Evergreen Vines in Deciduous Woods

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Provisional Preface

I have drafted this booklet during the winter of 2012–13 in order to focus attention on special problems posed by evergreen vines in deciduous woods. As invasive species, some of these vines thrust unwelcome urgent issues into the science of conservation. Understanding their general ecology helps to deal with these issues. As the reader will discover, this ecology appears much connected to mammalian herbivory—or lack thereof. I urge a broader approach to conservation of temperate forests in eastern North America, involving more consideration of intense seasonal browsing as a natural force. There has been excessive interest in burning for some habitats. I am particularly interested in stimulating more work on the restoration of eutrophic woodlands in the central Ohio Valley, where so little remains of the original ecosystem. Despite the pitiful condition of our remnants and difficulties in developing a coordinated effort among conservationists, some progress is possible. We do know that Virginian settlers established 'woodland-pastures' in more affluent areas, with the help of their slaves. The majestic old oaks and ashes of these sites accelerated growth and developed their large spreading limbs during the early decades of settlement—but during the 18th Century a more shady condition had prevailed over the landscape (Campbell 1989, McEwan & McArthy 2008). In recent years, conservationists have secured land with the best remnant of such woods (Griffith Woods in Harrison Co., Kentucky), but management remains unsettled (see p. 147–156). I aim to develop the framework of this booklet further with more information from these woods, plus extensions eventually into a general work on forest ecology in temperate regions. Much of this current draft will be tightened up after more analysis of plot data, better review of herbivory and secondary chemistry, deeper discussion of morphology—including sexuality (see p. 139–141)—and paleontology. I invite comment and collaboration.

Evergreen Woody Vines in Deciduous Mid-Temperate Forests: a Review of Habit, Habitat, Mammalian Herbivory, Secondary Chemistry and Biogeographic Context

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Abstract. Prompted by local invasion of East Asian *Euonymus fortunei* (‘purple winter creeper’) into eutrophic woodlands of eastern U.S.A, this paper reviews the ecology of all evergreen vines in mid-temperate regions across the Northern Hemisphere (Hardiness Zones 6 and 7). Only about 15–20 species of moderate (3–5 m) to extreme (15–20+ m) height are largely evergreen—in *Bignonia*, *Celastrus*, *Euonymus*, *Hedera*, *Holboellia* and *Lonicera* and *Smilax*. Additional species have ‘semi-evergreen’ leaves that tend to senesce gradually during hard winters. Some of these evergreen-tending vines also cover much ground below deciduous trees. They are concentrated on nutrient-rich soils, in marked contrast to evergreen trees and shrubs—a trend that may be linked with a ‘contrarian’ strategy in these vines: to capture light during winter in deciduous forests. However, these plants are often eaten by mammalian herbivores, especially during winter. None are severely toxic, and woody vining taxa in general tend to have less defensive chemistry than their closest non-vining relatives. Diverse evidence suggests that large native herbivores and livestock reduce vines, as well as other undergrowth. It is suggested that, in eutrophic woodlands of humid mid-temperate regions before human influences, intense seasonal browsing was a major ecological factor and that it remains more important than burning for maintenance of native biological diversity. Biogeography and phylogeny indicate that genera with evergreen-tending vines diverged from their subtropical ancestors during mid- to late-Tertiary eras, long after deciduous genera first appeared in the fossil record. These vines grew into the expanding, drying, cooling deciduous biome—and proliferated locally—but became susceptible to browsing in winter by migrating megafauna.

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APPENDICES [3 and 4 are unfinished working drafts]

Figures

Front cover. Woods behind Henry Clay High School (he would be shocked), where *Euonymus fortunei* has taken over several acres; Layton Register to right, 6 feet tall. These woods used to form one of the best little remnants in the city of Lexington, Kentucky, with several uncommon wildflowers, including trout-lilies (*Erythronium* spp.) and Dutchman's breeches (*Dicentra canadensis*). Much good could be done if youthful energy of the school was directed.
Intersections and back cover. Views of crossvine (*Bignonia capreolata*) in garden and wild. Although gone from many woods around town, it can be easily reestablished. It is probably the "jasmine" that Jessamine County was named after—then well-known and much-loved.

Tables

Introduction

The ‘purple winter creeper’—*Euonymus fortunei* [= *E. hederaceus*, *E. radicans*]—is native to East Asia. But it has become widely promoted by the horticultural industry as an ‘ornamental’ ground-cover across the eastern U.S.A. during 1950-2000, together with closely related segregates or cultivars such as the non-climbing *E. kiautschovicus* (Graves 1940, Zouhar 2009). In warm- and mid-temperate zones on base-rich soils, *fortunei* climbs up trees, cliffs and walls, where it flowers and fruits, leading to widespread invasion of woods and thickets. Escapes initially occurred mostly in or near urban areas of east-central states, from Massachusetts to Missouri,. They have now spread across most of the Ohio watershed and elsewhere (Kartesz 2012, SE-EPPC 2012). *E. fortunei* has become one of the most problematic invasive plants in woodland of central Kentucky, often dominating shady ground. But its degree of spread over the ground, versus up trees, varies much among sites (Campbell 2012).

Euonymus fortunei is one of only a few species of evergreen woody vines (lianas) that are native to mid-temperate regions of the Northern Hemisphere. Species of European ivy—*Hedera*—are the most well-known in traditional Anglo-European horticulture. Also, the popular evergreen to semi-evergreen *Lonicera japonica* from East Asia is now an abundant invasive species in much of eastern North America (Nuzzo 1997, Larson et al. 2006). The only widespread native vine with an pronounced evergreen tendency in mid-temperate regions of the eastern U.S.A is *Bignonia capreolata* (cross-vine). Other natives are just semi-evergreen, tending to loose some leaves in most winters: *L. sempervirens* and the greenbriars, *Smilax bona-nox* and *S. glauca*. *Decumaria barbara* (wood-vamp) is also semi-evergreen but extends only into warmer parts of mid-temperate zones (Duncan 1967).

Such vines are largely restricted to warm- plus mid-temperate zones, as are many other broad-leaved evergreen trees and larger shrubs. These zones correspond to Heinrich Walter's "moist warm temperate forest" plus warmer parts of his "deciduous temperate forest" (Breckle 2002). In North America (USDA 1990, 2012), they have often been referred to as Hardiness Zones 9 and 8 (warm-temperate) plus 7 and 6 (mid-temperate), with mean annual minimum temperatures of about -5° C to -10° C (warm-temperate) or -15° C to -20° C (mid-temperate).

The physiological basis of adaptation by evergreen plants to winter cold has been the subject of much research (e.g., Öquist & Huner 2003). Seasonal development of hardiness in *Hedera* involves complex changes in sugars, proteins and anthocyanins (Parker 1962, Bauer & Koffler 1987, Oberhuber & Bauer 1991). The protective role of xanthophylls has been shown in *Euonymus* (Adams & Demmig-Adams 1995, Verhoeven et al. 1998). But, despite the distinctive increase of purple coloration in much *E. fortunei* during winter, there is no published research on the possible role of anthocyanins in hardiness of this species. (Purplish winter coloration also occurs often in *B. capreolata*, *L. japonica* and *S. glauca*.) And even general understanding of differences among evergreen plants remains limited—what exactly allows the conifers to extend so much further north than most woody angiosperms? Their somewhat inexplicable supercooling ability must be a critical factor (Margesin et al. 2007, and their citations), with significant implications for secondary chemistry.

Meanwhile, refinements of the Hardiness Zone system are being developed (e.g., DeGaetano & Schulman 1990, McKenney et al. 2007, Daly et al. 2012), as well as more global and functional approaches (Magarey et al. 2008, Harrison et al. 2009). The combined effects of mean annual (overall) temperature, mean annual (extreme) minimum temperature, and precipitation patterns on vegetation still need much more analysis. For example, in East Asia, relatively evergreen forest extends into zones with cooler mean annual temperatures than in North America and Europe. As noted by Walter and others, this contrast can be attributed to the generally less extreme minimums within temperate zones of East Asia (Wolfe 1987, Widrlechner 1997). In Eastern North America, standard deviation of the annual extreme minimum temperate exhibits a remarkable peak in the Ohio Valley, extending locally into the Appalachians (Daly et al. 2012). A detailed comparative analysis of such patterns in relation to vegetation patterns across all North Temperate regions has yet to be done, building on Greller's work (1989, 2003).

Evergreen vines are potentially vigorous, aggressive competitors in forests of mid-temperate regions, given suitable soils—and they are often concentrated on moist fertile soils. Some can also survive on the ground in cool-temperate regions (Zone 5 and even 4), although they do not generally climb high, flower and fruit there except near coasts with ameliorated winters. These vines are able to keep photosynthesizing during the winter in mid-temperate zones, where most trees are deciduous on moist fertile soils. However, the evergreen habit does make them susceptible to browsing by mammalian herbivores, especially during the winter when other green leafy forage is often scarce on richer soils.

There has already been considerable interest in the generally high degree of herbivory on vines, and whether aliens are favored more than natives in North America (e.g., Schierenbeck et al 1994, Schweitzer & Larson 1999, Ashton & Lerdau 2007, Knapp et al 2008, Lieurance et al. 2012). Secondary chemistry in plants is generally known to influence mammalian herbivory in varied ways, through deterence, toxicity or more complex interactions (Harborne 1991a). An attempt is made below to summarize relevant information from the vast and complex literature on chemical patterns and their potential effects. This effort is based on natural history rather than theory, although a moderate course for understanding is suggested (following Grubb, 1992) between simple starting points (as offered by Feeney, 1976) and the quagmire of potential complexity (as reviewed by Stamp, 2003).

This paper is in three parts. The first summarizes distributions of evergreen-tending woody vines along habitat gradients in east-central U.S.A. The second part presents an ecological summary of all evergreen vines in mid-temperate regions of the Northern Hemisphere, together with reports of mammalian herbivory, patterns in secondary chemistry and comparisons with deciduous vines. Notes are added on some deciduous woody vines and on some herbaceous or ‘subshrubby’ vines that are relatively robust or allied with the woody vines. In several taxa, it is not possible to classify them clearly as evergreen, deciduous or herbaceous. The third part provides a general discussion of evolutionary trends and ecological factors, with a focus on potential relationships to mammalian herbivory.

The species of central interest are evergreen-tending vines with the following features.
(1) All climb onto trees and shrubs, or occasionally cliffs and walls, up to a height of at least 3 m. Only a few species can generally climb up limbless boles of larger trees using adventitious roots or similar means—perhaps just *Decumaria*, *Euonymus fortunei*, *Hedera* and, in a special way, *Bignonia*. Some can also spread much on the ground.
(2) All are truly evergreen, with leaves usually persisting through winter, or semi-evergreen, with leaves persisting until damaged by cold, rather than by physiologically-timed abscission.
(3) They all extend significantly into mid-temperate zones (Hardiness Zones 7 or 6).
These characteristics are well-known for native evergreen-tending vines in North America (Duncan 1967) and in Europe (with only *Hedera*). There are diverse evergreen-tending species in East Asia, but published information on them in English is much sparser. It is hoped that this

initial review will lead to more thorough assessment of East Asian species, deeper functional understanding across the temperate world, and improved management of their invasive tendencies. Eventually, the framework used here could be extended to functional comparisons of whole floras. Campbell (1982) presented an initial foray along those lines for trees.

Genera with strictly herbaceous vines in temperate regions are not compared here in detail. In Kentucky, these include Apocynaceae (*Cynanchum, Gonolobus, Matelea*), Asteraceae (*Mikania*), Convolvulaceae (*Calystegia, Convolvulus, Cuscuta, Ipomaea*), Cucurbitaceae (*Cayaponia, Cucurbita, Echinocyctis, Melothria, Sicyos*), Dioscoreaeae (*Dioscorea*), Euphorbiaceae (some *Tragia*), Fabaceae (*Amphicarpaea, Apios, Clitoria, Galactia, Lathyrus, Phaseolus, Vicia*), Lygodiaceae (*Lygodium*), Passifloraceae (*Passiflora*), Polygonaceae (*Fallopia*), Rubiaceae (some *Galium*) and Sapindaceae (*Cardiospermum*). Trends in several features that are outlined below (e.g., Tables 7–9) could be extended with inclusion of herbaceous vines, but not trends in dioecy—which is remarkably rare amongst them (only in *Dioscorea* and perhaps some cucurbits). An expanded treatment will eventually embrace these genera as well.

Taxonomic nomenclature generally follows Weakley (2011) and Flora of China (1996–2011). See also Campbell & Medley (2012) for notes on species in Kentucky. Authors of taxa can be checked in those sources, and are not listed here. Suggested common names for genera are listed in Table 7 below, but these are not widely accepted in some cases.

Fig. 1a. ***Bignonia capreolata*** **(purplish) and** ***Smilax bona-nox*** **on 14 Dec 2012, 3-5 m high.**

Fig. 1b. ***Smilax bona-nox*****: climbing shoots in Dec (above); juvenile shoots in Jan (below).**

Fig. 1c. Unusually pronounced camoflouage in *Smilax bona-nox*; Feb, Grayson Co., KY.

Fig. 1d. ***Smilax glauca*** **on 6 Jan 2013: climbing shoots (above); juvenile shoots (below).**

Fig. 1e. January mix of *Euonymus fortunei* and *Hedera helix* in front-yard of Lexington, Kentucky, a common sight in urban areas of east-central U.S.A.; note striped venation.

Fig. 1f. *Euonymys fortunei* in February. Purplish color of lower leaf surfaces increases through the winter. F.N. Meyer selected more colored plants as "forma *colorata*" in 1914.

Fig. 1g. Shoots of alien *Lonicera japonica* (upper) and native *L. sempervirens* (lower), on 18 Jan 2013, Lexington, Kentucky; note flower buds at lower left, and yellowing leaves.

PART ONE: Distributions of Species along Ecological Gradients in East-central U.S.A.

Typical Positions of Species along Hydrological Gradients

Figure 2 presents a simplified summary of two major ecological gradients among tree species in more natural habitats of east-central U.S.A.—from mesic to xeric conditions, and from mesic to hydric conditions. The topology of this diagram was initially developed to allow two-dimensional displays of all natural vegetation types recognized by NatureServe (2012) across this region. Each species is located at its approximate modal position, as derived from much review of the literature and much general experience in the woods. These gradients are interpreted to reflect the somewhat independent stresses from xeric and hydric conditions, based on a general analysis of compositional data from across east-central U.S.A. (Campbell 1987) and on much local detail in environmental pattern (e.g., Braun 1950, Jones et al. 1984, Campbell & Grubbs 1992, Campbell 2004a, Kupfer et al. 2010, Campbell & Seymour 2011). Sites with 'xerohydric' tendency (e.g., 'post oak glades') experience relatively large ranges of dry versus wet conditions through the seasons. Unfortunately, there has been little definitive research into the independent nature of xeric and hydric stresses on forests in North America, and a one-dimensional concept of the 'moisture gradient' persists in most environmental analysis (e.g., Schaetzl et al. 2009). However, a rigorous approach has been recently initiated in Germany (Schwärzel et al. 2009).

Of course, there are also complicating relationships with past and present disturbance regime. In particular, burning and browsing over several millenia have probably been positively correlated with the gradient from deeper woods at the mesic extreme (often on more rugged terrain) to more open grassy conditions at the 'xerohydric' extreme (usually on more gentle terrain). And the special effects of forceful flooding are largely confined to the ‘rheic’ (lower left) sector of the diagram. But more short-term or small-scale patterns of disturbance have relatively little projection along these gradients. For example, abundance of *Liriodendron* after disturbance in *Fagus*-dominated woods involves only a small shift away from the mesic extreme. And the extensive artificial edges in modern landscapes are not sampled here.

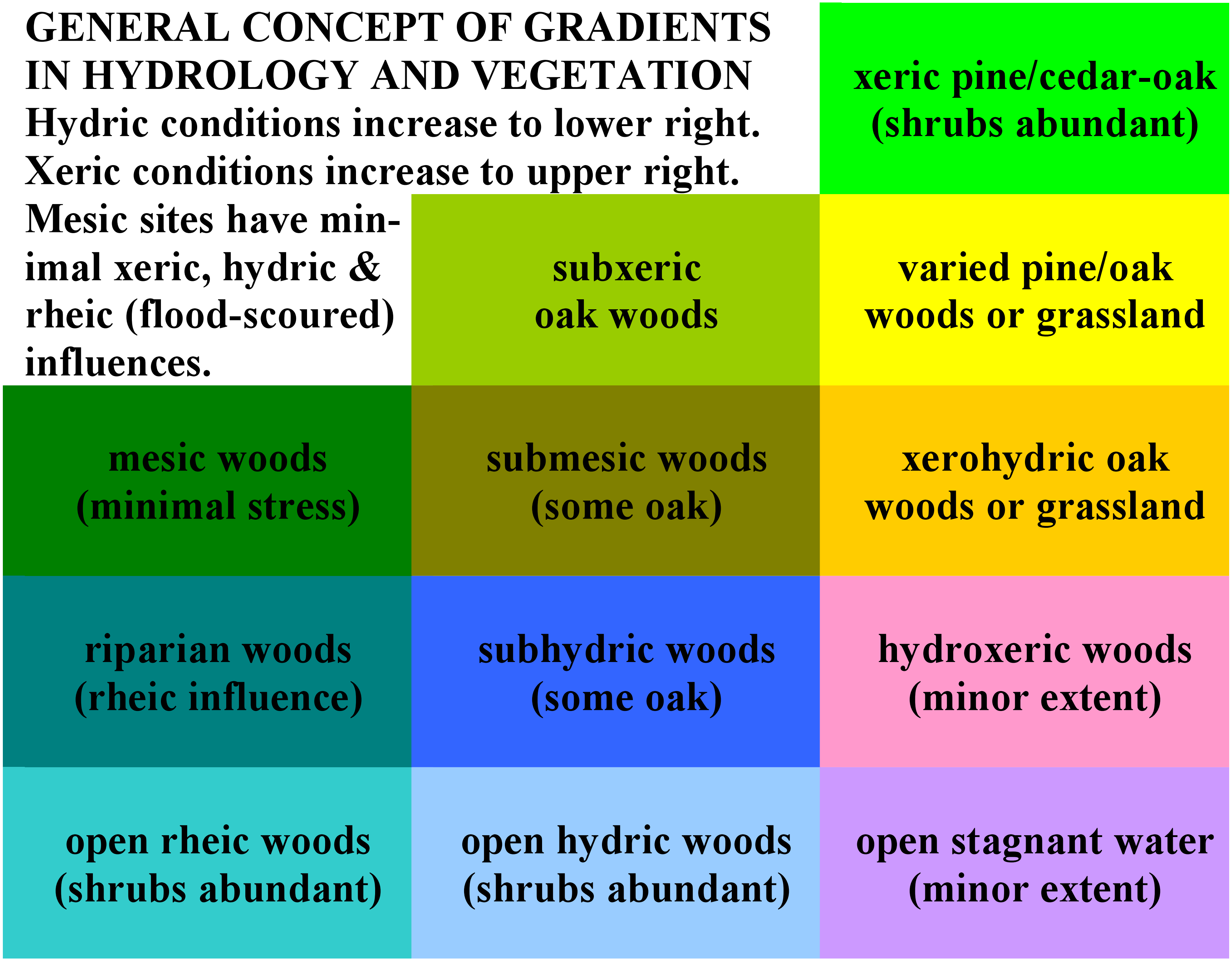
The most commonly associated tree species for each vine are gleaned from descriptions of vegetation types in NatureServe (2012) and from other sources; see caption to Figure 2. These tree species are abbreviated in the overlays for each vine species. The eight species of evergreen-tending vine in mid-temperate regions have broad overlapping distributions along these gradients of tree composition (Figure 2c-j). There is a sequence from relatively hydric or riparian habitats to relatively xeric or disturbed uplands, as follows: *Decumaria barbara*, *Hedera helix*, *Euonymus fortunei*, *Bignonia capreolata*, *Lonicera* species (abundant *japonica*, local *sempervirens*) and the *Smilax* species (*bona-nox*, *glauca*). The more distinctly evergreen species of *Smilax* that occur in warmer zones are not included here (Weakley 2011): *laurifolia* (esp. swampy sites), *smallii* (esp. drier bottoms) and *auriculata* (esp. submesic to xeric sands).

Except for the wetter habitats of some *Decumaria*, there is a general absence of association between these vines and trees typical of more hydric sites (e.g., *Salix nigra, Fraxinus pennsylvanica, Taxodium distichum, Quercus lyrata, Q. phellos*). *Hedera* and *Euonymus* are aliens with only local abundance, but they are centered in habitats transitional from *Decumaria* to *Bignonia*. And the alien *Lonicera* has now filled in much of the potential habitat between *Bignonia* and *Smilax*.

Figure 2a–k. Simplified summary of hydrological gradients in mid-temperate forests of eastern states, with overlays of evergreen vines. Mesic conditions (M) are at center-left; more open, stressed or disturbed conditions increase to upper right (xeric extreme/X), to lower right (hydric extreme/H), or to lower left (riparian/rheophytic with active scouring/R).
(a) [Next page] General concept of gradients in hydrology and vegetation.
(b) Six-letter codes indicating approximate modal positions of species, using first three letters of genus and species (see Appendix 1); if more than one mode, the average is shown.
Red letters = codes for species associated with strongly acid soils; green = medium acid; blue = circumneutral. Dark grey fill = generally continuous forest; medium grey = more open woods, often mixed with shrubland or grassland; pale grey = zones usually dominated by shrubs or graminoids. Parentheses indicate species with relatively northern ranges, which are replaced by other species to the south within this region. ** Ring-porous wood; * semi-ring-porous.
(c–j) Distribution of evergreen-tending vines along the gradients, based on general review of common woody associates (including forest types of NatureServe 2012, VegBank of Peet et al. 2012) and personal experience. Shadings indicate concentrations.
(c) *Decumaria barbara*; see also on Jones+ (1984), Bledsoe+ (2000), Boyle+ (2009) etc.
(d) *Hedera helix*; based largely on Waggy (2010).
(e) *Euonymus fortunei*; based largely on Zouhar (2009).
(f) *Bignonia capreolata*; see also Goebel et al. (2001).
(g) *Lonicera japonica*; see also Ladwig & Meiners (2010).
(h) *Lonicera sempervirens*; see also Waters+ (1974), Martin+ (2002), Campbell+ (2011).
(i) *Smilax bona-nox*; see also Goebel et al. (2001).
(j) *Smilax glauca*; see also Bazzaz (1968), Clinton et al. (1993), Goebel et al. (2001).
(k) Sequence of classes for vertical dimension in Figure 3.

GENERAL CONCEPT OF GRADIENTS IN HYDROLOGY AND VEGETATION

Hydric conditions increase to lower right.
Xeric conditions increase to upper right.
Mesic sites have minimal xeric, hydric & rheic (flood-scoured) influences.

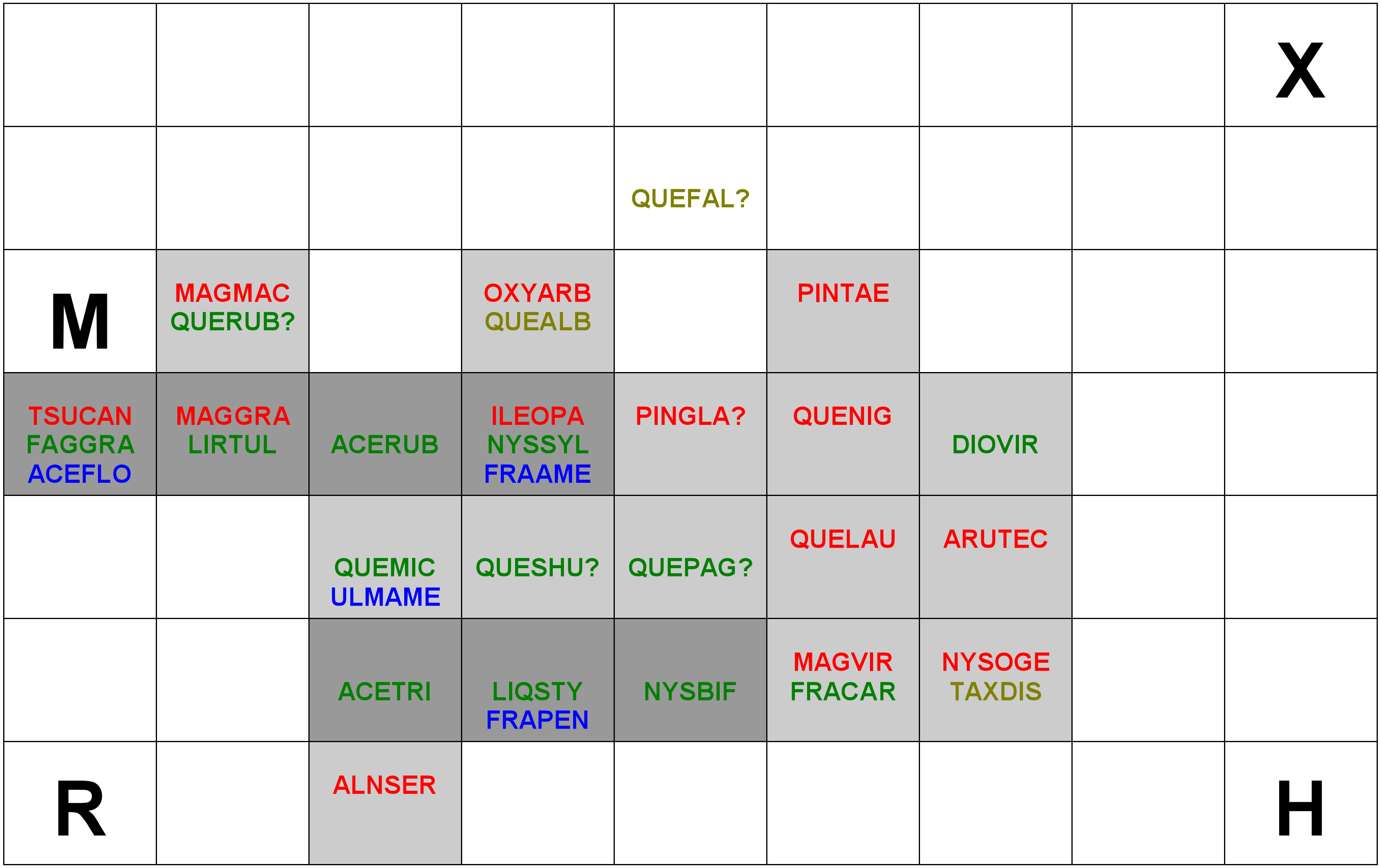


		xeric pine/cedar-oak (shrubs abundant)
	subxeric oak woods	varied pine/oak woods or grassland
mesic woods (minimal stress)	submesic woods (some oak)	xerohydric oak woods or grassland
riparian woods (rheic influence)	subhydric woods (some oak)	hydroxeric woods (minor extent)
open rheic woods (shrubs abundant)	open hydric woods (shrubs abundant)	open stagnant water (minor extent)

(b) Hydrological gradients among trees of east-central states.

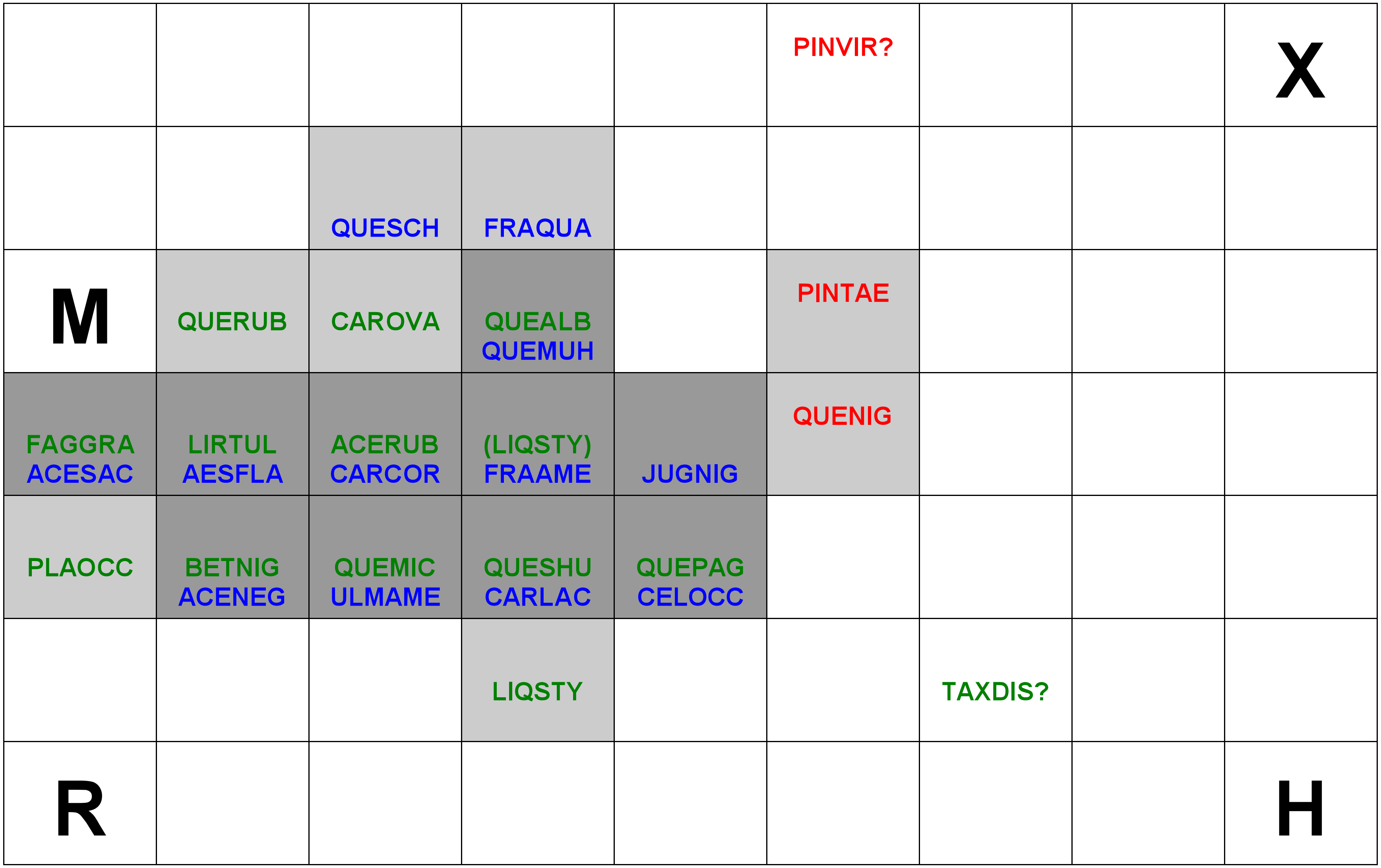
		CLIFFS	CLIFFS	CLIFFS	PINVIR JUNVIR ULMSER**	PINRIG QUEPRI** ULMALA**	QUELAE** QUEILI** CELTEN**	XERIC EXTREME
MESIC SLOPES (below)	CLIFFS	QUECOC** QUEVEL** QUESCH**	QUEMON** CARGLA** FRAQUA**	VACARB QUEFAL** (ULMTHO)**	PINECH (POPGRA) FRABIL**	QUEMAR** MALCOR* GLETRI**	QUEMRG** MALANG* (RHUTYP)**	GRASS-LAND
TSUCAR HALTET CLAKEN	MAGMAC QUERUB** TILAME	CASDEN** CAROVA** ULMRUB**	OXYARB QUEALB** QUEMUE**	CARPAL** CARTOM** CARCAR**	PINTAE SASALB* PRUSER*	PINPAL QUESTE** GYMDIO**	QUEINC** (QUEIMB)** (QUEMAC)**	GRASS-LAND
TSUCAN FAGGRA ACESAC	BETLEN LIRTUL AESFLA	MAGACU ACERUB CARCOR*	ILEOPA NYSSYL FRAAME**	(PINSTR) (JUGCIN)* JUGNIG*	QUENIG** ROBPSE** MORRUB*	QUEHEM** DIOVIR* MACPOM**	PINSER QUEPHE** QUESIN**	GRASS-LAND
PLAOCC	MAGTRI BETNIG ACENEG	QUEMIC** ULMAME**	QUESHU** CARLAC**	QUEPAG** CELSPP**	QUELAU** ILEDEC FRAPEN**	(QUEPAL)** CHATHY (QUEBIC)**	PINELL TAXASC QUELYR**	BOG or MARSH or FEN
POPDEL	ACESNM CATSPE**	ACETRI CARILL*	LIQSTY FRASUB**	NYSBIF PLAAQU	MAGVIR FRACAR** FORACU	PERPAL TAXDIS POPHET	CYRRAC NYSAQU GLEAQU**	STAGNANT WATER
RHEIC EXTREME	SALSER SALCAR SALINT	ALNSER SALNIG	CORSTR	CEPOCC	DECVER	STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

(c) Common associates of *Decumaria barbara* (in more southern region).



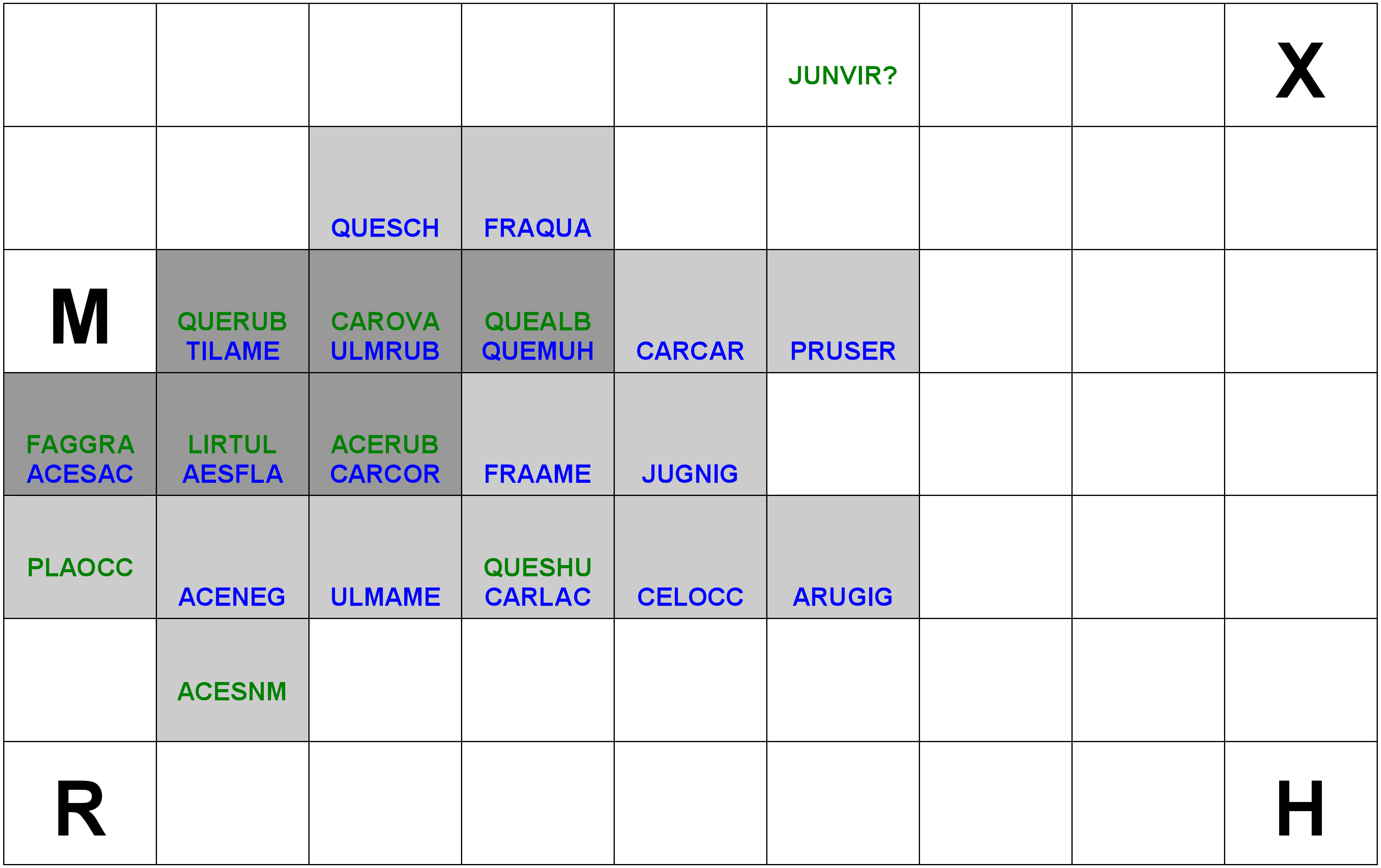
								X
				QUEFAL?				
M	MAGMAC QUERUB?		OXYARB QUEALB		PINTAE			
TSUCAN FAGGRA ACEFLO	MAGGRA LIRTUL	ACERUB	ILEOPA NYSSYL FRAAME	PINGLA?	QUENIG	DIOVIR		
		QUEMIC ULMAME	QUESHU?	QUEPAG?	QUELAU	ARUTEC		
		ACETRI	LIQSTY FRAPEN	NYSBIF	MAGVIR FRACAR	NYSOGE TAXDIS		
R		ALNSER						H

(d) Common associates of *Hedera helix* (English Ivy).



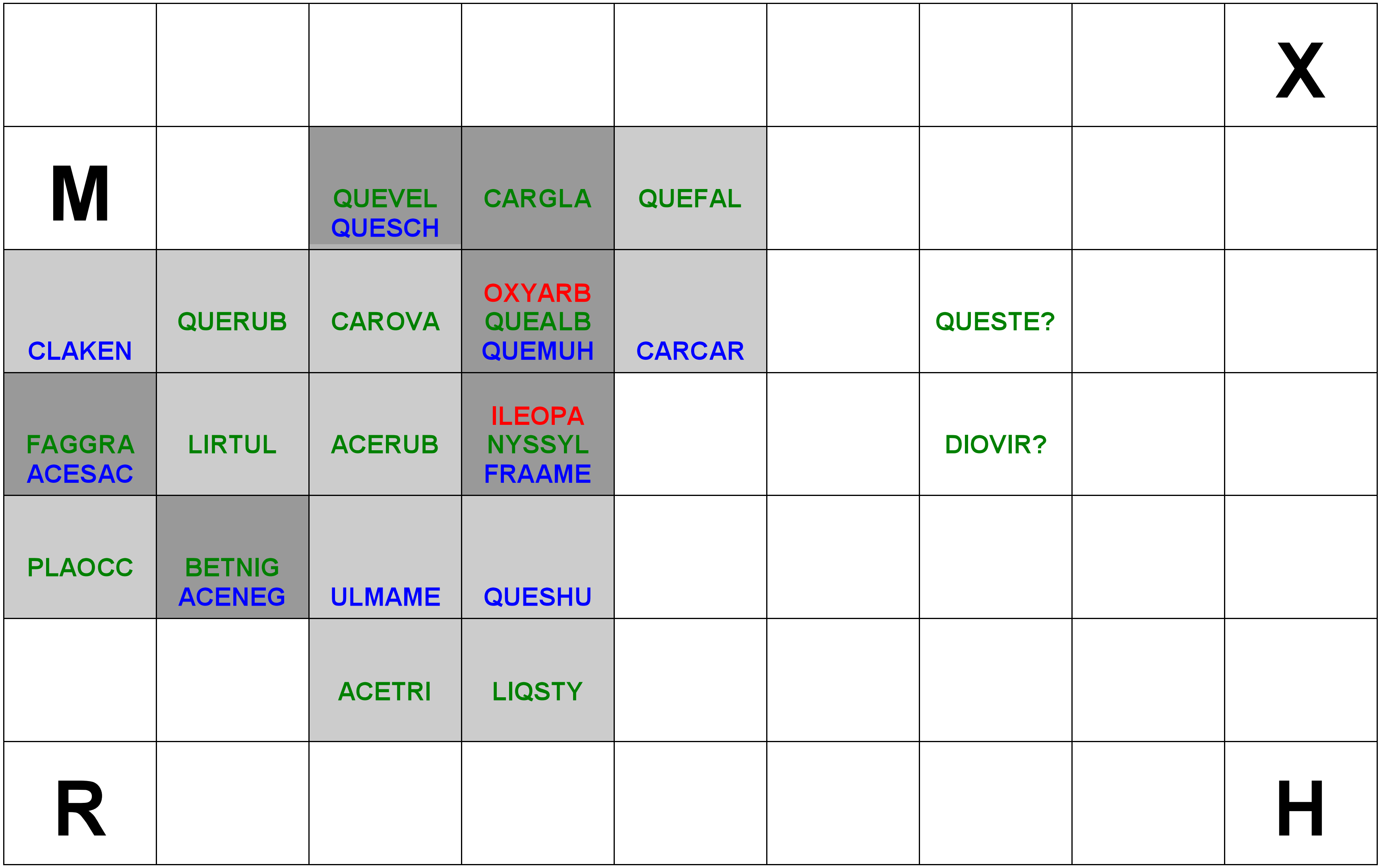
					PINVIR?			**X**
		QUESCH	FRAQUA					
M	QUERUB	CAROVA	QUEALB QUEMUH		PINTAE			
FAGGRA ACESAC	LIRTUL AESFLA	ACERUB CARCOR	(LIQSTY) FRAAME	JUGNIG	QUENIG			
PLAOCC	BETNIG ACENEG	QUEMIC ULMAME	QUESHU CARLAC	QUEPAG CELOCC				
			LIQSTY			TAXDIS?		
R								**H**

(e) Common associates of *Euonymus fortunei* (Winter-creeper).



