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THE DISTRIBUTION OF LIANAS AND THEIR CHANGE IN ABUNDANCE IN TEMPERATE FORESTS OVER THE PAST 45 YEARS

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Abstract. Lianas (woody vines) are an important and dynamic component of many forests throughout the world, and increases in CO_2, mean winter temperature, and forest fragmentation may promote their growth and proliferation in temperate forests. In this study, we used a 45-year data set to test the hypothesis that lianas have increased in abundance and basal area in the interiors of 14 deciduous temperate forests in Wisconsin (USA) since 1959. We also censused woody plants along a gradient from the forest edge to the interior in seven of these forests to test the hypothesis that the abundance of lianas declines significantly with increasing distance from the forest edge. We found that lianas did not increase in abundance within the interiors of temperate forests in Wisconsin over the last 45 years. However, relative and absolute liana abundance decreased sharply with increasing distance from forest edges. Our findings suggest that forest fragmentation, not climate change, may be increasing the abundance of lianas in northern deciduous temperate forests, and that lianas may further increase in abundance if the severity of forest fragmentation intensifies.

Key words: climate change; edge effects; forest fragmentation; lianas, distribution and abundance; temperate forests; Wisconsin, USA, deciduous forests.

INTRODUCTION

Lianas (woody vines) are a key component of forests around the world, competing intensely with trees and reducing tree growth, establishment, fecundity, and survivorship (Dillenburg et al. 1993, Pérez-Salicrup 2001, Schnitzer et al. 2005). In tropical forests, lianas commonly compose 10–45% of the woody stems and species (Schnitzer and Bongers 2002) and may be increasing in size and abundance, possibly due to elevated levels of atmospheric CO_2, forest productivity, and disturbance (Phillips and Gentry 1994, Phillips et al. 2002, Wright et al. 2004). Lianas are also common in temperate forests, where they may also be increasing in size and abundance for some of the same reasons. Approximately 215 species of lianas occur in the contiguous United States (USDA NRSC 2005), and both native and invasive lianas, such as *Celastrus orbiculatus, Hedera helix, Parthenocissus quinquefolia*, *Pueraria montana*, *Toxicodendron radicans,* and *Vitis* spp. may alter tree regeneration and forest dynamics in North America (Smith and McCay 1979, McNab and Loftis 2002).

Increasing levels of CO_2 may enhance growth and proliferation of temperate lianas more than of competing growth forms (e.g., trees; Hättenschwiler and Körner 2003, Mohan et al. 2006, Zotz et al. 2006), thus allowing lianas to increase in relative abundance. Globally, atmospheric CO_2 levels have risen substantially, from ~280 ppm in the industrial revolution (ca. 1850) to ~375 ppm in 2005, with 60% of this increase occurring after 1958 (Keeling and Whorf 2005).

Warmer winter temperatures may also increase the abundance and distribution of temperate lianas, which are limited in their distribution by their vulnerability to freezing-induced xylem embolism in cold climates (Sperry et al. 1987, Ewers et al. 1991, Schnitzer 2005). Both annual and winter temperatures in North America have risen over the past half century, possibly allowing lianas to increase in abundance and expand their ranges poleward (sensu Parmesan and Yohe 2003). Since 1960 in Wisconsin, USA, mean annual temperatures have increased by 0.94°C (range: 4.9 to 8.1°C; $P = 0.02$, $R^2 = 0.12$, $n = 45$ annual data points) and mean winter temperatures (December–February) increased by 2.40°C (range: −12.8 to −3.2°C; $P = 0.02$, $R^2 = 0.13$, $n = 45$; NOAA/NESDIS/NCDC 2005). In contrast, mean annual precipitation, a likely driver of liana distributions in tropical forests (Schnitzer 2005), has not changed significantly in Wisconsin during the period from 1960 to 2005 (33.76 to 35.50 cm/yr; $P = 0.21$, $R^2 = 0.04$, $n = 45$; NOAA/NESDIS/NCDC 2005).

Lianas also increase in abundance with increased disturbance and forest fragmentation, as has been shown in tropical forests (reviewed by Schnitzer and Bongers [2002]). If this association also holds true for temperate forests (e.g., McNab and Loftis 2002, Merriam 2003), then increased forest fragmentation (Vogelmann 1995, Radeloff et al. 2005) should cause an increase in liana abundance in these forests. Aside from species-specific studies (e.g., McNab and Loftis 2002), however, little is known about the factors that explain

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the abundance and distribution of lianas in temperate forests, and whether liana abundance is increasing with changes in land use and climate.

