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LIANA CELASTRUS ORBICULATUS (ORIENTAL BITTERSWEET)

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THE ECOLOGY OF THE EXOTIC, INVASIVE TEMPERATE LIANA CELASTRUS ORBICULATUS (ORIENTAL BITTERSWEET)

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ABSTRACT

THE ECOLOGY OF THE EXOTIC, INVASIVE TEMPERATE LIANA CELASTRUS ORBICULATUS (ORIENTAL BITTERSWEET)

By

Timothy Jay Tibbetts

The exotic liana (woody vine) *Celastrus orbiculatus* was compared to co-occurring plants of the native species *C. scandens* and *Vitis riparia* in south central Michigan. The successful invasion of *C. orbiculatus* does not appear to be related to hydraulic advantages over native lianas. *Celastrus orbiculatus* lacks the root pressure mechanism seen in *V. riparia* and lacks any advantage in hydraulic conductance. These findings indicate that root pressure is not a requisite characteristic for success as a temperate liana.

Reproductive characters observed in *C. orbiculatus* indicate a clear advantage over the native congener *C. scandens*. *Celastrus orbiculatus* produces more seeds that are smaller and have a greater chance of germinating than seeds of *C. scandens*. These trends hold true across several sites, and over two years.

Shoot elongation measurements of *C. orbiculatus* and *V. riparia* over two years failed to demonstrate differences in maximum shoot length. In one year, *C. orbiculatus* enjoyed a longer growing season by maturing earlier and retaining

leaves longer than *V. riparia*. Incidence of herbivory was similar in these species, however, *V. riparia* shoots suffered a higher rate of mortality.

Dendrochronology proves to be a useful tool in the investigation of liana invasion. Both *C. orbiculatus* and *V. riparia* demonstrate sensitivity in annual ring widths that is reproducible within individuals and between individuals at the same site. The chronologies developed indicate that Kellogg Biological Station was invaded by *C. orbiculatus* at least by 1952, Hidden Lake Gardens by 1971, and the Petrides farm by 1972.

Celastrus orbiculatus appears to thrive in Michigan for numerous reasons: reduced effects of herbivory and competitors in the form of other plant species using the same niches. The frequent and large scale disturbances characteristic of many temperate ecosystems also enhance the opportunities for exotic species such as *C. orbiculatus* to establish, persist, and invade.

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CHAPTER 1

Exotic lianas in temperate ecosystems: invadable communities or effective invaders?

Introduction

Vines occur across taxonomic divisions, in ferns, gymnosperms and angiosperms. Climbers occur in monocots as well as dicots and in 133 plant families, indicating that the adaptation for a climbing habit has evolved numerous times (Gentry 1991). However, the distribution of lianas (woody vines) across the globe is disproportionate. Lianas are generally more prevalent in tropical ecosystems (19% of floras) than in temperate ecosystems (6% of floras) (Gentry 1991). In Michigan, lianas comprise only about 1% of the flora (29 species of 2465 total as reported in Voss, 1972, 1985, 1996). The relative rarity of the climbing growth form in the temperate landscape indicates that there may be factors that limit their distribution, probably low temperatures and limited moisture (Ewers 1985, Sperry and Sullivan 1992, Hargrave et al. 1994).

Although lianas are generally minor components of temperate forest communities, there are some notable exceptions in eastern North America: *Pueraria lobata* Willd.(kudzu), *Lonicera japonica* Thunb. (Japanese honeysuckle), *Celastrus orbiculatus* Thunb. (Oriental bittersweet), *Passiflora mollissima,* and *Rosa* (*multiflora* Wechsler 1977, Patterson 1974, Slezak 1976). These introduced lianas have become temperate zone "weeds" displacing native species and are capable of changing community dynamics (Penfound 1966) and damaging native species (Trimble and Tryon 1974, Lutz 1943). In light of these temperate weedy lianas, we can explore two hypotheses that are not mutually exclusive: 1) some temperate plant communities are particularly prone to invasion, and 2) some exotic lianas are preadapted or predisposed to becoming successful invaders.