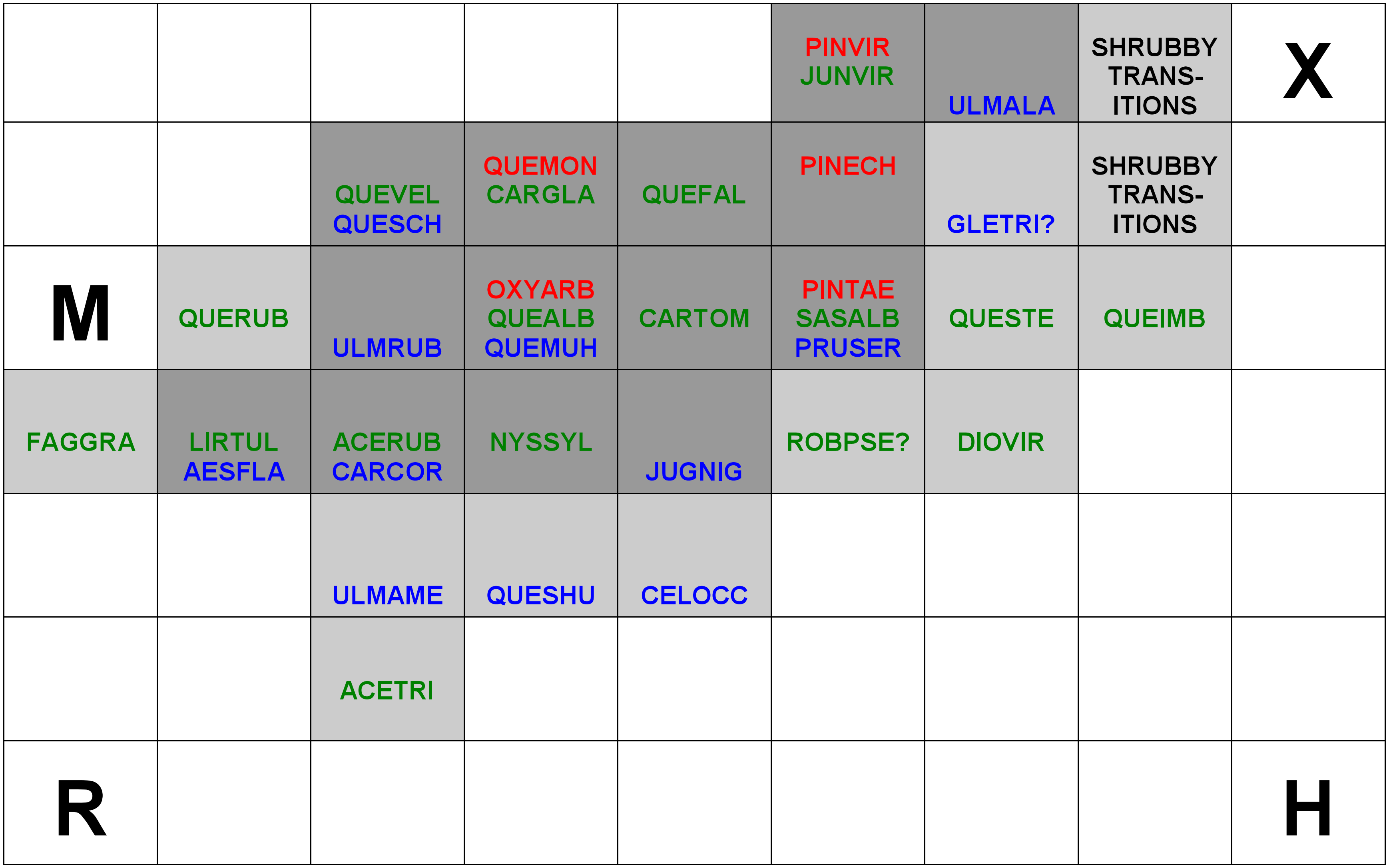
					JUNVIR?			X
		QUESCH	FRAQUA					
M	QUERUB TILAME	CAROVA ULMRUB	QUEALB QUEMUH	CARCAR	PRUSER			
FAGGRA ACESAC	LIRTUL AESFLA	ACERUB CARCOR	FRAAME	JUGNIG				
PLAOCC	ACENEG	ULMAME	QUESHU CARLAC	CELOCC	ARUGIG			
	ACESNM							
R								H

(f) Common associates of *Bignonia capreolata* (Crossvine).



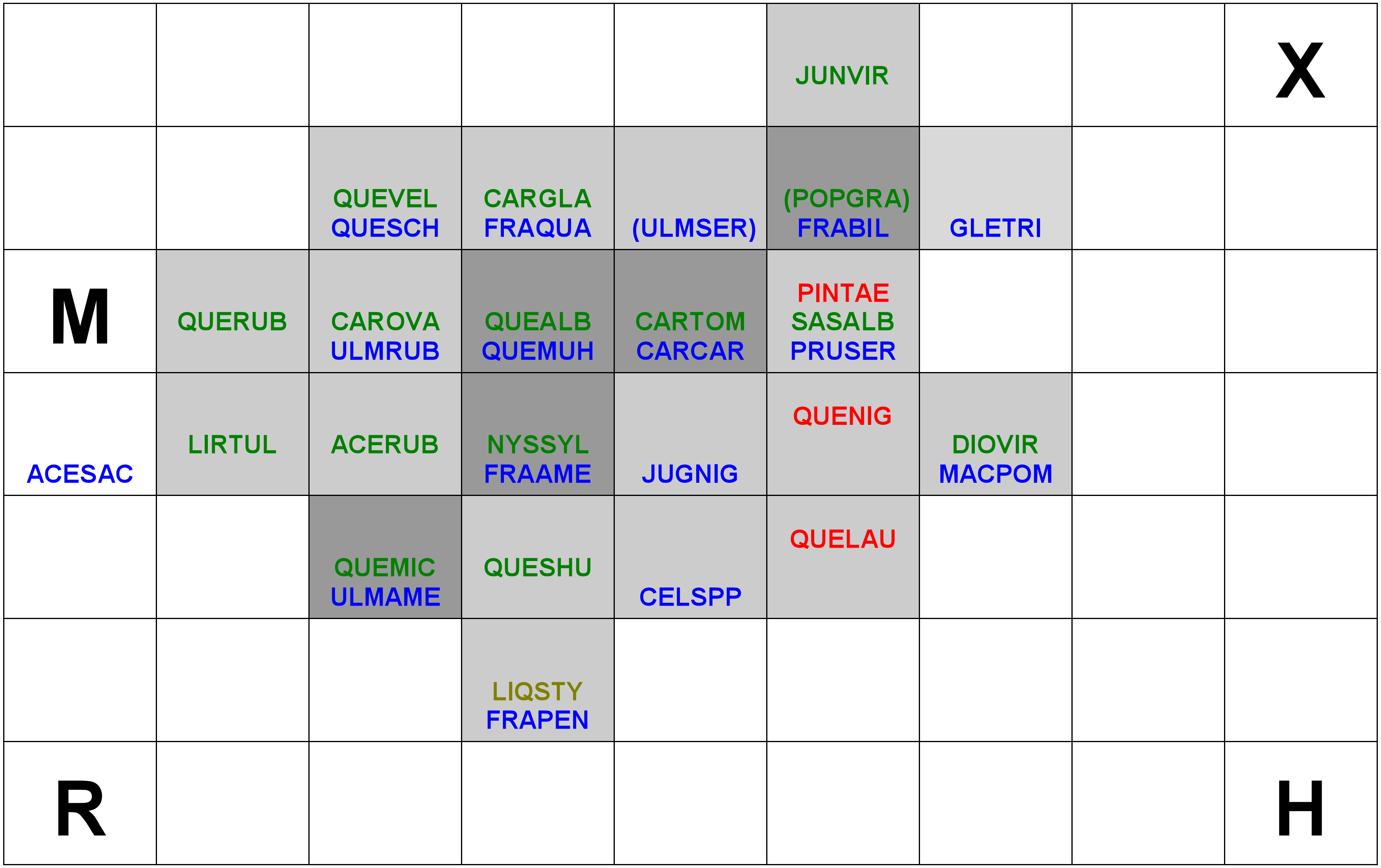
								X
M		QUEVEL QUESCH	CARGLA	QUEFAL				
CLAKEN	QUERUB	CAROVA	OXYARB QUEALB QUEMUH	CARCAR		QUESTE?		
FAGGRA ACESAC	LIRTUL	ACERUB	ILEOPA NYSSYL FRAAME			DIOVIR?		
PLAOCC	BETNIG ACENEG	ULMAME	QUESHU					
		ACETRI	LIQSTY					
R								**H**

(g) Common associates of *Lonicera japonica* (Japanese Honeysuckle).



					PINVIR JUNVIR	ULMALA	SHRUBBY TRANSITIONS	X
		QUEVEL QUESCH	QUEMON CARGLA	QUEFAL	PINECH	GLETRI?	SHRUBBY TRANSITIONS	
M	QUERUB	ULMRUB	OXYARB QUEALB QUEMUH	CARTOM	PINTAE SASALB PRUSER	QUESTE	QUEIMB	
FAGGRA	LIRTUL AESFLA	ACERUB CARCOR	NYSSYL	JUGNIG	ROBPSE?	DIOVIR		
		ULMAME	QUESHU	CELOCC				
		ACETRI						
R								H

(h) Common associates of *Lonicera sempervirens* (Trumpet Honeysuckle).

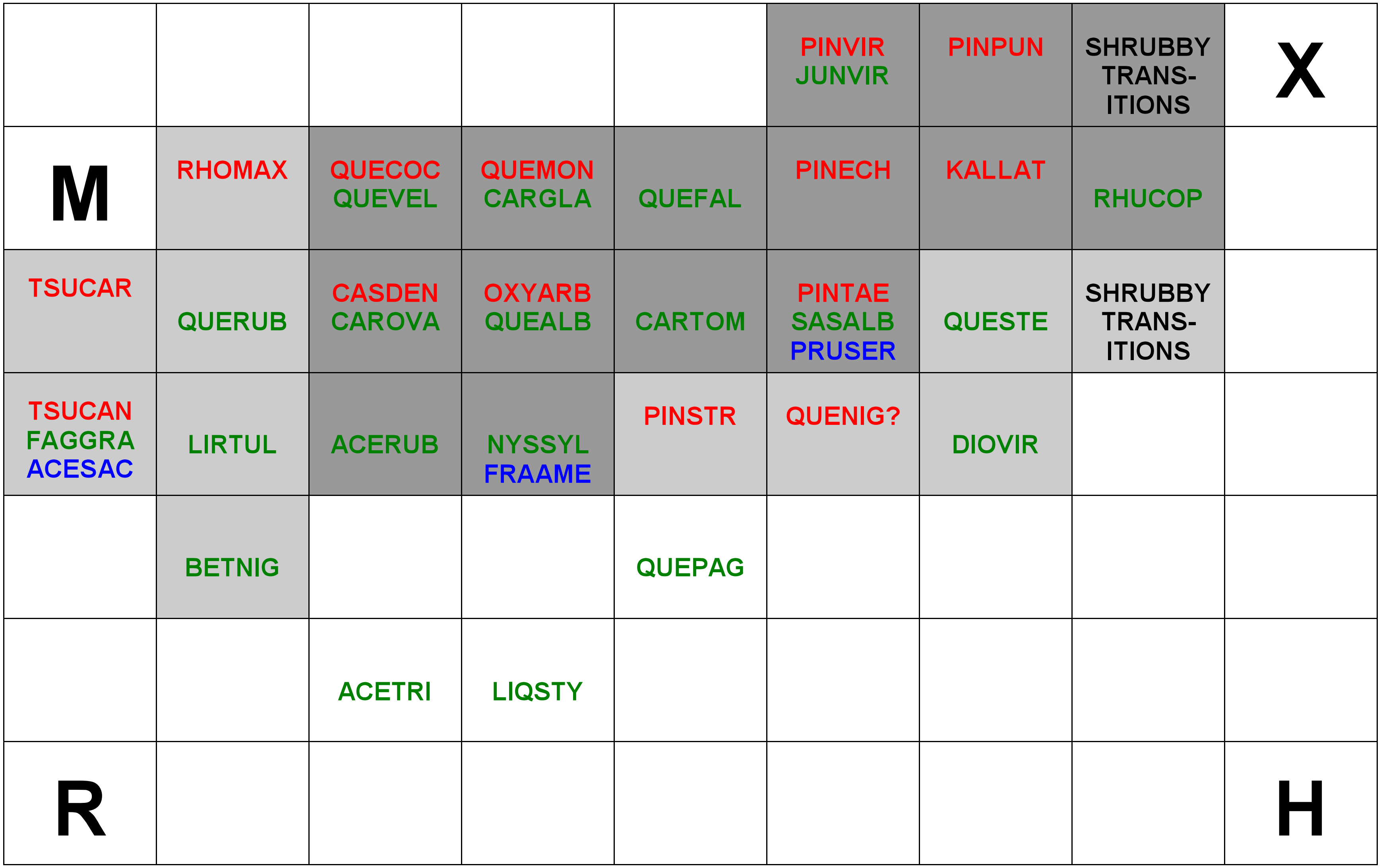


					JUNVIR			X
		QUEVEL QUESCH	CARGLA FRAQUA	(ULMSER)	(POPGRA) FRABIL	GLETRI		
M	QUERUB	CAROVA ULMRUB	QUEALB QUEMUH	CARTOM CARCAR	PINTAE SASALB PRUSER			
ACESAC	LIRTUL	ACERUB	NYSSYL FRAAME	JUGNIG	QUENIG	DIOVIR MACPOM		
		QUEMIC ULMAME	QUESHU	CELSPP	QUELAU			
			LIQSTY FRAPEN					
R								H

(i) Common associates of *Smilax bona-nox* (Saw-brier).

					PINVIR JUNVIR	ULMALA	CELTEN	X
		QUECOC QUEVEL QUESCH	QUEMON CARGLA FRAQUA	VACARB QUEFAL	PINECH FRABIL		RHUGLA	
M	QUERUB	CAROVA ULMRUB	QUEALB QUEMUH	CARTOM CARCAR	PINTAE SASALB PRUSER	QUESTE	SHRUBBY TRANSITIONS	
FAGGRA ACESAC	LIRTUL	ACERUB CARCOR	NYSSYL FRAAME	JUGNIG	ROBPSE	DIOVIR		
	ACENEG	QUEMIC ULMAME	QUESHU CARLAC	QUEPAG CELLAE	ILEDEC ARUGIG			
			LIQSTY					
R								H

(j) Common associates of *Smilax glauca* (Cat-brier).



					PINVIR JUNVIR	PINPUN	SHRUBBY TRANSITIONS	**X**
M	RHOMAX	QUECOC QUEVEL	QUEMON CARGLA	QUEFAL	PINECH	KALLAT	RHUCOP	
TSUCAR	QUERUB	CASDEN CAROVA	OXYARB QUEALB	CARTOM	PINTAE SASALB PRUSER	QUESTE	SHRUBBY TRANSITIONS	
TSUCAN FAGGRA ACESAC	LIRTUL	ACERUB	NYSSYL FRAAME	PINSTR	QUENIG?	DIOVIR		
	BETNIG			QUEPAG				
		ACETRI	LIQSTY					
R								**H**

(k) Typical species for the nine divisions in vertical gradient of Figure 3.

					8	8	9	9
	5	6	6	7	7	8	8	9
4	4,5	5	6	7	7	8	8	9
3,4	3,4	4,5	6	7	8	8	8	9
2,3	2,3	3	3	7	8			
	2	1	1					
	2	1						

The pH-related Gradient: General Floristic Patterns in Kentucky

The third major gradient among tree species in east-central states is indicated by pH (Table 1, Figure 2). This gradient has been revealed by several analyses (e.g., Campbell 1987, Ulrey 2002, Peet et al. 2003, Simon et al. 2005, Bledsoe & Shear 2000), but it is undoubtedly caused by a complex of trends in soil chemistry and associated environmental factors, rather than just pH. Parallel gradients in Europe have been well-documented by Ellenberg (1988, and previous German editions), leading to many applications of botanical indices for pH and nutrient levels (e.g., Wittig & Neite 1986, Meerts 1997, Thompson et al. 1997, Ertsen et al. 1998, Wamelink et al. 2002, Chytrý et al. 2003, Ewald 2003, Thimonier et al. 2006, Verheyen et al. 2012). However, physiological mechanisms remain poorly understood for most non-crop plants, even in Europe (Fisher & Binkley 2000, Mengel & Kirkby 2001, Brady & Weil 2002, Sparks 2003). Soils with pH about 5.5–6.5 tend to have the highest natural levels of available nitrogen and phosphorous, and pH itself need have little or no simple direct relationship to the gradient. But the prevalent form of nitrogen changes from ammonium at lower pH to nitrate at higher pH (e.g., Aciego-Petri & Brooke 2008). Also, aluminum and manganese can become more soluble and toxic to some plants in strongly acid soils (e.g., Vanguelova et al. 2007).

Table 1 summaries trends in some ecomorphological features of the woody flora in Kentucky as a whole. Each of the 279 native species has been assigned to its most typical (modal) position along the pH-related gradient. (Although perhaps absent from Kentucky in 1492, *Maclura pomifera* is included here since it has become widely naturalized from the southwest, and it has instructive ecology.) The following five classes are used to represent the pH-gradient: A to E (Campbell & Medley 2012).

A. Association with strongly acid soils (ca. pH 4–5) and low overall fertility; usually with a sandy component or on Devonian black shale. *Tsuga canadensis* is potentially dominant on mesic sites; common upland oaks include *Quercus montana* and *Q. coccinea*; *Castanea dentata* was formerly frequent; Ericaceae are common. Typical species are concentrated in the Knobs and Appalachian regions, coupled with virtual absence in calcareous regions.

B. Transitional or uncertain assignment between A and B; usually on soils derived from sandstone or acid shales.

C. Association with medium acid soils (ca. pH 5–6) and medium overall fertility; soils often have mixed origin with some sand. *Fagus grandifolia* is potentially dominant on mesic sites; common upland oaks include *Q. alba, Q. velutina, Q. stellata* and *Q. falcata*; Ericaceae are uncommon to absent. Typical species are scattered over most of the state, including hills of the Bluegrass, other calcareous regions, Knobs and Appalachian hills.

D. Transitional or uncertain assignment between C and E; soils often have mixed origin, sometimes with much sand. Species that are common on farmland or alluvial soils with relatively high fertility (especially in N and P) are generally assigned here.

E. Association with weakly acid to neutral soils (ca. pH 6–7) and medium to high overall fertility, especially in bases (Ca, Mg, K); soils generally lack much sand. *Acer saccharum* (sensu lato) is potentially dominant on mesic sites; common upland oaks include *Q. muhlenbergii*, *Q. shumardii*, *Q. macrocarpa* and locally *Q. imbricaria*. Typical species have higher frequency in calcareous regions, especially the Bluegrass, compared to the Knobs and Appalachian hills (where they are absent or restricted to unusually fertile valleys and local base-rich shales).

The majority of native woody species (60%) are assigned to classes C or D, but the subset of woody vines have a much stronger concentration in these two classes (88%). The two vines with most evergreen tendency (*Bignonia capreolata* and *Smilax bona-nox*) are both typical of class D, together with the evergreen mistletoe (*Phoradendron leucarpum*). *S. glauca* is centered in class B, but it has less persistent leaves, often falling during colder winters. In contrast, the evergreen habit among trees and shrubs is strongly concentrated among species of class A, on more acid and infertile soils. Among large tree species, those with entire simple leaves are concentrated in class B, while those with compound leaves are concentrated in classes D and E. And, among trees, other features have increased occurrence from A to D or E: dioecious flowering (large trees only); potential for clonal spread with lateral roots; unusually large edible fruits; and thorns (large trees only).

Table 2 shows patterns in some functional groups among the herbaceous flora of Kentucky. Again, distinctly evergreen species—ferns, subshrubs and herbs (excluding graminoids)—are concentrated on strongly acid soils (class A). Mycotrophic and parasitic species also tend to be associated with more acid soils. Herbaceous vines, including annuals, are most frequent among species typical of moderate position along the gradient (class C). Other annuals, biennials or monocarpic perennials tend to be concentrated at higher pH, especially winter-annuals.

The pH-related Gradient: Vine Frequencies in Plots from Central Kentucky & VegBank

Figure 3 is designed to combine the pH-related gradient with the general gradient from mesic or riparian woods to more open xeric or disturbed woods on uplands (as expressed in Figure 2k). Distinctly hydric vegetation is generally excluded, although riparian woods and subhydric transitions to thin swampy woodland are included in the lowest rows. Figure 3b indicates approximate modal positions for each common tree species, and the approximate correspondence of vegetation classes depicted here to the associations of NatureServe (2012).

Figure 3d–j presents overlayed data from 746 plots surveyed in central Kentucky. These are plots of 15 m radius (706.5 m^2) for trees over 9.5 cm dbh, with subplots of 10 m radius (314 m^2) for smaller stems and ground vegetation. They include 628 plots surveyed on Daniel Boone National Forest during 1993–1995 (with M. Hines & D. Taylor); plus 118 surveyed in the central Bluegrass region during 1977–79 (Campbell 1980). Plots were located regularly along subjectively selected, diverse topographic transects in order to represent the full range of species composition as equitably as possible. They do not systematically cover the whole landscape. They were selected to include some canopy trees of at least 25 cm dbh, and they exclude obvious edges or transitions to recent old fields. But in most cases there has been some cutting of trees, and in many cases the woodland is successional, especially from old pastured areas. These plot data are supplemented with other general information on occurrence of each vine species based on selected published sources and VegBank (Appendix 2). Data from VegBank (Peet et al. 2012) were checked on 6 Dec 2012, and refer only to the 1485 plots from southeastern states (AL, MS, NC, SC, TN, VA, WV). These plots mostly range from 100 to 1500 m^2 in area, with miscellaneous sampling methods.

Evergreen trees—plus minor amounts of evergreen shrubs—are most abundant, as a proportion of basal area, in vegetation typical of strongly acid soils, and at the xeric or disturbed extreme (Figure 3c). In contrast, six of the seven evergreen-tending vines are concentrated in vegetation typical of medium acid to base-rich soils, and most of them are concentrated in mesic to subxeric woods (Figure 3d-j). Each vine has relatively little occurrence in vegetation typical of mesic to subhydric alluvial sites on base-rich soils. However, there is a curious tendency for extension into subhydric vegetation on medium acid soils, especially by *Lonicera japonica*. Could rarity on damp base-rich soils be caused by the history of herbivory?

Other Distributional Data for Species in East-central U.S.A.

Geographic distributions of these vines across the U.S.A. are fairly well-documented by BONAP (Kartesz 2012) and others (e.g., Tables 3 and 4), but there are inconsistencies and gaps, especially in ranges of the less widespread aliens, *Hedera helix* and *Euonymus fortunei* (Figure 4). Although many thousands of plots have been surveyed for flora and vegetation in eastern states during recent decades, there has, unfortunately, been little synthesis of these data until the recent efforts of VegBank (Peet et al. 2012). A much larger database, begun in 1930, is the continuing Forest Inventory Analysis (FIA) of US Forest Service, providing a systematic-random sample of forested area that is “at least 37 m wide; 0.4-ha in size; covered, or formerly covered, by trees; capable of tree-growth; and not developed for nonforest uses” (Rudis et al. 2005). The FIA has been largely limited to better known woody species, but more details of other plants are now being collected (e.g., Miller et al. 2008; see Table 3).

Lonicera japonica. The map of this species produced by recent FIA for southeastern states (Figure 5) shows its frequency by county in the subplots of 168 m^2 (groups of four subplots are dispersed within ca. 6000 m^2). This alien vine is most abundant, with frequencies of 50-90%, in the Piedmont (from Virginia to Georgia), in the Upper East Gulf Coastal Plain, and in other low hills where much forest has been fragmented and farmland has been abandoned. It is infrequent

(< 10%) to absent in some counties of the Mississippi Alluvial Plain, Nashville Basin, Kentucky Bluegrass, and Ridge-and-Valley regions.

With these plot data from southeastern states, Wang et al. (2012) showed a positive relationship of *L. japonica* to site productivity (site index), and negative to recent occurrence of fire (within past 5 years). Across northeastern states, Schulz & Gray (2012) found relatively high frequency in whole FIA plots (subplots combined) that were classified as mixed upland forest (17.1%); less in white oak (13.9%), oak-hickory (13.6%), and hard maple (11.4%) types. They found little difference comparing plots of intact forest to plots at edges (9.0% versus 11.7% overall), but the difference was much greater for the subset of plots classified as white oak (9.1% to 21.4%). Possible relationships of these data to patterns in deer populations do not appear to have been studied. Some recent statistical models have focussed on the likely effects of forest fragmentation and global warming, and on the extent to which *L. japonica* currently saturates its potential habitat or has room for further expansion (Lemke et al. 2012, Wang et al. 2012). The species is clearly concentrated at edges of forests, especially roadsides, where is often the most abundant alien plant. It appears to have spread relatively fast into most suitable habitat across southeastern states within the past century or so (Merriam 2003).

Smilax. A large amount of plot data exists for these species in the literature, but there has been virtually no general analysis in relation to habitat gradients. Data in a recent thesis by Ulrey (2002) does allow some confirmation of the trends reported here for *S. glauca* (Table 4)—much more synthesis of such information is warranted for this important genus.

Table 1. Some pH-related trends in ecomorphological features of Kentucky's native woody plants, as indicated by typical positions for each species along the pH-related gradient. See text for explanation of gradient; see Appendix 1 for species abbreviations; see Campbell & Medley (2012) for listings and distributions of large trees, small trees, large shrubs, small shrubs and vines. Varieties are counted in total taxa. Features are as follows.

Percentage of all trees and shrubs with evergreen leaves. All trees are listed.

Percentage of trees with entire simple leaves. These do not include needle-leaved gymnosperms. Trends are weak to absent among shrubs and vines.

Percentage of total that are vines (or parasitic epiphytes). All species with evergreen leaves are noted plus the parasitic mistletoe, *Phoradendron leucarpum*; those with semi-evergreen to deciduous species are in parentheses.

Percentage of large trees with compound leaves. These do not include needle-leaved gymnosperms. Trends are absent among smaller trees, shrubs and vines.

Percentage of all trees with clonal spread. These have frequent lateral spread by root-suckering or layering. Large trees are listed. Clear trends are absent among shrubs.

Percentage of large trees that are dioecious. Included here are 'polygamo-dioecious' species: with sexes concentrated on separate trees but with some bisexual flowers in some cases. Clear trends are absent among smaller trees, shrubs and vines.

Trees with unusually large fruit. These are large or small trees with the largest fruits (in Kentucky) within their genus if more than one species, or the largest within their family if only one species per genus, or the largest within their order if one species per family. Excluded are species with normal types of bird-dispersed or wind-dispersed seeds.

Large trees with thorns. Trends are absent among smaller trees and shrubs. *Ilex opaca*, with prickles on leaves, is classified here as a small tree. *Juniperus* might also be added.

Ecomorphological Features	Percentages of species (and noted species) at their typical positions along the pH-related gradient				
	A: strongly acid	B: intermediate	C: medium acid	D: intermediate	E: base-rich
% of all trees and shrubs with evergreen leaves; trees listed below	29% Pinrig Tsucan (Rhomax)	9.5% Pinvir Pinech Pinstr (Ileopa)	0	6% Junvir Thuocc	0
% of all trees with entire simple leaves	30%	21%	14%	10%	11%
% of total that are vines; evergreen species listed below	0	3% (Smigla)	17% (Lonsem)	21% Bigcap Pholeu (Smibon)	4%
% of large trees that are strictly dioecious (*) or partially so	0	0 [smaller tree: Ileopa*]	23% Acerub Divir* Nysaqu* Nyssyl* Popgra* Sasalb*	38% Acescn Diopub* Fra(5) Gleaqu Junvir* Morrub Pop(2)* Salnig*	26% Aceneg* Gletri Gymdio* Frapro Macpom*
% of all trees with compound leaves	0	14%	7%	25%	25%
% of all trees with clonal spread (lateral roots or layers); large trees listed	10%	14%	12% Diovir Sasalb	19% Robpse Salnig (Thuocc) Ulmrub	30% Gymdio Gletri ?Ulmtho Macpom
Trees with unusually large edible fruits (versus related taxa)		Casden	Diovir Malcor	Carlac Aesfla Asitri	Quemac Jugnig Gymdio Prumun Macpom Cramol
Large trees with thorns				Robpse (Gleaqu)	Gletri Macpom
Total large trees	7	9	25	35	19
Total small trees	3	5	18	17	9
Total large shrubs	9	19	16	6	9
Total small shrubs	5	6	10	11	7
Total woody vines	0	2	14	18	2
Combined Totals	24	39	83	87	46

Table 2. pH-related trends in some functional groups among Kentucky's native herbaceous vascular plants, as indicated by the distribution of typical positions for each species along the pH-related gradient. See text for explanation of the pH-related gradient; see database of Campbell & Medley (2012) for listings and distributions of functional groups. Groups without clear trends are not shown, but they are included in the totals (determinate spring woodland perennials, rosette perennials, shorter spring-summer perennials, summer woodland perennials with simple broad leaves, shorter graminoids of more open land, and aquatic plants). Numbers of species within each group are provided in parentheses. Percentages are based on the total numbers of all woody plus herbaceous native species at each position along the gradient (A to E); these totals are provided in the bottom row. Shadings indicate concentrations. Details of functional groups are as follows.

Evergreen ferns, herbs and subshrubs. These are species with tough evergreen leaves usually evident above the litter, excluding the many species with only basal tufts of leaves that are protected near ground level. Nevertheless, some assigments are tentative, and species of rock outcrops deserve may deserve distinction; sandstone species are mostly assigned to A, limestone species to E. Graminoids are excluded. The exceptional plants under D and E are mostly ferns, also *Hepatica acutiloba* and *Paxistima canbyi*.

Mycotrophic plants. Partially or (in a few cases) completely dependent on fungi for nutrition; most species are in Orchidaceae. Further refinement of concepts is needed.

Parasitic plants. Partially or completely dependent on host plants for nutrition; most species are in Orobanchaceae.

Larger summer-fall graminoids. These are all C4 species in Cyperaceae and Poaceae that are typical of open sunny sites. Excluded are those with short stature, ca. 0.1–0.2(–0.4) m tall, which are mostly typical of wetlands, shorelines and trampled areas; also excluded are "woodland" species such as *Muhlenbergia* spp.

Later woodland graminoids. These are C3 panic-grasses (*Dichanthelium* spp.) plus a few C4 muhly-grasses (*Muhlenbergia* spp.).

Herbaceous Vines. These include annual vines. A similar trend (with peak in C–D) occurs among woody vines (Table 1).

Earlier woodland graminoids. These all have C3 photosynthesis.

Distichous woodland lilioid perennials. This small group is affiliated with some woodland graminoids or herbs.

Tall summer-fall perennials. Plants reach ca. 1–3 m. Trends are similar for running and non-running subgroups.

Tall annuals. These plants reach ca. 1–3 m and are self-supporting; vines are excluded. Note also tall annual crops on fertile soils: okra, hemp, tobacco, corn (maize).

Summer woodland perennials with large divided leaves. Trends are similar for early and late flowering subgroups.

Biennials and monocarpic perennials. Trends are similar for early and late flowering subgroups.

Winter-annuals. Trends are similar for subgroups of woodlands, old fields and rocky glades.

Functional Groups of Native Herbaceous Species (total numbers in parentheses)	Percentages of species in divisions of the pH-related gradient				
	A: strongly acid	B: inter-mediate	C: medium acid	D: inter-mediate	E: base-rich
Evergreen ferns, herbs and subshrubs (58)	**16%**	**2.4%**	**1.4%**	**1.0%**	**3.5%**
Mycotrophic plants (51)	**8.9%**	**3.4%**	**3.4%**	**0.7%**	**0.5%**
Parasitic plants (27)	**2.4%**	**2.0%**	**2.0%**	**1.2%**	**2.0%**
Larger summer- to fall-flowering graminoids of grassland (49)	**1.6%**	**5.1%**	**2.4%**	**1.8%**	**1.5%**
Later woodland graminoids (28)	**1.6%**	**2.4%**	**1.6%**	**1.0%**	**0.5%**
Herbaceous vines (43)	**0.8%**	**0.3%**	**3.3%**	**2.1%**	**2.0%**
Earlier woodland graminoids (28)	**0**	**0**	**0.8%**	**2.7%**	**2.0%**
Distichous woodland lilioids (21)	**0**	**1.0%**	**1.0%**	**1.3%**	**1.0%**
Tall summer-fall perennials (66)	**0**	**1.0%**	**3.0%**	**5.2%**	**3.5%**
Tall annuals (15)	**0**	**0**	**0.3%**	**1.6%**	**1.0%**
Summer woodland perennials with large divided leaves (37)	**0**	**1.0%**	**1.7%**	**1.9%**	**4.5%**
Biennials and monocarpic perennials (51)	**0.8%**	**0.7%**	**1.0%**	**4.1%**	**6.4%**
Winter-annuals (34)	**0%**	**0%**	**1.1%**	**2.4%**	**5.9%**
Total Species (herb. + woody)	**123**	**293**	**693**	**660**	**200**

Figure 3a–j. The pH-related gradient and dryness/disturbance gradient among trees of east-central U.S.A., with trends in evergreen-tending woody plants as overlays.

Figure 3a,b. Diagrams combining the pH-related and dryness/disturbance gradients. See text for explanation of the pH-related gradient (left to right). The vertical gradient with nine divisions, as outlined below, expresses the broadly defined trend from lowlands to uplands, with increasing dryness and associated disturbance (Figure 2k). Purely hydric vegetation is excluded. Six-letter codes for species (as in Figure 2b) show approximate positions of their maximum frequency (with alternatives in parentheses for a few bimodal or broadly ranging species); some smaller species are excluded due to lack of space, especially Rosaceae. Four-number codes indicate approximate positions of most native vegetation types (CEGLs) that have been described by NatureServe (2012) for non-hydric sites in Kentucky plus adjacent states.

9. Grassy openings due to xeric conditions, burning or browsing.
8. Xeric to subxeric woods plus open shrubby or grassy savannas.
7. Subxeric/seral woods, plus thin or shrubby transitions/savannas.
6. Transitions from subxeric/seral to more mesic woods.
5. Transition from mesic to subxeric/seral woods, often ‘submesic’.
4. Mesic colluvial woods, especially toeslopes and NE-faces.
3. Mesic alluvial woods, often transitional to riparian woods.
2. Riparian woods, with forceful but temporary flooding.
1. Subhydric woods, but often transitional to submesic woods.

Figure 3c. Percentage of evergreen species in basal area of forest, based on plots from central Kentucky. See text for sources of data; plots are 15 m radius for stems >9.5 cm dbh, with subplots of 10 m radius for stems 1–9 cm dbh and ground vegetation. The evergreen species are *Juniperus virginiana*, *Ilex opaca*, *Pinus* spp. (*echinata, rigida, strobus, virginiana*) and *Tsuga canadensis*, plus local *Kalmia latifolia* and *Rhododendron maximum* in the shrub layer.

Figures 3d–j. Distribution of evergreen-tending vines. Shadings indicate concentrations based on the following data.

> In parentheses: (numbers/total plots) indicate occurrences of the species in plots of 10 m radius (0.314 ha); see text for sources of data.
>
> To left: + indicates added observations of the author from central Kentucky;
> ++ indicates observed concentrations observed by the author.
>
> To right: + indicates typical presence in CEGL descriptions of NatureServe (2012); or concentrations reported by Ulrey (2002), Biggerstaff & Beck (2007), Waggy (2010), Zouhar (2009), Campbell & Seymour (2011), etc.
>
> # indicates plot numbers with the species in VegBank, based on searches in Dec 2012; see Appendix 2 for lists of individual plots.

(a) Summary diagram, with common names of predominant trees.

GRADIENT IN DRYNESS AND DISTURBANCE	pH-RELATED GRADIENT (A: strongly acid to E: circumneutral)				
	A	B	C	D	E
xeric or seral (to subxeric)	PINES, HEATHS and transitions with sassafras, persimmon		Varied mixes esp. post oak blackjack o.	RED CEDAR, LOCUSTS CHERRIES, PLUMS diverse hawthorns, briars	
subxeric or seral (to submesic)	OAK-CHESTNUT (former)	OAK-HICKORY: esp. white oak, black oak, s. red oak; pignut, mockernut, shagbark; local red maple, blackgum			OAK-ASH+ chink. oak bur oak+
mesic (to submesic or subxeric)	HEMLOCK BIRCHES +	BEECH, SUGAR MAPLE TULIP, BUCKEYES, BASSWOODS and drier transitions with n. red oak			BLACK MAPLE bitternut+
riparian (to mesic)	absent or rare	RIVER BIRCH, SYCAMORE shrubby willows		BOX ELDER, SILVER MAPLE, SYCAMORE local willow, cottonwood	
subhydric	absent or rare	SWEETGUM, SWAMP RED MAPLE, ALDER		GREEN ASH,WHITE ELM taller willows	

(b) Details of pH-related and dry/open gradients among trees of east-central U.S.A.

GRADIENT IN DRYNESS AND DISTURBANCE	pH-RELATED GRADIENT (A: strongly acid to E: circumneuntral)				
	A	**B**	**C**	**D**	**E**
9 openings	Danser 4061 7805	Andter Danspi 2417 4756 7707	Schsco Andger Andvir Pananc 4044 4686 7705	Setgen Rhuspp Rubspp 2024 4624 4738	Spocom Trifla 4078
8 xeric-sx.+	Pinrig Oxyarb 3617	Pinvir Quemar 3765 6327 7500	Queste Diovir Chivir Popgra 4217 5018 7121	Junvir Queimb Robpse Arugig 3836 4732 7279	Quemac Gletri Macpom Fracar 3835 4436 4544
7 subxeric+	Quecoc Steova 4412 6271 8431	Pinech Carpal 2591 7247 7493	Quefal Cartom Sasalb Corflo 7244 7746 7795	Pruser Cercan Vibruf Ulmala 3836 4133 7699	Jugnig Celocc Ulmtho/ser 4693 7180 7879
6 sx.-mesic	Quemon Magmac 4425 7267	Pintae Casden 7196 7268 8521	Quealb Cargla Quevel Nyssyl 2067 7219 8428	Carova (Ulmame) Morrub Asitri 2070 6445 7240	Quemuh Queshu Carlac Claken 3876 4697 4741
5 submesic+	Betlen Rhomax 6923 7102 7565	Pinstr Ileopa 6192 7286 7300	Querub Lirtul Acerub (Liqsty) 7220 7218 7881	(Carcor) Ulmrub Fraame Ostvir 4793 7698 7233	Aesgla Gymdio Fraqua 4437 6237 8442
4 mesic coll.	Tsucan Betall 7136	Magtri 5043 8407	Faggra Magacu 6055 7200 7201	Acesac Aesfla Tilhet Carcar 2411 5222 7695	Acenig Tilame (Car cor) 4411 6471 8412
3 mesic all.		transitions/mixes 7143 7565	transitions/mixes (Quemic) 2099 7281 7340	transitions/mixes (Ulmame) 7184 7334 8429	transitions/mixes Cellae (Queshu) 4697 7339
2 riparian		Salser 3895 7314	Betnig Salcar 7312 8471	Plaocc Acescn 2431 2586 4626	Aceneg Popdel 2018 4690 5033
1 subhydric		Alnser 3737 3894 7443	Acetri Quepal (Liqsty Quepag) 2438	Frapen Salnig (Quemic) 6548 7703	Salint 8562

(c) Percentage of evergreen trees in basal area of Kentucky plots

GRADIENT IN DRYNESS AND DISTURBANCE	pH-RELATED GRADIENT (A: strongly acid to E: circumneuntral)				
	A	**B**	**C**	**D**	**E**
9 openings	**66**	**no plots**	**no plots**	**no plots**	**63**
8 xeric-sx.+	**51**	**56**	**61**	**no plots**	**29**
7 subxeric+	**7.9**	**9.4**	**8.5**	**12**	**27**
6 sx.-mesic	**34**	**17**	**14**	**3.3**	**4.4**
5 submesic+	**50**	**37**	**4.2**	**0.4**	**2.3**
4 mesic coll.	**65**	**36**	**8.6**	**0**	**0**
3 mesic all.	**no plots**	**41**	**3.1**	**0**	**0**
2 riparian	**no plots**	**(1 plot)**	**0.2**	**0.1**	**0**
1 subhydric	**no plots**	**33**	**3.3**	**0.5**	**0**

(d) ***Hedera helix*: in only 2 of 746 Kentucky plots and 6 of 1485 VegBank plots.**

GRADIENT IN DRYNESS AND DISTURBANCE	**pH-RELATED GRADIENT (A: strongly acid to E: circumneutral)**				
	A	**B**	**C**	**D**	**E**
9 openings	**(0/19)**				**(0/2)**
8 xeric-sx.+	**(0/22)**	**(0/25)**	**(0/16)**		**(0/9)**
7 subxeric+	**(0/43)**	**(0/72)**	**(0/27)**	**(0/5) +**	**(0/10)**
6 sx.-mesic	**(0/12)**	**(0/47)**	**(0/56) +**	**(0/45) +**	**+ (0/41)**
5 submesic+	**(0/7)**	**(0/19)**	**(0/24) + #3,4,6**	**+ (0/25) +**	**+ (1/26)**
4 mesic coll.	**(0/11)**	**(0/14)**	**(0/22) #1,5**	**+ (0/26)**	**+ (1/8)**
3 mesic all.		**(0/8)**	**(0/13) +**	**+ (0/3) #2**	**+ (0/2)**
2 riparian		**(0/1)**	**(0/9)**	**(0/9)**	**(0/4)**
1 subhydric		**(0/7)**	**(0/48)**	**(0/4)**	**(0/5)**

(e) *Euonymus fortunei*: in only 8 of 746 Kentucky plots and 1 of 1485 VegBank plots.