In this study we examine the change in liana abundance over the last 45 years in the interiors of 14 temperate deciduous forests in southern Wisconsin. We compared historic data that were collected in 1959–1960 in forest interiors (F. R. Swan, *unpublished data*) to data that we collected during the summer months of 2004–2005 using the same census methods (based on detailed field notes of F. R. Swan). Although historic data on forest edge effects do not exist, we tested whether liana abundance increased with increasing proximity to the forest edge by comparing liana abundance in plots along forest edges to plots in the interior. We tested two specific hypotheses: (1) lianas have increased in abundance in the interior of temperate forests over the last 45 years; and (2) liana abundance is highest at forest edges and it declines with increasing distance from the edge.

METHODS

We surveyed lianas in 14 temperate, mixed-hardwood forests located in southern Wisconsin, USA (between 42°29′42″ N and 43°25′00″ N latitude, 88°40′00″ W and 90°05′00″ W longitude); all forests were >18 ha in area and had little or no disturbance since the 1960 measurements. The trees were predominantly of seven genera: *Quercus*, *Acer*, *Carya*, *Fraxinus*, *Ulmus*, *Tilia*, and *Prunus*, and lianas of two predominant genera: *Vitis* and *Parthenocissus*.

The change in liana abundance over the last 45 years

In each forest stand we measured the abundance and diameter of lianas in the same area of forest surveyed in 1959–1960, closely following the methods described by F. R. Swan (*unpublished manuscript*). Swan used a point-quarter census at 40 points along randomly selected transects in each stand (Greig-Smith 1982), as well as a 1-m^2 plot ground-cover survey at each of the 40 points. Points were located ~15 m apart and were >40 m from the nearest forest edge, at which distance edge effects are greatly reduced (Saunders et al. 1999, Matlack 1994). At each point, we measured and identified four canopy trees ≥10 cm in diameter at breast height (dbh) (one tree in each quadrant), and we counted, identified, and measured the diameter of all lianas that were climbing these trees. We measured the stem diameter of each liana at 130 cm along the stem from the rooting point (methods follow Gerwing et al. 2006, Schnitzer et al. 2006). We also identified and counted all woody stems in each 1 m^2 ground-cover plot located in the southeastern quadrant at each point ($n = 40$ points). We collected data on all of the liana species present; however, for the 45-year comparison, we compared only the taxa targeted by Swan: *Celastrus* spp., *Parthenocissus quinquefolia*, *Toxicodendron radicans, Vitis* spp. Species omitted by Swan constituted <3% of the contemporary liana community (Londré 2005).

We analyzed the difference in overall and species-specific liana abundance between 1959–1960 and 2004–2005 using nonparametric Wilcoxon sign-rank tests (Sokal and Rohlf 1995, SAS Institute 2005). To determine whether liana diameter distribution changed over the 45-year period, we classified overall liana abundance per diameter size class using 10 bins ranging from 0–0.125 inch (0–0.32 cm) to 2.5–3.0 inches (6.35–7.62 cm), following methods of F. R. Swan (*unpublished manuscript*). We used pairwise comparisons of overall liana abundance in the bins between 1959–1960 and 2004–2005 using a nonparametric Wilcoxon sign-rank test. Because we included and measured all lianas climbing on the trunks of the point-quarter trees that reached 130 cm from the ground, our sampling methods deviated slightly from those of Swan, who had measured all lianas that reached 30 cm on the trunk of the trees. We corrected for sampling differences in liana abundance by randomly surveying 885 lianas on 120 trees in 2 of the 14 forests using both methods. We found that our method recorded 3.4% fewer lianas than did that of Swan; however, correcting our data by this percentage did not alter our findings ($T_S = -7.5$, $P = 0.67$, $n = 14$ comparisons; Wilcoxon sign-rank test).

