Körner, C., 2006. *In situ* growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO_2. Functional Ecology 20, 763–769.