GRADIENT IN DRYNESS AND DISTURBANCE	**pH-RELATED GRADIENT (A: strongly acid to E: circumneuntral)**				
	A	**B**	**C**	**D**	**E**
9 openings	**(0/19)**				**(0/2)**
8 xeric-sx.+	**(0/22)**	**(0/25)**	**(0/16)**		**+ (1/9)**
7 subxeric+	**(0/43)**	**(0/72)**	**(0/27) +**	**+ (1/5)**	**+ (1/10) +**
6 sx.-mesic	**(0/12)**	**(0/47)**	**(0/56) +**	**+ (1/45)**	**++ (2/41) +**
5 submesic+	**(0/7)**	**(0/19)**	**(0/24) +**	**+ (0/25) +**	**++ (0/26)**
4 mesic coll.	**(0/11)**	**(0/14)**	**(0/22) #1**	**+ (1/26) +**	**++ (0/8)**
3 mesic all.		**(0/8)**	**(0/13)**	**+ (1/3) +**	**+ (0/2)**
2 riparian		**(0/1)**	**(0/9)**	**+ (0/9) +**	**+ (0/4)**
1 subhydric		**(0/7)**	**(0/48)**	**(0/4)**	**(0/5)**

(f) *Bignonia capreolata*: in 126 of 746 Kentucky plots but only 5 of 1485 VegBank plots.

GRADIENT IN DRYNESS AND DISTURBANCE	pH-RELATED GRADIENT (A: strongly acid to E: circumneuntral)				
	A	B	C	D	E
9 openings	(0/19)				(0/2)
8 xeric-sx.+	(0/22)	(1/25)	(0/16)		(2/9)
7 subxeric+	(0/43)	(1/72)	(2/27)	(2/5) +	(1/10)
6 sx.-mesic	(2/12)	(2/47)	(11/56)	(19/45)	(15/41)
5 submesic+	(0/7)	(2/19) +	(5/24) #4	(5/25)	(11/26) +
4 mesic coll.	(0/11)	(1/14)	(10/22) +	(6/26)	(4/8)
3 mesic all.		(0/8)	(5/13)	(1/3) #?	(0/2)
2 riparian		(0/1)	(5/9)	(1/9)	(0/4) #3
1 subhydric		(0/7)	(11/48)	(0/4) #1,2,5,?	(1/5)

(g) *Lonicera japonica*: in 66 of 746 Kentucky plots and 17 of 1485 VegBank plots.

GRADIENT IN DRYNESS AND DISTURBANCE	**pH-RELATED GRADIENT (A: strongly acid to E: circumneutral)**				
	A	**B**	**C**	**D**	**E**
9 openings	**(0/19)**				**(0/2)**
8 xeric-sx.+	**(0/22)**	**(0/25)**	**(0/16)**	**(0/0) + #13**	**(2/9)**
7 subxeric+	**(0/43)**	**(1/72) + #1**	**(1/27) + #17**	**(0/5) + #5,15,16**	**(2/10) +**
6 sx.-mesic	**(0/12)**	**(0/47)**	**(5/56)**	**(2/45) #9?**	**(7/41)**
5 submesic+	**(0/7)**	**(0/19) +**	**(2/24) +**	**(3/25) + #2,7,8,10,11**	**(3/26) + #4**
4 mesic coll.	**(0/11)**	**(1/14)**	**(2/22) +**	**(1/26)**	**(0/8)**
3 mesic all.		**(0/8)**	**(2/13) #6**	**(0/3) #3**	**(0/2)**
2 riparian		**(0/1)**	**(1/9)**	**(0/9) #12**	**(0/4)**
1 subhydric		**(0/7)**	**(7/48)**	**(4/4) #14**	**(0/5)**

(h) *Lonicera sempervirens*: in zero Kentucky plots and zero VegBank plots.

GRADIENT IN DRYNESS AND DISTURBANCE	pH-RELATED GRADIENT (A: strongly acid to E: circumneuntral)				
	A	**B**	**C**	**D**	**E**
9 openings	(0/19)				(0/2)
8 xeric-sx.+	(0/22)	(0/25)	(0/16) +	(0/0) +	(0/9) +
7 subxeric+	(0/43)	(0/72)	(0/27) +	(0/5) +	(0/10) +
6 sx.-mesic	(0/12)	(0/47) +	(0/56) +	(0/45) +	(0/41) +
5 submesic+	(0/7)	(0/19)	(0/24) +	(0/25) +	(1/26) +
4 mesic coll.	(0/11)	(0/14)	(0/22) +	(0/25) +	(1/8) +
3 mesic all.		(0/8)	(0/13)	(0/3) +	(0/2) +
2 riparian		(0/1)	(0/9)	(0/9)	(0/4)
1 subhydric		(0/7)	(0/48)	(0/4)	(0/5)

(i) *Smilax bona-nox*: in 17 of 746 Kentucky plots and 9 of 1485 VegBank plots.

GRADIENT IN DRYNESS AND DISTURBANCE	**pH-RELATED GRADIENT (A: strongly acid to E: circumneutral)**				
	A	**B**	**C**	**D**	**E**
9 openings	**(0/19)**			**(0/0) #6**	**(1/2)**
8 xeric-sx.+	**(0/22)**	**(0/25)**	**(0/16)**	**+ (0/0)**	**+ (1/9)**
7 subxeric+	**(0/43)**	**(0/72) #2,4**	**(0/27) + #1**	**+ (0/5)**	**+ (1/10)**
6 sx.-mesic	**(0/12)**	**(0/47)**	**(0/56)**	**(4/45)**	**(5/41)**
5 submesic+	**(0/7)**	**(0/19)**	**(0/24)**	**(1/25)**	**+ (2/26)**
4 mesic coll.	**(0/11)**	**(0/14)**	**(0/22)**	**(0/25)**	**(2/8)**
3 mesic all.		**(0/8)**	**(0/13) #5**	**(0/3) #7,8**	**(0/2)**
2 riparian		**(0/1)**	**(0/9)**	**(0/9)**	**(0/4)**
1 subhydric		**(0/7)**	**(0/48)**	**(0/4) #9**	**(0/5)**

(j) *Smilax glauca*: in 254 of 746 Kentucky plots and 7 of 1485 VegBank plots.

GRADIENT IN DRYNESS AND DISTURBANCE	**pH-RELATED GRADIENT (A: strongly acid to E: circumneutral)**				
	A	**B**	**C**	**D**	**E**
9 openings	**(6/19)**				**(0/2)**
8 xeric-sx.+	**(17/22) + #3,9**	**(18/25) + #4,8**	**(10/16) +**		**(0/9)**
7 subxeric+	**(28/43) ++ #5,6**	**(47/72) ++ #7**	**(20/27) +**	**(0/5)**	**(0/10)**
6 sx.-mesic	**(5/12) +**	**(24/47) +**	**(25/56) +**	**(12/45)**	**(0/41)**
5 submesic+	**(2/7) +**	**(6/19) +**	**(9/24) +**	**(7/25)**	**(1/26)**
4 mesic coll.	**(1/11)**	**(3/14) +**	**(2/22) +**	**(0/25)**	**(0/8)**
3 mesic all.		**(2/8)**	**(2/13)**	**(0/3)**	**(0/2)**
2 riparian		**(0/1)**	**(2/9)**	**(0/9)**	**(0/4)**
1 subhydric		**(3/7)**	**(14/48)**	**(1/4)**	**(0/5)**

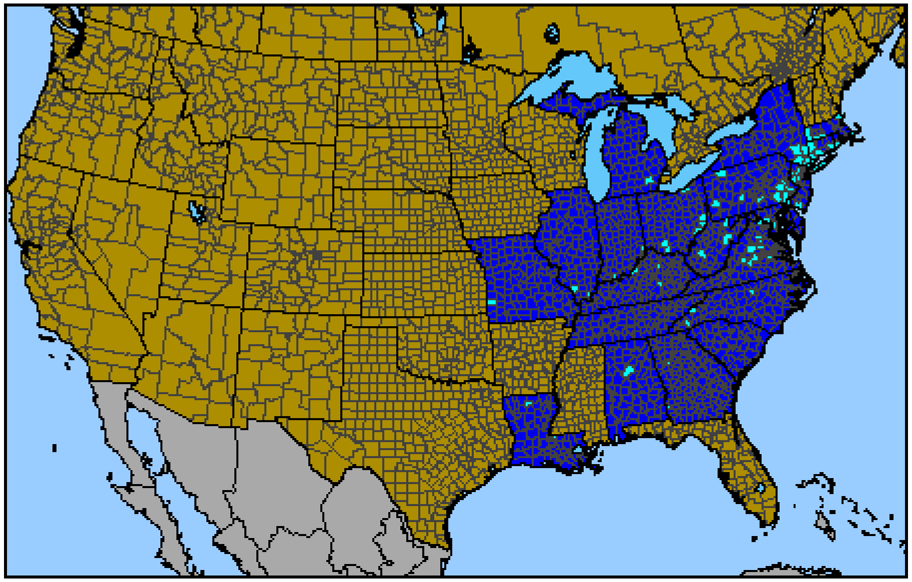
Table 3. Estimated "cover" percentages of alien evergreen vines within the "forested" area of southeastern states, based on Forest Inventory and Analysis by US Forest Service. Data come from Miller et al. (2008); see text. Euofor = *Euonymus fortunei*; Hedhel = *Hedera helix*; Lonjap = *Lonicera japonica*. In Texas, only eastern forested regions are included.

SPECIES	ESTIMATED PERCENT COVER IN EACH STATE											
	AL	AR	FL	GA	KY	LA	MS	NC	SC	TN	TX	VA
Euofor	0	0.0004	0	0	0.06	0	0	0.0009	0	0.03	0	0.00004
Hedhel	0.007	0.00004	0	0.00008	0	0	0.02	0.008	0.02	0.007	0	0.02
Lonjap	12.9	2.1	0.02	3.0	4.8	0.7	9.0	3.0	6.3	9.7	2.1	5.8

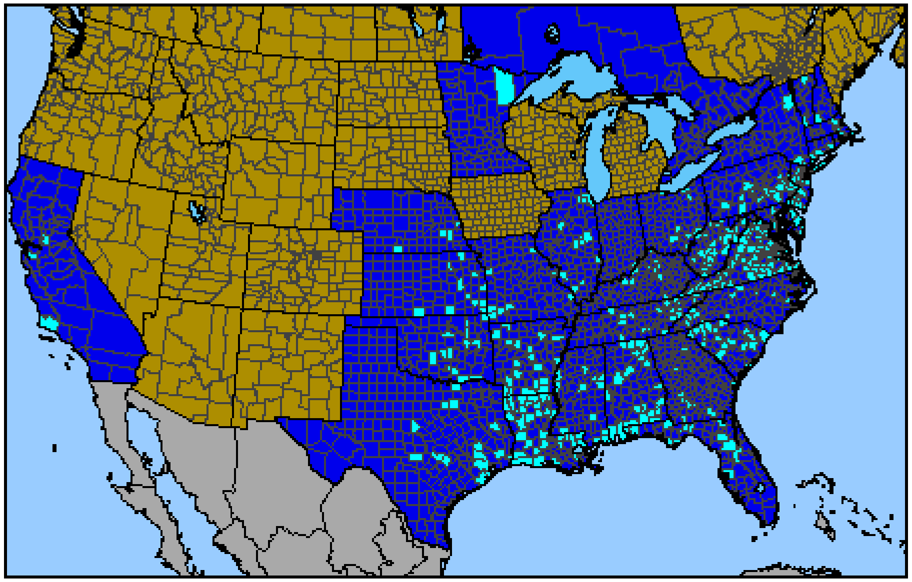
Table 4. Distribution of *Smilax glauca* among forest types < 4500 ft elevation in the southern Appalachian region, based on information assembled by Ulrey (2002: Table 4). Each cell indicates the forest type name and the percentage of occurence in 0.1 ha plots.

HABITAT DESCRIPTORS	**STRONGLY ACID approx. = A of Fig. 3**	**INTERMEDIATE approx. = B of Fig. 3**	**MEDIUM ACID approx. = C of Fig . 3**
7. XERIC-SX.	**Table Mt. Pine** **78**	**Shortleaf Pine** **74**	**(no plots)**
6. SUBXERIC	**Chestnut Oak** **78**	**Oak-hickory** **94**	**Calcareous oak** **+**
5. MESIC-SX.	**Carolina Hemlock** **86**	**White Pine** **65**	**Red oak** **52**
4. MESIC	**Canada Hemlock** **24**	**Acid cove forest** **50**	**Rich cove forest** **75**

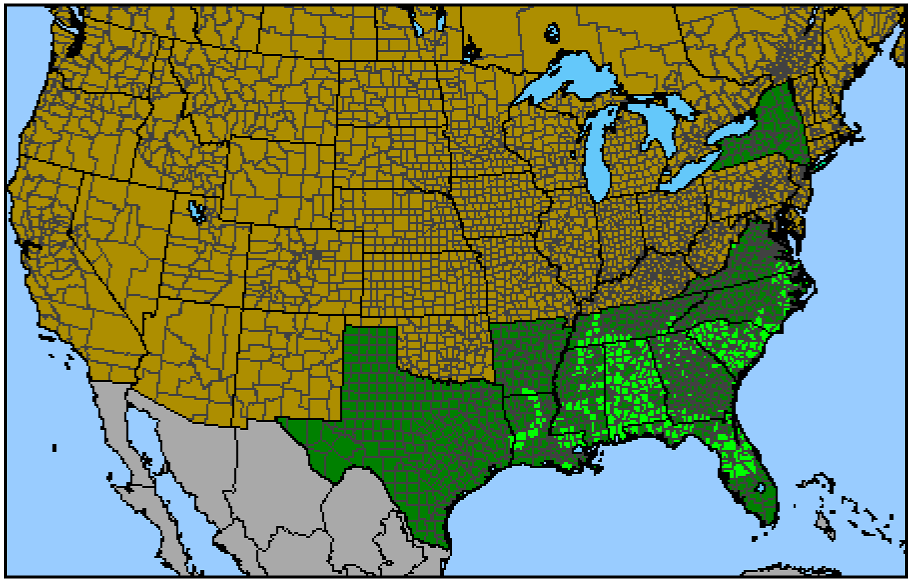
Figure 4. Maps of documented counties with evergreen or semi-evergreen vines of mid-temperate regions in east-central states, from BONAP (Kartesz 2012).
Pale green on dark green indicates native species; pale blue/pink on dark blue indicates alien species, with pink indicating official noxious status. The current Hardiness Zones occupied by these species are indicated after each name (USDA 2012). *Clematis terniflora* has little or no woody growth above ground in Zones 6–7; see notes in text under Ranunculid Orders.



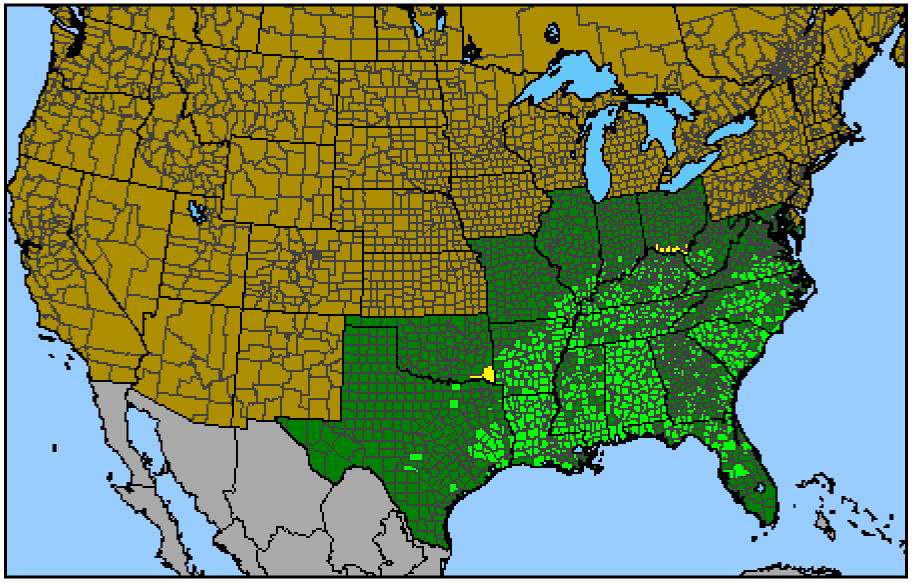
***Akebia quinata*: Zones 6a to 7b (?)**



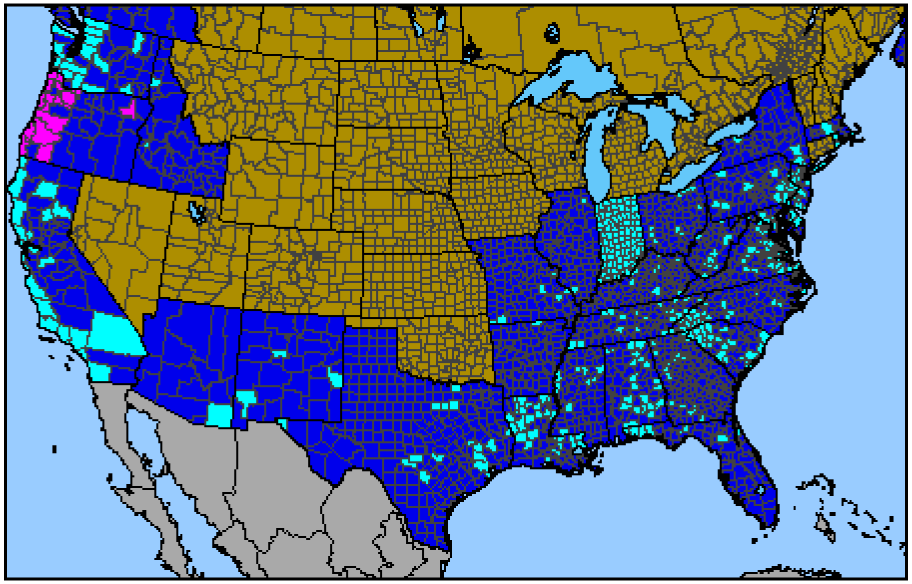
***Clematis terniflora*: Zones 6a to 9a**



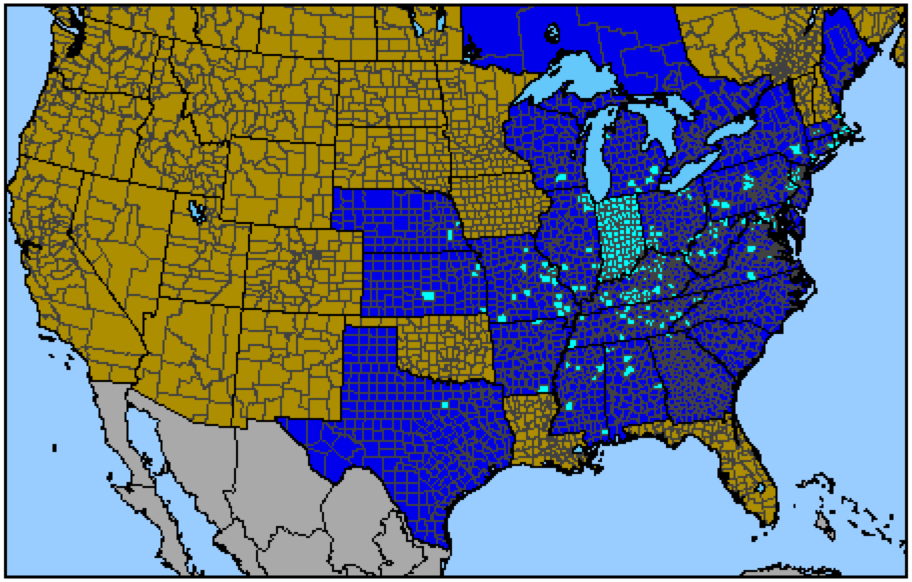
***Decumaria barbara*: Zones 7b to 9b**



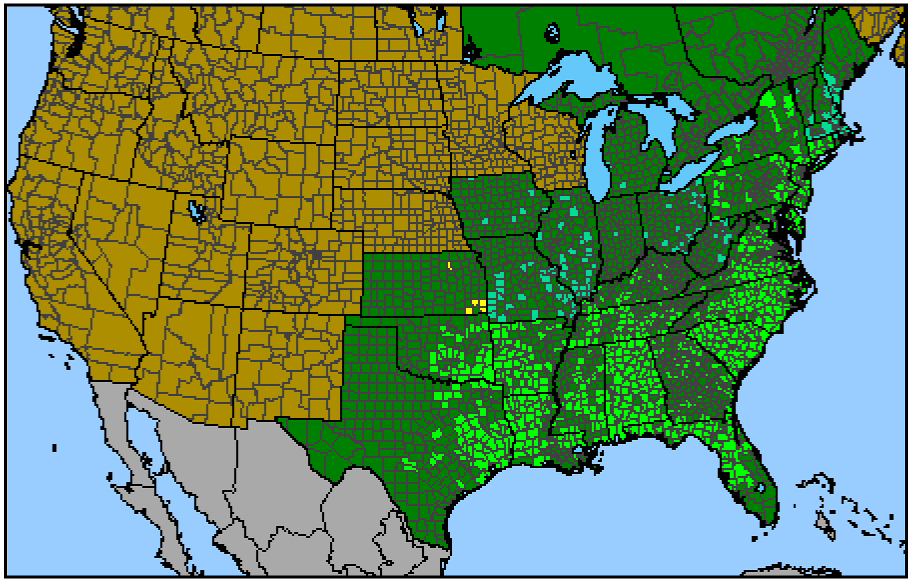
***Bignonia capreolata*: Zones 6b to 9b**

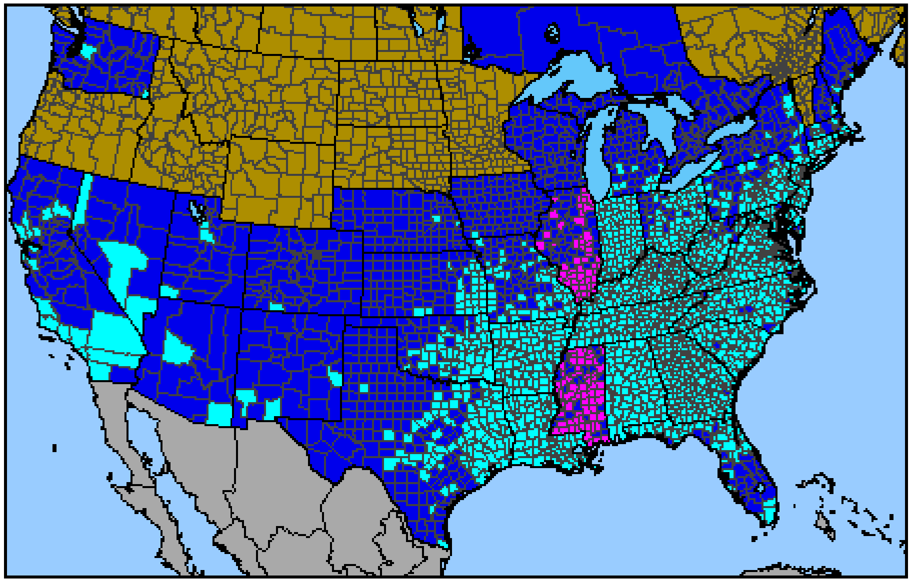


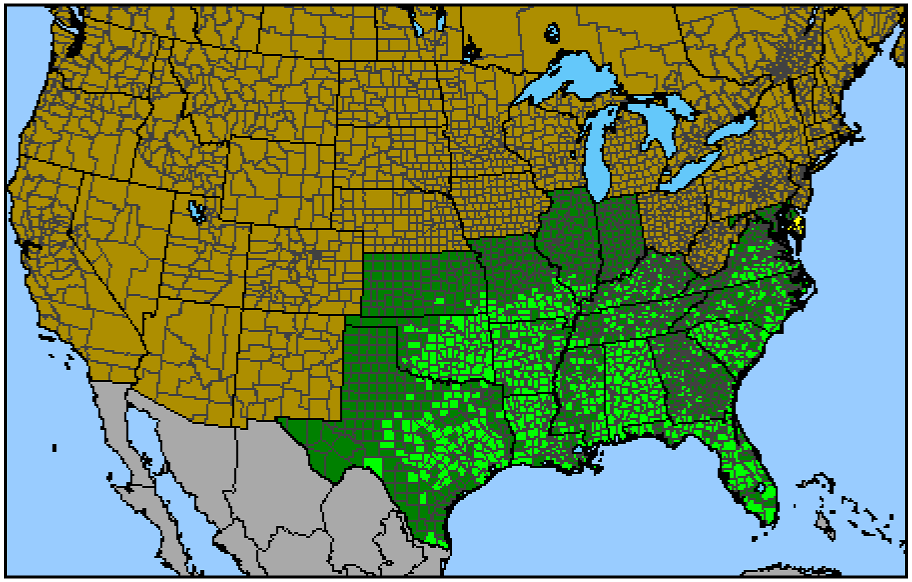
***Hedera helix*: Zones 6a to 9a (?)**



***Euonymus fortunei*: Zones 6a to 8a (?)**


***Lonicera sempervirens*: Zones 5b to 9b**


***Lonicera japonica*: Zones 5b to 9b**


***Smilax bona-nox*: Zones 6b to 10a**

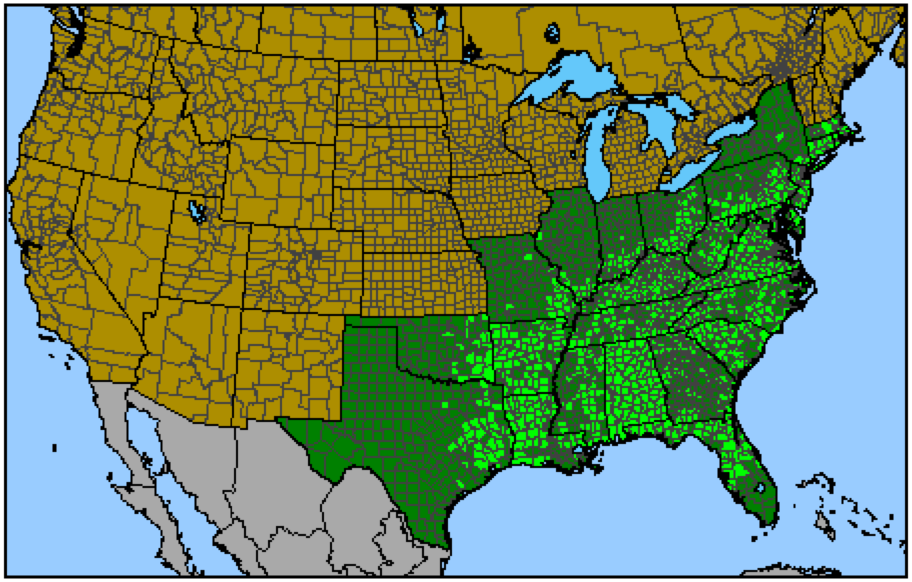
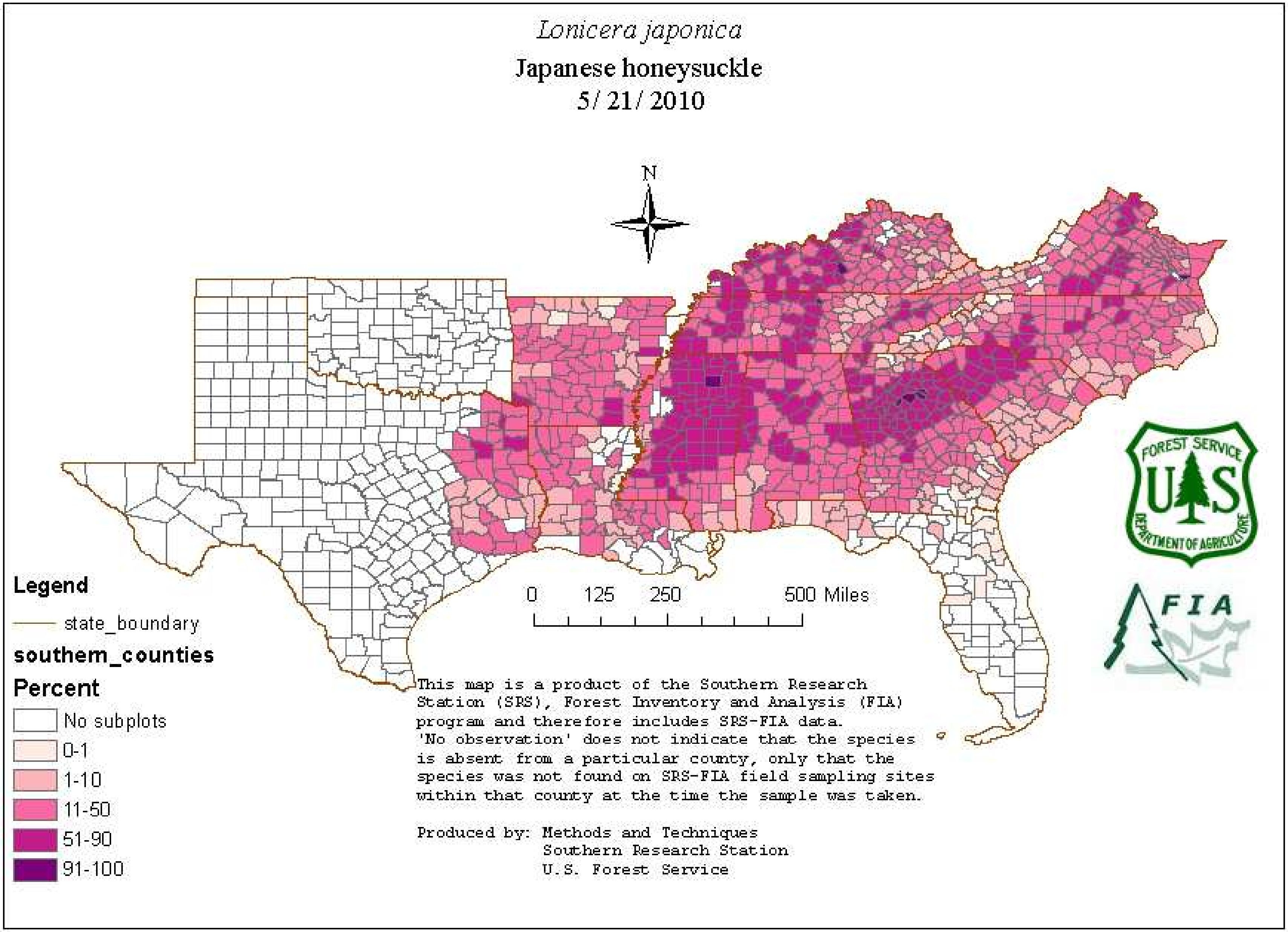

***Smilax glauca*: Zones 6a to 9b**

Figure 5. Forest Inventory Analysis Map of *Lonicera japonica* in southeastern states (from USDA 2010, http://srsfia2.fs.fed.us/images/srsfia/nni/a09_3101.pdf).



This map is a product of the Southern Research Station (SRS), Forest Inventory and Analysis (FIA) program and therefore includes SRS-FIA data. 'No observation' does not indicate that the species is absent from a particular county, only that the species was not found on SRS-FIA field sampling sites within that county at the time the sample was taken.

Produced by: Methods and Techniques
Southern Research Station
U.S. Forest Service

PART TWO: Evergreen-tending Vines in Mid-temperate Regions

Notes on Individual Taxa

The notes below cover all evergreen or semi-evergreen vines that extend into mid-temperate regions of the Northern Hemisphere, plus brief consideration of excluded taxa. The taxonomic sequence follows current concepts of angiosperm phylogeny and its usual linear projection (Stevens 2012), except that Monocots are placed after Eudicots since they are generally more distinct in biological and ecological features, compared to the presumed common ancesters in early Magnoliid plants. The only Monocots included here are species of *Smilax*, which are the only mid-temperate woody vines without cambium; they are almost the only ones with thorns; they may have the most diverse non-alkaloidal chemistry; they have the most consistent consumption by mammalian herbivores; they are the only ones that are strictly dioecious; and they have almost the largest number of species per genus (Table 7).

Table 5 summarizes general information on the ecology of each species, including provisional information on mammalian herbivory (with listed references), and indicators of secondary chemistry. General information on ranges, zones, habits and habitats comes largely from the following sources: Flora Europaea (1964–80), Flora of North America (1993–2010), Flora of China (1996–2011), Ohwi (1965), Duncan (1967), Raulston (1992), Yuan et al. (2009), Fang et al. (2011), Weakley (2011), JSPS (2012), and Kartesz (2012). Additional references are listed under each taxon. Data on chemistry or toxicity are widely scattered in voluminous literature, and a comprehensive listing of all sources is not provided here. Much older information is summarized in Muenscher (1961), Darnley-Gibbs (1974), Levin & York (1978), Glasby (1992), Beckstrom-Sternberg & Duke (1994), Harborne et al. (1999), Burrows

& Tyrl (2001), Hegnauer & Hegnauer (2002) plus associated databases. There has been no access to the more complete databases that exist in some institutions (e.g., Ehrman et al. 2007).

MAGNOLIID ORDERS: excluded. There are a few vines in these orders that extend into warm-temperate zones—often as evergreens, or into mid-temperate zones but there strictly deciduous or just herbaceous: Schisandraceae (*Kadsura, Schisandra*); Menispermaceae (*Cocculus,Calycocarpum, Menispermum*); Aristolochiaceae (*Aristolochia*, *Isotrema*). Among species of eastern North America, *Cocculus carolinus* is semi-evergreen in Zones 8–9a. It does extend into Zones 6b–7 but just as a largely deciduous plant with little or no woody stem.

RANUNCULID ORDERS

Lardizabalaceae. *Akebia* contains five species of evergreen to deciduous vines in warm- and mid-temperate zones in China, Korea and Japan. *A. trifoliata* and *A. quinata* (Figure 4) extend into Zone 7 as wild plants, and can remain semi-evergreen there except in colder winters (Raulston 1992). In Japan, taller shoots of *A. trifoliata* loose most leaves during winter, but shoots in the understory tend to retain a greater proportion of leaves, especially those formed late in the summer (Koyama & Kikuzawa 2008). *A. quinata* is widely cultivated and has escaped locally in the eastern U.S.A., tangling up the shrub layer, covering ground and suppressing native vegetation. It is able to grow through regularly mowed grass and spreads into adjacent woods (J. McCandless, Louisville, pers. comm.). In Louisville, Kentucky (currently transitional from Zone 6 to 7), *quinata* retains some leaves during most winters in gardens and parks, at least on the ground where leaf litter protects it from the coldest winds (J. Wysor, pers. comm.). Flowering is occasionally observed here but fruiting in this self-incompatible species is rare.

Holboellia is a closely related, larger genus of evergreen vines, centered in warm- and mid-temperate zones of the Sino-Himalayan region. It is weakly separated from the more tropical genus, *Stauntonia*, in which it has been merged by Christenhusz (2012). Some species extend into montane cloud forest zones or mid-temperate zones and remain evergreen: *angustifolia* (= *fargesii*), *grandifolia*, *latifolia* and *coriacea* (Shi & Zhu 2009, Chettri et al. 2010). The only deciduous species of *Holboellia* may be *medogensis* of southeast Tibet.

There is only sparse information about mammalian browsing on *Akebia* or *Holboellia*. Some use of *A. quinata* by Sika deer has been indicated in Japan (Takatsuki & Hirabuki 1997), but this plant is reportedly avoided by white-tailed deer in North America (Jull 2001). Squirrels can feed intensively on its buds and fresh shoots during April in Japan (Setoguchi 1990). *H. angustifolia* is used to feed cattle and other livestock during the winter in Nepal (Samant 1998), and some feeding on its shoots by monkeys has been reported (Grueter et al. 2009).

Ranunculaceae: excluded. Several species of *Clematis* are evergreen-tending woody vines of warm temperate regions, but these do not generally extend into mid-temperate zones. Such species include *armandii*, *uncinata* and allies of East Asia, and *cirrhosa* of southern Europe. The species that is most persistent above ground in mid-temperate zones may be the East Asian *terniflora* (= *maximowicziana*, *dioscoriaefolia* or *paniculata* or some authors). In Zones 8–9a, it can climb to 9 m high with semi-evergreen foliage and semi-woody stems; in Zones 6a–7 it tends to be tardily deciduous, and stems usually die above ground by end of winter (Figure 4).

ROSID ORDERS

Celastraceae. The widespread genus *Celastrus* comprises many scandent to twining woody species, but these are mostly deciduous in temperate regions (Hou 1955). *C. hindsii* is an evergreen twining shrub of mountains in Southeast Asia, native but becoming a “noxious weed” in some areas of southern China, as well as *Pueraria lobata* (Peng et al. 2009). Several other species of the genus in China and Japan are evergreen, especially section Sempervirentes, but most are restricted to warmer zones. The common invasive East Asian species, *orbiculatus*, is consistently deciduous, as is the North American native, *scandens*. Schaller et al. (1986) reported eating of *hindsii* by takin (a goat-antelope) in China. The genus in general appears to be relatively palatable, with potential for reduction under intense browsing (Asnani et al. 2006, Rossell et al. 2007, Ashton & Lerdau 2008, Averill 2012; but see Burroughs & Dudek, 2008).

Euonymus fortunei is a persistently evergreen vine that can climb trees and cover ground in woods (Brothers & Springarn 1992, Zouhar 2009)—and it can also spread into mowed lawns from wooded edges, becoming invasive in North America (Figure 4). Unfortunately, there is little published information in English that describes the ecology of this species in its native range of southern China, Korea and Japan. There are several related evergreen species of vine or “ascending subshrub” in *Euonymus* section *Ilicifolia*, and their taxonomy has been confused. Some reports of *E. vagans*, a “shrub or ascending subshrub to 3 m” (according to the Flora of China) may refer to *fortunei*, sensu lato (e.g., Shi & Zhu 2009). The common cultivar of eastern U.S.A. named “Manhattan” is often placed in *kiautschovicus*, which is a poorly defined species that appears intermediate between *fortunei* and *japonicus*—a shrub centered in warm temperate to subtropical zones. Cuttings from ‘adult’ climbing stems tend to remain upright and retain branch mutations in leaf shape or coloration (Dirr 1998; see also, US Patents).

In East Asia, species of the *E. fortunei* group are locally common from montane forests to urban lowlands, especially on base-rich soils. They are often planted for revegetation of steep slopes or for ornamental uses (e.g., Wang et al. 2009, Xia et al. 2007). However, the author's experiences in some wilder parts of Sichuan and Yunnan suggest that *Euonymus* climbers or scramblers there are largely restricted to two types of site: (1) steeper slopes and cliffs where browsing animals have less easy access—often in generally undisturbed forest (Yuan et al. 2009); and (2) fenced or walled areas near buildings. In central Japan, Sakai et al. (2002) reported it as the second-most common vine (after *Wisteria*) in a deciduous oak-dominated woods that had been recovering for three decades from burning and grazing.

From ornamental plantings of *E. fortunei* in North America, there is much anectodal evidence that this species is often preferred for browse by deer, especially during the winter (Table 5). In Kentucky, there can be locally intense browsing by deer, beaver, cattle, horses and sheep, based on personal observations or conversations with land managers. From East Asia, there are few direct indications of browsing in English literature, but the observations of Sika deer by Takatsuki & Hirabuki (1997) are suggestive. In a caging experiment at Brookhaven, New York, Ashton & Lerdau (2008) found that *fortunei* actually grew more with exposure to deer and rabbits. But, due to competition or other complicating factors in the experiment, its growth there was generally weak—even negative in some individuals, unlike compared species; the data did show more damage from herbivory among the uncaged plants (I. Ashton, pers. comm.). The species does proliferate with mowing under some conditions, especially in partial shade, but it does not seem to invade unmowed grassland.

Outside section *Ilicifolia*, there are several other shrubby species of *Euonymus* that are described as "scandent" but these do not appear to be truly robust tall vines exceeding 3 m.

They occur mostly in section *Echinococcus* (Flora of China Vol. 11), with both evergreen and deciduous species in mid-temperate zones, and they can be browsed (e.g., Samant et al. 2007). In eastern North America, *americanus* and *obovatus* are semi-evergreen to deciduous plants of warm/mid-temperate and mid/cool-temperate zones, respectively—and stems stay distinctly green. Both spread on or near the ground with rooting stems. *E. americanus* also grows up to become a deciduous shrub if it can escape from deer. Several reports indicate strong preference for browsing on the these American species by deer and other mammalian herbivores, especially during winter: for *americanus*, Lay (1967), Blair et al. (1980), Moreland (2003), Segelquist & Pennington (1968), Thrift (2007) and Webster et al. (2005); for *obovatus*, Asnani et al. (2006). The larger deciduous shrub of North America, *E. atropurpureus*, is also among the more sensitive woody plants to mammalian browsing in eutrophic woodland, based on personal observation, Dennis (1997) and others. The invasive tardily deciduous shrub, *E. alatus*, can also become intensively browsed, despite the corky wings along its winter-green twigs.

Other Rosid families excluded. There are many vines in these families that occur in warm-temperate zones (often as evergreens), and extend into mid-temperate zones but there largely deciduous or just herbaceous: Vitaceae (*Ampelopsis, Parthenocissus, Vitis*); Anacardiaceae (*Toxicodendron*); Rosaceae (*Rosa, Rubus*); Rhamnaceae (*Berchemia*); Cannabaceae (*Humulus*); Fabaceae (*Lackeya, Pueraria, Wisteria*). Some roses have more persistent leaves.