Edge effects and liana abundance

In 7 of the 14 forests we compared liana abundance and basal area between five 15 × 15 m plots on the forest edge and five same-sized plots in the interior. We selected edge plots randomly and we delimited the forest edge by the presence of canopy trees (≥10 cm dbh). The location of each interior plot was at least 40 m from the edge and was selected randomly. We counted and measured the diameter (130 cm from the roots) of all individually rooted lianas that were ≥130 cm tall and were rooted in the plots. We included all liana taxa present in the plot, which consisted of *Celastrus* spp., *Clematis virginiana*, *Menispermum canadensis*, *Parthenocissus quinquefolia*, *Smilax tamnoides*, *Toxicodendron radicans*, and *Vitis* spp. We also measured the diameter of all trees and shrubs ≥1 cm dbh to determine the change in liana abundance as a proportion of all woody plants between the forest edge and interior. We further divided edge plots into 5 × 15 m sections oriented with the long axis parallel to the forest edge for fine-scale analysis of liana abundance with distance from the edge. We used a nonparametric Wilcoxon sign-rank test to compare liana abundance and basal area between the edge and interior plots and among the 5 × 15 m plot sections (SAS Institute 2005).

We quantified abiotic edge effects in each of the seven forests by measuring photosynthetically active radiation (PAR), canopy density, and gravimetric and volumetric soil moisture from the forest edge to the interior during the months of June and July (2005). We measured these variables every 5 m along five randomly selected 40-m transects that were oriented perpendicular to the edge of each forest. We measured PAR on clear days using a LI-

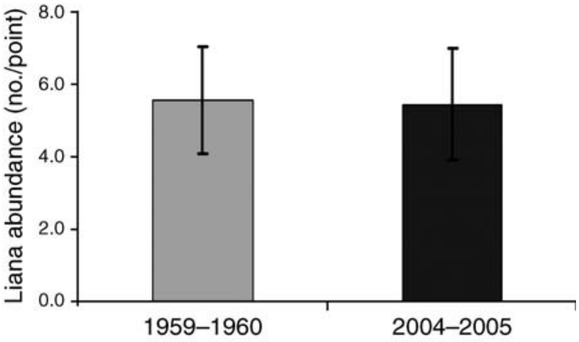

FIG. 1. Change in liana abundance from 1959–1960 to 2004–2005 in 14 temperate deciduous forests in southern Wisconsin, USA, using the point-quarter census method. There were no significant changes in liana abundance during this 45-year period. Data are means ± SE.

COR Quantum Line Sensor (LI-COR, Lincoln, Nebraska, USA) and converted the measurements to relative PAR by dividing them by mean full-sun measurements taken outside of the forest immediately before and after measuring each transect. As an additional test of available light, we measured canopy density with a spherical crown mirror densitometer (Model C; Forestry Suppliers, Jackson, Mississippi, USA) and converted the canopy density data to values relative to no canopy. We measured volumetric soil moisture with a Quick Draw Soil Moisture Probe tensiometer (Model 2900F1; SoilMoisture Corporation, Santa Barbara, California, USA) and gravimetric soil moisture by calculating the difference in mass between fresh and oven-dried soil samples using the equation and methods provided by Robertson et al. (1999). We were unable to acquire volumetric soil-moisture measurements at one site (Abrahams Woods) because the low soil-moisture levels were outside the effective range of the tensiometer (>80 KPa). We used linear regression to quantify the change in abiotic conditions from the edge to the interior and to examine the relationship between liana abundance and relative PAR, canopy density, and volumetric and gravimetric soil moisture (Sokal and Rohlf 1995, SAS Institute 2005). Replication for the regressions was at the forest level, using the mean of the five transects for each point.

RESULTS

Liana abundance and diameter did not increase in the interiors of Wisconsin (USA) forests over the last 45 years. Between 1959–1960 and 2004–2005, total liana abundance did not change considering either the point quarter method ($T_S = -9.5$, $P = 0.58$, $n = 14$ forests; Fig. 1), the 1-m^2 plot method (6.47 ± 1.2 SE vs. 7.40 ± 1.9; $T_S = 4.5$, $P = 0.81$, $n = 14$ forests), or the mean number of lianas per tree (1.39 ± 0.4 vs. 1.36 ± 0.4; $T_S = -9.5$, $P = 0.58$, $n = 14$ forests; Appendix). Liana diameter distribution also did not change over the 45-yr time period (abundance within each of the diameter bins did not differ significantly; $T_S = 12.5$, $P = 0.23$, $n = 10$ diameter size-class bins). Species-specific analyses, however, suggest that the abundance of some species changed over the last 45 years. Specifically, the density of *Vitis* spp. increased significantly over this period as measured using the point quarter method (from 0.13 ± 0.04 to 0.51 ± 0.20 individuals per census point [mean ± SE]; $T_S = -33.5$, $P = 0.01$, $n = 14$ forests). In contrast, the density of *Toxicodendron radicans* decreased significantly using both methods, with a mean of 1.71 ± 0.78 vs. 0.19 ± 0.15 individuals per point ($T_S = 19.0$, $P = 0.05$, $n = 14$ forests) and 1.92 ± 0.76 vs. 0.38 ± 0.21 individuals per 1-m^2 plot ($T_S = 32.5$, $P = 0.02$, $n = 14$ forests). The abundance of *Parthenocissus quinquefolia* and *Celastrus* spp. did not change over the 45-year period (Londré 2005).