A note is inserted here on the temperate mistletoes: *Phoradendron* and *Viscum* (Viscaceae) in Santalales—which phylogenetic models have rooted above the Rosid clades and below the base of Caryophyllid and Asterid clades (Stevens 2012). These epiphytic evergreen parasites on trees have some ecological similarities to the evergreen vines. They have abrupt northern limits that are close to the vines. Their hosts are usually deciduous trees (often late-leafing species in Kentucky), usually in thin woods on soils with moderate to high fertility. Mistletoes in general have high mineral contents and digestible carbohydrates, and perhaps highly variable protein (from 6–10% to 24% in Littlefield et al.); they are often preferred browse by larger mammalian herbivores, when access is possible (Atwood 1941, Troels-Smith 1960, Watson 2001, Dillard et al. 2005, Mathiasen et al. 2008, Umcalilar et al. 2007, Littlefield et al. 2011). Their leaves have little direct structural or chemical defense, with simple phenolics, flavonols or tannins predominant. But some species have unusual proteins (thionins, lectins) that can have varied medicinal or cytotoxic effects. Mammalian toxicity is not documented among livestock or wild animals, although excessive consumption of *Viscum* by misguided humans can cause digestive problems or death in extreme cases (Kienle et al. 2011, Evens & Stellpflug 2012).

ASTERID ORDERS

Hydrangeaceae. In the small genus *Decumaria*, *sinensis* is an evergreen climbing shrub of central China, and *barbara* is a semi-evergreen vine of the southeastern U.S.A. (Figure 4). The allied genus *Pileostegia* comprises a few evergreen vines in warm-temperate zones of East Asia. The large complex genus *Hydrangea* also contains a few tall vines, but they are strictly deciduous. In all three genera, the climbing plants use adventitious roots. There is little information on herbivory of *Decumaria*, except for a few indications of moderate use by deer in North America (Moreland 2003, ?Thrift 2007). There is more information on shrubs in *Hydrangea*: *arborescens* and *quercifolia* are reported to have moderate use by deer in North America (e.g., Nixon et al. 1970, Fargione 1991, Knox 2007); and *paniculata*, much use by

Sika deer in Japan (Takatsuki 1986, Yokoyama et al. 2000). However, the popular ornamental, *macrophylla*, is reportedly toxic in Japan despite high nutritional content (Ogura 2011).

Actinidiaceae. *Actinidia henryi* [not = *A. callosa* var. *henryi*] is reportedly semi-evergreen, as are several other Chinese species of this genus, at least in warm temperate zones (Table 5, Flora of China Vol. 12). The evergreen-tendency appears to have evolved at least four different times, in different sections of the genus (Chat et al. 2004). But Japanese species are reportedly all deciduous. The allied monotypic genus, *Clematoclethra*, is a strictly deciduous vine that occurs only in mid-temperate to subalpine zones of China. Schaller et al. (1986) reported eating of *A. henryi* by takin in China, and there are several reports of the deciduous species being eaten by various mammals (Table 5).

Bignoniaceae. *Bignonia* is considered by some authors to contain just one species, *capreolata* (Weakley 2011), but some uncertainty remains (Lohmann 2006, Olmstead et al. 2009). It reaches an abrupt northern limit in southern Indiana and southern Ohio—with a similar range to *Smilax bona-nox* (Figure 4) and other notable evergreens such as the mistletoe, *Phoradendron leucarpum*, and the bamboo, *Arundinaria gigantea*. Yet at the edge of its interior range in southern Illinois, Indiana and Ohio, the species is locally proliferating on south-facing bluffs and terraces (D. Nickrent & D. Boone, pers. comm.). It climbs with tendrils that develop into pads (as reviewed by Seidelmann et al., 2012), and adventitious roots are formed on lower stem sections after 2–3 years (pers. obs.). It can also spread widely on the ground, but does not form dense mats of leaves like *Euonymus* or *Hedera*. The plant can be preferred browse for some mammals in the winter, a phenomenon that is particularly well-documented in the case of swamp rabbits (Table 5). There is little information on use by deer—the few reports indicate only moderate usage. But the plant has among the best-tasting leaves of any evergreen vine in this author's experience (rivaling *Smilax* but much more fibrous).

Araliaceae. *Hedera* is an evergreen vine with adventitious roots, flowering in late summer to fall. Its species are concentrated in warm- to mid-temperate zones, with a center of diversity in the Mediterranean region (Ackerfield & Wen 2003, Green et al. 2011). The widespread European *H. helix* (sensu stricto) is most common in western regions with relatively mild winters (Metcalfe 2005). Towards the east, it is more restricted to lowland riparian habitats, where cold winters appear to limit its height. In North America, *helix* (a tetraploid) has become locally abundant at scattered sites across southeastern states, with much local vegetative spread (Figure 4, Okerman 2000, Waggy 2010). The closely related species, *hibernica* (an octoploid), is concentrated in regions with more oceanic climate, and has become the prevalent taxon in western North America (Clarke et al. 2006). In more interior regions of North America, *Hedera* has not been able to tolerate winters as a high vine, although it may persist as a sterile ground-cover. In Kentucky, there has been virtually no evidence of establishment from seed until recent years—seedlings have begun to appear in gardens of the Lexington area during 2000–2012 (as observed by this author and Richard Weber, Springhurst Garden).

Other species of *Hedera* occur in warm- to mid-temperare regions further east: *colchica* and *pastuchowii* in northern Turkey and the Caucasus region; *nepalensis* in the Sino-Himalayan region; *rhombea* in Taiwan and Japan. *H. nepalensis* is becoming widely used in Chinese horticulture. It may have less tolerance of shade and drought than *Euonymus fortunei* (Jiang et al. 2007, Chen & Wang 2008), but it is reportedly more tolerant of SO_2 pollution than most ornamental plants in Chinese cities (Chen et al. 2007).

Although *Hedera* is quite bitter, there is ample evidence that it can provide relatively nutritious browse for ruminants, especially during winter (Table 5). Its general concentration within hedgerows, hawthorn scrub and younger woods across Britain (Rackham 2003) can be partly interpreted in terms of escape from herbivory. During medieval times, it was common practice in Europe for *H. helix* to be cut down for feeding to livestock during the winter (see also Troels-Smith, 1960). Cattle can eliminate it from the forest floor after several years of concentrated influence (Uytvanck & Hoffmann 2009), and goats have been used recently to reduce the invasion of *Hedera* in Oregon (Ingham 2008). But there is much variation in usage. Boulanger et al. (2009) found the plant to be generally avoided by deer, with an index based largely on summer browsing. And outside deer-exclosures, Rossell et al. (2007) found more reduction in *Lonicera japonica*, and much more in *Celastrus orbiculatus*. In East Asia, *H. nepalensis* is also a traditional source of fodder for livestock in the Sino-Himalayan region (Bajracharya et al. 1978, 1985). It is probably a significant winter-forage for wild ungulates (e.g., Shah et al. 2009), but rhesus monkeys appear to avoid it (Goldstein & Richards 1989).

The general ecology of *Hedera helix* is well-known within its native Europe (Metcalfe 2005). Schnitzler & Heuzé (2006) have documented its association with nutrient-rich soils on floodplains of the Rhine, as well as its sensitivity to waterlogging. The plant maintains a relatively constant, conservative flow of water to leaves, in marked contrast to associated trees (Leuzinger et al. 2011). Heuzé et al. (2009) have explored how growth responds to annual variation in temperature, indicating that warmer summers have most effect on uplands, while increases in Feb–Mar temperature have most effect on lowlands. There has been considerable research on the photosynthesis of *H. helix*. Oberhuber & Bauer (1971) initially found that "adult ivy leaves possess an enormous capacity to repair light-induced damage to the photosynthetic apparatus in winter" (see also Bauer & Kofler, 1987); this allows growth to resume in early spring before trees leaf out. The maximum photosynthetic rate of *H. helix* is relatively low compared to other vines, including *L. japonica* (Carter & Teramura 1988). However, 'adult' leaves on climbing shoots have distinct morphology and physiology, with higher photosynthetic rates per leaf area than 'juvenile' leaves on lower shoots, largely due to increased leaf thickness (Bauer & Bauer 1980). But 'adult' leaves are less able to adjust physiologically to short-term changes in light (Bauer & Thoni 1988). Zotz et al. (2006, plus cited studies) found that *H. helix* responds much to increases in CO_2—more so than associated shrubs and trees. They measured more stimulation of photosynthesis by CO_2 in the forest understory (where sugar content remained low), as compared to plants high on trees (where sugar content was already higher and increased with more CO_2).

Caprifoliaceae. *Lonicera japonica* is largely evergreen, as well as allies that include *acuminata*, *etrusca*, *ferruginea* and the *macrantha* complex. These plants are mostly twiners of Southeast Asia that extend into mid-temperate zones, where they are locally common in mixed successional deciduous forest (e.g., Lee et al. 1990). The only native species elsewhere is *biflora*, which occurs in scattered parts of the Mediterranean region but is reportedly rather short (< 3 m) and deciduous; it is not included in Table 5. *L. japonica* is widely cultivated, and it has become an abundant invasive alien in North America—while its native congeners tend to decline in some areas (Stransky 1984, Hardt 1986, Nuzzo 1997, Clemants & Moore 2005). *L. acuminata* sensu lato (including *henryi*) has a more western range than *japonica*, largely Sino-Himalayan. It has been cultivated under the name *henryi* in Europe, where it has recently become invasive at several sites (Weber 2005, Verloover 2006).

Mammalian toxicity from *L. japonica* is unknown, and standard tests on rats have revealed no pathological effects after high doses of leaf extract (Thanabhorn et al. 2006). In North

America, the plant is well known to be eaten much by deer and cattle during hard winters, for which it has been promoted (e.g., Handley 1945, Noland & Morrison 1954, Segelquist & Rogers 1975, Stransky 1984, Hardt 1986, Dyess et al. 1993, Frederick & Kennedy 1995). Even in summer, there is evidence that it can be used more than other vines (Nixon et al. 1970, Ashton & Lerdau 2003). Dense deer populations appear to reduce the plant's abundance (e.g., Beaver 2011). However, *japonica* is able to regrow rapidly after damage (Schierenbeck et al. 1994), and it is relatively plastic in its overall growth rate and form (Schweitzer & Larson 1999). Sasek & Strain (1991) found that its growth-response to CO_2 enrichment was greater than that of the native *sempervirens*.

The native *Lonicera* vines of North America and Eurasia—in subgenus *Caprifolium*—are generally rather short and semi-evergreen to deciduous in mid-temperate regions. *L. sempervirens* is largely evergreen in warmer zones of the southeastern U.S.A., but it usually reaches only 3–4 m. It seems to have spread north into mid-western states during recent decades (Kartesz 2012, see also state floras), but it may be limited by intensive deer-browsing in northeastern states (Table 5; Clemants & Moore 2005). In two caging experiments, *sempervirens* was more damaged than *japonica* by deer or rabbits (Schierenbeck et al. 1994, Ashton & Lerdau 2008). *L. albifolia* of southwestern U.S.A. and Mexico (Nelle 1996), and the European species (*implexa*, *etrusca*, *caprifolium*, *periclymenum*) are also favorites of deer and livestock (Appendix 4).

In South Carolina, Schierenbeck & Marshall (1993) found that both *sempervirens* and *japonica* produce new leaves during Janurary. But *sempervirens* abscissed its old leaves during mid-December, while *japonica* retained its old, photosynthetically active leaves through March. Moreover, the new leaves of *japonica* had significantly higher photosynthetic rates than *sempervirens* during January—although for most of the growing season there was no significant difference in sun or in shade. The greater shade tolerance of *japonica* may involve morphological differentiation rather than photosynthetic rates, since plants exhibit a somewhat distinct prostrate growth form on the ground, without twining behavior (Larson 2000). Yet *japonica* is also more responsive to the presence of climbing structures, as measured by morphological changes and increase in overall biomass (Schweitzer & Larson 1999).

Other Asterid families excluded. There are several low vines or subshrubs affiliated with Gentianales (sensu lato) that extend into warm-temperate zones—often as evergreens—but much less into mid-temperate zones—where strictly deciduous or restricted to ground vegetation. Families include Loganiaceae (*Gardneria*), Gelsemiaceae (*Gelsemium*), Apocynaceae (*Trachelospermum, Thyrsanthella, Vinca*) and Oleaceae (*Jasminum*). Most have bitter iridoids or alkaloidal toxins (with Levin indices of 3 to 6) and may be generally avoided, e.g., *Jasminium* according to Le Houérou (1980). But deer are able to browse some species to a moderate or high degree (e.g., Samant et al. 2007), especially *Gelsemium sempervirens* in the southeastern U.S.A. during winter (e.g., Atwood 1941, Lay 1967, Blair & Burnett 1980, Thill 1984, Thill & Martin 1989, William & Baxley 2008, Wade & Mengak 2010). *Thyrsanthella difforme* is a reasonable North American segregate of *Trachelospermum* (Livshultz et al. 2007). It extends far into Zone 7, and is occasionally browsed (Thill 1984). *Vinca minor* has anomalous growth form, being an evergreen trailing subshrub of mid- to cool-temperate zones in southern Europe, and now widely planted elsewhere. It can spread to dominate the forest floor, with much potential to suppress tree seedlings (Darcy & Burkhart 2002). It has some reputation for toxicity, and there is no more than occasional use by deer (e.g., Sotala & Kirkpatrick 1973, Heinrich & Predl 1993, Jett 1995, Jull 2001). However, cattle can largely eliminate it after several years of grazing and trampling (Uytvanck & Hoffmann 2009).

MONOCOT ORDERS

Smilacaceae. In the large widespread genus *Smilax*, many species climb and hang with tendrils and thorns, but few have a pronounced evergreen tendency in zones colder than warm-temperate. In eastern North America, the ‘green-briars’ of east-central states are evergreen to deciduous vines: *bona-nox*, *glauca*, *hispida* (= *tamnoides* var. *hispida*), and *rotundifolia*. *S. bona-nox* has the strongest tendency to evergreenness. At the northern edge of its range this species is largely restricted to south-facing calcareous slopes, where it often hangs off the sides of the sheltering evergreen tree, *Juniperus virginiana*. In Kentucky, *glauca* also has some persistent leaves well above the ground during most winters. Leaves of *hispida* leaves stay green only on low shoots (< 1 m high). Leaves of *rotundifolia* leaves are generally all dropped during Oct–Nov, but its stems stay quite green all winter (like several species of *Euonymus*)—more so than its congeners. Species of *Smilax* are well-known to provide frequent browse for deer and other large herbivores in the eastern U.S.A., especially on fresh vigorous growth in spring or after cutting, burning or thinning of the woods (Table 5). However, seasonal and spatial variation in abundance or palatability may often obscure the general preferences (e.g., Halls 1975, Blair & Brunett 1980, Crimmins et al. 2010). Dense deer populations can cause large reductions in cover of *Smilax* (e.g., Beaver 2011). Rabbits can also be a major herbivore on fresh shoots, especially after fires that stimulate much new growth, sometimes leading to declines in cover (e.g., Niering & Dreyer 1989).

In mid-temperate regions elsewhere, there are a few other high-climbing *Smilax* species. (a) *S. californica* of the western U.S.A. is reportedly semi-evergreen but rarely gets more than 3 m tall (Nevin Smith, Suncrest Gardens, pers. comm.).

(b) *S. aspera* of the Mediterranean region and western Asia is evergreen, but it does not get higher than 4 m or extend into mid-temperate zones. It is often browsed by livestock, and young shoots are traditionally eaten by humans (D'Antuono & Levato 2003, Samant et al. 2007; but see Lev-Yadun 2009).
(c) *S. ferox* and *megalantha* of the Sino-Himalayan region climb to 5 m or more and extend into cool-temperate zones, but it is not clear if they have persistent leaves.
Additional East Asian species may extend into mid-temperare zones, but, again, their degree of evergreenness remains obscure. Samant (1998) reported use of *ferox* and *vaginata* by livestock in the Himalayas. (*S. vaginata* is one of several East Asian species in the genus that are low unarmed shrubs, often resembling deciduous *Vaccinium* species of North America.)

Other Monocot families excluded. Dioscoreaceae (*Dioscorea*) are only herbaceous in mid-temperate zones. Poaceae include some scandent evergreen bamboos but only in warmer temperate zones (*Ampelocalamus*).

Table 5. Features of range, habit, habitat, mammlian herbivory and secondary chemistry for evergreen and semi-evergreen vines that extend into mid-temperate zones. Abbreviations in each column are as follows.

Range and Habitat: abbreviated regions.

Chi = China; Him = Himalayan region; Jap = Japan; Kor = Korea; Tai = Taiwan.
Plus following data.
HZ: Hardiness Zones where most of the species occurs in the wild.
AL: Altitude above sea level in Sino-Himalayan region and southern China.
Habitats descriptors, based on varied sources, with some added standardization.

Habit Column: following sequence of data

EG = evergreen leaves; SEG = semievergreen; DEC = deciduous; underlined species have more or less coriaceous (leathery) leaves (versus papery or membranaceous).
Typical maximum height in m
ADH = adventitious roots and specialized holdfasts formed on tree trunks.
ADR = adventitious roots usually formed along stems that climb tree trunks.
TEN = climbs with tendrils
THO = thorny, which sometimes enhances climbing ability
TWI = climbs only with twining stems (no roots)

Herbivory Column: references to mammals eating leaves or stems of the plant.

BUT/NOT: indicates that partial/general avoidance is indicated by the research
* Asterisks indicate sources with data on protein contents; see "pr" in last column.

Chemistry Column: classes of compound reported from the species or its relatives.

? indicates reports only from related species.

Top line indicates predominant types of secondary chemicals as follows:

C = condensed tannins (but not always distinguished from hydrolysable tannins)

N = alkaloids or other nitrogen containing compounds, and their derived glycosides; numbers after / are the alkaloidal toxicity indices of Levin & York (1978).

P = phenolics (including tannic acids, hydrolysable tannins, flavonoids, lignans, stilbenes) and furans, or their derived glycosides.

T = terpenoids (including iridoids, saponins) and their glycosides, lactones, etc.

S = sterols or steroids and their derived glycosides.

TOX: severe (non-digestive) toxicity reported in mammals, with chemical cause if known; excluding reports clearly attributed to fruits or seeds (i.e., perhaps the source of reports in *Celastrus* and *Euonymus*)

TAS: provisional description of human taste, from this author's reaction.

pr = crude protein content of leaves, with references in Herbivory Column indicated by asterisks; where possible, these are from leaves sampled in summer (not fresh spring shoots); crude protein is calculated as N content × 6.25, but is often an overestimate of the digestible protein (Conklin-Brittain et al. 1999).

TAXA	**RANGE**	**HABIT**	**HERBIVORY**	**CHEMISTRY**
RANUNCULID				
Lardizabalaceae *Holboellia angustifolia coriacea, grandiflora* and *latifolia* (genus combined with *Stauntonia* by some authors)	seChi Him HZ 6-8? AL (10)15-27 mesic mountain forest edges, open hillsides, stream-sides	EG 5-10+m? TWI Monoecious	**cattle+** (Samant 1998); **monkeys** (Grueter+ 2009, Fan+ 2009, Huang+ 2010*)	**?TP** (based partly on *brachyanthera, chinensis, hexaphylla*) ?phenolics ?triterpenoid-glycosides ?saponins **pr = 7-12** (Kusumoto+2012)
Lardizabalaceae *Akebia quinata, trifoliata* and allies	eChi Jap HZ 7-8? AL 2-21 mesic open forest, scrub	SEG-DEC 5-12m TWI Monoecious	**?deer** (Takatsuki+ 1997; BUT Jull 2001) **squirrel**. esp. Apr (Setoguchi 1990) **?monkey** (Iwamoto 1982* just fruits/seeds)	**T** triperpenoids saponins **TAS**: strongly bitter **pr = 10%***
ROSID				
Celastraceae *Celastrus hindsii* and perhaps allied species (*virens, monospermus, ?homaliifolius*), but these are mostly in warmer zones	SE Asia HZ 7-9? AL 3-25 forests, thickets (?mesic to sub-xeric)	EG 5-19m TWI ?Dioecious	**takin** (Schaller+ 1986*) **?monkeys** (based on *orbiculatus*, Nakagawa 1989; and on *gemmatus*, Fan+ 2009) **?deer** (based on *orbiculatus*, Rossell+ 2007; Averill 2012) BUT note also reported	**?TPNS** (partly based on *angulatus, hypoleucus, orbiculatus, scandens*) phenolics (rosamarinic acid) ?flavonoids ?diterpenoides triterpenoids saponins sesquiterpene-

			toxicity of *scandens* to horses (Schaffner 1904) and low-moderate preference by deer (Fargione+ 1991, Wade+ 2010)	-esters and -pyridine alkaloids glycoalkaloids (solanine) **?TOX**: solanine (glycoside of an indolizidine alkaloid) **?pr = 10%***
Celastraceae *Euonymus fortunei* and perhaps allies (*kiautschovicus*, *vagans* of some authors, *bockii*, ?*pseudovagans*, ?*kengmaensis*, ?*hupehensis*, ?*theacola*) but most of these species occur in warmer zones or do not usually exceed 3 m in height)	East Asia HZ 6-8? AL 0-34 mesic to subxeric forests, scrub, urban areas	EG 10-20m ADR	**deer**, esp. winter (Burroughs+ 2008, Conover+ 1988, 1995, Fargione+ 1991, Masters+ 1991, Masters+ 2004, ?Takatsuki+ 1997; ?NOT Ashton+ 2008); **cattle** (JC+ pers. obs., ?Pan+ 2005*); **beaver** (JC+ pers. obs.); **horses** (JC+ pers. obs.); **sheep** (JC+ pers. obs.); **rabbits** (Stafne+ 2005); **monkeys** (Nakagawa 1989)	**TPNS** (based partly on *alatus, americanus, atropurpurea, europaeus*, *japonicus*, etc.) phenolics, flavonoids lignans; ?furans sesquiterpene-esters -pyridine alkaloids triterpenoids ?sesquiterpenoids ?steroids (cardenolide) ?steroidal glycosides **?TOX**: cardenolide **TAS**: mealy-bitter **?pr = 9-12%***

ASTERID				
Hydrangeaceae *Decumaria sinensis*	eChi HZ 7-9 AL 6-13 mesic thickets on slopes, rock crevices	EG 2-5m ADR	**?monkeys** (based on allied genus *Schizophragma*; Nakagawa 1989, Enari+ 2010)	**?PT** phenolics, flavonoids ?saponins ?glucosides **?pr = 9%** (Kusumoto+ 2012)
Hydrangeaceae *Decumaria barbara*	seUSA HZ 7-9 mesic forests	SEG 4-10m ADH	**?deer** ("moderate" Moreland 2003, ?Thrift 2007)	**?PT** (see other Hydrangeae) ?flavonoids ?glycosides
Actinidiaceae *Actinidia henryi* and perhaps *rubricaulis* (but excluding species of warmer zones: *cylindrica, zhejiangensis, rufotricha, fulvicoma, liangguanensis*)	seChi HZ 7? AL 14-25 mesic mountain forests, thickets	SEG 15m? ADR/TWI Poly-Dio.	***henryi*: takin** (Schaller+ 1986). Also following deciduous species. ***arguta*: deer** (Takah.+ 2001, Takatsuki 2009); **monkeys** (Enari+ 2010) ***deliciosa*: deer** (Palomo 2012) ***pilosula*: monkeys** (Grueter+ 2009) ***polygama*: monkeys** (Enari+ 2010)	**?TPCN** (from *chinensis*, *polygama*, *rufa*) ?tannins, ?flavonoids (benzopyran) ?saponins ?triterpenoids ?monoterpenoids ?actinidine (from pyridine)/2.0 **?pr = 12%** (Kusumoto+ 2012)
Araliaceae *Hedera rhombea*	Tai Kor Jap HZ 6-8? mesic forests, edges	EG 10+m ADR	**deer** (Takatsuki 1988, ?Takatsuki+ 1997)	**T** (see also *helix*) triterpenoids saponins

Araliaceae *Hedera nepalensis*	seChi Him HZ 6-8? AL (0)12-26(35) mesic forests, rocky slopes	EG 10+m? ADR	**cattle+**, esp. winter (Bajracharya+ 1985, Samant 1998) **?deer** (Shah+ 2009); NOT rhesus monkeys (Goldstein+ 1989)	**T** (see also *helix*) saponins monoterpenoids sesquiterpenes
Araliaceae *Hedera pastuchowii* and *H. colchica*	Caucasus HZ 6-7? mesic forests, edges	EG 5+m ADR		**?T** (based on *helix*)
Araliaceae *Hedera helix* group, including *H. hibernica*	WC Europe HZ (6)7-8(9) mesic forests, cliffs, walls	EG 10-30m ADR	**deer**, esp. winter (Burroughs+ 2008, Fargione+ 1991, Gill+ 2001, Gonzalez-H.+ 1996, 1999*, Kirby 2001, Masters+ 1991, 2004, McEvoy+ 2006, Metcalfe 2005*, Pettorelli+ 2001, 2003, Rackham 2006, Tixier+ 1997, Krafft 2011, Perrin+ 2011; NOT Papageorgiou+ 1981* in summer, Boulanger+ 2009) **cattle+** in winter (Metcalfe 2005, Troels-Smith 1960, Uytvanck+	**TP** phenolics monoterpenoids polyacetylenes (falcarinol) saponins **(TOX):** saponins and falcarinol **TAS:** strongly bitter **pr = 9%***

			2009) **goats** (Bartolomé+ 1998, Ingham 2008, Rogosic+ 2006) **sheep** (Metcalfe 2005, Rogosic+ 2007)	
Bignoniaceae *Bignonia capreolata*	seUSA HZ 7-9 mesic to subxeric forests, thickets	EG 10-25m TEN-ADH (+ADR)	**rabbits**, esp. winter (Fowler+ 2007, Smith 1982*, Toll+ 1960). **deer**, moderate use (Atwood 1941, Lay 1967, Wolters+ 1977, Moreland 2003, Wade+ 2010; Blair+ 1980)	**?TPS** (see other Bignoniaceae) ?phenolics ?triterpenoids ?iridoid-glycosides ?steroids **TAS:** mealy-sweet (invigorating) **pr = 13.5%***
Caprifoliaceae *Lonicera sempervirens*	seUSA HZ 6-9 submesic thickets, edges	SEG (varies) 3-7m TWI (weak)	**deer**: high-medium use but variable (Schierenbeck+ 1994, Ashton+ 2008, Jull 2001, Wade+ 2010)	**PT** phenolics, flavonoids iridoids **TAS**: slightly bitter, slightly sweet **?pr = 7-11%** (Apx. 4)
Caprifoliaceae *Lonicera japonica* or allies (*affinis*, *hypoglauca* etc.)	eChi Jap+ HZ 6-9 AL 8-15 mesic to subxeric, thin	EG-SEG 5+m TWI	**deer**, esp. winter (Handley 1945, Lay 1967, Moreland 2003, Shierenbeck+ 1994, Ashton+ 2003, Nixon+	**TP** phenolics, flavonoids saponins iridoid-glycosides sitosterol

	forests, scrub, rocky ground		1970, Sotala+ 1973, . Wolters+ 1977, Thrift 2007, Beaver 2011*; NOT Shaw 2008* in summer); **monkeys** (Nakagawa 1989*, Go 2010, Huang+ 2010*); **?squirrels** (Setoguchi 1990)	?other glycosides **TAS**: mealy-bitter (more acrid than *sempervirens*) __pr = 8-15%*__ (also Segelquist+ 1975, Dyess+ 1993, Jones+ 2008, Kusumoto+ 2012 Lashley 2009; higher includes fertilized)
Caprifoliaceae *Lonicera acuminata*, or allies (*henryi* etc.)	sChi Him HZ 6-9? AL 1-32; mesic forests & scrub	SEG 15+m TWI	**takin** (Schaller+ 1986); **monkeys** (Bleisch+ 1998*, Xiang+ 2007, Grueter+ 2009)	**?TP** (see also *japonica*) phenolics etc. __pr = 12%*__
MONOCOTS				
Smilacaceae *Smilax ferox*, *S. megalantha*	seChi HZ 5-8? AL 9-34 thin forests, thickets	SEG? 5m? TEN+THO Dioecious	**cattle+** (Samant 1998); **?monkeys** (Huang+ 2010*; *Heterosmilax*, Fan+ 2009).	**?PTSC** (based largely on *china*, *chinensis*, *officinalis*, *glabra*) phenolics (quercetin, glucopyranosides) ?tannins saponins, steroids ??tropane-alkaloid (scopolamine) __pr = 13*__

Smilacaceae *Smilax* species esp. *bona-nox* also *glauca* not *hispida* not *rotundifolia*	HZ 6-9 **bon**: seUSA **gla**: seUSA **his**: seCan-USA **rot**: seUSA+ thin forests, thickets, old fields (esp. on subxeric to xeric sites in north, but also lowlands in south)	TEN+THO Dioecious EG-SEG 5-8+ m SEG 5+m SEG-DEC 7+ m SEG-DEC 5-6+m	**deer** (Beaver 2011*, Castleberry+ 1999, Dillard+ 2005, Halls 1975, Halls+ 1982*, Klein+ 2010, Korschgen+ 1980, Lay 1967, Lashley+ 2011, Lopes+ 1984, Masters+ 2004, Moreland 2003, Nixon et al. 1970, Shaw+ 2010*, Soper+ 1993*, Sotala+ 1973, Thill+ 1984, 1989, Thrift 2007, Wade+ 2010; BUT Blair+ 1980) **cattle** (Thill+ 1984, 1989, Wolters+ 1977); **rabbits**, esp. Apr (Niering+ 1989)	**PTCS** phenolics tannins ?steroidal saponins **TAS**: mealy to slightly bitter then slightly sweet (sweetness pronounced in *bona-nox* but more of an aftertaste in *glauca*) **pr = 9-15+%** (more if fertilized or in spring*; also Torgenson+ 1971, Jones+ 2008)

Mammalian Herbivory and Secondary Chemistry

The foliage of most evergreen or semi-evergreen vines in mid-temperate regions is eaten by varied mammalian herbivores (Table 5). Only *Hedera* is sometimes reported to be toxic for generalist herbivores, due to its saponins, but even this plant has been much used during the winter within its native range. Cattle, goats and sheep are able to consume large amounts, especially in combination with other plants that contain tannins (Rugosic et al. 2006, 2007). There are no regular published reports of severe disease or mortality from mammals eating *Hedera*—although its bitterness would probably prevent excessive consumption by mammals not adapted to the plant. Some potentially toxic compounds are known from *Celastrus* and *Euonymus* (Table 5), but there are no regular reports of toxicity from the few evergreen vines within these two genera. In the case of *E. fortunei*, there are zero published reports of toxicity to wild mammals or livestock, despite much exposure during recent decades within North America.

For an initial assessment of chemical variation in these plants, it is useful to recognize the following general classes of compounds, as detailed in Table 5; see also Harborne (1991a, 1999), Wink & Schimmer (2010), etc., for general background.

Phenolics/flavonoids and derived glycosides (including tannic acids, stilbenes, lignans, catechols, quinones). Varied types are known in most of the ten genera with evergreen or semi-evergreen mid-temperate vines, but they appear less developed in *Akebia* and *Hedera*. These compounds have diverse physiological effects on mammals, but severe to fatal reactions are uncommon in the wild. Lignans are estrogen-like and some are toxic. Catechols, quinones and their derivatives are more often highly irritant or toxic to mammalian physiology.

Condensed tannins (polyphenols based on flavone units). These have been reported only from *Actinidia*, *Lonicera* and *Smilax*. Tannins—especially condensed tannins— are large molecules that bind to proteins and generally reduce the digestibility of vegetation (e.g., Adams et al. 2009). However, ruminants such as deer may seek to ingest small amounts of hydrolysable tannins (esters of sugars and tannic acids) for benefits in digestion (Verheyden-Tixier & Duncan 2000).

Terpenoids and derived glycosides/lactones (including saponins and iridoids). These diverse deterrent compounds have been found in all 10 genera except *Decumaria* and *Bignonia* (sensu stricto), where they are expected. Secondary chemistry remains virtually unexplored in those two genera, but terpenoids are known from close tropical relatives of *Decumaria* in *Pileostegia* and *Schizophragma* (Hufford et al. 2001, Li 2011), and of *Bignonia* in *Tanaecium* and *Dolichandra*, etc. (Von Poser et al. 2000, Mitaine-Offer 2002, Olmstead et al. 2009, Choudhury et. al. 2011). As I can attest for *Akebia* and *Hedera*, terpenoids tend to be more aggressively bitter than tannins. Negative physiological effects in mammals are well-known (e.g., Harbourne 1991b, Langenheim 1994, Nyahangare et al. 2012). Sesquiterpene lactones occur widely in vascular plants (from *Ginkgo* to *Artemisia*), and are often foul-smelling. Saponins are triterpenoids that have been shown to limit mammalian herbivory in many cases. Yet saponins can often inhibit urease in the gut, reducing production of ammonia and methane (e.g., Veit et al. 2011). Ruminants—especially goats—are much less affected by saponins, although digestive problems and abortions can still result from large amounts in the diet (e.g., Cheeke 1971, Francis et al. 2002, Rugosic et al. 2006, 2007). Iridoids are monoterpenes typical of asterid taxa that have much general deterrent activity and other physiological effects in mammals.

Sterols/steroids and derived glycosides. These are generally derived from triterpenoid precursours, and share some biosynthetic steps with saponins. Among genera considered here, such chemicals are known from *Celastrus*, *Euonymus, Lonicera* and *Smilax*, and may also be expected in *Bignonia.* Some of these compounds have intense physiological effects on mammals, especially the cardiac glycosides (including cardenolides)—which stop hearts. However, specific analyses of the vines listed here have revealed no more than benign sterols/steroids: none in *C. hindsii* (e.g., Sung et al. 2008); sitosterols in *E. fortunei* and *L. japonica* (or allies), which can reduce cholesterol (e.g., Qu 2001); and steroidal saponins in several species of *Smilax*, which can reduce blood sugar, dementia and cancer (Challinor et al. 2012, Zhang et al. 2012).

Alkaloids and diverse other nitrogen-containing compounds. These are unknown in the 10 temperate genera, except *Actinidia* (e.g., Maddumage et al. 2013), *Celastrus* (e.g., Feng et al. 2007) and *Euonymus* (e.g., Ying et al. 2011), which have pyridine derivatives (actinidine etc.) or sesquiterpene-pyridine alkaloids. These types of compounds tend to have significant inhibitory effects on insects, tumor cells and viruses. Some exhibit attractant, irritant or neuroleptic-like effects on mammals, but without mortality (e.g., Sousa & Almeida 2005). Other groups of alkaloids, not found at all in these 10 genera, are well-known to reduce herbivory or cause mortality in mammals (Levin & York 1978, Harborne 1999).

Relationships of Chemistry to Life-form

Evergreen versus deciduous taxa. Genera with vines that are largely deciduous in mid-temperate zones have a different chemical spectrum and a greater variety, especially in alkaloids or other nitrogen-containing compounds (Table 6). Such compounds are known or suspected in about 9 of the 21 genera, mostly belonging to Magnoliid or Ranuncilid families and Fabaceae. However, there are no reports of pyridine alkaloids as found in Celastraceae. Among phenolics, condensed tannins are known only in *Humulus* and *Wisteria*; tannic acids are common in Vitaceae and *Toxicodendron*; and the latter is also infamous for its allergenic derivatives of catechol. Ten of the 21 genera have well-developed terpenoid chemistry, but concentrated in Asterid families. *Berchemia, Clematoclethra*, *Cocculus* and *Humulus* are known to produce sterols or steroids. These trends are summarized further below (Table 7).

Vines in general versus shrubby relatives. Within the following families or genera with woody plants that mostly have a climbing habit (evergreen or deciduous), current information on phylogenetic patterns indicates a halt or loss in evolution of some significant defensive compounds. This trend can be explored through comparisons with their closest non-climbing relatives, following Gianoli (2004), Stevens (2012) and other relevant sources.

(1) **Schisandraceae**. All species are vines, comprising deciduous *Schisandra* and evergreen *Kadsura*. There are no reports of alkaloids or mammalian toxicity; moderate use by deer is reported from Japan (Yokoyama et al. 2000). The closely allied Illiciaceae (*Illicium*) are all shrubs or small trees with mammalian toxicity, due to sesquiterpenes or the protoalkaloid skimmianine (Nakamura et al. 1996, Tsuji & Takatsuki 2004, Wang et al. 2011).

(2) **Lardizabalaceae**. Almost all species are vines, mostly high-climbing evergreen-tending species, and they lack benzylisoquinoline alkaloids. But these alkaloids are generally found in the allied clade that comprises the much shorter climbers in Menispermaceae (deciduous in temperate regions) plus non-climbers in Berberidaceae and Ranunculaceae (Stevens 2012).

(3) **Celastraceae: *Euonymus***. Section Ilicifoliae (including *fortunei*) are mostly scandent shrubs to high climbers, generally evergreen and with diverse secondary chemicals, but there are no reported significant problems or intense physiological effects in mammalian herbivores (Table 5). Other sections of the genus are all non-climbing shrubs and small trees (mostly deciduous in temperate regions), including two well-known Old World species that have added chemical defenses such as cardenolides. *E. europaeus* also produces gut-damaging lectins that may reduce herbivory by rabbits; it is just moderately preferred by generalist herbivores (Hart et al. 1988, Motta 1996, Boulanger et al. 2009, Thomas et al. 2011). *E. alatus* can have varied medicinal to cytotoxic effects in mammals, partly due to cardenolides (e.g., Kitanaka et al. 1996, Kim et al. 2009). It may be preferred much less than *fortunei* during the winter in North America (Conover & Kania 1988; but see Fargione et al., 1991), although moderate use by deer has been reported in its native range (Yokoyama et al. 2000). As noted above, however, the North American shrubs remain highly palatable (*americana, atropurpurea, obovatus*), so this trend from climbers to shrubs within *Euonymus* is not consistent.

(4) **Anacardiaceae: *Toxicodendron***. The only climber in this genis is *radicans* (sensu lato)—a widespread deciduous vine of southern China and eastern North America. Despite the dermatis in humans that is often caused by its catechol derivatives, “Cattle, horses, sheep, hogs, goats, birds and many other animals appear completely immune to poison ivy” (Mulligan & Junkins 1977, and their citations). Moreover, deer and other herbivores (moose, cattle, goats, deer,

rabbits, muskrat) often eat the plant with low to moderate preference, although there is much variation in the degree of selection (e.g., Atwood 1941, Habeck 1960, Sotala & Kirkpatrick 1973, Wolters et al. 1977, Korschgen et al. 1980, Ludewig & Bowyer 1985, Paul 1993, Castleberry et al. 1999, Pederson and Wallis 2004, Ward 2000, Dillard et al. 2005, Forrester et al. 2006, Thrift 2007, Shaw 2008, Beaver 2011); see also Mohan et al. (2008) and their citations for recent review. *T. radicans* was among the preferred woody species in taste-tests performed with captive American bison in Kentucky (personal trials of the author).

In contrast, the other species of *Toxicodendron* are mostly tall shrubs or trees (*parviflorium, potaninii, succedaneum, sylvestre, vernicifluum, vernix*, etc.), and they tend to have stronger toxicity (Vogl & Mitchell 1998, Frankel 1999). From literature reviewed here, there are few reports of mammalian herbivory: one case of rabbits on *vernix* in a severe winter (Siegler 1937); one case of deer on *vernix* (Lay 1967); one case of deer on *pubescens*, which is relatively close to *radicans* (Thill & Martin 1989); and an occasional young shoot of *succedanum* by monkeys (Tsuji & Takatsuki 2004).

(5) **Rhamnaceae, section Rhamneae**. *Berchemia* contains just vines, but other temperate genera are small trees or shrubs, sometimes reportedly “scandent” but not high-climbing: *Rhamnus*, *Frangula* and (mostly in drier regions) *Sageretia*. Deeper phylogenetic comparisons may also be appropriate within this complex family (Richardson et al. 2012). The secondary chemistry of *Berchemia* foliage appears largely limited to phenolic compounds, derived glycosides and tannins, plus some non-toxic sterols of medicinal value. But phenyl-ethylamine alkaloids are added in *Sageretia* and *Frangula* (*F. alnus* = *R. frangula*); triterpenes and steroids are added in *Rhamnus alnoides* (Villar et al 1986). Also, the foliage of various *Rhamnus* species, when eaten by mammals, can be strongly laxative—probably due to anthraquinone

glycosides, or it can depress and potentially damage nervous systems, or it can damage livers (Smyth 1903, Cotton et al. 1933, Lichtensteiger et al. 1997, Mahady 2004, Crowch & Okello 2009). The yellowish inner bark of North American species tends to be ill-scented (E. Wofford, pers. comm.).

In North America, several reports indicate moderate to high preference of deer for *B. scandens* (e.g, Blair 1960, Lay 1967, Wolters et al. 1977, Blair & Brunett 1989, Thill 1984, Nelle 1996, Castleberry et al.1999, Shaw 2008). Elsewhere, species of *Berchemia* are used locally to feed goats (e.g., Wambui et al. 2011), and shoots are eaten occasionally by monkeys (e.g., Tsuji & Takatsuki 2004). There are no reports of toxic effects in mammals from eating leaves. To compare *Berchemia* with *Frangula*, a meaningful sympatric contrast can be made between *B. scandens* and *F. caroliniana*, which are both well-known species of the southeastern U.S.A. The latter is apparently browsed much less by deer—the few reports indicate generally zero to moderate preference (Lay 1967, Wolters et al. 1977, Lay & Murry 1978, Blair & Brunett 1980, Grabner et al. 2005, Shaw 2008, Wade & Mengak 2010), except in one case that may have included goats (Nelle 1996). The European *Frangula alnus* is often browsed, but typically with just moderate preference (Staines & Welch 1981, Gill 1992, Borkowska & Konopko 1994, Knapp et al. 2008, Aday & Wyckoff 2010).

The common European species, *Rhamnus cathartica*, appears to have little general use by ruminants (Godwin 1943, Heinrich & Predl 1993, Qaderi et al. 2009), except hungry goats (e.g., Decandia et al. 2000). Most species of *Rhamnus* in Mediterranean and Himalayan regions also have generally low but highly variable preference; there is some use by camels and goats, or as fodder prepared for livestock (e.g., LeHouérou 1980, Samant et al. 2007). In eastern North America, foliage of *R. alnoides* is completely avoided by ruminants (e.g., Wright &

Long 2002) and lagomorphs (e.g., DeVos 1964), and there are no published reports of mammals eating *R. lanceolatus*—although fatal girdling by rodents can occur in arboreta (2 observations of this author).

(6) **Cannabaceae**. The vine *Humulus* has been traditionally used for fodder, salad greens, beer and varied medicinal uses (e.g., Hampton et al. 2009, Al-Mamun et al., 2009, Guo et al. 2009, Srečec et al. 2011). It has diverse chemistry, but is generally not considered toxic. The allied tall annual herb, *Cannabis*, produces some distinct phenolics which have various benign, medicinal or debilitating effects in mammals, especially through the nervous system (e.g., Hall & Degenhardt 2009). There are virtually no reports of *Cannabis* foliage being eaten for food by deer, although fruited material may be rarely used in winter (as cited by Atwood, 1941) and seeds are much used by birds and small mammals. Fresh foliage is generally avoided by livestock, but cattle may rarely consume a toxic amount (Driemeir 1997), and moderate amounts are sometimes processed into silage for livestock (e.g., Fisher 1975).

(7) **Hydrangeaceae**. *Decumaria, Pileostegia* (both evergreen) and *Schizophragma* (deciduous) form a clade of vines (Hufford et al. 2001) that appear to have a rather simple, largely phenolic chemistry without significant toxicity (Bohm et al. 1985, Li 2011). The allied deciduous genus *Hydrangea* mostly contains shrubs, and it has more diverse chemistry that includes cyanogenic glycosides and alkaloids in some East Asian species (e.g., Chang et al. 2003, Ishih et al. 2007, Nakamura et al. 2009). There is only sparse chemical information from the few climbers classified within *Hydrangea* (*anomala*, *integrifolia*, *petiolaris, integrifolia, peruviana, seemanii*, *serratifolia*), but it suggests that flavonoids are less developed (Bate-Smith 1978).

(8) **Bignoniaceae**. The tribe Bignonieae are virtually all climbers (mostly evergreen), and they tend to have low levels of iridoids or less complex forms of them (Von Poser et al. 2000). Iridoids are generally more common in the allied taxonomic groups based on *Tabebuia*, *Tecoma* and *Catalpa*, which are mostly trees (Lohmann 2006, Olmstead et al. 2009). The evergreen vines *Bignonia* (Table 5) and the deciduous vine *Campsis* are both browsed by rabbits or deer at moderate degrees in eastern U.S.A. (e.g., Blair et al. 1977, Wolters et al. 1977, Castleberry et al. 1999, Fargione et al. 2001, Halls & Boyd 1982, Williams & Baxley 2008). In contrast, there are virtually no published reports of deer browsing on the temperate tree, *Catalpa* (Atwood 1941, Heinrich & Predl 1993, Jull 2001), which produces toxic napthaquinones, iridoids and a phthalide lactone (e.g., McDaniel 1992, Park et al. 2010, Lampert et al. 2011). Further comparison is needed among the tropical genera.

(9) **Caprifoliaceae**. Climbers in *Lonicera* consist of the largely deciduous section Caprifolium plus the more evergreen *japonica-macrantha* group. The many species of non-climbers are mostly deciduous shrubs, including the European *xylosteum* and the East Asian invaders in North America: *standishii*, *fragrantissima*, *maackii*, *morrowii* and *tatarica*. Available data (Appendix 4) suggest that species of Caprifolium are highly nutritious, and have relatively low levels of phenolics, iridoids and tannins, compared to the shrubs (e.g., LeHouérou 1980, González-Hernández & Silva-Pando 1999, Cabiddu et al. 2000, Nostro et al. 2000, González-Hernández et al. 2003, Peñuelas et al. 2006, Lieurance et al. 2012). Indeed, the old latin taxonomic name—Caprifolium—means ‘goat’s leaf’ due to their love of these plants, which have generally been called ‘woodbine’ in England.

> “But chief the flower beyond compare,
> the flaunting Woodbine revell’d there,
> Sacred to Goats; and bore their name
> ‘Till Botanists of modern fame
> New fangled titles chose to give
> To almost all the plants that live.”
> (Whitehead 1777)

However, increases in nutrient supply, damage or stress in the climbers can promote iridoids that tend to deter herbivory, especially by insects.

Deer appear to have only moderate preference for the shrubby species of *Lonicera*, in general (Appendix 4). Leaves of *maackii* produce relatively high concentrations of the flavonoids, apigenin and luteolin plus their glycosides (Cipollini et al. 2008), and varying levels of these chemical have been found in several other species of the genus. Apigenin stimulates apoptosis in cells (programmed death), including red blood cells (Zbidah et al. 2012), and it has many physiological effects in animals and plants. Luteolin is less toxic and it has many potential medical uses, but high doses tend to be nauseous. Both chemicals can have oestrogeneic effects and disrupt molting cycles (as reviewed by Cipollini et al.). Further comparisons among genera of Caprifoliaceae and Adoxaceae would be useful, since there are significant differences in chemistry and use by ungulates.

(10) **Smilacaceae (*Smilax*)**. Most species are woody or herbaceous climbers, with diverse secondary chemicals but little or no mammalian toxicity (Table 5). They are sister to Liliaceae

(sensu stricto), which are strictly non-climbing and contain many species with alkaloids or derivatives of methylene-butanoates that have mammalian toxicity (Keeler 1979).

In other families with vines, there are no clear differences in chemistry or herbivory between climbers and allied non-climbers based on available information. However, relevant data remain sparse or absent in several cases.

(1) **Aristlochiaceae**. Appropriate comparisons need more attention, given the complex taxonomy (Ohi-toma et al. 2006). Both *Isotrema* and *Aristolochia* (sensu stricto) contain vines, shrubs and herbs. All are alkaloidal and probably avoided by mammalian herbivores.

(2) **Ranunculaceae**: *Clematis* versus *Anemone* (sensu lato). Both tend to be somewhat toxic due to anemonin or other compounds, often with a sharp-peppery taste. But there are reports of local browsing, especially by deer (Habeck 1980, Fargione et al. 1991, Nelle 1996, González-Hernández & Silva-Pando 1999, Samant et al. 2006, Xiang et al. 2007, Wallach et al. 2009). Much chemistry in *Clematis* involves saponins rather than nitrogenous alkaloids, and despite many medicinal uses severe mammalian toxicity has rarely been reported (Pei et al. 2009, Hao et al. 2012).

(3) **Celastraceae, tribe Celastreae**. Appropriate comparisons need more attention, given the complex phylogeny and chemistry (Simmons et al. 2001).

(4) **Vitaceae**: Vitoideae versus Leeoideae (*Leea*). There is much documented browsing by deer on *Vitis* (except perhaps *rotundifolia*), *Ampelopsis* and *Parthenocissus*, though perhaps less on the latter (e.g., Atwood 1941, Blair & Burnett 1980, Yokoyama et al. 2000, Samant et al. 2007, Shaw 2008, Williams & Baxley 2008, Beaver 2011; see also Borchard et al., 2010). Their tropical climbing relatives include *Tetrastigma*, which is eaten by varied mammals including

humans (e.g., Sawian et al. 2007; D. Nickrent, pers. comm.), and *Cissus*, which can have sublethal toxicity and varied medicinal effects (as reviewed by Nyahangare et al., 2012). Little available information exists on herbivory of *Leea*, which is more arboreal and strictly tropical; there is a report of human consumption (Barua et al. 2007).

(5) **Rosaceae**: climbers/trailers versus more shrubby species within *Rosa* and perhaps *Rubus*. There is much browsing by deer in both of these complex genera, which are defended largely by tannins and thorns.

(6) **Fabaceae**: Phaseoleae (including *Lackeya* and *Pueraria*) plus Milleteae (including *Wisteria*) versus Indigoferae, or perhaps deeper comparisons to be established within these complex groups. The toxic amino acid canavanine is typical of *Dioclea* and some other largely tropical genera within Phaseoleae, but it is absent from *Pueraria*; the chemistry of *Lackeya* remains unknown (Lackey 1977). *Wisteria* is quite toxic due to other compounds (Table 6).

(7) **Actinidiaceae**: *Actinidia* and *Clematoclethra* are climbers that should be compared to non-climbing *Saurauia*, but the latter is tropical. Within Ericales as a whole, it may be reasonable to just compare other temperate taxa—mostly Ericaceae, which have well-known toxicities in many evergreen species (benzo- and napthoquinones) but less in deciduous (e.g., *Vaccinium*).

(8) **Gentianales:** Oleaceae (*Jasminium*), Loganiaceae (*Gardneria* etc.), Gelsemiaceae (*Gelsemium*), Apocynaceae (*Trachelospermum, Vinca,* etc.). Appropriate comparisons for temperate vines in these families remain unclear, given their complex phylogeny (Livshultz et al. 2007, Frasier 2008). See "Notes on individual taxa" above; although alkaloidal, some of these plants can be browsed much in the winter.

(9) **Araliaceae**: *Hedera* versus *Acanthopanax*, *Schefflera* and allies. Sublethal toxicity due to varied terpenoids has been reported from these plants; deeper review is needed.

But there is, remarkably, almost no opposite trend among temperate plants—that is, more defensive secondary chemistry in a largely climbing clade compared to the most closely allied non-climbing clade. **Ranunculales** might present the only example: Menispermaceae have a greater diversity of alkaloids and terpenoids than their largely non-climbing relatives in Berberidaceae plus Ranunculaceae (Barboso-Filho & Leitão da-Cunha 2000). However, all three of these families are somewhat toxic to mammalian herbivores, and the chemistry of some temperate Menispermaceae remains poorly known (especially *Calycocarpum*). Moreover, some *Cocculus* and other species are reported to have moderate or high usage by goats and deer (Nelle 1996, Shinde et al. 2000, Bhatta et al. 2001, Samant et al. 2007). It would be interesting to compare general chemistry of vines in Menispermaceae with the few derived shrubby lineages within this family (Ortiz et al. 2007, Jacques et al. 2011).

A deeper and broader analysis will eventually be interesting to pursue, including herbaceous vines as well as woody. Chemical evolution within Solanales is particularly complex, but possible associations with the frequent herbaceous climbing habit in this group do not seem to have been explored (Eich 2008).

Table 6. Features of secondary chemistry in vine genera that are strictly deciduous within mid-temperate regions.

Genera are listed in phylogenetic order, as in Table 5. Those that contain only vines are underlined. Included here are some largely herbaceous genera with close woody relatives. Several additional genera not listed here have both deciduous and evergreen species (*Actinidia, Akebia, Celastrus, Lonicera, Smilax*). Abreviations are generally the same as for Table 5.

( ): occurrence in mid-temperate zones is marginal, more common in warmer zones
? indicates uncertain ecological or chemical assignment
LF: EG = leaves often evergreen in warmer zones; underlined are often coriaceous
LF: eg = leaves partially as above, at least somewhat coriaceous
LF: HE = plants herbaceous in mid-temperate zones but often exceeding 3 m
LF: he = plants partially as above
HZ = Hardiness Zones of mid-temperate species (excluding species of warmer zones)
Predominant types of chemistry are indicated by the following symbols (see also Table 5).
    C = condensed tannins
    N = alkaloids or other nitrogen-containing compounds
    P = phenolics/flavonoids and derived glyciosides
    T = terpenoids (with saponins, iridoids, etc.) and derived glycosides
    S = sterols/steroids and derived glycosides
TOX: indicates genera with reported severe toxicity to mammals.
TAS: provisional descriptors of taste to humans.
pr = typical protein contents of leaf dry weight, with references.

FAMILY: GENUS	**LF**	**HZ**	**SECONDARY CHEMISTRY**
MAGNOLIID FAMILIES			
Schisandraceae: (<u>*Schisandra*</u>) TWI Monoecious	eg?	7-8	**PT:** polyphenols, ?flavanols, ?tannins/acid? lignans, triterpenoids **pr = 9-13%** (Nakagawa 1989, Huang.+ 2010, ?Kusumoto+ 2012)
Aristolochiaceae: <u>*Isotrema*</u> TWI	eg?	6-8	**N:** unusual alkaloids* (aristolochic acid)/2.38 TOX* **?pr = 11-22%** (Bostan+ 2012, Kusumoto+ 2012)
Menispermaceae: <u>*Calycocarpum*</u> TWI Dioecious		7-8	?NP: unknown but probably as in *Cocculus* ?TOX
Menispermaceae: <u>*Cocculus*</u> TWI Dioecious	he <u>EG</u>	6-9	**NPS:** flavonoids, alkaloids of aporphine, erythrina, or isoquinoline* type/3.68, ?sterols, ?tannins/acids ?TOX* **?pr = 11%** (Bhatta+ 2001)
Menispermaceae: <u>*Menispermum*</u> TWI Dioecious	HE	4-7	**NPT:** flavonoids, alkaloids (aporphine, chlorinated, isoquinoline* or phenolic types)/3.0, cyanogenic glucosides, terpenoid lactones TOX* TAS: “rank”
RANUNCULID FAMILIES			
Ranunculaceae: <u>*Clematis*</u> (s.s.) TWI Partly dioecious	he <u>EG</u>	6-9	**PNT:** anemonin* (pentadienoic dimer), aporphine alkaloids, ?triterpenoids/saponins/glycosides (roots) TOX* TAS: acrid-peppery **pr = 13-19%** (Nakagawa 1989, Papageorgiou+ 1981)

ROSID FAMILIES			
Vitaceae: *Ampelopsis* TEN		6-10	**P:** phenolics (ampelopsin, myrecetin, gallates, quercetin; lupeol, ethyl gallate, stilbenes), flavanols (catechin) **pr = 12%** (Iwamoto 1982)
Vitaceae: *Parthenocissus* ADR +TEN		3-10	**P:** phenolics (leucantho-cyanidins, stilbenes), tannic acids, flavanols (catechin) **pr = 10-16%** (Conklin-B+ 1999, Shaw 2008, Lashley 2009, Beaver 2011)
Vitaceae: *Vitis* TEN Polygamo-dioecious		3-10	**P:** phenolics (caffeic acid), phenolic acids (gallic acid, stilbene trimers), flavonoids (quercetin), ?flavanoids **pr = 10-20%** (Torgenson+ 1971, Conklin-B. 1999, Shaw 2008, Lashley 2009, Beaver 2011)
Anacardiaceae: *Toxidodendron* ADR Polygamo-dioecious		4-10	**P:** phenolics, flavonoids, tannic acids (gallotannic acid) ALLERGENS: pentadecyl-catechols, biflavonoids **pr = 10-16%** (Torg.+ 1971, Lash. 2009, Beaver 2011)
Rosaceae: *Rosa* THO Rarely dioecious (*setigera* is cryptically dioecious)	eg	4-8	**PC:** phenolics, flavonoids/glycosides, tannins TAS: mealy-slightly astringent **pr = 8-15%** (Torgenson+ 1971, Nakagawa 1989, Hedtcke+ 2009, Ammar+ 2004)
Rhamnaceae: (*Berchemia*) TWI	eg	7-10	**P(S):** benzoquinones, tetralones*, glucosyl-oxybenzoates, lignans, ?sterols; ?TOX* **pr = 12-15%** (Shaw 2008; Kusumoto+ 2012; based partly on *floribunda, racemosa*)
Cannabaceae: *Humulus* TWI Dioecious	HE	3-7	**PTSC:** phenolics, tannins, monoterpenoids, triterpenoids (humulone), prenylated flavonoids (steroid-like), sterols, furans **?pr = 17-23%** (Al-Mamun+ 2009, Guo+ 2009)

Fabaceae: *Lackeya* (segregate of *Dioclea*) TWI	he	7-8	**N:** ?canavanine/similar*, ?lectins* ?TOX* **?pr = 7%** (Hecht 1979)
Fabaceae: *Pueraria* TWI	he	6-10	**PTN:** isoflavones (genistein, and puerarin—an oestrogenic glucoside), triperpenoids, indole alkaloids (roots); **pr = 18-23%** (Corley+ 1997, Deguchi+ 2001, Samant+ 2007)
Fabaceae: *Wisteria* TWI		6-9	**NC:** wisterine* (uncharacterized glycoside), lectins*, tannins TOX* (lectins = proteins that bind to sugars)
ASTERID FAMILIES			
Hydrangeaceae: (*Schizophragma*) ADR		7-9?	**?TP** (based on *Pileostegia*; Li 2011) **?pr = 8-9%** (Nakagawa 1989, Kusumoto+2012)
Hydrangeaceae: *H. anomala, integrifolia, kawakamii, petiolaris* ADR		6-9?	**PT (?NS):** flavonoids, iridoids, ?isoquinoline- and ?quinazalone-alkaloids*/3.0, ?cyanogenic glycosides*, (coumarins), ?tannins, ?steroidal glycosides ?TOX* (or perhaps only shrubs) **?pr = 13-18%** (Togenson+ 1971, Deguchi+2001)
Actinidiaceae: *Clematoclethra* TWI? Dioecious		4-7?	**PTS:** phenolics (caffeic acid, coumarins, mangiferin), flavonoids (kaemferol), tripterpenoids (betulin), sterols
Apocynaceae: (*Trachelospermum*), *Thyrsanthella** TWI (?ADR; Cai et al. 2005)	eg	7-9	**PTN:** phenolics, flavonoids, lignan glucosides, triterpenoids, saponins, indole alkaloids* ?TOX* **pr = 6-8%** (Iwam. 1982, Nakag. 1989, Kusum.+ 2012)
Bignoniaceae: *Campsis* ADR (nodal)		5-9	**TP:** iridoids, phenolic acids (ferulic), phenyl propanoid glycosides, flavonoids **pr = 8-12%** (Jones+ 2008)

PART THREE: General Discussion of Evolutionary Trends and Ecological Factors

Patterns in Phylogeography, Morphology and Physiology

Phylogeographic context. All species of evergreen-tending vines in mid-temperate regions belong to genera with largely temperate ranges, except *Celastrus*. However, several of them, especially those that often reach 10 m (*) and have relatively coriaceous leaves, are in largely tropical families (Stevens 2012): Bignoniaceae (*Bignonia**), Araliaceae (*Hedera**), Actinidiaceae (*Actinidia**) and Celastraceae (*Celastrus**, *Euonymus**). The largely temperate families represented here are Caprifoliaceae (*Lonicera*), Hydrangeaceae (*Decumaria**) and Lardizabalaceae (*Akebia*, *Holboellia**). Smilacaceae (*Smilax*) are a more widespread family of humid tropical and temperate regions—the only family represented here that occurs in all three major realms of the Northern Hemisphere, but largely semi-evergreen in eastern North America and just short, shrubby and southern within Europe. These families represent all major superorders of angiosperms, except the relatively primitive Magnoliidae, which do have several temperate deciduous vines (see Table 5 and text above). They are concentrated among the relatively advanced Asteridae (with *Decumaria*, *Actinidia*, *Hedera*, *Bignonia* and *Lonicera*).

The 11 genera or subgeneric sections with some vines that are evergreen-tending tend to have more restricted global ranges than deciduous or herbaceous taxa (Tables 7, 8a). The six that are strictly evergreen, or nearly so, are as follows: the Sino-American disjunct *Decumaria*—with two species; the Sino-Himalayan *Holboellia*—with ca. 20 species but reasonably merged into the paleotropical *Stauntonia* (Christenhusz 2012); the East Asian *Euonymus* section *Ilicifolia*—with perhaps only 1–4 vining species; the eastern North American *Bignonia*—with maybe just one species but close to the neotropical *Cydista* (Lohmann 2006, Olmstead et al. 2009); *Lonicera* section *Nintooa*—with ca. 5–10 East Asian species (plus one short, reportedly deciduous species in Mediterranean regions); and the Eurasian *Hedera*—a distinct genus with at least 13 species (Green et al. 2011). Only *Hedera* has radiated widely from its original center in the Mediterranean region, but was absent in North America until recently introduced. The genera/subgenera with mixed evergreen and deciduous condition include two that are restricted to East Asia (*Akebia, Actinidia*), two that are moderately widespread but lacking in most of Europe (*Celastrus, Smilax*), and one that occurs in all three regions (*Lonicera* subgenus *Caprifolium*).

Among these 11 evergreen-tending taxa, only *Decumaria* has a disjunct distribution in East Asia and eastern North America. Such disjunctions are generally considered to result from fragmentation of the Arcto-Tertiary Flora about 5–10 million years ago (Wen 1999, 2001, Xiang et al. 2000, Milne & Abbott 2002, Donoghue & Smith 2004, Milne 2006). In contrast, among the 23 genera or subgeneric sections with vines that are largely deciduous to herbaceous (Tables 7, 8a), 11 are largely restricted to East Asia and Eastern North America; six have relatively broad distributions across temperate or montane regions; and only five are restricted to one continent. Deeper phylogeographic analysis may reveal similar disjunctions within some largely deciduous to herbaceous sections of more widespread vining genera centered in warmer zones: *Cocculus*, *Berchemia*, *Trachelospermum* (with its segregate *Thyrsanthella*).

Is evergreenness more recent than the deciduous habit? The more restricted ranges of evergreen-tending mid-temperate genera might be attributed, in part, to a generally more recent origin. Synthesis of phylogenetic evidence—calibrated in some cases with fossils—does indicate that the evergreen-tending taxa are less old than the deciduous (Table 10). Such evidence assumes that currently evergreen or deciduous genera have largely remained so since they originated. More comprehensive analysis of phylogeography, fossils and functional traits will be needed eventually to provide a rigorous test of this hypothesis. Another consideration is that repeated cold climatic periods during the past 5–10 million years might have prevented evergreenness from becoming a widespread feature among mid-temperate vines. There is indeed some evidence that disjunctions among evergreen Asian-American plants in general tended to develop earlier than in deciduous plants, presumably caused by more sensitivity to cold (Milne & Abbott 2002).

The oldest evergreen-tending mid-temperate vining genus appears to be *Decumaria*, estimated to have diverged during the Oligocene (ca. 20–30 million years ago) from the subtropical to warm temperate genera, evergreen *Pileostegia* and deciduous *Schizophragma* (Samain et al. 2010, Xiang et al. 2011). As reviewed by Green et al. (2011), molecular and fossil evidence indicates that *Hedera* originated in subtropical to warm temperate forest during the Miocene, about 10–15 million years ago, when disjunctions among the older Arcto-Tertiary genera were being formed. Based on the biogeographic context of *Stauntonia* (sensu lato with *Holboellia*) and *Bignonia* (sensu lato), it is likely that their radiation into temperate zones is no older than the origin of *Hedera* (Burnham & Graham 1999, Wang et al. 2002). Within the largely shrubby genus, *Euonymus*, the evergreen vines—*fortunei* and allies—occur only in section *Ilicifolia*, which is restricted to East Asia. The *fortunei* group are closely related to more shrubby species, suggesting a recent divergence, but a molecular analysis of their phylogeny is not yet available.

Genera with both evergreen and deciduous vines in temperate regions will provide special insight to evolutionary processes when their phylogeny is clarified: *Actinidia, Akebia, Celastrus, Hydrangea* (sensu lato), *Lonicera* and *Smilax*. Based on morphological patterns outlined in Flora of China (1996–2011) plus recent molecular analysis, evergreenness of mid-temperate species could be a derived character within most of these genera (Chat et al. 2004, Wang et al. 2002, Mu et al. 2012, Smith 2009, Samain et al. 2010, Xiang et al. 2011). Patterns within the complex genus, *Lonicera*, are particularly interesting, since it contains a largely deciduous vining group—subgenus *Caprifolium*—that is widespread across the Northern Hemisphere, plus a semi-evergreen vining group—section *Nintooa*—that has much less geographic radiation within the largely deciduous and shrubby subgenus *Lonicera* (Appendix 4). As indicated by Smith (2009), *Nintooa* probably had a more recent origin than *Caprifolium* (ca. 20 versus 25–30 million years ago). However, most of the radiation within both groups appears to have occurred within the past 10–15 million years. Another complex genus, *Hydrangea* sensu lato—including *Decumaria*, could also provide an instructive comparison of deciduous and evergreen lineages, which seem to have diverged much earlier than in *Lonicera* (Xiang et al. 2011). The deciduous climbing habit may be ancestral within the Arcto-Tertiary "Hydrangea 1" clade of Samain et al. (2010). In *Smilax*, some morphological patterns suggest that evergreenness is derived among the largely temperate clades (Chen et al. 2006), but molecular analyses suggest that it is ancestral within the whole genus (Cameron & Fu 2006).

Despite their smaller ranges and evidence of more recent appearance, the evergreen-tending vines tend to have more species per genus and more current invasiveness than the deciduous vines (Table 8a). These are weak trends, but they affirm that evergreenness has special benefits for these plants in some modern contexts.

Climbing habits. There are diverse climbing patterns in vining plants (Putz & Mooney 1991, Isnard & Silk 2009). The evergreen-tending species of mid-temperate regions—as well as other temperate vines—are loosely divisible into two broadly defined ecological groups, although a few species combine features of both. At the generic level, this division has associations with several biological features (e.g., Table 9, Figure 6).

(1) Typical twiners, scramblers and tendrillers. These climb on supporting branches but not vertical surfaces, often to no more than 5–10 m high, without adventitious roots but usually twining around the supports: *Akebia, Holboellia, Celastrus, Lonicera, Smilax* and perhaps some *Actinidia*. Although not able to climb up larger trees by themselves, such species—especially Vitaceae among deciduous taxa—can sometimes climb up other vines (Putz 1995) or up smaller trees and shrubs, then move to larger hosts (Ichihashi & Tateno 2011). *Smilax* uses tendrils and thorns to climb, but its shoots do not twine. *Holboellia* is the only strictly evergreen genus in this group. In contrast, the 23 genera or subgeneric sections with strictly deciduous to herbaceous vines in mid-temperate regions (Table 7) mostly belong here, except *Parthenocissus*, *Toxicodendron* (*radicans* group), *Schizophragma*, *Hydrangea* (*anomala* group) and *Campsis*, which belong with the following.

(2) Surface-ascenders. These are able to ascend tree trunks, cliffs or walls, often up to 10-20 m and usually with adventitious roots, at least on lower stem sections: *Decumaria* (both species), *Hedera* (all species), *Euonymus fortunei* and allies, ?*Actinidia henryi* and *Bignonia capreolata*. Assignment of *A. henryi* remains uncertain since the extent of adventitious roots is not published, but such roots are known in the genus and *A. kolomicta* is reported to climb trees "by means of adventitious roots in the lower parts, or by the twining of long whip-like shoots higher up, or rambling after the fashion of brambles over the undergrowth, or in clearings trailing on the ground by means of adventitious roots in the lower parts" (Stapf 1926). In the case of *Bignonia*, climbing is accomplished by versatile tendrils that are able to curl around narrow stems or to attach in small crevices of most tree barks. Its tendrils "form into irregularly shaped attachment pads when they come into contact with a suitable substrate surface. These attachment pads grew around presented fibers and into surface cavities and excreted a resin-like substance" (Seidelmann et al. 2012, summarizing Charles Darwin's observations of 1875). But only larger lower stem sections of *Bignonia* eventually form adventitous roots.

There has been insufficient synthesis of research on growth rates and shade tolerances to allow thorough physiological comparisons of these two groups, but several studies have provided useful insight (e.g., Forseth & Teramura 1987, Carter et al. 1988, 1989, Schierenbeck & Marshall 1993, Baars & Kelly 1996, Cai 1999, Sakai et al. 2002, Cai et al. 2005, Jiang et al. 2007, Allen 2007, Ichihashi et al. 2009, 2010, 2011, Leicht-Young 2010, Kusumoto et al. 2012). Typical twiners and scramblers appear to have more rapid potential growth and less shade tolerance, on average, often resulting in lower leaf:stem mass ratios and establishment on smaller hosts. *Akebia* and *Lonicera japonica* are somewhat exceptional in having a moderate degree of shade tolerance, and often sending prostrate shoots into understories. But they are still concentrated in young or thin woods with more small trees and shrubs—for example, on the Carolina Piedmont, *L. japonica* has declined in maturing woods where *Vitis rotundifolia* and *Rubus* spp. have increased (Taverna et al. 2005). Also, the thick rhizomes of *Smilax* often maintain low shoots that are thinly scattered in the shade, exposed to herbivory but able to grow up if fresh canopy gaps occur. These shoots are sometimes more thorny or variegated than taller flowering shoots.

In contrast, the 'surface-ascenders'—especially *Hedera*, *Euonymus* (evergreen) *Toxicodendron* and *Parthenocissus* (deciduous)—can often produce leafy shoots that dominate much ground in shade between trees. In *Hedera* and *Euonymus* the leaves of low creeping 'juvenile' shoots often have distinct coloration, morphology, physiology, compared to those of root-climbing shoots and flowering ‘adult’ shoots (Metcalfe 2005, Bauer & Bauer 2006, Yang et al. 2006). Also, *Decumaria*, *Schizophragma* and *Toxicodendron* are able to produce much thinner and broader leaves in shade. However, *Campsis* is relatively intolerant of shade and among the most rapidly growing species—it is the only ‘surface-ascender’ with pinnate leaves.

To summarize, this initial review of the literature indicates that most of the 11 evergreen-tending genera or subgenera (Table 7) are ‘surface-ascenders’ with simple leaves (or paired in *Bignonia*), moderate to high shade tolerance, relatively low specific leaf area (mm^2/mg dry weight), and generally moderate growth rates. *Holboellia* and *Akebia* (which is partially deciduous) are exceptional in their more twining habit and palmate leaves. In contrast, the 23 largely deciduous to herbaceous taxa are mostly twiners, scramblers or tendrillers (except for five genera), with compound leaves in 10 cases. Deciduous vines appear to have a broader distribution of overall stature, leaf forms, nitrogen contents, shade tolerances and growth rates. Among twiners or tendrillers, *Ampelopsis*, *Berchemia*, most *Vitis* (except *rotundifolia*), most *Actinidia*, most *Celastrus* and most *Lonicera* subgenus *Caprifolium* generally do not grow into more shady understories. In contrast, *Parthenocissus, Schizophragma* and *Toxicodendron* are ‘ascenders’ that also have a pronounced ability to grow over the ground under forest canopies—often exhibiting unusually high and variable specific leaf area (e.g., Ichihashi et al. 2009). Moreover, deciduous species with compound leaves have some of the fastest growth rates, in terms of annual extension by both ‘ordinary shoots’ and longer ‘searcher shoots’ in twiners (e.g, *Akebia, Pueraria, Wisteria*) and in the somewhat anomalous ‘ascender’, *Campsis*.

Hydrological associations. Figure 7 summarizes, for forests of east-central U.S.A., the apparent distribution of all native woody or subshrubby vine species in terms of their typical modal positions along hydrological gradients. The format follows that of Figure 1a, with abbreviations for vines rather than trees (Appendix 1), but their positions are based on general knowledge and review of the literature rather than data from plots. Although most species have wide overlapping ranges of habitat, there is a concentration of modal positions along the zone between two major sectors: (1) mesic-to-subxeric-to-xeric woods; versus (2) wetlands and open shrubby-to-grassy uplands. Such concentration is confirmed by detailed observations at specific sites (e.g., Waters et al. 1974, Collins & Wein 1993, Goebel et al. 2001, Allen 2007, p. 105). It is suggested that the core habitat for woody vines, in general, has been developed within this broad 'vining zone'—where deeper woods typical of more hilly terrain come into contact with riparian interruptions, wetlands, browsed or burned uplands and plains.

Figure 7 marks (with underlining) those species that have evergreen-tendency, including some that are largely deciduous within Kentucky but evergreen-tending further south. The few native 'ascenders' (group 2)—including evergreen-tending *Decumaria* and *Bignonia*—are mostly positioned in slightly more mesic wooded habitats. The other evergreen-tending species are mostly clustered at the drier end of the vining zone: *Smilax* spp., *Lonicera sempervirens* and *Cocculus*.

Physiology of water-relations. There is a need for deeper comparative review than is possible here. One basic theme would be the extent to which xylem anatomy is correlated with the twining versus trunk-climbing habit, or with deciduous versus evergreen habit. An initial reading of scattered incomplete literature suggests that several of the 'twining and scramblers' (group 1) have 'ring-porous' clustering of particularly wide vessels in early wood, which can allow rapid growth to be concentrated in a delayed spring to early summer, before onset of droughts—a trait also found in most temperate trees of summer-dry sites (Woodcock 1994, Zanne 2006, Boura & DeFranceschi 2007). Ring-porous vines include *Akebia trifoliata* (Sun et al. 2003), *Clematis* spp. (Schoch et al. 2004), *Celastrus* spp. (Davis & Evert 1970, Tibbets &

Ewers 2000), *Vitis* spp. (Schoch et al. 2004), *Rosa* spp. (Schoch et al. 2004), *Wisteria floribunda* (Sun et al. 2003), some *Actinidia* spp. (Condon 1991, Xiao et al. 2010), and *Lonicera japonica* (Bell et al. 1988, Chiu & Ewers 1992). *Vitis* maintains unusually wide and late-produced vessels throughout most of its wood, together with strong root-pressure until frost and active phloem into the winter (Tibbets & Ewers 2000).

In contrast, distinctly ring-porous patterns (versus just 'semi-ring-porous')—or presence of unusually wide vessels throughout—are not documented among 'surface-ascenders' like *Parthenocissus* and *Hedera* (group 2). Further research is needed like that of Bell et al. (1988), who found: "Most significant among the species differences in water relations were the conservative water use patterns of *P. quinquefolia*, and [in contrast] the midday maxima of transpirational water loss measured in *L. japonica* compared to the morning peaks in transpiration for the two deciduous species." Slower growth, more stomatal control and diffuse-porous wood in the 'surface-ascenders' could also reduce problems from cavitation of xylem during droughts or freezes.

There is, however, no evidence so far of general differences in wood anatomy between the evergreen and deciduous vines. In oaks as well, Cavender-Bares & Holbrook (2001) showed no clearcut relationship between hydraulic properties and evergreenness. And additional traits that may be largely independent of evergreenness are the structure, extent and function of rhizomes or other underground storage organs, as in the monocot *Smilax* (without cambial growth). Cobb et al. (2007) concluded that: "Strong root pressure can account for *Smilax*'s survival in temperate regions with severe frosts, where few monocots with persistent aboveground organs are found." The rhizomes of *Smilax* must also be involved in the remarkable ability of these plants to recover from repeated damage (e.g., Boggs et al. 2012).

Leaf-longevity in general and its temperate associations. Evergreenness itself deserves more precise definition in most of these vines, ideally based on measurements of longevity in individual leaves (Koyama & Kikuzawa 2008). Most of the evergreen-tending species in mid-temperate zones appear to have leaves that live up to a year, until shortly before or shortly after the next flush of growth in spring—these would be "brevi-deciduous" to "semi-evergreen" in the sense of Kikuzawa & Lechowisz (2011, Chapter One). *Hedera helix*, which has relatively tough frost-resistant leaves, tends to loose them after spring—then providing a pulse of nutrients from their decomposition (Badre et al. 1998). But even in this well-known species, longevity of leaves is not well-documented. Fischer & Feller (1994) worked with *Hedera* leaves up to two years old, which may be expected as a typical mean for broad-leaved evergreen woody plants in humid temperate zones. Yet there is much variation even within species (Escudero & Mediavilla 2003, Hikosaka 2005, Wright et al. 2005).

Within humid temperate regions, the proportion of evergreen woody plants is greatest on relatively acid, infertile soils (e.g., Monk 1966, Reich et al. 1992, Givnish 2002, Ordoñez et al. 2008; Table 1). It has been suggested that this trend simply results from selection of more conservative nutrient-cycling strategies on less fertile soils, where annual shedding of leaves during autumn might allow leaching of critically limiting nutrients during winter or spring. Slower decomposition of evergreen leaves could also be involved (Cornelisson et al. 1999). But a more profound cause may be that the generally slower maximum rates of photosynthesis on infertile soils must directly reduce the potential for summer-growth to offset any lack of leaves during winter.

Moreover, there is a correlated set of foliar traits among all vascular plants (Wright et al. 2004), including temperate vines (e.g., Ichihashi et al 2009). These traits are greater longevity, more thickness (or mass/area), lower N and P contents, and slower maximum photosynthesis (even per area)—but not leaf size. The more long-lived, slower metabolizing leaves in this global 'spectrum' are associated with dry climates and infertile soils. Yet much mystery remains concerning the local variation along this continuum, within particular environments or functional groups (Grubb 2002), and there are further relationships with leaf shape. Among woody plants such as temperate vines, evergreen leaves are more often simple versus compound (with the notable exception of *Holboellia*), unlobed (with the notable exception of 'juvenile' *Hedera*) and entire-margined, compared to deciduous taxa (Table 9). And although cordate leaf bases are generally associated with the vining habit (Givnish & Vermeij 1976), none of the strictly evergreen mid-temperate vines are distinctly cordate (0/6 versus 11/28 in Table 7); 'juvenile' *Hedera*, again, is somewhat exceptional. Possible causes of such associations remain largely untested, although increase in perimeter/area of leaves may enhance photosynthetic rates (with more gas-exchange, cooling and vascular supply), and it may reduce some effects of herbivory (Givnish 1987, Brown & Lawton 1991, Nicotra et al. 2011).

Correlations with leaf nitrogen content. Provisional information on nitrogen contents in mature leaves of several vines are scattered in the literature. These are generally reported as "crude protein" (= 6.25 × N content from the Kjeldahl method), as reviewed by Conklin-Brittain et al. (1999). Among the evergreen-tending vines considered here (Table 5), most have moderate protein contents of about 9–13% dry weight. Leaves of *Hedera* (and perhaps also *Decumaria* and *Holboellia*) have consistently low content (about 9%), in accord with their thickness and slow photosynthetic rates (Carter & Tamura 1988). *Smilax* tends to have relatively high content but quite variable (9–17%), increasing in fresh growth after disturbance (e.g., Dewitt & Derby 1955; and refs. of Table 5). The largely deciduous genera of mid-temperate zones (Table 6), tend to have higher protein contents (mostly 10–18%), but there is much overlap with the evergreen-tending taxa. The highest contents (18–22%) have been reported among more herbaceous-to-subshrubby species in *Aristolochia*, *Clematis* and *Pueraria*—which have much nitrogen-based secondary chemistry and rapid weedy growth. However, relatively low contents (6–9%) have been reported from other herbaceous-to-subshrubby genera, especially some with more subtropical or evergreen ancestry (?*Dioclea, Schizophragma, Trachelospermum*).

Kusomoto et al. (2012) have recently reported nitrogen contents and other functional characters for 20 largely evergreen vines in a subtropical forest of southern Japan, including several species in the same genera as temperate vines. Their data support the concept that thin, nitrogen-rich leaves are loosely associated with a deciduous or herbaceous tendency, and with the twining or scrambling habit rather than climbing with adventitious roots (Figure 6a). Leaf nitrogen content and the deciduous/herbaceous tendency—but not specific leaf area (mm^2 per mg)—were correlated with concentration of the species on more concave topography (Figure 6b), There were no significant relationships of functional characters with tree basal area or density in the forest. Wood density of the vines was not correlated with the foliar characters, but it was relatively high among the few species of thorny scramblers and nitrogen-fixers.

More collection and analysis of functional data such as these would allow much better understanding of the diversity in vining behaviors. It will be important to add data for expanding displays like Figure 6. A provisional expansion (not shown) using information from Ichihashi et al. (2009, 2010, 2011), Han et al. (2010) and other miscellaneous sources confirms that variation in both leaf nitrogen contents and in specific leaf area tends to increase at higher levels of those parameters. The variation suggests that species are clustered along two branches: towards high N at moderate SLA (with more herbaceous species at the extreme); and towards higher SLA at moderate-low N (with deciduous ‘ascender’ *Schizophragma* at the extreme). Thorny scramblers and nitrogen-fixers cluster with the high N branch, but might be divisible. Overlays of secondary chemistry on such figures would be quite interesting.

Concentration of evergreen-tending vines on eutrophic soils. Within humid temperate forests of the Northern Hemisphere, vines are generally most frequent on moist to damp, fertile soils (e.g., Tables 1, 2; Schnitzer & Bongers 2002, Morrisey et al. 2009, Chettri et al. 2010, Kusomoto 2012). The few species of evergreen-tending vine follow this trend. In eastern North America (Table 2, Figure 2), *Bignonia capreolata* and other such species are mostly concentrated on mesic to submesic sites with moderately high pH (ca. 5–7), where the highest overall fertilities tend to occur. In most of Europe, *Hedera helix* (sensu lato) is the only native evergreen vine, and it is most common on nutrient-rich sites with pH of 4.5–7 (Rackham 2003, Metcalfe 2005, Schnitzler & Heuzé 2006). In the Himalayan region, *H. nepalensis* is concentrated on similar soils—together with *Holboellia latifolia* and *Lonicera glabrata* in eastern sections (e.g., Saima et al. 2009, Chettri et al. 2010). Further east in Asia, there is much less published information in English. *Euonymus fortunei*, *E. vagans* and their allies are sometimes associated with base-rich soils, but their associated forest may often be largely evergreen in montane cloud forest with much leaching of minerals from upper soil horizons (Shi & Zhu 2009, Yuan et al. 2009).