Lianas were 4 times more abundant at the edge than in the interior plots ($T_S = 14$, $P = 0.008$, $n = 7$ forests; Fig. 2a). Liana basal area was >2 times greater on the forest edge than in the interior: 99.70 ± 38.69 cm^2/ha vs. 41.49 ± 25.15 cm^2/ha ($T_S = 13$, $P = 0.02$, $n = 7$ forests). These trends were consistent for each of the liana species (Fig. 2b) and for all seven forests (data not shown). Liana abundance decreased sharply within the first 5 m from

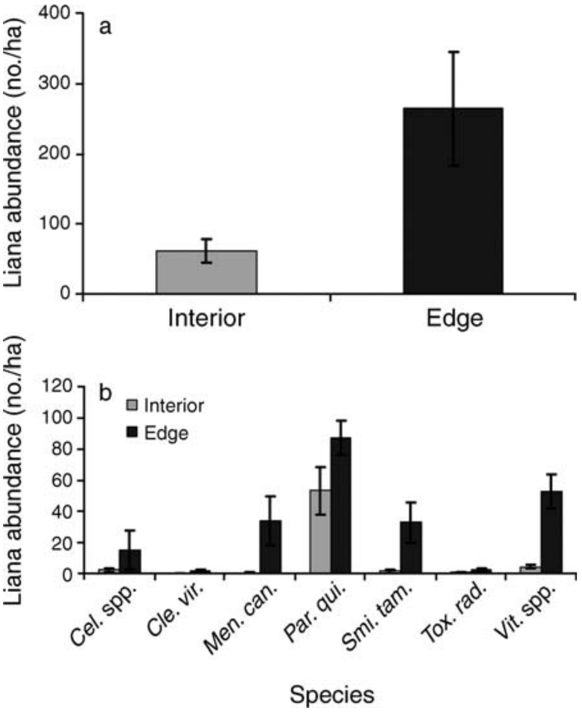

FIG. 2. Difference in mean liana abundance on the edge vs. the interior of seven forests in southern Wisconsin, USA (five plots at each location per forest). Mean liana abundance was significantly greater ($P < 0.01$) on the edge than in the interior for (a) all liana species combined and (b) for each species separately. Species included in this figure are: *Celastrus* spp., *Clematis virginiana, Menispermum canadensis, Parthenocissus quinquefolia*, *Smilax tamnoides*, *Toxicodendron radicans*, and *Vitis* spp. Data are means ± SE.

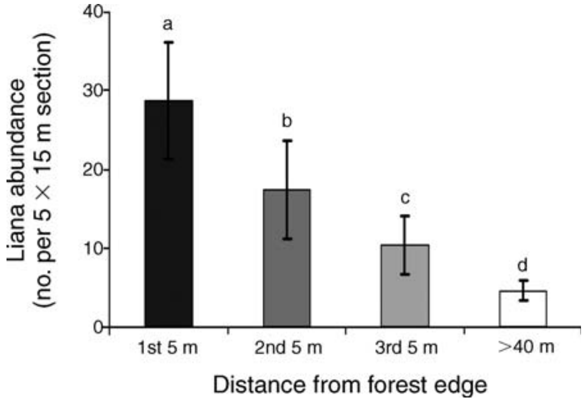

FIG. 3. Decrease in mean liana abundance from the edge to the interior of seven forests in southern Wisconsin, USA. Data are based on five edge plots and five interior plots (>40 m from the forest edge) per forest. Each plot was divided into three contiguous 5 × 15 m sections starting at the forest edge, and plot sections were oriented with the long axis parallel to the forest edge. Interior plots were originally 15 × 15 m and were scaled to the comparable 5 × 15 m size. Mean liana abundance was significantly different between all edge-distance classes ($P < 0.05$). Data are means ± SE.