This association of evergreen vines with fertile soils is the opposite of trends in other evergreen vascular plants (e.g., Tables 1, 2), and fundamentally different selective factors must have operated. It is likely that the vines are taking advantage of the deciduous season in the tree canopy, continuing to photosynthesize through some of the winter, at least during early or late periods, as shown for *Hedera* (Bauer & Kofler 1987). *Hedera* even flowers and fruits during the late summer to fall, an unusual trait among woody plants of mid-temperate zones (also in some *Hamamelis*, *Lonicera*, ?*Viburnum* and Viscaceae). Among evergreen-tending vines of east-central U.S.A., *Smilax glauca* is somewhat exceptional as it occurs mostly on subxeric sites with moderately to strongly acid soils (Figure 2j). But its associated trees are mostly deciduous oaks that form a broad ecological wedge between *Tsuga*-with-*Rhododendron* on more mesic sites and *Pinus*-with-*Kalmia* on more xeric sites.

As noted above, evergreen-tending vines probably spread into temperate zones of the Northern Hemisphere after deciduous trees had largely replaced evergreen trees—including some conifers—during the climatic cooling and drying of mid- to late-Tertiary Eras (Table 10; Axelrod 1966, 1983; Davis 1983, Wolfe 1987, Graham 1999, Manos & Stanford 2001, Manos et al. 2007, Wallander 2008). These vines appeared later than most of the strictly deciduous vines. Moreover, the dominant deciduous tree genera of subxeric sites—*Castanea, Quercus, Carya, Fraxinus*—appear to have proliferated much later than radiation of the original Arcto-Tertiary flora. In the temperate forests of the Southern Hemisphere, one would then expect less shade-tolerant evergreen vines, due to general lack of deciduous trees—this can be tested.

The concept that some life-forms of plants settle on a contrarian strategy to complement the ecology of their dominants, is of course an old idea. Similar selection must have shaped the concentrations of winter annuals and biennials (with overwintering rosettes) in forest on base-rich soils (Table 2). It is also implicated in the much-researched ephemeral flushes of diverse life-forms among vernal perennials, which capture light before new tree leaves expand to cast deep shade, and which capture nutrients from decomposing deciduous litter (e.g., Muller 1978, Grubb & Marks 1989). However, the evolution of evergreen-tending vines and their allies seems to have been generally more recent and more plastic, leaving many questions.

Evolutionary ‘loose ends’ may include the few odd evergreen-tending ‘subshrubby’ life-forms that can cover ground in deciduous woods—as in *Euonymus* of eastern North America (*obovatus* and, sometimes, *americanus*), and especially the whole genus *Vinca* of Mediterranean regions. Are these constrained evolutionary branches that might have developed into evergreen vines if climates were less harsh during the late Tertiary and Quaternary Eras? Or do these plants still have potential for selection of more rampant forms, as occur in other branches of their families—Celastraceae and Apocynaceae?

Potential interactions with herbivory. Varied direct and indirect effects of herbivory may complicate patterns in evergreen versus deciduous plants, reducing the value of simple theories (Grubb 1992). Even recent global analysis of multiple factors in such patterns leaves much residual variation (VanOmmen-Kloeke et al. 2012). Consumption of evergreen leaves by overwintering herbivores is a problem for many plants (e.g., Karban 2008). Among evergreen woody vines, species like *Euonymus fortunei*, *Bignonia capreolata* and *Hedera helix* can become especially important for mammalian herbivores during the winter (Table 5). Yet browsing on some relatively deciduous *Smilax* species is often most intense during the early growing season, when thick new rapidly growing shoots emerge from the ground—somewhat like bamboos (e.g., Halls 1975).

Uniform addition of herbivory to the landscape might select for more physically- or chemically-defended leaves of the ‘neutral’ type (unspecialized fibre, tannins etc.)—an investment that could lead to mutual benefits with nutritional or photosynthetic strategies for more expensive evergreen leaves on infertile soils. But herbivores—especially larger animals—are expected to concentrate on more productive soils with mineral-rich forage during the winter (Kirby 2001, Jones et al. 2008). Such soils would include valleys, gullies, swales and saddles in montane bamboo forests with diverse vines (Igota et al. 2004, Tang 2006, Shi et al. 2012). The direct selective effects of such herbivory could amplify any general trends in nutrient-cycling and photosynthetic strategy that lead to evergreen woody plants being concentrated on infertile soils. Alternatively, young vining shoots on eutrophic sites—more than other woody plants—may often escape from most mammals by growing rapidly into the tree canopy. In that case, there could be special advantages to minimizing structural support and chemical defense, at least temporarily, so that upward growth rate is increased.

For both reasons, defenses of the ‘neutral’ type might be less useful on more fertile soils. It is notable that decreases of foliar phenolic concentrations have been indicated within several woody species along gradients of increasing soil fertility in temperate regions (e.g. Muller et al. 1987, Nicolai 1988). Also, a recent intensive analysis of rain forest in Peru has shown generally lower levels of chemical defenses on more fertile soil, and levels are especially low among woody vines (Asner & Martin 2011).

Patterns in secondary chemistry. As detailed above (at end of Part Two), vining taxa tend to have less defensive chemistry than their closest non-vining relatives. In 10 of these phylogenetic comparisons, there are indications of this trend; in 9 cases there is neutral or uncertain information; and only one case provides a possibly opposing trend. Moreover, shorter woody plants in general may be better defended against mammals than high-climbing vines and trees (Borchard et al. 2011). In particular, most of the species of evergreen shrubs or small trees in largely deciduous forests of north temperate zones have strongly deterrent to toxic chemistry that includes complex terpenoids, steroidal alkaloids or cyanogenic glycosides (Grubb 1992)—*Ilex* species may be exceptional, lacking toxicity, but some of them have prickly leaves instead.

Most vines still have some chemical defense, and Table 7 summarizes the predominant types of secondary chemicals produced by different groups of vines in mid-temperate regions. Largely herbaceous or subshrubby genera have diverse chemistry that includes alkaloids or other N-containing compounds in most cases (7 of 9 taxa). Largely deciduous woody genera have less diverse chemistry, with relatively simple phenolics predominating (minus condensed tannins or steroidal compounds in almost all cases) and with less occurrence of N-containing compounds (3 of 14 taxa). In genera that have mixed deciduous-evergreen or largely evergreen habit, there is more diverse phenolic chemistry that includes condensed tannins, terpenoids and steroidal compounds in several cases. But again there are relatively few of these genera with N-containing compounds (3 of 11 taxa; $P = 0.02$ with chi^2 test), none of which are acutely toxic to mammals (see notes on herbivory and chemistry above).

Indications of moderate to acute toxicity for mammalian herbivores (Table 7) are concentrated among the largely herbaceous vining genera (6 of 9), plus a few in the largely deciduous woody group (6 of 14). There may be no indications of acute toxicity among the mixed or largely evergreen groups, although a few of these genera are known to cause digestive problems if eaten in quantity (2 of 11; $P = 0.09$ with chi^2 test). Miscellaneous reports of consumption by mammals, especially ruminants, suggest a trend of increasing use from herbaceous to deciduous to evergreen vines (Table 7). These trends remain just suggestive without a more definitive and comprehensive analysis. There is a growing abundance of information on secondary chemicals in vascular plants and their miscellaneous effects. Clearly more synthesis and experimenation could provide answers to the central questions here—which of these chemicals influence consumption by generalist mammalian herbivores, and can the general edibility of many vines in temperate regions be directly attributed to low levels of defensive compounds?

Table 7. Summary of genera (or subgeneric segregates) with woody or subshrubby vines in mid-temperate zones: herbaceous or deciduous versus evergreen-tending groups. This relates (with abbreviations) to Tables 5, 6, 8 and 9, plus further literature review for TOX (toxicity) and EAT (edibility) ratings. Growth habit and species numbers are based just on vines in mid-temperate zones. Underlining shows taxa that contain only vines; EG are more evergreen in warmer zones; taxa with minor extent into mid-temperate zones are in ( ).

HERBACEOUS TO SUBSHRUBBY	SPP	VEG	SEX	RAN	CHE	TOX	EAT
Aristolochia [without *Isotrema*] (EG) 2n = 6-16, 24, 28, 36 Birthwort	2-4	TWI	Bisexual	Wide+ (AfEu)	N	XX	–?
Cocculus (EG) 2n = 26, 52, 78 Southern Moonseed	2	TWI	Dioec.	Wide (Af)	NPS	X?	+?
Menispermum 2n = 52 Northern Moonseed	2	TWI	Dioec.	AsAm	NPT	XX?	–
Clematis subgenus *Clematis* (EG) 2n = 16, 32, 48 Clematis	c. 50-80	TEN	Partly Dioec.	Wide+ (AfEu)	PNT*	X	+?
Humulus 2n = 16-20 (40) Hop	3	TWI	Dioec.	Wide+ (Eu)	PTSC		++
Lackeya [= *Dioclea multiflora*] 2n = ? <22 in allied genera> Clusterpea	1	TWI	Bisexual	Am	N	X?	++?
Pueraria~ 2n = 22-24 (44) Kudzu	5*	TWI	Bisexual	As++	PTN*		+++
(*Trachelospermum*+*Thyrsanthella* EG) 2n = 20 Star-jasmine	2	TWI	Bisexual	AsAm	PTN*	X?	+?
Smilax subgenus *Nemexia* 2n = 26 Carrion-flower	5-7*	TEN	Dioec.	AsAm	PTS		+?

WOODY, LARGELY DECIDUOUS	**SPP**	**VEG**	**SEX**	**RAN**	**CHE**	**TOX**	**EAT**
(*Schisandra*) 2n = 28 Magnolia Vine	c. 9	TWI	Monoec.	AsAm	PT		+?
Isotrema [*Aristolochia* segregate] (EG) 2n = 28-32 Pipe Vine	c. 10	TWI	Bisexual	AsAm	N	XX	−?
Calycocarpum 2n = ? <26 allied genera> Cupseed Vine	1	TWI	Dioec.	Am	?NP	X?	−?
Ampelopsis 2n = 20, 40 Pepper Vine	c. 6*	TEN	Bisexual	AsAm++	P		++
Parthenocissus 2n = 40 Virginia Creeper	3	ADH	Bisexual	AsAm	P		++?
Vitis [*Muscadinia* could be split] 2n = 38, 40* Grape Vine	c. 16	TEN	Poly-Dioec.	Wide+ (AfEu)	P		++
Toxidodendron 2n = 30 Poison-ivy	2	ADV	Poly-Dioec.	AsAm	P	X	++?
Rosa (EG) 2n = 14, 21, 28, 35 (42) Rose	c. 2-5*	THO	Rare Dioec.	Wide++ (AfEu)	PC		++
(*Berchemia*) (EG) 2n = ? <24 in allied genera> Supplejack	c. 9	TWI	Bisexual	Wide (Af)	P	X?	++
Wisteria 2n = 16 (32) Wisteria	c. 3-6*	TWI	Bisexual	AsAm++	NC	XX	−
(*Schizophragma*) 2n = 28 Lesser Climbing Hydrangea	1-3	ADV	Bisexual	As	?TP		+?
Hydrangea: *anomala* group 2n = 36 Climbing Hydrangea	2-4	ADV	Bisexual	AsAm?	PT	X?	+?
Clematoclethra 2n = 48 Lesser Chinese Gooseberry	1-4	TWI?	Dioec.	As	PT		??

Campsis 2n = 40 Trumpet Creeper	2	ADV	Bisexual	AsAm	TP		++
WOODY WITH MIXED DECID. AND EG	**SPP**	**VEG**	**SEX**	**RAN**	**CHE**	**TOX**	**EAT**
Akebia (EG) 2n = 16, 32 Chocolate Vine	3-5*	TWI	Monoec.	As+	T		+?
Actinidia (EG) 2n = 58 (116, 174) Chinese Gooseberry	10-15	TWI-ADV	Poly-Dioec.	As+	TPCN*		+?
Celastrus (EG) 2n = 46 Bittersweet	8-12	TWI	Partly Dioec.	Wide++ (Af)	TPNS*	X?	+?
Lonicera subgenus *Caprifolium* (EG) 2n = 18, 36 Woodbine Honeysuckle	c. 8	(TWI)	Bisexual	Wide+ (Eu)	P(T)		+++
Smilax subgenus *Smilax* (EG) 2n = 32 (64) Greenbriar	c. 25-35	TEN	Dioec.	Wide (Af)	TPCS		+++
WOODY, LARGELY EVERGREEN	**SPP**	**VEG**	**SEX**	**RAN**	**CHE**	**TOX**	**EAT**
Holboellia 2n = 32 China Blue Vine	c. 5*	TWI	Monoec.	As	?TP		+?
Decumaria 2n = 28 Woodvamp	2	ADV	Bisexual	AsAm	?PT		+?
Euonymus section *Ilicifolia* 2n = 32, ?64 Winter Creeper	1-8*	ADV	Bisexual	As++	TPNS*		++
Hedera 2n = 24, 48, 72, 96, 144, 192 Ivy	5*	ADV	Bisexual	EuAs++	TP	X	++
Bignonia 2n = 40 Crossvine	1	TEN-ADH	Bisexual	Am	?TPS		++
Lonicera section *Nintooa* 2n = 18 (36) Asian Honeysuckle	5-11	TWI	Bisexual	As++	PT		++

Table 8a. Comparison of range size, species-richness and invasive tendency between herbaceous-tending, deciduous and evergreen-tending genera of mid-temperate vines. See Table 7 for list, classes of genera and abbreviated groups. For B, numbers of species (SPP) are estimates; the intermediate class (4–6) is marked with askerisks (*). For C, "some" invasive tendency is "+" under RAN in Table 7; in these cases, the genus is established outside the native range but not widely abundant. Genera with "much" invasive tendency are "++" under RAN; these have become locally abundant in at least one region outside the native range. P is from Fisher's exact tests with 2×2 cells (a,b,c,d) or extended to all 3×3 cells (Ghent 1972).

A. RANGE WIDTH P= 0.24 (3×3); 0.06 (2×2)	Native to one temperate region	Native to two temperate regions	More widespread (in Africa/Europe)
Herbaceous or subshrubby	2a	3b	4b
Largely deciduous	3a	8b	3b
Largely evergreen or mixed	6c	2d	3d
B. SPECIES-RICHNESS P= 0.27 (3×3); 0.12 (2×2)	1–3 mid-temperate vining species	4–6 mid-temperate vining species	>6 mid-temperate vining species
Herbaceous or subshrubby	6a	2a	1b
Largely deciduous	7a	3a	4b
Largely evergreen or mixed	2c	4c	5d
C. INVASIVE TENDENCY P= 0.31 (3×3); 0.17 (2×2)	No invasive tendency	Some invasive tendency	Much invasive tendency
Herbaceous or subshrubby	5a	3a	1b
Largely deciduous	10a	1a	3b
Largely evergreen or mixed	4c	3c	4d

Table 8b. Comparison of range size, species-richness and invasive tendency between bisexual/monoecious, partly dioecious & strictly dioecious genera of mid-temperate vines. See Table 7 for list, classes of genera and abbreviated groups. For B, numbers of species (SPP) are estimates; the intermediate class (4–6) is marked with askerisks (*). For C, “some” invasive tendency is “+” under RAN in Table 7; in these cases, the genus is established outside the native range but not widely abundant. Genera with “much” invasive tendency are “++” under RAN; these have become locally abundant in at least one region outside the native range. P is from Fisher’s exact tests with 2×2 cells (a,b,c,d) or extended to all 3×3 cells (Ghent 1972).

A. RANGE WIDTH P= 0.03 (3×3); 0.008 (2×2)	Native to one temperate region	Native to two temperate regions	More widespread (in Africa/Europe)
Bisexual or monoecious	7a	10a	3b
Partly dioecious (various)	1c	0c	5d
Strictly dioecious	2c	2c	3d
B. SPECIES-RICHNESS P= 0.015 (3×3); 0.013 (2×2)	1–3 mid-temperate vining species	4–6 mid-temperate vining species	>6 mid-temperate vining species
Bisexual or monoecious	8a	7c	5c
Partly dioecious (various)	0a	2c	4c
Strictly dioecious	6c	0d	1d
C. INVASIVE TENDENCY P= 0.009 (3×3); 0.09 (2×2)	No invasive tendency	Some invasive tendency	Much invasive tendency
Bisexual or monoecious	11a	3b	6b
Partly dioecious (various)	0a	4b	2b
Strictly dioecious	6c	1d	0d

Table 9. Tests of associations among some biological features of mid-temperate vines. See Table 7 for listing and classification of genera, plus abbreviations.
P is from Fisher's exact tests with 2×2 cells (a,b,c,d) or extended to all 3×3 cells (Ghent 1972).
Note also that the 'evergreen-tending' condition is weakly associated with the 'surface-ascending' condition ($P = 0.1$ in 2×2 test among the 24 woody genera).

1-5 [next page]. Comparisons between genera of herbaceous-subshrubby vines; versus woody twiners, tendrillers or scramblers; versus woody surface-ascenders. Ascenders have ADR or ADH under VEG in Table 7.

6-10 [second page]. Comparisons between genera of herbaceous-subshrubby vines; versus largely deciduous; versus evergreen-tending genera. Note that in 10 the strictly evergreen group are all strictly non-dioecious (see text).

1. SERRATED LEAVES **P= 0.94 (3×3); 0.32 (2×2)**	**Entire unlobed**	**Partly serrated or lobed**	**Consistently serrated**
Herbaceous to subshrubby	4a	4a	1b
Woody twiners/tend./scram.	4c	5c	3d
Woody surface-ascenders	3c	4c	3d
2. DIVIDED LEAVES **P= 0.80 (3×3); 0.42 (2×2)**	**Simple unlobed**	**Lobed or varied**	**Compound**
Herbaceous to subshrubby	3a	2a	4b
Woody twiners/tend./scram.	6c	4c	4d
Woody surface-ascenders	5c	1c	4d
3. OPPOSITE LEAVES **P=0.005 (3×2); 0.004 (2×2)**	**Alternate leaves**	**Opposite leaves**	
Herbaceous to subshrubby	9a	0b	
Woody twiners/tend./scram.	12a	2b	
Woody surface-ascenders	4c	6d	
4. CHEMISTRY (Table 6) **P= 0.03 (3×3); 0.13 (2×2)**	**Alkaloids etc. (N 1st or 2nd under CHE)**	**Mixed (marked * under CHE)**	**Terpenoids or phenolics (T/P)**
Herbaceous to subshrubby	4a	3a	2b
Woody twiners/tend./scram.	3a	1a	10b
Woody surface-ascenders	0c	2c	8d
5. SEXUALITY (Table 6) **P= 0.22 (3×3); 0.05 (2×2)**	**Bisexual or monoecious**	**Partly dioecious (various)**	**Strictly dioecious**
Herbaceous to subshrubby	4a	1a	4b
Woody twiners/tend./scram.	9a	3a	3b
Woody surface-ascenders	8c	2c	0d

6. SERRATED LEAVES **P= 0.39 (3×3); 0.07 (2×2)**	**Entire unlobed**	**Partly serrated or lobed**	**Consistently serrated**
Herbaceous or subshrubby	4a	4a	1b
Largely deciduous	3c	6c	5d
Largely evergreen or mixed	6a	4a	1b
7. DIVIDED LEAVES **P= 0.74 (3×3); 0.12 (2×2)**	**Simple unlobed**	**Lobed or varied**	**Compound**
Herbaceous or subshrubby	3a	2b	4b
Largely deciduous	6a	3b	5b
Largely evergreen or mixed	7c	1d	3d
8. OPPOSITE LEAVES **P=0.06 (3×2); 0.07 (2×2)**	**Alternate leaves**	**Opposite leaves**	
Herbaceous or subshrubby	9a	0b	
Largely deciduous	11a	3b	
Largely evergreen or mixed	6c	5d	
9. CHEMISTRY (Table 6) **P= 0.004 (3×3); 0.30 (2×2)**	**Alkaloids etc. (N 1st or 2nd under CHE)**	**Mixed (marked * under CHE)**	**Terpenoids or phenolics (T/P)**
Herbaceous or subshrubby	4a	3a	2b
Largely deciduous	3a	0a	11b
Largely evergreen or mixed	0c	3c	8d
10. SEXUALITY (Table 6) **P= 0.44 (3×3); 0.21 (2×2)**	**Bisexual or monoecious**	**Partly dioecious (various)**	**Strictly dioecious**
Herbaceous or subshrubby	4a	1a	4b
Largely deciduous	9a	3a	2b
Largely evergreen or mixed	8c	2c	1d

Table 10. Geological eras from first appearance up to early radiation of each vine genus. Estimates vary much in reliability. Darker shading indicates based on fossils and/or dated phylogenetic analysis; lighter, same but weaker evidence. Question marks are estimates only from phylogeny and biogeography. Within each genus, later dates indicate when relatively diverse lineages are likely to have begun, including some in mid-temperate zones. Genera are listed in approximate order of age, but with additional separation as follows.

(a) Genera that are largely deciduous in mid-temperate regions; * evergreen in warmer.

(b) Evergreen-tending genera with at least one modern mid-temperate evergreen vine; asterisks indicate partially evergreen genera (*) or fully evergreen genera (**) today.

(c) Largely herbaceous taxa in mid-temperate zones today (not a comprehensive list); these are included for comparative purposes, since they do have woody relatives.

# Indicates genera with at least some ability to climb trees using adventitious roots or pads.

Bottom two rows show first North American indications of genera with deciduous trees in temperate regions, based largely on fossils, in the following two groups.

(d) Largely typical of mesic to submesic or subhydric habitats, mostly diffuse-porous: 1, *Acer* (Renner et al. 2008); 2, *Aesculus* (Manchester 2001); 3, *Alnus* (Forest+ 2005); 4, *Carpinus* (Forest+ 2005); 5, *Liquidambar* (Pigg+ 2004); 6, *Nyssa* (Wen+ 1993); 7, *Platanus* (Feng+ 2005); 8, *Tilia* (Manchester 1994); 9, *Fagus* (Manchester+ 2004); 10, *Liriodendron* (Nie+ 2008); 11, *Morus* (Zerega+ 2005); 12, semi-ring-porous *Catalpa* (Olmstead+ 2009).

(e) Largely typical of more subxeric or disturbed habitats, mostly ring-porous (except *Ostrya*): 1, *Carya*-like pollen (Muller 1981); 2, *Castanea* (Manos+ 2001); 3, *Carya* (Manos+ 2007); 4, *Fraxinus* (Wallander 2008); 5, *Juglans* (Stanford+ 2000); 6, *Gledistsia* & *Gymnocladus* (Schnabel+ 1998); 7, *Ostrya* (Forest+ 2005); 8, *Quercus* sections *Quercus* and *Lobatae* (Manos+ 1999, 2001); 9, *Robinia* (Lavin+ 2003); 10, *Maclura* (Martinez-C.+ 2006).

GEOLOG. ERA	**uCret.**	**Paleo.**	**Eoc.**	**Oligo.**	**Mio.**	**Plio.**	**References**
Millions of years	**84-65**	**65-56**	**56-34**	**34-23**	**23-5**	**5-2.5**	St = Stevens 2012 ref.
(a) DECIDUOUS VINES							
Schisandra	▓	▓	▓				Denk+ 2006
Aristolochia	░	░	░				St: Wikstrom+ 2004
*Cocculus**		░	░				Jacques+ 2011
Ampelopsis		▓	▓	▓			Nie+.10; Zecca+.12
Clematoclethra			?				Chat+ 2004
# *Parthenocissus*			▓	▓			Nie+.10; Zecca+.12
# *Campsis*			░	░			Xiang+ 2000
Isotrema			?	?			Ohi-toma+ 2006
Calycocarpum			?	?			Jacques+ 2011
Vitis			▓	▓	▓		Nie+.10; Zecca+.12
*Rosa**			░	░	░		DeVore+ 2005
# *Schizophragma*				▓			Samain+.10; Xiang+.11
# *Hydrangea*				▓	▓		Xiang+ 2011
Menispermum				▓	▓		Jacques+ 2011
*Clematis**				▓	▓		Xie+ 2011
*L. Caprifolium**				▓	▓		Smith 2009
# *Toxicodendron*					▓		Nie+ 2009
Berchemia					▓		Smiley+.75, Rich.+.04
Wisteria				?	▓	?	Wang+ 2006

GEOLOG. ERA	**uCret.**	**Paleo.**	**Eoc.**	**Oligo.**	**Mio.**	**Plio.**	**References**
Millions of years	**84-65**	**65-56**	**56-34**	**34-23**	**23-5**	**5-2.5**	St = Stevens 2012 ref.
(b) EVERGREEN-TENDING VINES							
_S. Smilax_*		░	▓				Dilcher+ 2005
_Celastrus_*			?	░	?	?	Mu+ 2012
# _Actinidia_*			?	?	?		Schönenberger+ 2001
# _Decumaria_**				▓			Samain+.10; Xiang+.11
# _Hedera_**					▓		Green+ 2011 & cited.
L. Nintooa**					▓		Smith 2009
_Akebia_*					?		Wang+ 2002
Holboellia**					?	?	Wang+ 2002
# _Bignonia_**					?	?	Olmstead+ 2009
# _E. fortunei_ s.l.**					?	░	Li+.84; Simmons+.01
(c) HERBACEOUS VINES							
S. Nemexia			?	░	?		St: Qi+ 2012
Humulus					▓		Zerega+ 2005
Pueraria					▓	▓	Lavin+.05; Wang+.10
Lackeya						?	Kajita+ 2001
Thyrsanthella						?	Livshultz+ 2007
(d,e) DECIDUOUS TREES							
Mesic Genera		1-8	9-11	12?			See also: Graham 1999, Muller 1981 etc.
Subxeric Genera		1?	2-5	6-9	10?		

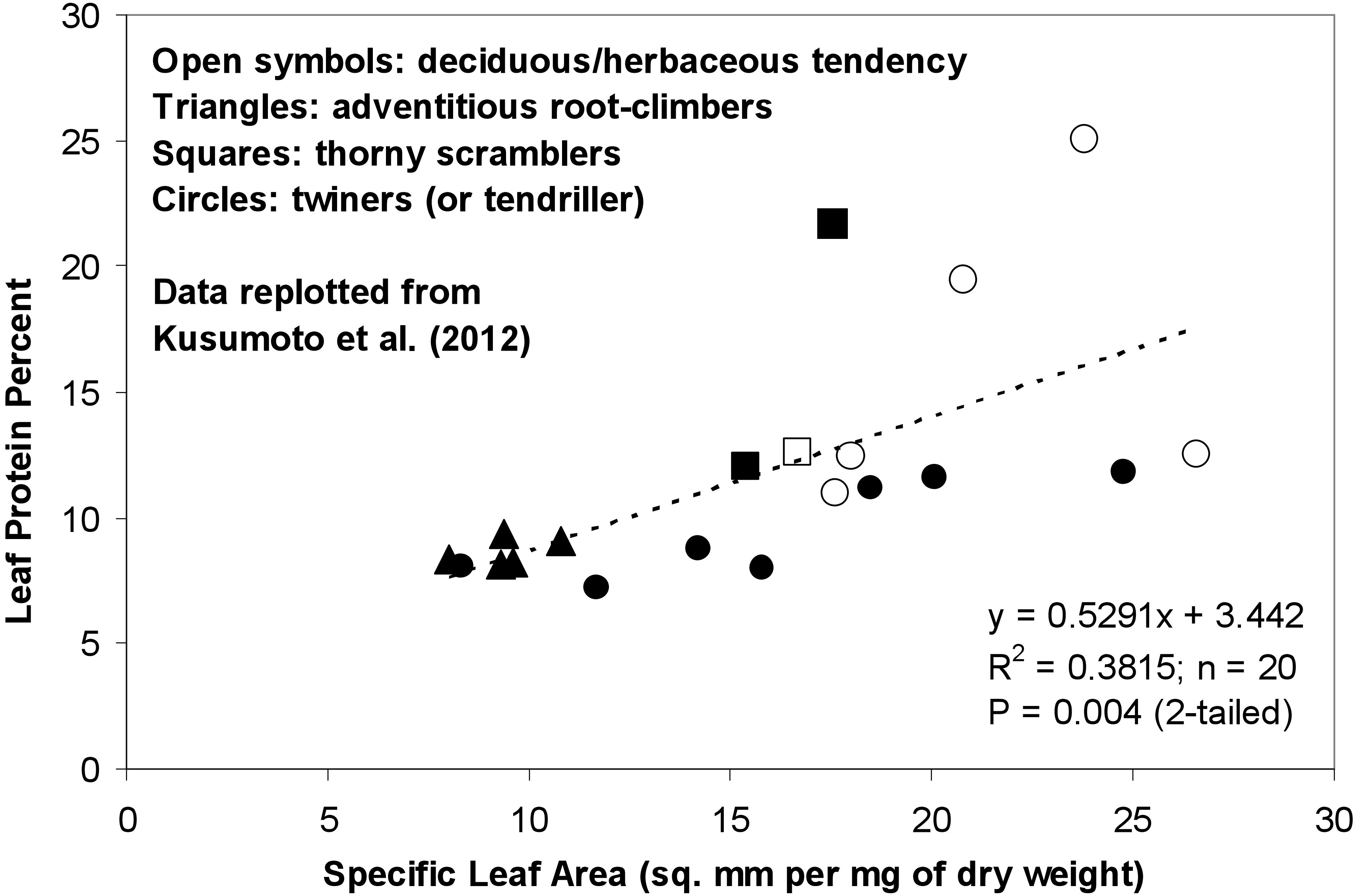


Figure 6a. Estimated leaf protein content (= 6.25 × N% of dry weight) in relation to specific leaf area for the 20 species of vine ('lianas') studied by Kusumoto et al. (2012) in subtropical forest of southern Japan. The three species with >15% protein are the one herbaceous plant with tendrils (at top) and the two N-fixing species among all 20.

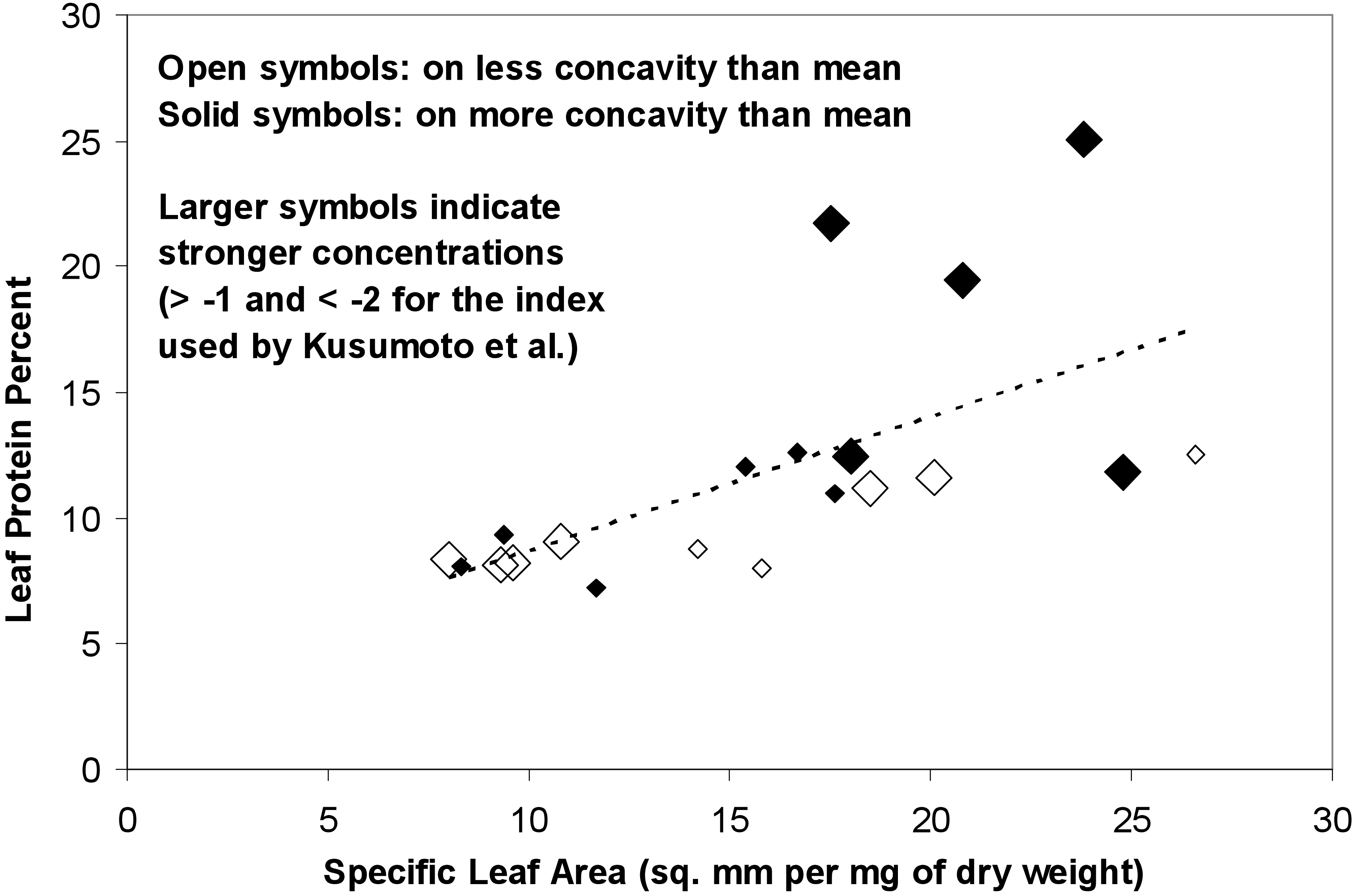
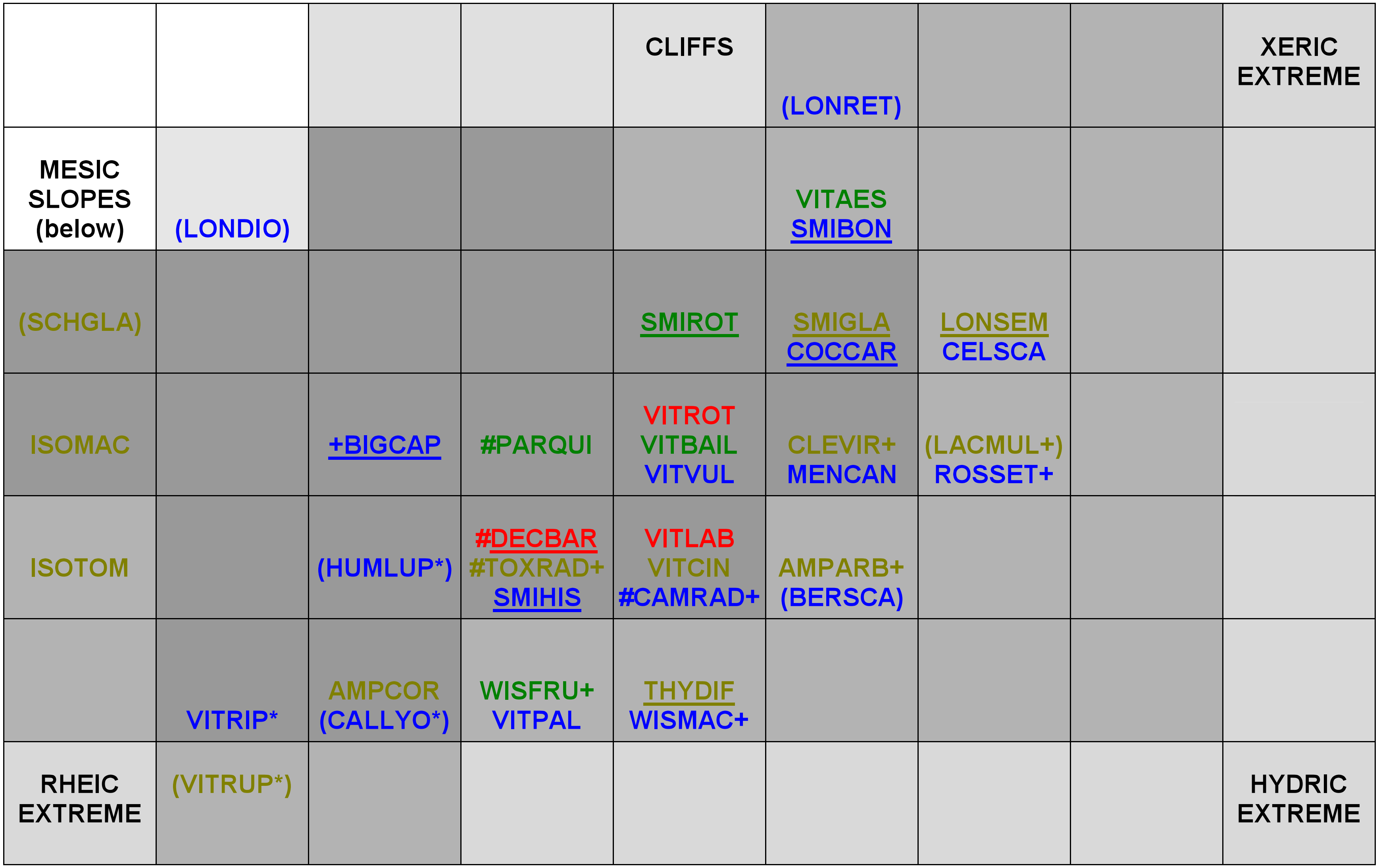


Figure 6b. As in Figure 6a, adding overlay of associations with topographic concavity for each of the species, from the "relief index" calculated by Kusumoto et al. (2012). Their index was significantly correlated with leaf nitrogen ($P < 0.01$) and climbing habit ($P < 0.05$). But there was no correlation of forest basal area with functional characters.

Figure 7. Approximate modal positions of woody vine species along hydrological gradients of Figure 1. See text for further explanation. Underlined species are evergreen-tending; # climb trees; + have pinnate leaves; ( ) are rare/local species.



				CLIFFS	(LONRET)			XERIC EXTREME
MESIC SLOPES (below)	(LONDIO)				VITAES SMIBON			
(SCHGLA)				SMIROT	SMIGLA COCCAR	LONSEM CELSCA		
ISOMAC		+BIGCAP	#PARQUI	VITROT VITBAIL VITVUL	CLEVIR+ MENCAN	(LACMUL+) ROSSET+		
ISOTOM		(HUMLUP*)	#DECBAR #TOXRAD+ SMIHIS	VITLAB VITCIN #CAMRAD+	AMPARB+ (BERSCA)			
	VITRIP*	AMPCOR (CALLYO*)	WISFRU+ VITPAL	THYDIF WISMAC+				
RHEIC EXTREME	(VITRUP*)							HYDRIC EXTREME

Development of Hypotheses, Experiments and Applications

Competition, invasion and herbivory of evergreen-tending vines. There has been much interest in potential interactions of vines with trees, but rather little conclusive experimental work (e.g., Putz & Mooney 1991, Schnitzer & Bongers 2002, Morrisey et al. 2009, Ichihashi & Tateno 2011). Even the effects of smothering species with adventitious roots like *Hedera* remain uncertain, as commented upon by Rackham (1990, p. 24). Some statistical analysis of patterns in woodland has suggested a negative effect of *Hedera* on larger trees (e.g., Garfi & Ficarrota 2003), and "ivy is often regarded as a problem as it is believed to reduce tree growth rates" (Castagneri et al 2013). Dillenberg et al. (1993) used a trenching and trellising experiment to show that root competition of *Lonicera japonica* has more effect on growth of *Liquidambar* than does canopy competiton, which was only significant in combination with root competition; *Parthenocissus quinquefolia* had much less overall effect. Skullman et al. (2004) showed allelopathic effects of *L. japonica* on pines. There is little evidence that high-climbing vines have distinct 'host-preferences' for tree species independent of tree size, succession and environmental factors (Ladwig & Meiners 2010, Leicht-Young et al. 2010, Castagneri et al. 2013, Kusumoto et al. 2012). But Talley et al. (1996) did show that seed-germination of the deciduous vine, *Toxicodendron radicans*, is inhibited by bark chemistry of some trees, especially *Juglans nigra*.

Effects of these vines on ground vegetation within woodland are more obvious in some cases. Across its native and invaded ranges, *Hedera* appears to suppress growth of associated plants (including *Lonicera*) due to direct competition for space and resources—based on long-term observations of succession without ungulates (Harmer et al. 2001) and short-term manipulations (Biggerstaff & Beck 2007a,b). In Kentucky, the local dominance of *Euonymus* *fortunei* has clearly led to much local reduction in cover of native grasses (especially *Elymus* spp.) and herbs (especially summer perennials), as documented in the Shady Lane Walnut Woods at University of Kentucky Arboretum (J.J.N. Campbell & Kim D-H., in prep.). However, Smith & Reynolds (2012) have recently experimented with potted plants, and showed that *Asarum canadense* can depresses growth of *E. fortunei* by ca. 60% through changes in the chemistry of associated soil. They found no significant effect of *Euonymus* soil (versus *Asarum* soil) on growth of *Asarum*.

Rather than invoking direct competition or inhibition (Grubb 1992), parameters of disturbance that are correlated with these vines can sometimes be used to indicate more significant relationships with associated plants than parameters of the vines themselves. For example, Surrette & Brewer (2008) found that environmental factors including prescribed fire provided stronger correlations with native plant diversity than did cover of *Lonicera japonica* itself—a species that is reduced by frequent fire. It would be interesting to extend such research to include patterns of browsing by deer—which can also reduce *L. japonica* (Table 8).

Given the apparent competitive ability of some evergreen-tending vines, why do they do not dominate temperate deciduous woodlands in general—what ecological factors could control their populations? The invasion of vines like *Hedera*, *Lonicera* and *Euonymus* species into the southeastern U.S.A. has been partly attributed to release from 'natural enemies' that may control them in their native ranges (Schierenbeck et al. 1994, Ding et al. 2006, Ashton & Lerdau 2008). Perhaps the most obvious type of 'enemy' to consider first would be livestock (pigs, cattle, goats, sheep)—which have been a major ecological factor in much woodland of Europe and East Asia for several thousand years, often replacing wild ungulates that roamed before human settlement. Livestock have been especially influential in transitions from grassland to woodland on more fertile soils, where invasion by vines is most common. They remain locally important, especially in more hilly regions—although original effects of extinct megafauna were probably concentrated on plains (e.g., Bullock & Pakeman 1997, Pykälä 2000, Vera 2000, Mountford & Peterken 2003, Willson 2006, Melick et al. 2007, Hodder & Bullock 2009, Smith 2010, Garcia 2012). In contrast, although livestock tended to replace large native herbivores in the southeastern U.S.A. during initial centuries of European settlement, open range has been greatly reduced in woodlands here after the 1930s, especially around more densely populated areas. Moreover, fencing generally provides ideal support for vines such as *Lonicera japonica*, while also reducing the movement of larger animals through the tangles.

The 'herbivore hypothesis' and its extensions. This hypothesis—with some corollaries—can be stated as follows (Campbell 2012): "Before human civilization, patterns of herbivory in space and time, especially by larger animals, were a major factor maintaining the diversity of woodland on eutrophic soils in temperate regions. If so, the modern decline in naturally-behaving larger animals has often allowed browsing-sensitive plants to increase in situations where they would have been more controlled in the past. Such plants would include some aliens that have now prospered in more populated regions, where even deer and livestock are restricted. In contrast to fire, the original impact of herbivory was concentrated on mineral-rich soils with the most productive vegetation. Moreover, regular browsing as well as rapid decomposition would have reduced fuel-loads in woodland on such soils."

The general elimination of larger herbivores from civilized landscapes, especially on more eutrophic soils suitable for agriculture, has left fundamental questions about the original ecology, how to conserve remnants, and how to restore functional systems in a post-modern world. These difficult questions have not received sufficient attention around the temperate world, except during recent years in Europe (Mitchell & Kirby 1990, VanWieren 1995, Pykälä 2000, Vera 2000, Kirby 2001, Bradshaw et al. 2003, Bakker et al. 2004, Mitchell 2005, Rackham 2006: 90–100, Takatsuki 2008, Hodder et al. 2009, Johnson 2009, Hédl et al. 2010, Kuijper 2011, Garcia 2012, Garcia et al. 2013). In eastern North America, the 'herbivore hypothesis' can be developed to help explain much vegetational pattern on more base-rich soils (e.g., Campbell 1989). A central concept is that prolonged intensive browsing is expected eventually to thin out relatively palatable plants on productive soils, but also to select for more tolerant or deterrent species that can predominate in the recovery from disturbance. Thus, a somewhat cyclical process can be envisaged—especially if trails and glades maintained by larger animals form a continually shifting dynamic network over the landscape, responding to changes in the browsable quality of vegetation (Campbell 2012). Such trails and glades might cover a small proportion of the landscape, but have a large influence on regeneration of trees.

Productivity, herbivory, morphology and chemistry. In eastern North America, effects of mammalian herbivores may have been most influential on the most fertile, productive soils—usually with moderate to high pH (ca. 5.5–6.5). Among large trees, in particular, there is a concentration on fertile soils of most species with thorns (Table 1) or with strongly repellant to toxic chemistry: these include *Aesculus*, *Carya* Sect. *Apocarya*, *Gymnocladus*, *Juniperus*, *Maclura*, *Platanus*, *Prunus* and *Robinia* on more fertile soils, versus *Pinus* and *Liquidambar* on less fertile soils (e.g., Atwood 1941, Burrows & Tyrl 2001). There is a similar concentration of trees with large fruits and seeds that appear adapted to dispersal in guts of large animals (Table 1)—cattle and deer in the central Ohio Valley still disperse some seeds of the ungulate-adapted tree, *Gymnocladus diocica*, despite a recent claim to the contrary (Zaya & Howe 2009). In addition, herbivory might have contributed to some trends in the gross vegetative morphology of trees, such as the tendency for clonal spread and compound leaves to be more frequent on more fertile soils (Table 1). But the potential selective effects of herbivory on morphology (Brown & Lawton 1991, Grubb 1992) will be difficult to separate from the effects of other disturbances.

As summarized in Table 7 and text above, many mid-temperate vines have deterrent chemistry, especially relatively short, herbaceous or deciduous species, but vining taxa tend to have less defensive chemistry than their closest non-vining relatives. The evergreen-tending genera typically lack toxic alkaloids and other complex, specialized compounds that do occur in the deciduous taxa. Instead, their deterrent chemistry is largely based on tannins, terpenoids (including saponins) and steroidal compounds. Such trends would accord with the concept that these evergreen-tending vines are more 'accessible' or 'apparent' to generalist herbivores during the winter, causing selection for more 'quantitative' unspecialized defenses (Feeney 1976, Grubb 1992, Stamp 2003).

Most temperate vines also lack 'spines'—woody thorns, cauline and foliar prickles. Among evergreen-tending species, spines form only in *Smilax*. A few deciduous species of *Rosa* and *Rubus* are somewhat vining and densely prickly, but also relatively short. Several species of herbaceous vines have rasping prickles (e.g., *Humulus*, some *Mimosa*) or stinging hairs on stems (e.g., *Tragia*), but only *Humulus* is a robust climber. Spines increase among vines of warmer zones (adding species of *Elaeagnus*, *Saurauia* and *Zanthoxylum* in East Asia), especially in the tropics (adding *Calamus* and many other genera)—where hooked spines enhance climbing ability as well as defense from herbivores (e.g., Putz & Mooney 1981, Grubb 1992, Kusumoto et al. 2012). One can hypothesize that most mid-temperate vines have been able to suffer the seasonal herbivory of larger mammals by recovering with vigorous growth in general, escaping into the canopy (Ashton & Lerdau 2008). The few spiny species (*Smilax,* *Rosa, Rubus*) are mostly short and concentrated in brushy transitions from woodland to grassland where larger herbivores may be more frequent. The many shrubs and trees with a thorny tendency (especially deciduous Araliaceae, Berberidaceae, Fabaceae, Rosaceae, Rutaceae) or with a prickly tendency (including the evergreen leaves of some *Ilex*, *Juniperus, Mahonia, Ulex*) are also typical of such habitats. The relatively defenseless *Ilex vomitoria* of southeastern U.S.A. is much browsed by deer (Halls & Boyd 1982).

An unusual feature in a few vines is variegated coloration on lower leaves, with yellowish to whitish stripes or mottles. Among temperate vines, this occurs only in some species of *Euonymus* (which also becomes purplish during the winter), *Hedera* (*helix* more than *hibernica*) and *Smilax* (especially *bona-nox* and *aspera*)—all evergreen-tending (Figure 1). Variegation of leaves is usually associated with relatively narrow or lobed shape, forming a 'juvenile' syndrome that is generally restricted to low shoots in the woods. Such shoots are more exposed to herbivores, especially during winter, and their coloration may have been selected as camouflage from larger animals with poor visual acuity (Givnish 1990). However, in *Smilax* these shoots often also extend into more open sunny areas, where their potential for warning coloration has been suggested (Lev-Yadun 2009). As reviewed by Givnish and Lev-Yadun, one can conceive of various interactions between leaves like these and the structure, chemistry or herbivory of vegetation, but there has been almost no experimental investigation.

Sexuality. Another character that may be influenced by herbivory is the dioecious tendency, including various subdioecious or polygamo-dioecious conditions (with bisexual plus unisexual individuals). Such sexual separation occurs in only 5-10% of all vascular plants but it is relatively frequent among vines (Renner & Ricklefs 1995). In the complete native plus alien flora of the Carolinas, Conn et al. (1980) reported an increase in dioecy (broadly defined) from

12.3% of 173 tree species, to 13.8% of 282 shrubs, to 15.7% of 102 woody or subshrubby vines. This trend is enhanced in Kentucky (Campbell & Medley 2012), with higher proportions of species overall: 21.5% of 107 trees, 16.7% of 156 shrubs, and 47.7% of 44 vines (or 41.7% of 24 vining genera). Included here as dioecious vines are *Celastrus scandens* (Mu et al. 2012) and *Rosa setigera,* a somewhat vining plant (Kemp et al. 1993), plus the eight species of *Vitis*—which are generally described as dioecious or polygamo-dioecious (Moore 1991, Olien 2001, Aradya et al. 2012). If the eight alien vines in Kentucky are excluded (of which only *C. orbiculatus* is dioecious-tending), the proportion is 55.6% (or 47.6% of 21 genera). These high proportions—as elsewhere in the Ohio Valley—may be part of a general association with nutritional factors. Among trees of Kentucky, at least, the dioecious tendency is associated with moderate to high soil fertility (Table 1).

Dioecious percentages of 15–45% (including polygamous transitions) may be typical for vines in subtropical to mid-temperate regions. High proportions among woody plus herbaceous vines are also reported from subtropical to mid-temperate, mineral-rich regions of China: 31.5% of 130 species in part of Zhejiang (Cai 1999); 32.4% of 330 in part of Hunan (Yan 2007); 35.5% of 62 in part of north Yunnan (Chen & Li (2008b); and 35.5.% of all 661 in southeast China (Cai & Song 2000). Lower proportions have been reported from some of the most tropical regions in China: 28.7% of 115 in part of south Yunnan (Chen & Li 2008a); 22.1% of 340 in Taiwan (Tseng et al. 2008). At the depauperate extreme, in Europe plus the Mediterranean region, there are only about eight native woody vines, of which two southern species are dioecious (*Smilax aspera*) or partially so (*Vitis vinifera*); the proportion could be higher if herbaceous vines are included (with several species of *Bryonia* and *Tamus* but also *Aristolochia*). In contrast, only 1–20% of vines (lianas) in most fully tropical floras are reported to be dioecious—proportions that are generally lower than among the trees (e.g., Renner & Ricklefs 1995, Gillespie 1999, VanDulmen 2001, Matallana et al. 2005, Machado 2006).

It is notable, then, that none of the six genera with strictly evergreen vines in mid-temperate regions have any degree of dioecy (Table 7)—despite several other strictly evergreen woody plants of mid-temperate zones being strictly dioecious (hollies, junipers, mistletoes, yews). In contrast, 3/5 of the genera with mixed evergreen and deciduous condition are dioecious or partially so; 4/14 of the largely deciduous genera; and 4/9 of the herbaceous to subshrubby taxa considered here ($P = 0.08$ with chi^2 test of strictly evergreen versus the rest). There is also a negative association between strict dioecy and the 'ascending' growth form with adventitious roots or pads (Table 9.5). Globally, vining taxa tend to have higher numbers of species than sister taxa (Gianoli 2004) and dioecious taxa tend to have fewer (Heilbuth 2000), but there are interesting exceptions. Among mid-temperate taxa, strictly dioecious genera have few species and are rarely invasive, but dioecious-tending genera tend to have wide global ranges (Table 8b). Moreover, genera with more than 10 vining species (Table 7) all have labile sexuality (partially dioecious or polygamo-dioecious: *Clematis, Vitis, Actinidia, Celastrus*) except for *Smilax*, which is strictly dioecious. Among woody plants of Kentucky, there are also intriguing associations between dioecy and habitat gradients (Table 1, Appendix 3).

How might these varied trends in sexuality be explained? Renner & Ricklefs (1995) suggested that successful fruit production by vines is particularly expensive—in terms of resources diverted from critical upward vegetative growth—and that this functional problem has led to delayed femaleness and then sexual specialization. Their hypothesis might apply to dioecious deciduous species, especially typical twiners, scramblers and tendrillers that are relatively light-demanding. But it may not apply to more the more shade-tolerant, slow-growing, ground-covering, evergreen-tending tree-ascenders. Moreover, the obligate outcrossing from sexual specialization in deciduous vines might be critical for rapid local genetic segregation (micro-evolution) in the more unpredictable biotic environments of larger forest gaps and transitions to open land. Instead, some of the evergreen-tending genera have relatively high chromosome numbers (Table 6), suggesting that polyploidy or other duplication of genome sections has been more important in their success.

It is also conceivable that intense herbivory in vine-rich eutrophic woodland has contributed to dioecy through sexual selection, with more defense in females than males. Again, evergreen-tending species can be excepted since they are more 'apparent' to larger herbivores during winter, increasing selection for general chemical defense. In those species, it is likely that any unusual male-tending genotypes with less defense would be extirpated by continual consumption for several months of the year. Some studies have shown that males in dioecious plant species often suffer higher degrees of herbivory than females, and tend to grow faster or have other vegetative diferences (e.g., Ågren 1987, 1988, Jing & Cooley 1990, Dawson & Ehleringer 1993, Ashman 2002, Stevens & Esser 2009; but see, Niesenbaum 1992, Retuerto et al. 2006). Differential responses to pathogens may also be involved, which needs much more investigation (Williams et al. 2011, Vegas-Frutis et al. 2012). While varied theories linking dioecy with consumers exist, it will be impossible to make real advances in understanding without directly measuring the effects of consumption.

Effects of larger herbivores on vines and associated vegetation. Table 11 summarizes evidence from studies of browsing effects of deer or livestock on evergreen-tending vines, which indicate general reductions of at least 25–90% within periods of several years. Deciduous vines and shrubs were much reduced in most cases as well. But statistical significance is lacking for some individual results, and most of these observations refer just to *Smilax* species, *Lonicera japonica* or *Hedera helix* in the southeastern U.S.A. or western Europe. Much more long-term research, in diverse regions and with a wide variety of vegetational parameters, will of course be essential for deeper understanding (Hester et al. 2000, Russell et al. 2001).

In a more general review of deer effects, Rooney (2009) showed that there is a general shift from dicot herbs and woody plants towards graminoids, ferns or lycopods. It should not be surprising that large herbivores can reduce palatable plants, but there are more fundamental issues in overall ecology and conservation—what plants replace the more sensitive species; are the replacements native (or otherwise desirable); and can the effects of herbivores be used to restore functioning systems? Details of the research summarized in Table 11 do provide some initial insights—abundant replacing species are native in some cases (e.g. *Asimina, Impatiens, Pteridium, Toxicodendron*) but weedy aliens have invaded in other cases. It is likely that results vary much depending on the timing and intensity of browsing. In particular, the appropriate seasons for more intense browsing deserve special consideration.

Remarkable insight to some montane East Asian bamboo forests was provided by Takatsuki (2009), who found that exclosure from dense populations of sika deer led to large increases in woody vines, shrubs and tree regeneration. The vines—deciduous *Actinidia arguta* and *Celastrus orbiculatus*—were virtually absent from the browsed forest. Initial work in the U.S.A. has confirmed that the highly invasive vine, *C. orbiculatus*, can be greatly reduced by deer (Rossell et al. 2007, Averill 2012). The associated evergreen bamboo in Takatsuki’s study (*Sasa nipponica*) also increased initially but after 12 years its biomass had become more or less equalized and leafy cover was 70% lower than the browsed condition, apparently due to strong competition from the released woody dicots. His observations—plus evidence that deer concentrate in temperate bamboo forests during winter (Igota et al. 2004)—accord with the idea that large herbivores have enhanced the cover of bamboo in such zones. Similar ungulate effects are suggested for much of the *Arundinaria gigantea* that used to cover lowlands in the southeastern U.S.A. (Campbell 1989, Platt & Brantley 1997). Yet other research on East Asian mountains has shown that browsing can sometimes allow relatively unpalatable weeds, shrubs and trees (such as *Picea*) to grow up within bamboo thickets (Takahashi & Kaji 2001, Nomiya et al. 2003, Darabant et al. 2007, Seki et al. 2012).

How might browsing effects vary in space and time? Dennis (1997) has provided perhaps the only detailed published research on effects of different seasons for browsing in temperate woodland. Although not based on a true experiment, her observations of woodlots compared those with no recent browsing by cattle (but probably more deer), cattle mostly in Apr to Nov, cattle mostly in late Jun to Nov, and cattle mostly in Dec to Mar; there were two sampled transects of 50 m^2 per treatment. The 'deferred' browsing of cattle in late Jun to Nov appeared to support the most native species among grasses, herbs and shrubs (ca. 83 versus 48 in the controls); there were few additional aliens (8 versus 4)—but *Lonicera japonica* was most abundant in this treatment, compared to all others. Woodlots browsed by cattle in Dec to Mar had the lowest cover of vines, shrubs and tree seedlings, with *Lonicera* completely absent, but alien grasses and other weeds were relatively frequent (19 species).

Patterns of herbivory may be substantially different on the modern landscape, compared to earlier periods. For example, historical records of "buffalo" (*Bison bison*) during 1750–86 in north-central Kentucky show distinct concentrations during May–Jun and Nov (Campbell 2012), and some of the pioneer literature suggested seasonal migrations from north in summer to south in winter (Roe 1951, Belue 1996). Extinct megafauna of eastern North America probably migrated in similar ways (Hoppe & Koch 2007, and their citations)—expanding licks into glades and moving much matter (Haynes 2012). In contrast, the current effects of white-tailed deer on woodland in Kentucky tend to be spread through the whole year, or may be most intense during winter. It is likely that the modern abundance of food for deer in farmland and along edges for much of the year—especially during summer—has substantial effects on browsing within many adjacent wooded areas. And the general lack of predators today, except for humans during hunting seasons, probably allows deer to forage in openings that would have been more exposed, dangerous, avoided places before Virginian settlement.

It is hypothesized here that (Aug–)Sep to Nov(–Dec) would be the most effective season for intense browsing to shift the balance from alien to native plants in eutrophic woodlands of east-central U.S.A. During those months, most natives have stopped growing new shoots or are dormant, while most of the more problematic alien plants tend to remain exposed and some keep growing—especially evergreen-tending vines like *Euonymus fortunei*, tardily deciduous shrubs like *Lonicera maackii*, biennials with rosettes like *Alliaria petiolata*, and fall-germinating winter annuals like *Stellaria media*. Tests of such hypotheses will be as important to restoration of eutrophic woodlands in east-central states as research on the effects of different fire seasons in pine-oak woodland of more southeastern states (e.g., Glitzenstein et al. 1995, Sparks et al. 1998, Flory & Lewis 2009).

It is also important to pursue more systematic research into how herbivory varies from deeply shaded forest interiors to tree-fall gaps to more open woodland, because the regeneration (and natural selection) of many vines, shrubs, trees and other plant species has probably been concentrated in gaps and openings (Grubb 1977, 1992, Hulme 1996). Although much information has been accumulated on spatial patterns in deer browsing, there have been surprisingly few studies that have linked this information to models of forest dynamics (Russell et al. 2001). Gap-related patterns appear to be highly varied. Some recent research has indicated little or no concentration of herbivory by deer in smaller gaps (e.g., Moser et al. 2008). But browsing on woody plants can be greatly influenced by presence of alternative higher quality shrubs (especially *Rubus*), herbs and grasses (e.g., Moser et al. 2006, Rackham 2006: 538, Abbas et al. 2012). Deer often forage into nearby farmland rather than focussing on small interior forest-gaps, where unusually dense populations may nip regenerating plants in the bud before substantial forage grows up. And sheep are clearly lured away in the winter from deeper deciduous woods with evergreen-tending undergrowth, if there is better forage nearby amongst cool-season grasses and herbs (e.g., Garin et al. 2000).

Comparison of browsing with burning effects. A corollary of the general 'herbivore hypothesis' for eutrophic woodland (as stated above) is that burning should decrease in relative importance with more browsing on damper, richer soils. Again, there have been surprisingly few studies in temperate forests that explore such relationships. However, general knowledge of forests in the east-central U.S.A. indicates that fires are most frequent on somewhat dry infertile soils—in the upper left sector of Figure 2 (e.g., Campbell et al. 1991). In contrast, effects of bison, elk, deer and beaver appear to have been most intense on more moist and fertile soils—in the lower right sector of Figure 2 (e.g., Campbell 1989).

It is well known that *Lonicera japonica* often occurs on moderately dry or infertile soils sites (Figure 1f), and that it can be reduced by repeated burning (Barden & Mathews 1980, Nuzzo 1997, Kush et al. 2000, Munger 2000, Wang et al. 2012). However, its vigorous resprouting after fires can produce more accessible browse for deer (Stransky 1984), and the potential for interaction with deer deserves further investigation. *Hedera* (ivy) provides an interesting contrast with *Lonicera*. Metcalfe (2005) noted: "Cutting and grazing generally reduce the competitive abilities of ivy, and it shows low tolerance of fire when it does burn [see also Úbeda et al., 2006]. However, being evergreen and with a relatively high water content, ivy is slow to burn and will not readily spread fire well. Consequently, ground planting with ivy has been proposed to reduce fire risk in seasonally dry areas (e.g. Utah Bureau of Land Management 2001)." Species of *Vinca* have also been recommended for living firebreaks in some states (e.g., Lippi & Kuypers 1998).

Potential importance of smaller herbivores and pathogens. Could consumers other than large herbivores influence vine populations? This question remains largely unanswered. For example, there might be considerable effects of small mammals on evergreen vines that cover the ground. In western Europe, the bank vole (*Clethrionomys glariolus*) is often associated with *Hedera*, but its potential use of the plant in winter does not seem to have been investigated (Alain et al. 2006). Larger birds (Anseriformes, Galliformes) can also feed much on these vines, which provide relative palatable forage that can sometimes balance effects of more toxic evergreen plants in the diet (e.g., Hewitt & Kirkpatrick 1977). It is likely that turkeys and geese, in particular, can influence establishment of woody seedlings in some habitats (Clark & Gage 1995, Hulme 1996, Rinkes 2004, Vera 2009). One might expect invertebrates to play an insignificant role during winter, compared to warm-blooded animals, but do evergreen leaves allow populations to build up on them in dormant states? Some types of insects, such as adelgids and scales, are often associated with evergreen plants (McClure 1989, Ward et al. 1995).

Ding et al. (2006) outlined prioritized “natural enemies” for trials in biological control of East Asian plants in North America, including *Euonymus fortunei* and some deciduous vines (*Ampelopsis brevipaniculata, Celastrus orbiculatus, Pueraria montana*). They identified 40 species of arthropods, fungi and microbial pathogens on *Euonymus* in China, 13 of which are limited to this genus and thus potential agents to develop. For *Ampelopsis*, these numbers are 22 and 4; for *Celastrus*, 9 and 5; for *Pueraria*, 200+ and perhaps 3+, but some of these can also feed on *Amphicarpaea* and *Glycine* (Frye et al. 2007, Imai et al. 2011, Ruberson et al. 2012). For *Hedera helix*, they are 122+ and perhaps 22+ (Metcalfe 2005); for *Lonicera japonica*, at least 16 (Larson et al. 2006).

There is little published evidence that any of the evergreen-tending vine species are controllable to a large extent by arthropods or pathogens, but further investigation is needed. Most information comes from cultivated plants. The ‘euonymus scale’ insect (*Unaspis euonymi*) is an Asian pest of *E. fortunei* and other Celastraceae, that was estimated to cause about 10% annual mortality in planted *E. fortunei* across southern New England (VanDriesche et al. 1998)—considered an economic problem for the horticultural industry! Also, a cosmopolitan anthracnose fungus (*Colletotrichum gloeosporoides*) has caused much loss to *fortunei* in nurseries (Ningen et al. 2005). Both the scale and the anthracnose generally cause more damage in sun than shade, and there is no evidence that they have caused significant damage to populations of the plant that have escaped into wooded areas. Several ‘leaf spot’ fungi are common aesthetic problems on *Hedera helix*, but, again, none are documented to cause significant problems for wild plants (Metcalfe 2005, Waggy 2010).

There has been much recent interest in potential biological control of the largely herbaceous vine, *Pueraria montana* (= *P. lobata*, kudzu). This species has been common in the southeastern U.S.A. for 90 years, with virtually no reduction by pests or pathogens until spread of the Asian plataspid (shield bug), *Megacopta cribraria*, after 2009. In Georgia, Zhang et al. (2012) found that feeding of this bug led to a total biomass reduction of 32.5 % during the first year of infestation. Frye et al. (2012) showed that such levels of damage could cause reduction but only if repeated for several years. However, the bug also damages soybeans and some native legumes, so will not be promoted for biological control of *Pueraria*.

Integration of experimental trials, woodland restoration and land economy. Several vines have become problematic invasive species outside their native ranges, especially among the evergreen-tending genera (Table 7, 8a). Is there any evidence that substantial control of alien vines—evergreen or deciduous—is possible, as a cost-effective enterprise within the context of modern society?

Many papers have been written about these aliens, much has been recommended, and considerable effort has been made at control within some tracts of land. Leaders in the U.S.A. have included organizations such as the The Nature Conservancy, National Park Service, U.S. Forest Sevice and their partners in state governments. Methods for manual, mechanical or chemical control have been generally determined. But the potential for biological control is still uncertain, and trials with livestock have been been rare. Moreover, the fundamental ecological and economic questions remain largely unanswered.
(1) Can naturalistic ‘macro-management’ of habitats shift the composition from alien to native species, so that expensive ‘micro-management’ of individual species is minimized?
(2) Can any management plan be implemented across large areas and be sustained by regular income and fees from that land, or (less likely) by donations and taxes from afar?

There has been remarkably little published evaluation of success versus failure in our varied options for management to control these vines across North America. For *Hedera*, Biggerstaff & Beck (2002, 2007a,b) studied the effectiveness of manual versus chemical control and subsequent recovery of native plants. Ingham (2008) compared control of *Hedera* by goats with mowing. However, these projects covered only a few years, and did not address deeper issues of economics or ecological sustainability. The direct or indirect costs of invasive species to society in general have sometimes been estimated (Pimentel et al. 2005). But while mechanical and chemical control are often prescribed for control of alien plants, there have been few publications on the direct continuing costs of using these methods for keeping populations down to an acceptably low standard—other than general reviews and theories (D'Antonio 2004, Olson 2006, Kim et al. 2007, Epanchin-Neill & Hastings 2010, Kettenring et al. 2011). Even simple statistics are inconsistently published in most regions, if at all, such as annual expenditures per acre and degrees of reduction in aliens at specific sites. And there appears to have been no proper analysis of the costs and benefits from using livestock—or perhaps wildlife management—to help control unwanted plants within temperate woodlands designed for native biological diversity. A more systematic approach is needed, as is being developed for rangelands in western states (Masters & Sheley 2001, Finnoff et al. 2008).

Even at well-known sites with much visibility in eastern states, background research and repeated effort, there does not seem to be an adequate stream of public information. For example, parks in or near Washington D.C. have had much invasion of *Hedera* that has been studied for over 30 years (Thomas 1980, 1988, Putz 1995, Swearingen & Diedrich. 2004). Organized control has been tried for up to a decade (e.g., Young et al. 2012). The National Park Service is now reportedly cooperating on *Hedera* reduction with the Rock Creek Conservancy (2012). And in addition to staff and volunteers, a private company was contracted for at least five years to work on 176 acres (Invasive Plant Control Inc. ca. 2008). Yet the recent General Management Plan for the park made no mention of invasive plant species (NPS 2007 and associated documents), and there does not appear to be any freely available official report about invasive plant reduction. Moreover, the recent Environmental Impact Statement for control of deer in Rock Creek Park (NPS 2012) makes virtually no reference to one potential benefit of high deer density in some places—reduction of some alien plants. A photograph was shown (p. 22), with caption: "Deer exclosure/fenced plot at edge of forest overrun by invasive plants. The plot was discarded because the number of nonnative plants biased the data."

There is currently a dearth of institutional interest in using large herbivores to reduce alien plants, recover natives, and restore structure within eutrophic deciduous woodlands. There have been a few experiments, with promising results (Brockway & Lewis 2003, Compton et al. 2003, Darabant et al. 2007, Harrington & Kathol 2009, Hedtcke et al. 2009). But there has been virtually no extension to larger scales on a continuing schedule. A few conservationists have urged deeper involvement (Cramer 1991, Dennis 1997, Williams 1997, Brower & Dennis 1998), and agriculturalists have sometimes outlined concepts of 'agroforestry' (Rule et al. 1994, Buffum et al. 2009, Guyer & Ponder 2012), but there appears to be general disinterest or resistance. Critics usually point to the ecological damage that extended use of livestock can cause (Dambach 1944a,b; Johnson 1952), without considering the value from short periods of intensive browsing that could simulate the original seasonal patterns of larger herbivores. With deer alone, there are well-documented cases of high densities promoting some aliens—such as *Alliaria petiolata* or *Microstegium vimineum* (Webster et al. 2008, Eschtruth & Battles 2009, Knight et al. 2009). More basic problems are the lack of generally accepted ecological models for original vegetation, a decline of knowledge and experience with livestock in modern society, and general aversion to dealing with large animals.

In the Bluegrass region of Kentucky, with unusually fertile soil on phosphatic limestone, there is evidence of much ancient interaction between larger herbivores and native vegetation—but no evidence of regular fires before Virginian settlement (Campbell 1989, McEwan & McCarthy 2008). Griffith Woods is a 745 acre farm that presents the best opportunity to restore something like the original woodland. The Nature Conservancy and University of Kentucky initiated a partnership here in 2003 for research and management, including comparisons of browsing, burning and mowing effects (Crowley 2002, Berry 2007). In association with this project and the National Fish & Wildlife Foundation, a cooperative weed committee was supposed to be established for the region (Campbell 2004b). *Euonymus fortunei* is one of the most problematic invasive plants in Bluegrass Woodlands, together with bush-honeysuckle (*Lonicera maackii*) and garlic-mustard (*Alliaria petiolata*). Yet there is much circumstantial evidence that cattle have kept the *Euonymus* out of woodland pastures at Griffith Woods and elsewhere (Figure 8). Ideally, cooperative planning for this site will enable long-term studies of how livestock can be used to advance ecological goals, integrated into a sustainable economy.

Just as a return to prescribed fire has proliferated within recent decades, it is reasonable to expect diverse benefits from a careful return to more management of ungulates. For example, the concept of regular browsing by sheep and goats in fenced blocks of larger urban parks has considerable traction—to reduce some alien plants at their most sensitive season, to provide local meat for the community, to allow long-term research with much visibility, to reconnect people with more ecological and economic heritage (Berry 1990). Both animals are known to relish vines like *Hedera* (Table 5), and sheep appear to consume *Alliaria* (garlic mustard). The latter is virtually absent from pastures of all types in Britain (Tansley 1939), and W. Berry (pers. comm.) observed substantial reduction of it after autumnal grazing by sheep in a large enclosed plot near Port Royal, Kentucky.

It is suggested here that satisfactory control of invasive plants in the remnants of temperate woodland on eutrophic soils of the eastern U.S.A. will only be possible with three basic organizing principles among human beings.
(1) Regional networks at a moderate spatial scale, large enough to allow a critical mass of local knowledge focussed on relatively homogeneous regions, not spread over too many states.
(2) Regular sharing and pooling of data on native composition and trends in invasive species—especially at managed sites, providing transparent accounting for costs and benefits.
(3) Reasonable discussion and debate about how to approach methods for long-term sustainability that includes overall well-being of human communities.

We should avoid sentimental attachments to the past, but still try to understand it better. With the ‘post-modern’ age of conservation, which has actually been brewing for millenia, a deeper functional understanding is needed to manage the reassembled plants and animals—retaining as much of the old as possible but applying the new towards reasonable balances. For clear thinking in North America (e.g., Porter & Underwood 1999, Wright 1999), it is good to compare notes from around the world (e.g., Vera 2009, Hughes et al. 2012). Some of the most difficult lessons may come from New Zealand, where extinct large avian herbivores were replaced by mammals but left many endemic spiny or cryptic plants (Brown & Lawton 1991, Grubb 1992). Conservationists and ecologists there are grappling with some of the most radical current changes within temperate forests anywhere (Parkes 2008, Tanentzap et al. 2009).

Table 11 [next page]. Summarized apparent effects of cattle or deer on evergreen-tending vines, from studies of exclosures or from comparisons of different browsing histories. Studies are listed alphabetically by authors (right column). Note that statistical significance is lacking in several individual cases, and only the studies of exclosures include proper controlled experiments; see text for discussion. See Appendix 1 for abbreviations of vine species. Responses indicated here are estimates based on varied measures of stem density or cover (not frequency in plots), unless otherwise stated; ? indicates unclear or varied response. The entries from Griggs et al. (2006) and Webster et al. (2005) summarize trends in importance values for exclosures and changes in Cades Cove attributed to deer over 20 years.

Species	**Treatment summary**	**Decrease amount**	**Other vine responses**	**Other changes in ground vegetation**	**Author, date, state**
Lonicera japonica	deer for 12 years versus exclosures	>90%	−Toxrad 80% − Parqui 60%	general decrease but increases in *Asimina*, other native tolerators	Asnani+ 2006 OH
Lonicera japonica	high versus low deer density	>90% in winter	− Smirot 80% − Toxrad 70% ? Parqui ? Vitspp	much less shrub layer (*Rosa multiflora, Ligustrum sinense*, etc.) esp. summer	Beaver 2011 TN
Smilax glauca	high versus low deer density	ca 90% in summer	as above	as above	Beaver 2011 TN
Smilax bona-nox	high versus low deer density	>90% in summer	as above	as abore	Beaver 2011 TN
Euonymus fortunei	cattle for 20 years in open woods versus excluded	>90%	decreases in Camrad Parqui Toxrad Smihis Vitvul	general decrease in shrub layer (*Rubus, Lonicera maackii* etc.) but more saplings of *Carya laciniosa*	Berry 2007 KY; + author's observa-tions
Lonicera japonica	cattle in winter for >15 years	>90%	+Toxrad 300% −Vitrip 30%	much less shrub layer; more annuals, weeds	Dennis 1997 IL
Hedera helix	numbers of trends outside 6 deer-exclosures	decrease in 83%	− Lonper in 2 + in other 2	general decrease in *Quercus, Salix, Rubus Carpinus, Sorbus* etc.	Gill+ 2001 EU (review)

Smilax glauca	deer for 8+ years versus exclosures and initial data	>90%	less vines in general − Smirot>50% − Lonjap (?)	much less shrubs, (Euoame, Gayurs, Vacspp etc.) and seedlings, but increases in Acerub, Tsucan, Rhomax	Griggs+ 2006; Webster+ 2005
Hedera helix	deer for 2 years versus exclosures	ca 50%		shrubs reduced by half (*Rubus, Vaccinium*); but *Erica* increased	Gonzalez-Herdandez + 1996 SP
Smilax spp.	deer for 7 years versus exclosures	ca 80%		also ca 90% reduction in *Rubus*; less of most trees except *Robinia*	Harlow+ 1970,1975
Hedera helix	deer for several years versus exclosures	ca 40%	− Lonper>90%	also reduction in *Rubus*; increases in *Pteridium*, grasses	Kirby 2001 EN Nagshead
Hedera helix	deer for 8 years versus exclosures	ca 10%	− others 40%: Ampbr Celorb Euofor Lonjap Parqui Smispp Toxrad Vitaes	general reduction of shrub layer by about half (incl. *Euonymus*, *Rubus*, *Vaccinium*)	Krafft+ 2011 DC
Lonicera japonica	cattle for 4 years (in 2 months/year)	>90%		much less shrub layer (*Robinia, Rosa multiflora, Rubus*)	Luginbuhl+ 2000 NC

Hedera helix	ponies, cattle and deer for 22 years versus deer only	60% less in plot frequency	− Lonper 60% less in plot frequency	>90% decrease in *Rubus* frequency; 40% increase in *Pteridium*; 100%+ in grasses	Putman+ 1989
Lonicera japonica	deer for 2 years versus exclosures	>90%	− Parqui 60% ? Smispp ? Vitrot	5-10% decrease in woody plants <1.4 m; esp. *Rubus*; increases in *Fagus, Vaccinium*	Thrift 2007 SC
Lonicera japonica	high versus low deer density (many years)	>90% ?	− Parqui 30% − Smispp 15% − Vitrot 15%	ca 40% decrease in woodies <13 cm dbh; esp. *Quercus, Prunus, Liriodendron, Oxydendrum*; increases in *Cornus, Nyssa*	Thrift 2007 SC
Decumaria barbara	high versus low deer density	>50%	as above	as above	Thrift 2007 SC
Smilax spp.	deer for 2-5 years versus exclosures	2–40% but recovered	− Vitspp 70%?	ca 15% decrease in woody plants <1.4 m; esp. *Acer saccharum, Prunus serotina, Betula lenta, Rubus*; but increase in *Fagus*	Thrift 2007 WV
Hedera helix	cattle continual for 4 years	> 90%	−Vinmin>90%	much less *Rubus*; less vernal herbs	Uytvanck+ 2009 BE

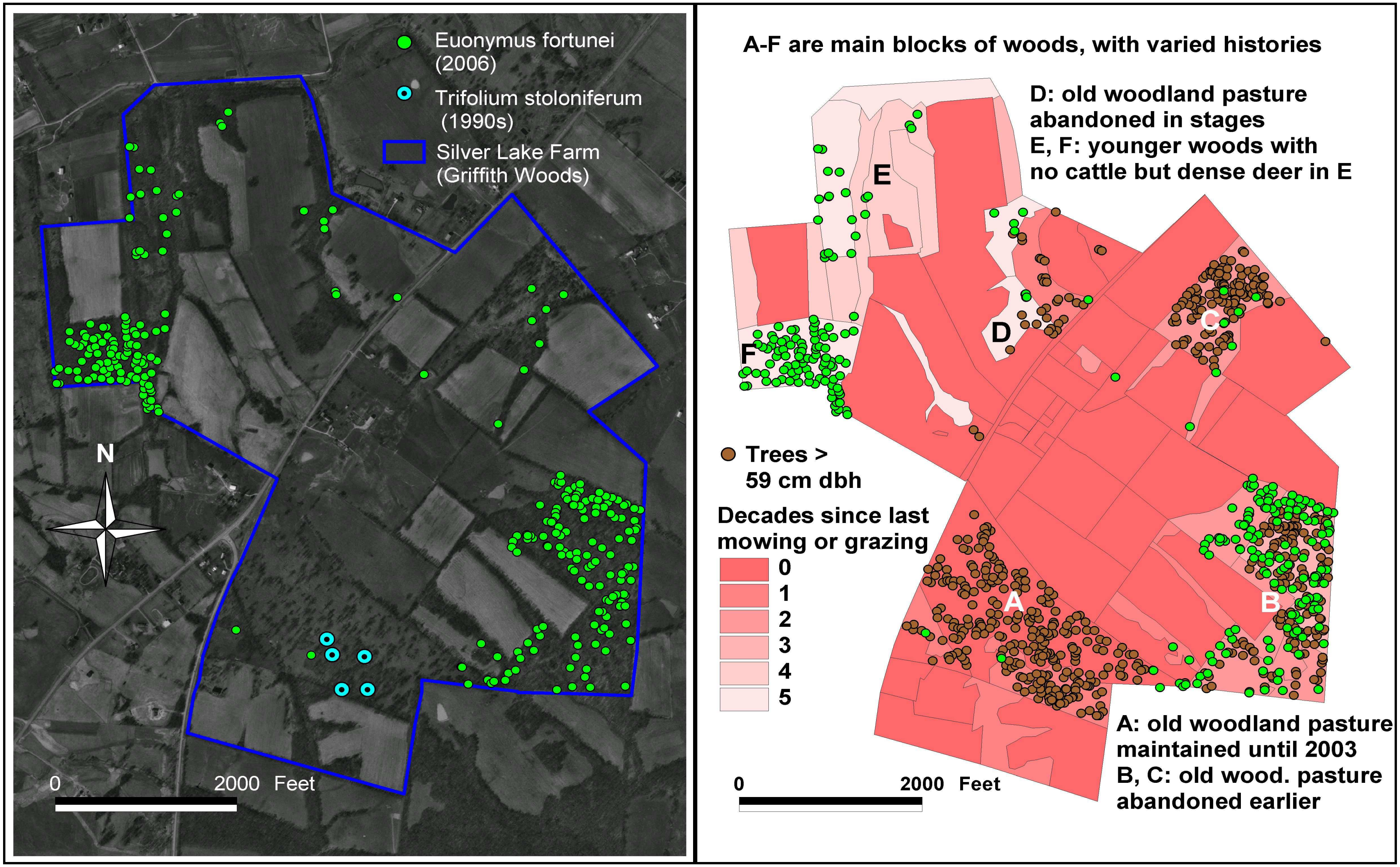


Figure 8. Maps of Griffith Woods (Harrison Co., Kentucky) showing locations of *Euonymus fortunei* and *Trifolium stoloniferum* in relation to management history. These data were assembled in 2003-2007, with assistance of Berry (2007). The old 'savanna' to south (A) was partly unmowed since 1986, leading to thickets of *Carya laciniosa*/*ovata* (which cattle do not eat) plus patches of the endangered clover.

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[*abstracts only seen, full papers not yet available in Kentucky; ** priorities to secure]

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APPENDIX ONE
Six-letter abbreviations for woody species used in Figures 2 and 3

T1 = large tree; T2 = small tree; S1 = large shrub; S2 = small shrub; V1 = large vine; V2 = small vine. See Campbell & Medley (2012) and Weakley (2012) for distributions, nomenclature, synonyms, etc.