the edge and continued to decrease 40 m into the forest interior (Fig. 3), a trend that was consistent for each forest. The abundance of trees was also significantly higher along the edge than in the interior plots ($T_S = 13.0$, $P = 0.03$, $n = 7$ forests; Fig. 4a), while shrubs showed no change with proximity to the edge ($T_S = 5.5$, $P = 0.19$, $n = 7$ forests; Fig. 4a). However, the relative edge-to-interior ratio of liana abundance (calculated as a proportion of all woody stems) was much greater for lianas than for either trees or shrubs (Fig. 4b), demonstrating that lianas are concentrated more at the edge than in the interior compared to other woody plants.

Photosynthetically active radiation (PAR), canopy density, and soil moisture gradients all varied with distance from the edges in our study forests. PAR was highest immediately along the forest edge ($P = 0.004$, $R^2 = 0.12$, $n = 63$ correlation data points), but dropped off rapidly and did not change after the first five meters. Similarly, canopy density was lowest immediately at the forest edge ($P = 0.001$, $R^2 = 0.25$, $n = 63$) and did not change after the first five meters. Both volumetric and gravimetric soil moisture decreased linearly with distance into the forest interior (volumetric, $P = 0.005$, $R^2 = 0.17$, $n = 54$; gravimetric, $P = 0.001$, $R^2 = 0.16$, $n = 63$). Liana abundance was positively correlated with PAR ($P = 0.03$, $R^2 = 0.17$, $n = 35$), negatively correlated with canopy density ($P = 0.005$, $R^2 = 0.27$, $n = 35$), and did not vary with either volumetric soil moisture ($P = 0.92$, $R^2 = 0.00$, $n = 30$) or gravimetric soil moisture ($P = 0.82$, $R^2 = 0.00$, $n = 35$).

DISCUSSION

Experimentally elevated levels of CO_2 in temperate forests have been shown to stimulate the growth of temperate liana species far more than that of trees, suggesting that lianas will increase in abundance and diameter with climate change (Hättenschwiler and Körner 2003, Mohan et al. 2006, Zotz et al. 2006). Despite increases in CO_2 over the past 45 years, we found no evidence that lianas have increased in abundance or diameter distribution in the interiors of Wisconsin (USA) deciduous temperate forests. In fact, *Toxicodendron radicans*, which grew markedly better under experimentally elevated CO_2 conditions than did competing trees (Mohan et al. 2006), actually decreased significantly in abundance in our study. The lack of change in overall liana abundance and diameter distribution in our study suggests that lianas are limited in the interiors of deciduous forests of Wisconsin by factors other than increased levels of CO_2.

In general, elevated minimum winter temperatures should increase liana abundance in temperate forests, because lianas grow and survive better in milder climates (Sperry et al. 1987, Ewers et al. 1991, Schnitzer 2005). The increase in mean winter temperatures from 1960 to 2005 in Wisconsin (2.40°C; NOAA/NESDIS/NCDC 2005), however, may not have been enough to reduce the threat of freezing-induced embolism. If minimum winter temperature is an important driver for the latitudinal distribution of lianas, then we might expect lianas to increase in abundance and size closer to the

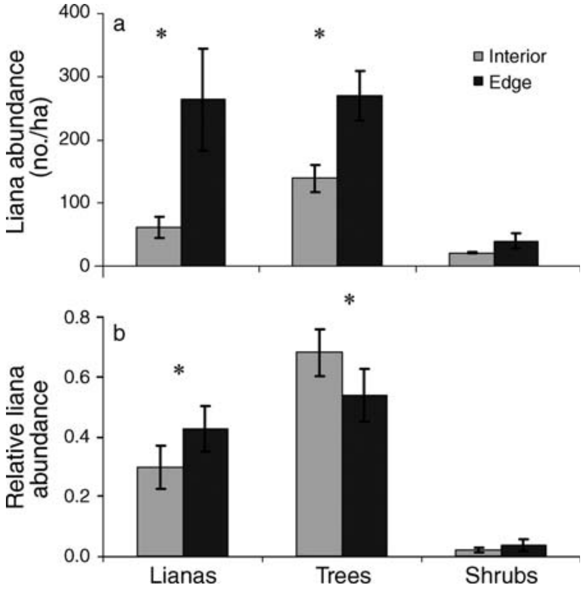

FIG. 4. Mean (a) absolute and (b) relative abundance of lianas, trees, and shrubs on forest edges vs. interiors in seven forests in southern Wisconsin, USA. The abundance of lianas and trees were both significantly higher in edge vs. interior plots ($P < 0.05$), as indicated by single asterisks. The mean relative abundance of lianas as a proportion of all woody stems was significantly higher in edge vs. interior plots, whereas the relative abundance of trees was significantly lower in edge vs. interior plots. The mean absolute and relative abundance of shrubs did not vary with plot location. Data are means ± SE.

winter freeze zone (see Schnitzer 2005), where a small increase in temperature could reduce the number of days below freezing, possibly allowing lianas to increase in abundance and move poleward, as has been the case with many other organisms (Parmesan and Yohe 2003, Root et al. 2003).

Alternatively, lianas may have been unable to benefit from elevated CO_2 and warmer winter temperatures because light availability was the most limiting factor in the forest understory. The extremely high proportion of lianas on the forest edge confirms the hypothesis that, as a group, lianas respond strongly to forest fragmentation. Compared to the forest interior, lianas were >4 times more abundant within 15 m of the forest edge (Fig. 2a) and >6 times more abundant within 5 m of the forest edge (Fig. 3). The strong gradient in liana abundance from forest edge to interior was probably due to light availability. The decreasing abundance of lianas with increasing distance from forest edge, particularly within the first five meters, was correlated significantly with PAR and increasing canopy density, but did not vary with soil moisture. Our results are similar to findings in tropical forests, where liana abundance is significantly higher along fragmented forest edges and within tree fall gaps (Putz 1984, Schnitzer and Carson 2000, 2001, Laurance et al. 2001, Schnitzer et al. 2004). Lianas could be increasing along temperate forest edges due to the interaction of light, CO_2, and temperature; however, we cannot assess this directly because of the lack of long-term data.

There may be additional, non-mutually exclusive factors that explain the high abundance of lianas at forest edges. For example, increased temperature, decreased relative humidity, increased wind turbulence (Matlack 1994, Saunders et al. 1999, Laurance et al. 2001), seed dispersal (Malmborg and Willson 1988, McEuen and Curran 2004), and trellis availability (Putz 1984) near the edge may all play a role. Lianas may colonize forest edges rapidly because of seed dispersal by avian frugivores, which spend proportionally more time consuming fruits and depositing seeds along edges than within the interiors of temperate forests (Malmborg and Willson 1988). In our study, *Vitis, Parthenocissus, Toxicodendron, Menispermum,* and *Smilax* all have bird-dispersed seeds and thus their relatively high abundance on the forest edge may by due in part to bird dispersal.

Because lianas increase substantially in abundance at forest edges, and given that forest fragmentation (and thus edge creation) has increased significantly over the last half-century, particularly in the northeastern and midwestern United States (e.g., Ritters and Wickham 2003, Radeloff et al. 2005), liana abundance has likely increased in temperate forests due to forest fragmentation. Currently within the continental United States, 20% of the total land area is within 127 m of a road (Ritters and Wickham 2003), suggesting severe habitat fragmentation across the landscape. Forested area in the midwestern and northeastern United States has nearly identical levels of fragmentation as that of the total land area (Ritters and Wickham 2003). Radeloff et al. (2005) found a strong positive correlation between suburban and rural sprawl and the fragmentation of temperate forests in the midwestern United States since 1940. Over the last 40 years in Wisconsin, the increase in the amount of houses and roads has compounded forest fragmentation substantially (Radeloff et al. 2005, Wisconsin Department of Natural Resources 2005). Moreover, as forest fragmentation continues, liana abundance will also likely continue to increase, and the effects of lianas on temperate forests, such as intense competition with trees (e.g., Schnitzer et al. 2005), reduced tree growth rates and biomass sequestration (e.g., Laurance et al. 2001), and the incidence of arrested gap-phase regeneration (e.g., Schnitzer et al. 2000) may become even more pronounced.

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APPENDIX

A table summarizing the abundance of lianas in 1959–1960 and 2004–2005 in 14 Wisconsin, USA, temperate deciduous forests, using both small-plot and point-quarter sampling methods (*Ecological Archives* E087-177-A1).