Abbrev	Full Binomial Name	LF
Aceflo	Acer floridanum (Chapman) Pax	T1
Aceneg	Acer negundo L.	T1
Acenig	Acer nigrum Michx. f.	T1
Acepen	Acer pensylvanicum L.	T2
Acepla	Acer platanoides L.	T1
Acertr	Acer rubrum L. var. trilobum Torr. & Gray ex K. Koch	T1
Acerub	Acer rubrum L. var. rubrum	T1
Acesac	Acer saccharum Marsh. var. saccharum	T1
Acesch	Acer saccharum Marsh. var. schneckii Rehd.	T1
Acesnm	Acer saccharinum L.	T1
Acespi	Acer spicatum Lam.	T2
Aesfla	Aesculus flava Ait.	T1
Aesgla	Aesculus glabra Willd.	T1
Aespav	Aesculus pavia L.	T2
Ailalt	Ailanthus altissima (P. Mill.) Swingle	T1
Albjul	Albizia julibrissin Durazz.	T1
Alnser	Alnus serrulata (Ait.) Willd.	S1
Amearb	Amelanchier arborea (Michx. f.) Fern.	T2
Amelae	Amelanchier laevis Wieg.	T2
Amesan	Amelanchier sanguinea (Pursh) DC.	S2
Amespi	Amelanchier spicata (Lam.) K. Koch	S2
Amocro	Amorpha croceolanata Wats.	S2
Amofru	Amorpha fruticosa L.	S1
Amonit	Amorpha nitens Boynt.	S2
Amparb	Ampelopsis arborea (L.) Koehne	V1
Ampcor	Ampelopsis cordata Michx.	V1
Araspi	Aralia spinosa L.	T2
Aroarb	Aronia arbutifolia (L.) Pers.	S1
Aromel	Aronia melanocarpa (Michx.) Ell.	S1
Aruapp	Arundinaria appalachiana Triplett, Weakley, & L.G. Clark	S2
Arugig	Arundinaria gigantea (Walt.) Muhl.	S2
Arutec	Arundinaria tecta (Walt.) Muhl.	S2
Asitri	Asimina triloba (L.) Dunal	T2
Bersca	Berchemia scandens (Hill) K. Koch	V2
Betall	Betula alleghaniensis Britt.	T1
Betlen	Betula lenta L.	T1
Betnig	Betula nigra L.	T1
Bigcap	Bignonia capreolata L.	V1
Brbcan	Berberis canadensis P. Mill.	S2
Bropap	Broussonetia papyrifera (L.) L'Hér. ex Vent.	T1
Calflo	Calycanthus floridus L. var. glaucus (Willd.) Torr. & Gray	S1
Callyo	Calycocarpum lyonii (Pursh) Gray	V2
Camrad	Campsis radicans (L.) Seem. ex Bureau	V1
Caraqu	Carya aquatica (Michx. f.) Nutt.	T1
Carcar	Carya carolinae-septentrionalis (Ashe) Engl. & Graebn.	T1
Carcor	Carya cordiformis (Wangenh.) K. Koch	T1
Cargla	Carya glabra (P. Mill.) Sweet	T1
Carill	Carya illinoinensis (Wangenh.) K. Koch	T1
Carlac	Carya laciniosa (Michx. f.) G. Don	T1
Carova	Carya ovata (P. Mill.) K. Koch	T1
Carovl	Carya X ovalis (Wangenh.) Sarg.	T1
Carpall	Carya pallida (Ashe) Engl. & Graebn.	T1
Cartom	Carya tomentosa (Lam. ex Poir.) Nutt.	T1
Casden	Castanea dentata (Marsh.) Borkh.	T1
Caspum	Castanea pumila (L.) P. Mill.	T2
Catbig	Catalpa bignonioides Walt.	T1
Catspe	Catalpa speciosa (Warder) Warder ex Engelm.	T1
Ceaame	Ceanothus americanus L.	S2
Cellae	Celtis laevigata Willd.	T1

Celocc	Celtis occidentalis L.	T1
Celten	Celtis tenuifolia Nutt.	T2
Cepocc	Cephalanthus occidentalis L.	S1
Cercan	Cercis canadensis L.	T2
Chivir	Chionanthus virginicus L.	T2
Claken	Cladrastis kentukea (Dum.-Cours.) Rudd	T1
Cleacu	Clethra acuminata Michx.	S1
Clecat	Clematis catesbyana Pursh	V2
Cleter	Clematis terniflora DC.	V2
Clevir	Clematis virginiana L.	V2
Clsorb	Celastrus orbiculatus Thunb.	V2
Clssca	Celastrus scandens L.	V2
Coccar	Cocculus carolinus (L.) DC.	V2
Comper	Comptonia peregrina (L.) Coult.	S2
Coralt	Cornus alternifolia L. f.	S1
Coramm	Cornus amomum P. Mill.	S1
Cordru	Cornus drummondii C.A. Mey.	S1
Corflo	Cornus florida L.	T2
Corobl	Cornus obliqua Raf.	S1
Corrac	Cornus racemosa Lam.	S1
Corsto	Cornus stolonifera Michx.	S1
Corstr	Cornus stricta Lam.	S1
Cracal	Crataegus calpodendron (Ehrh.) Medik.	T2
Crachr	Crataegus chrysocarpa Ashe ?	T2
Cracoc	Crataegus coccinea L. ?	T2
Cracol	Crataegus collina Chapman	T2
Cracru	Crataegus crus-galli L.	T2
Craeng	Crataegus engelmanii Sarg.	T2
Cragat	Crataegus gattingeri Ashe	T2
Crainc	Crataegus incaedua Sarg. ?	T2
Craint	Crataegus intricata Lange	T2
Craira	Crataegus iracunda Beadle	T2
Cramac	Crataegus macrosperma Ashe	T2
Cramar	Crataegus marshallii Egglest.	T2
Cramol	Crataegus mollis Scheele	T2
Craper	Crataegus persimilis Sarg. ?	T2
Crapru	Crataegus pruinosa (Wendl. f.) K. Koch	T2
Crapun	Crataegus punctata Jacq.	T2
Craspa	Crataegus spathulata Michx.	T2
Crasuc	Crataegus succulenta Schrad. ex Link	T2
Crauni	Crataegus uniflora Muenchh.	T2
Cravir	Crataegus viridis L.	T2
Crlame	Corylus americana Walt.	S1
Crpcar	Carpinus caroliniana Walt.	T2
Cyrrac	Cyrilla racemiflora L.	T2
Decver	Decodon verticillatus (L.) Ell.	S2
Diopub	Diospyros virginiana L. var. virginiana	T1
Diovir	Diospyros virginiana L. var. pubescens (Pursh) Dippel	T1
Dirpal	Dirca palustris L.	S2
Elamul	Elaeagnus multiflora Thunb.	T2
Eleumb	Elaeagnus umbellata Thunb.	S1
Eubrec	Eubotrys recurva (Buckl.) Britt.	S2
Euoame	Euonymus americanus L.	S2
Euoatr	Euonymus atropurpureus Jacq.	S1
Euofor	Euonymus fortunei (Turcz.) Hand.-Maz.	V1
Faggra	Fagus grandifolia Ehrh.	T1
Foracu	Forestiera acuminata (Michx.) Poir.	S1
Forlig	Forestiera ligustrina (Michx.) Poir.	T2
Fraame	Fraxinus americana L.	T1
Frabil	Fraxinus biltmoreana Beadle	T1
Frapen	Fraxinus pennsylvanica Marsh var. pennsylvanica	T1
Frasub	Fraxinus pennsylvanica Marsh. var. subintegerrima (-) Fern.	T1
Frapro	Fraxinus profunda (Bush) Bush	T1
Fraqua	Fraxinus quadrangulata Michx.	T1
Frasma	Fraxinus smallii Beadle	T1
Frncar	Frangula caroliniana (Walt.) Gray	T2
Gaybac	Gaylussacia baccata (Wangenh.) K. Koch	S2
Gaybra	Gaylussacia brachycera Michx.	S2
Gleaqu	Gleditsia aquatica Marsh.	T1
Gletri	Gleditsia triacanthos L.	T1
Gymdio	Gymnocladus dioicus (L.) K. Koch	T1
Haltet	Halesia tetraptera Ellis	T1
Hamvir	Hamamelis virginiana L.	S1
Hedhel	Hedera helix L.	V1

Humlup	Humulus lupulus L.	V2
Hydarb	Hydrangea arborescens L.	S2
Hyplob	Hypericum lobocarpum Gattinger	S2
Hyppro	Hypericum prolificum L.	S2
Iledec	Ilex decidua Walt.	S1
Ilemon	Ilex montana Torr. & Gray ex Gray var. montana	S1
Ileopa	Ilex opaca Ait.	T2
Ilever	Ilex verticillata (L.) Gray	S1
Isomac	Isotrema macrophylla (Lam.) C.F. Reed	V2
Isotom	Isotrema tomentosa (Sims) Huber	V2
Itevir	Itea virginica L.	S2
Jugcin	Juglans cinerea L.	T1
Jugnig	Juglans nigra L.	T1
Juncom	Juniperus communis L.	S1
Junvir	Juniperus virginiana L.	T1
Kalbux	Kalmia buxifolia (Berg.) Gift, Kron, & Stevens	S2
Kallat	Kalmia latifolia L.	S1
Lacmul	Lackeya multiflora (Torr. & Gray) Fortunato, Queiroz & Lewis	V2
Leufon	Leucothoe fontanesiana (Steud.) Sleumer	S2
Linben	Lindera benzoin (L.) Blume	S1
Liqsty	Liquidambar styraciflua L.	T1
Lirtul	Liriodendron tulipifera L.	T1
Londio	Lonicera dioica L.	V2
Lonpro	Lonicera prolifera (Kirchn.) Rehd.	V2
Lonsem	Lonicera sempervirens L.	V2
Lyolig	Lyonia ligustrina (L.) DC.	S1
Macpom	Maclura pomifera (Raf.) Schneid.	T1
Magacu	Magnolia acuminata (L.) L.	T1
Magfra	Magnolia fraseri Walt.	T1
Magmac	Magnolia macrophylla Michx.	T1
Magpyr	Magnolia pyramidata Bartr.	T1
Magtri	Magnolia tripetala (L.) L.	T1
Magvir	Magnolia virginiana L.	T2
Malang	Malus angustifolia (Ait.) Michx.	T2
Malbac	Malus baccata (L.) Borkh.	T2
Malcor	Malus coronaria (L.) P. Mill.	T2
Malioe	Malus ioensis (Wood) Britt.	T2

Malpum	Malus pumila P. Mill.	T1
Mencan	Menispermum canadense L.	V2
Moralb	Morus alba L.	T1
Morrub	Morus rubra L.	T1
Nesumb	Nestronia umbellula Raf.	S2
Nysaqu	Nyssa aquatica L.	T1
Nysbif	Nyssa biflora Walt.	T1
Nyssyl	Nyssa sylvatica Marsh.	T1
Ostvir	Ostrya virginiana (P. Mill.) K. Koch	T2
Oxyden	Oxydendrum arboreum (L.) DC.	T2
Parqui	Parthenocissus quinquefolia (L.) Planch.	V1
Perpal	Persea palustris (Raf.) Sarg.	T2
Phihir	Philadelphus hirsutus Nutt.	S2
Phiint	Philadelphus intectus Beadle ?	S1
Phipub	Philadelphus pubescens Loisel.	S2
Pholeu	Phoradendron leucarpum (Raf.) Reveal & M.C. Johnston	V0
Phyopu	Physocarpus opulifolius (L.) Maxim.	S2
Pinech	Pinus echinata P. Mill.	T1
Pinell	Pinus elliottii Engelm.	T1
Pinpal	Pinus palustris P.Mill.	T1
Pinpun	Pinus pungens Lam.	T1
Pinrig	Pinus rigida P. Mill.	T1
Pinser	Pinus serotina Michx.	T1
Pinstr	Pinus strobus L.	T1
Pintae	Pinus taeda L.	T1
Pinvir	Pinus virginiana P. Mill.	T1
Plaaqu	Planera aquatica J.F. Gmel.	T2
Plaocc	Platanus occidentalis L.	T1
Popdel	Populus deltoides Bartr. ex Marsh.	T1
Popgra	Populus grandidentata Michx.	T1
Pophet	Populus heterophylla L.	T1
Pruame	Prunus americana Marsh.	T2
Pruang	Prunus angustifolia Marsh.	T2
Pruavi	Prunus avium (L.) L.	T1
Pruhor	Prunus hortulana Bailey	T2
Prumah	Prunus mahaleb L.	T2
Prumex	Prunus mexicana S. Wats.	T2

Prumun	Prunus munsoniana W. Wight & Hedrick	T2
Pruser	Prunus serotina Ehrh.	T1
Pruvir	Prunus virginiana L.	S1
Ptetri	Ptelea trifoliata L.	S1
Puemon	Pueraria montana (Lour.) Merr.	V2
Pyrcal	Pyrus calleryana Dcne.	T1
Pyrcom	Pyrus communis L.	T1
Pyrpub	Pyrularia pubera Michx.	S1
Quealb	Quercus alba L.	T1
Quebic	Quercus bicolor Willd.	T1
Quecoc	Quercus coccinea Muenchh.	T1
Quefal	Quercus falcata Michx.	T1
Quehem	Quercus hemisphaerica Bartram ex Willd.	T1
Queili	Quercus ilicifolia Wangenh.	T2
Queimb	Quercus imbricaria Michx.	T1
Queinc	Quercus incana Bartram	T2
Quelae	Quercus laevis Walt.	T2
Quelau	Quercus laurifolia Michx.	T1
Quelyr	Quercus lyrata Walt.	T1
Quemac	Quercus macrocarpa Michx.	T1
Quemar	Quercus marilandica Muenchh.	T1
Quemic	Quercus michauxii Nutt.	T1
Quemon	Quercus montana Willd.	T1
Quemrg	Quercus margaretta Ashe ex Small	T2
Quemue	Quercus muehlenbergii Engelm.	T1
Quenig	Quercus nigra L.	T1
Quepag	Quercus pagoda Raf.	T1
Quepal	Quercus palustris Muenchh.	T1
Quephe	Quercus phellos L.	T1
Quepri	Quercus prinoides Willd.	T2
Querub	Quercus rubra L.	T1
Quesch	Quercus shumardii Buckl. var. schneckii (Britt.) Sarg.	T1
Queshu	Quercus shumardii Buckl.	T1
Quesin	Quercus sinuata Walt.	T1
Queste	Quercus stellata Wangenh.	T1
Quetex	Quercus texana Buckl.	T1
Quevel	Quercus velutina Lam.	T1

Rhalan	Rhamnus lanceolata Pursh	S1
Rhoarb	Rhododendron arborescens (Pursh) Torr.	S1
Rhocal	Rhododendron calendulaceum (Michx.) Torr.	S1
Rhocan	Rhododendron canescens (Michx.) Sweet	S1
Rhocat	Rhododendron catawbiense Michx.	S1
Rhocum	Rhododendron cumberlandense E.L. Braun	S1
Rhomax	Rhododendron maximum L.	T2
Rhomin	Rhododendron minus Michx.	S1
Rhoper	Rhododendron periclymenoides (Michx.) Shinners	S1
Rhopri	Rhododendron prinophyllum (Small) Millais	S1
Rhuaro	Rhus aromatica Ait.	S2
Rhucop	Rhus copallinum L. var. latifolia Engl.	S1
Rhugla	Rhus glabra L.	S1
Rhutyp	Rhus typhina L.	T2
Ribame	Ribes americanum P. Mill.	S2
Ribcyn	Ribes cynosbati L.	S2
Ribmis	Ribes missouriense Nutt.	S2
Robboy	Robinia boyntonii Ashe	S2
Robhis	Robinia hispida L.	S2
Robpse	Robinia pseudoacacia L.	T1
Roscar	Rosa carolina L.	S2
Rospal	Rosa palustris Marsh.	S2
Rosset	Rosa setigera Michx.	S2
Ruball	Rubus allegheniensis Porter	S2
Rubalu	Rubus alumnus Bailey	S2
Rubarg	Rubus argutus Link	S2
Rubcan	Rubus canadensis L.	S2
Rubdep	Rubus depavitus Bailey	S2
Rubfro	Rubus frondosus Bigelow	S2
Rublau	Rubus laudatus Berger	S2
Rubocc	Rubus occidentalis L.	S2
Rubodo	Rubus odoratus L.	S2
Rubpen	Rubus pensilvanicus Poir.	S2
Rubror	Rubus roribaccus (Bailey) Rydb.	S2
Salamy	Salix amygdaloides Anderss.	T2
Salcar	Salix caroliniana Michx.	S1
Saldis	Salix discolor Muhl.	S1

Saleri	Salix eriocephala Michx.	S1
Salhum	Salix humilis Marsh.	S2
Salint	Salix interior Rowlee	T2
Salnig	Salix nigra Marsh.	T1
Salocc	Salix occidentalis Walt.	S2
Salser	Salix sericea Marsh.	S1
Samcan	Sambucus canadensis L.	S1
Sampub	Sambucus pubens Michx.	S1
Sasalb	Sassafras albidum (Nutt.) Nees	T1
Sidlyc	Sideroxylon lycioides L.	T2
Smibon	Smilax bona-nox L.	V1
Smigla	Smilax glauca Walt.	V1
Smihis	Smilax hispida Muhl. ex Torr.	V1
Smirot	Smilax rotundifolia L.	V1
Spialb	Spiraea alba Du Roi	S2
Spitom	Spiraea tomentosa L.	S2
Sprvir	Spiraea virginiana Britt.	S1
Statri	Staphylea trifolia L.	S1
Steova	Stewartia ovata (Cav.) Weatherby	T2
Styame	Styrax americanus Lam.	S2
Symalb	Symphoricarpos albus (L.) Blake	S2
Symorb	Symphoricarpos orbiculatus Moench	S2
Taxasc	Taxodium ascendens Brong.	T1
Taxdis	Taxodium distichum (L.) L.C. Rich.	T1
Thuocc	Thuja occidentalis L.	T1
Thydif	Thyrsanthella difforme (Walter) Pichon	V2
Tilame	Tilia americana L.	T1
Tilhet	Tilia heterophylla Vent.	T1
Toxrad	Toxicodendron radicans (L.) Kuntze	V1
Toxver	Toxicodendron vernix (L.) Kuntze	S1
Tsucan	Tsuga canadensis (L.) Carr.	T1
Txscan	Taxus canadensis Marsh.	S2
Ulmala	Ulmus alata Michx.	T1
Ulmame	Ulmus americana L.	T1
Ulmpum	Ulmus pumila L.	T1
Ulmrub	Ulmus rubra Muhl.	T1
Ulmser	Ulmus serotina Sarg.	T1
Ulmtho	Ulmus thomasii Sarg.	T1
Vacarb	Vaccinium arboreum Marsh.	S1
Vaccon	Vaccinium constablaei Gray	S1
Vaccor	Vaccinium corymbosum L.	S1
Vacery	Vaccinium erythrocarpum Michx.	S2
Vacfus	Vaccinium fuscatum Ait.	S1
Vacpal	Vaccinium pallidum Ait.	S2
Vacsim	Vaccinium simulatum Small	S1
Vacsta	Vaccinium stamineum L.	S2
Vibace	Viburnum acerifolium L.	S1
Vibcas	Viburnum cassinoides L.	S1
Vibdea	Viburnum deamii Rehd.	S1
Viblan	Viburnum lantanoides Michx.	S1
Vibmol	Viburnum molle Michx.	S1
Vibnud	Viburnum nudum L.	S1
Vibpru	Viburnum prunifolium L.	T2
Vibraf	Viburnum rafinesquianum J.A. Schultes var. affine (-) House	S1
Vibrec	Viburnum recognitum Fern.	S1
Vibruf	Viburnum rufidulum Raf.	T2
Vitaes	Vitis aestivalis Michx. var. aestivalis	V1
Vitbai	Vitis baileyana Munson	V1
Vitcin	Vitis cinerea (Engelm.) Millard	V1
Vitlab	Vitis labrusca L.	V1
Vitpal	Vitis palmata Vahl	V1
Vitrip	Vitis riparia Michx.	V1
Vitrot	Vitis rotundifolia Michx.	V1
Vitrup	Vitis rupestris Scheele	V2
Vitvul	Vitis vulpina L.	V1
Wismac	Wisteria macrostachya (Torr. & Gray) Nutt. ex Rbns. & Fern.	V2
Xansim	Xanthorhiza simplicissima Marsh.	S2
Zaname	Zanthoxylum americanum P. Mill.	S1

APPENDIX TWO
List of plots in VegBank with occurrences of evergreen vines for Figure 2 (Dec 2012).

Figure 2c: ***Hedera helix***
#1 http://vegbank.org/cite/VB.Ob.4058.ROCR53
#2 http://vegbank.org/cite/VB.Ob.4059.ROCR54
#3 http://vegbank.org/cite/VB.Ob.4066.ROCR61
#4 http://vegbank.org/cite/VB.Ob.3930.ROCR24
#5 http://vegbank.org/cite/VB.Ob.4056.ROCR51
#6 http://vegbank.org/cite/VB.Ob.4057.ROCR52

Figure 2d: ***Euonymus fortunei***
1 http://vegbank.org/cite/VB.Ob.4056.ROCR51

Figure 2e: ***Bignonia capreolata.***
1 http://vegbank.org/cite/VB.Ob.25891.COSW115
#2 http://vegbank.org/cite/VB.Ob.25992.COSW212
#3 http://vegbank.org/cite/VB.Ob.25920.COSW248
#4 http://vegbank.org/cite/VB.ob.26507.CHAT43
#5 http://vegbank.org/cite/VB.Ob.25985.COSW205
#? see *Lonicera japonica* #14 and *Smilax bona-nox* # 8;

Figure 2f: ***Lonicera japonica***

#1 http://vegbank.org/cite/VB.Ob.3623.HAFE11
#2 http://vegbank.org/cite/VB.Ob.26027.027020553
#3 http://vegbank.org/cite/urn:lsid:cvs.bio.unc.edu:observation:7349-{CCCB9791-7B32-4428-B3D9-4F5BCB0FA01D}
#4 http://vegbank.org/cite/VB.Ob.26114.027090002
#5 http://vegbank.org/cite/VB.Ob.4081.ROCR79
#6 http://vegbank.org/cite/urn:lsid:cvs.bio.unc.edu:observation:8161-{7102FDB7-0DA9-4A1B-8D1C-7F81A39B2769}
#7 http://vegbank.org/cite/VB.Ob.4727.VAFO60
#8 http://vegbank.org/cite/VB.Ob.26108.027080400
#9 http://vegbank.org/cite/VB.Ob.3553.HAFE21
#10 http://vegbank.org/cite/VB.Ob.26028.027020554
#11 http://vegbank.org/cite/urn:lsid:cvs.bio.unc.edu:observation:8197-{A00CBEE5-2994-4DDC-9E2F-3A25B2AEC71E}
#12 http://vegbank.org/cite/urn:lsid:cvs.bio.unc.edu:observation:8162-{691FD52B-FE14-4293-8842-BA2CC63134C3}
#13 http://vegbank.org/cite/VB.Ob.4699.VAFO32
#14 http://vegbank.org/cite/VB.ob.27093.HOLL2; also has Bigcap
#15 http://vegbank.org/cite/VB.Ob.4711.VAFO44
#16 http://vegbank.org/cite/VB.Ob.4069.ROCR66
#17 http://vegbank.org/cite/VB.Ob.3952.ROCR74

Figure 2g: ***Lonicera sempervirens*****.**
With zero plot data, typical associates are gleaned from miscellaneous literature; see also caption to Figure 1 for some sources.

Figure 2h: ***Smilax bona-nox*****.**
#1 http://vegbank.org/cite/VB.ob.26361.CHAT96
#2 http://vegbank.org/cite/VB.ob.26694.CHAT38
#4 http://vegbank.org/cite/VB.ob.27160.HOLL22
#5 http://vegbank.org/cite/VB.ob.26497.BANK37
#6 http://vegbank.org/cite/VB.ob.26751.CHAT51
#7 http://vegbank.org/cite/VB.Ob.25961.COSW121
#8 http://vegbank.org/cite/VB.Ob.25893.COSW117; also has Bigcap
#9 http://vegbank.org/cite/VB.Ob.25992.COSW212

Figure 2i: Smilax glauca.
#1 http://vegbank.org/cite/VB.Ob.4565.FIIS44
#2 http://vegbank.org/cite/VB.Ob.4566.FIIS45
#3 http://vegbank.org/cite/VB.ob.26485.CHER29
#4 http://vegbank.org/cite/VB.ob.26474.CHAT3
#5 http://vegbank.org/cite/VB.ob.26688.CHAT32
#6 http://vegbank.org/cite/VB.ob.26505.CHAT41
#7 http://vegbank.org/cite/VB.ob.26654.BANK61
#8 http://vegbank.org/cite/VB.ob.26695.CHAT39
#9 http://vegbank.org/cite/VB.ob.26468.CHAT24
#10 http://vegbank.org/cite/VB.ob.26905.APAL74

#11 http://vegbank.org/cite/VB.Ob.4570.FIIS1
#12 http://vegbank.org/cite/VB.Ob.4608.FIIS39
#13 http://vegbank.org/cite/VB.ob.26793.APAL25

APPENDIX THREE

Modal positions of dioecious trees, shrubs and vines along hydrological gradients

The following figures compare typical habitats of dioecious woody species with all woody species for Kentucky or other eastern states, following the format of Figure 2.

Among trees, shrubs and vines, there appear to be concentrations in the broad zone between: (a) deeper woods on better drained terraces and hills; versus (b) wetlands, thin woods, shrubland and grassland on drier ground. It is also notable that among dominant herbaceous families typical of open lands, relatively few are dioecious or even dioecious-tending. Following is an incomplete initial listing for Kentucky; * most/all alien. In deeper woods, especially mesic woods of various types, there are virtually no typical dioecious herbaceous species, with the notable exception of those marked @.

Ranunculaceae: *Thalictrum@* (all?). Saxifragaceae: *Astilbe@*.
Rosaceae: *Fragaria*. Cannabaceae: *Cannabis*. Cucurbitaceae: *C. foetidissima* (check others).
Urticaceae: *Urtica* (esp. *dioica**); see also flexible monoecy in *Laportea@*.
Caryophyllaceae: some *Silene**. Polygonaceae: *Rumex acetosella*+*, *P. amphibium* (?).
Amaranthaceae: *Amaranthus tuberculatus* group (partly adventive).
Solanaceae: *S. carolinianum* (andromonoecious). Ericaceae: *Epigaea* (Conn et al. 1980).
Araliaceae: *Aralia nudicaulis@*; note also sex-changing *Panax.trifolium*.
Asteraceae: *Antennaria*, *Anaphalis*.
Naijadaceae: *Naijas marina**; see also sex-changing *Arisaema*.
Liliales: *Asparagus**; *Chamaelirium@*, *Dioscorea@*
Poales—Cyperaceae: only *Carex picta*; ?no Juncaceae (but see *Distichia, Oxychloe*);
?no Poaceae (but to west see *Buchloe* and allies, *Distichlis, Gynerium*).

(a) Trees of east-central states (same as in Figure 2a).

		CLIFFS	CLIFFS	CLIFFS	PINVIR JUNVIR ULMSER	PINRIG QUEPRI ULMALA	QUELAE QUEILI CELTEN	XERIC EXTREME
MESIC SLOPES (below)	CLIFFS	QUECOC QUEVEL QUESCH	QUEMON CARGLA FRAQUA	VACARB QUEFAL (ULMTHO)	PINECH (POPGRA) FRABIL	QUEMAR MALCOR GLETRI	QUEMRG MALANG (RHUTYP)	GRASSLAND
TSUCAR HALTET CLAKEN	MAGMAC QUERUB TILAME	CASDEN CAROVA ULMRUB	OXYARB QUEALB QUEMUE	CARPAL CARTOM CARCAR	PINTAE SASALB PRUSER	PINPAL QUESTE GYMDIO	QUEINC (QUEIMB) (QUEMAC)	GRASSLAND
TSUCAN FAGGRA ACESAC	BETLEN LIRTUL AESFLA	MAGACU ACERUB CARCOR	ILEOPA NYSSYL FRAAME	(PINSTR) (JUGCIN) JUGNIG	QUENIG ROBPSE MORRUB	QUEHEM DIOVIR MACPOM	PINSER QUEPHE QUESIN	GRASSLAND
PLAOCC	MAGTRI BETNIG ACENEG	QUEMIC ULMAME	QUESHU CARLAC	QUEPAG CELSPP	QUELAU ILEDEC FRAPEN	(QUEPAL) CHATHY (QUEBIC)	PINELL TAXASC QUELYR	BOG or MARSH or FEN
POPDEL	ACESNM CATSPE	ACETRI CARILL	LIQSTY FRASUB	NYSBIF PLAAQU	MAGVIR FRACAR FORACU	PERPAL TAXDIS POPHET	CYRRAC NYSAQU GLEAQU	STAGNANT WATER
RHEIC EXTREME	SALINT	SALNIG				STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

(b) Dioecious or polygamo-diocecious trees of east-central states.

		CLIFFS	CLIFFS	CLIFFS	JUNVIR			XERIC EXTREME
MESIC SLOPES (below)	CLIFFS				POPGRA FRABIL	GLETRI	(RHUTYP)	GRASS-LAND
					SASALB	GYMDIO		GRASS-LAND
		ACERUB	ILEOPA NYSSYL FRAAME		DIOVIR MORRUB	MACPOM		GRASS-LAND
	ACENEG				ILEDEC			BOG or MARSH or FEN
POPDEL	ACESNM	ACETRI	FRAPEN	NYSBIF PLAAQU	FRACAR FORACU	POPHET	NYSAQU GLEAQU	STAGNANT WATER
RHEIC EXTREME	SALINT	SALNIG				STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

(c) Small trees and shrubs of Kentucky (rare/local species in parentheses).

		CLIFFS (PHIPUB)	CLIFFS PHIHIR	CLIFFS VIBRAF	(RHOMIN) (JUNCOM) HYPFRO	(GAYBRA) CORRAC RHALAN	(AMESAN) ROBHIS RHUARO	(AMESPI) (SYMALB) PHYOPU
MESIC SLOPES (below)	(RHOCAT) PHIINT	STEOVA VIBACE DIRPAL	VACCSTA CORFLO OSTVIR	VACCOR AMEARB VIBRUF	KALLAT ROSCAR (RIBMIS)	GAYBAC CHIVIR PTETRI	(AMELAE) CRLAME PRUANG	(EUBREC) CRASPP CRACRU+
(LEUFON) (TAXCAN) (VIBMOL)	RHOMAX CORALT RIBCYN	PYRPUB (NESUMB) STATRI	RHOPRI HAMVIR EUOATR	RHOCAL (STYGRA) SIDLYC	AROMEL PRUAME CORDRU	RHUCOP RHUGLA ZANAME	(VACERY) HYPPRO (BRBCAN)	CASPUM CRASPP CRAMOL+
(VIBLAN)	CLEACU (ACEPEN) (ACESPI)	ILEMON LINBEN CRPCAR	RHOPER EUOAME VIBPRU	RHOCUM ASITRI FRACAR	ARUAPP ARASPI SYMOCC	AROPRU SALHUM ROSSET	(AMECAN) HYPLOB PRUMUN	(KALBUX) CRASPP CRASPP
(SAMPUB)	CALFLO VIBDEA HYDARB	XANSIM VIBCAS AESPAV	RHOCAN ILEDEC SAMCAN	VACFUS VIBNUD ARUGIG	ARUTEC ROSPAL (RIBEAME)	SPITOM SALOCC (SPIALB)	[CLEALN] (TOXVER) (COROBL)	BOG or MARSH or FEN
(COMPER) (SPIVIR) (SALERI)	RHOARB VIBREC COROBL	(SALDIS) CORAMM AMOFRU	ILEVER ITEVIR AMONIT	LYOLIG STYAME AMOCRO	CRAVIR+			STAGNANT WATER
RHEIC EXTREME	SALSER SALCAR SALINT	ALNSER	CORSTR	CEPOCC	DECVER	STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

(d) Dioecious or polygamo-diocecious small trees and shrubs of Kentucky.

		CLIFFS	CLIFFS	CLIFFS		RHALAN	RHUARO	XERIC EXTREME
MESIC SLOPES (below)						CHIVIR PTETRI		GRASSLAND
(TAXCAN)		PYRPUB (NESUMB)				RHUCOP RHUGLA ZANAME		GRASSLAND
		ILEMON LINBEN				SALHUM ROSSET		GRASSLAND
						SALOCC		BOG or MARSH or FEN
(COMPER) (SALERI)		(SALDIS)	ILEVER					STAGNANT WATER
RHEIC EXTREME	SALSER SALCAR SALINT					STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

(e) Woody vines of Kentucky (same as in Figure 7).

		CLIFFS	CLIFFS	CLIFFS	(LONRET)			XERIC EXTREME
MESIC SLOPES (below)	LONDIO				VITAES SMIBON			GRASSLAND
(SCHGLA)				SMIROT	SMIGLA COCCAR	LONSEM CELSCA		GRASSLAND
ISOMAC		BIGCAP	PARQUI	VITROT VITBAIL VITVUL	CLEVIR MENCAN	(LACMUL) ROSSET		GRASSLAND
ISOTOM		(HUMLUP)	[DECBAR] TOXRAD SMIHIS	VITLAB VITCIN CAMRAD	AMPARB (BERSCA)			BOG or MARSH or FEN
SCOURED SHORES	VITRIP	AMPCOR CALLYO	WISFRU VITPAL	THYDIF WISMAC				STAGNANT WATER
RHEIC EXTREME	(VITRUP)					STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

(f) Dioecious or polygamo-diocecious woody vines of Kentucky.

		CLIFFS	CLIFFS	CLIFFS				XERIC EXTREME
MESIC SLOPES (below)	CLIFFS				VITAES SMIBON			GRASS-LAND
				SMIROT	SMIGLA COCCAR	CELSCA		GRASS-LAND
				VITROT VITBAIL VITVUL	CLEVIR MENCAN	ROSSET		GRASS-LAND
		HUMLUP	TOXRAD SMIHIS	VITLAB VITCIN				BOG or MARSH or FEN
SCOURED SHORES	VITRIP	CALLYO	VITPAL					STAGNANT WATER
RHEIC EXTREME	VITRUP					STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

APPENDIX FOUR
Table of *Lonicera* spp., with notes on range, habit, browsing by ruminants and chemistry.

Species	**Range; approx. hardiness zone**	**Habit**	**Ruminant Use; with references**	**Chemistry; with references**
CAPRIFOLIUM GROUP				
ciliata	W North America HZ 4–6?	vine; DEC		+ apigenin + luteolin (Glennie 1969)
hirsuta	E North America HZ 3–4	vine; DEC	?medium-low use (Beals+ 1960, Weatherill+ 1969, Wright+ 2002)	low phenolics (Lieurance 2012)
dioica	E North America HZ 4–6	vine; DEC	??high use (JC)	
reticulata (= *prolifera*)	E North America HZ 5–6	vine; DEC	??high use (JC)	low phenolics (Lieurance 2012)
flava	E North America HZ 7	vine; DEC	?high use (Turner+ 2009)	low phenolics (Lieurance 2012)
sempervirens	E North America HZ 6–9	vine; SEG or delayed deciduous	high-medium on average but variable (Schierenbeck+ 1994, Ashton+ 2008, Jull 2001, Wade+ 2010)	low phenolics (Lieurance 2012) - apigenin + luteolin (Glennie 1969)

albifolia	S North America HZ 8–9	vine; SEG-DEC?	?high use (Nelle 1996)	
periclymenum	N Europe HZ 4–7	vine; DEC-SEG	high use (Gonzalez-H+ 1996*, 1999*, Gill+ 2001, McEvoy+ 2006)	?low phenolics; (Gonzalez-H.+ 2003) **pr = 10-11%***
caprifolium	S Europe HZ 7–8	vine; SEG-DEC?	high use (Mitchell+ 1990, Kirby 2001)	
× *heckrottii*, etc.	(horticultural) HZ 6–8?	vine; DEC-SEG	?medium-high use (Fargione+ 2001)	
implexa (*caprifolium* ssp. *implexa*)	SW Europe HZ 8–9?	vine; SEG-DEC?	high use (Cabbidu+ 2000, Decandia+ 2000*)	?low phenolics (Cabbidu+ 2000) + apigenin + luteolin (Flamini+ 1997) **?pr = 7%***
etrusca	S Europe HZ 8–9?	vine; DEC-SEG	high use (LeHouérou 1980, Kidjo+ 2007; NOT Papageorgiou+ 1981* in summer)	+ apigenin + luteolin (Guven.+ 2012) **pr = 8%***
tragophylla (*subaequalis, yunnanensis*)	S China HZ 6–9?	vines; DEC-SEG?		

JAPONICA GROUP				
biflora	Mediterranean HZ 6–9?	shrub <2m? DEC-SEG?	(grows with Nerium oleander, L. implexa)	
acuminata or allies (*henryi*)	Sino-Himalaya HZ 6–9?	vines; SEG	??medium-high use (see refs in Table 5)	
japonica or allies (*affinis, hypoglauca*, etc.)	East Asia HZ 6–9	vines; SEG	medium-high use esp. in winter (see refs. in Table 5)	high phenolics (Lieurance 2012) + apigenin (Son+ 1992) + luteolin (Zhang+ 2009) TAS: mealy-bitter
ferruginea or allies	East Asia HZ 6–9?	vines; SEG?		
macrantha or allies (*confusa, dasystyla, similis* etc.)	East Asia HZ 6–9?	vine; SEG-DEC		+ luteolin (Li+ 2001, Yao+ 2006, Qin+ 2008)

XYLOSTEUM GROUP				
xylosteum	Europe HZ 4–6	shrub; DEC	medium use (Mysterud+ 1999, Boulanger+ 2009)	high phenolics (Lieurance 2012) + apigenin + luteolin (Glennie 1969)
tatarica (also *ruprechtiana, chrysantha*)	East-Central Asia HZ 4–6	shrub; DEC	?low use (Heinrich+ 1995; see also Swihart+ 1983)	high phenolics (Lieurance 2012) + apigenin (Jiang+ 2008) - apigenin (Glennie 1969)
× *bella*, etc.	(horticultural) HZ 4–6	shrub; DEC	?low use (Mudrak+ 2009)	
morrowii	N East Asia HZ 4–6	shrub; DEC	?medium use or variable (Turner+ 2009, Averill 2012)	
maackii	East Asia HZ 5–7	shrub; DEC but delayed	low-medium use (Heinrich+ 1995, Trisel 1997; JC pers. obs.)	high phenolics; + apigenin + luteolin (Lieurance 2012) TAS: mealy-bitter(-acrid)

CAERULEA GROUP				
hypoleuca ? (position unclear)	Himalayas HZ 3–5?	shrub; DEC		
ligustrina or allies (*nitida, pileata*)	Sino-Himalaya HZ 5–7?	shrub; SEG-DEC		+/- apigenin + luteolin (Glennie 1969)
caerulea or allies	Eur Asi NAme HZ 3–5?	shrub; DEC		?high phenolics + luteolin (Chaovanalikit+ 2004, Borchard+ 2011)
villosa (*caerulea* var. *villosa*)	E North America HZ 3–4?	shrub; DEC		
REMAINING (regular flws)				
involucrata (or *ledbourii*)	W N. America HZ 3–4?	shrub; DEC	?low to medium use, esp. moose (Harry 1957, Weatherill+ 1969)	+ apigenin + luteolin (Glennie 1969)

gracilipes	Japan	shrub; DEC		+ apigenin + luteolin (Kikuchi+ 1996)
angustifolia group (*myrtillus rupicola, syrinantha*)	Sino-Himalaya	shrub; DEC		+ luteolin (Qian+ 2006) +/- apigenin (Glennie 1969)
REMAINING (bilabiate flws)				
canadensis	E North America HZ 4–5	shrub; DEC	medium-high on average but very variable (Howard 1937, Atwood 1941, Krefting 1941, Beals+ 1960, Christensen 1963, Telfer 1967, Petrides 1975, Belovski 1981 (?), Cornett+ 2000, Wright+ 2002)	
oblongifolia	E North America HZ 3–4?	shrub; DEC	?low use (Renton 2010; increases with cattle)	+ apigenin + luteolin (Glennie 1969)

utahensis	W N, America HZ 3–4?	shrub; DEC	?medium use, esp. moose (Harry 1957)	+ apigenin + luteolin (Glennie 1969)
maximowiczii and *nigra* groups	Eurasia HZ 3–8??	shrub; DEC		?high phenolics (Borchard+ 2011)
tangutica (*saccata*) and *albigena* groups	Eurasia HZ 3–8??	shrub; DEC	??low use (Winkler 1998, JC pers. obs.; increases in rough pasture)	+ apigenin + luteolin (Li+ 2001) (but Glennie 1969 did not)
hispida group	Eurasia HZ 3–5??	shrub; DEC	??low use (Winkler 1998)	
fragrantissima group (*microphylla*)	East Asia HZ 7–8	shrub; DEC-SEG	low use (Heinrich+ 1993)	high phenolics (Lieurance 2012) + apigenin + luteolin (Chumbalov+ 1978) TAS: mealy-slightly bitter

DIERVILLA				
lonicera	E North America HZ 3–5	shrub; DEC	medium use but often persists/regrows (see refs. under *L. canadensis*; also Murie 1934, Christensen 1963, Belovsky 1981, Cornett+ 2000, Crawford+ 1993)	?high phenolics (Lieurance 2012 etc.)
sessilifolia	E North America HZ 6?	shrub; DEC	?medium use but perists (Atwood 1941, Barden 1978; see also Todd 1927)	
rivularis	E North America HZ 7?	shrub; DEC