Communities and Disturbance

The harsh North American climate and poor liana habitat may help explain the paucity of temperate lianas relative to both temperate South America and temperate Asia, which have greater liana diversity (Gentry 1991). However, this low liana diversity and abundance also indicates that the liana niche is largely open in North American plant communities. Given the low potential for competition with native lianas, invading lianas may have the potential for explosive spread.

Disturbance and its effects on ecosystem function frequently favors invasion (Orians 1986). Successful invasion may only be possible if it coincides with disturbance. Crawley (1986) looked for pattern to explain Britain's alien plant problem. It is estimated that ten times more plant species have been introduced to the British Isles than are recognized as members of the "native" flora. Crawley (1986) found that successful establishment of an alien plant species depended on disturbance of the soil surface and the amount of exposed bare ground due to low plant cover in a given community. Secondary factors included proximity to sources of alien propagules and the rate of propagule dispersal. Clearly, since natural disturbances are stochastic, any community is potentially invadable (Crawley 1986).

Temperate forest communities are subject to natural disturbances including catastrophic wind-throw, tornadoes, downbursts accompanying thunderstorms, ice storms, fires, herbivory, and disease epidemics (Davis 1987). More mature stages of succession may suffer less frequent disturbance; their advanced stage is evidence of a long time period without disturbance (Robertson et al. 1996). However, the chance of disturbance still remains, and directly following disturbance the presence of bare ground can act as a catalyst for invasion. Indeed, one interpretation of the process of succession is the repeated invasion by new species.

Davis (1987) looked at the invasion of temperate forest communities using pollen records. Disturbance was responsible for opening the canopy, however secondary factors were important in determining the success of invasion. The presence of invaders in the successional communities depended on whether they were already present in the seed bank or as juveniles. Thus the timing of invading species introduction through dispersal is critical. Young, even-aged successional stands, more common following large disturbance, offered few gaps for invasion (Davis 1987).

Human disturbance of communities is not stochastic. Forestry practices such as logging create open space available for invasion. Wildlife management practices often intentionally create and maintain "edge" habitat using disturbance. In addition, humans increase the distribution and dispersal of alien propagules, either intentionally or unintentionally (Crawley 1987). The purposeful introduction of exotic species for wildlife use (food, cover) or ecological purposes (erosion control) can have undesired results. Human activities also continually reduce the size of natural areas and decrease the isolation of sites through road building and settlement. These practices can open space for invasion and lead to the establishment of exotic species.

Without detailed information on all the resource levels in a community and the requirements of the species present, predicting whether a community is likely to be invaded can be based only on plant cover as a surrogate and the local disturbance regime. This implies that communities are universally invadable. It will be useful to look at the attributes of species that make them effective invaders.

Models based on these characteristics may be helpful for predicting invasion.

Invasion ecology

Invading species are frequently considered weeds. A weed is subjectively defined as a plant growing where it is not desired. Weeds can be native or exotic species under this definition. Life-history patterns have been divided into *r*- and *K*-selected, with *r*-selected species maximizing reproduction by producing many, small young that mature rapidly and require little care while *K*-selected species target carrying capacity and produce fewer, larger young that mature slower and receive intensive care (MacArthur & Wilson 1967, Pianka 1970). This scheme is clearly an oversimplification, and any species will demonstrate traits of both strategies. However, in general one would expect weeds to be relatively *r*-selected, having rapid development, short life span, semalparity, small body size, and many small seeds (MacArthur & Wilson 1967, Pianka 1970).

Grime (1979) refined the *r*- selected pattern and defined weeds (ruderals) as being small herbs with short life spans, devoting most of their production into many seeds, having high potential relative growth rate, and having varied but often high palatability to herbivores. A number of these traits are found in exotic lianas.

Rejmánek and Richardson (1996) attempted to identify the characteristics of pines that explained why some species became successful invaders while others did not. They found that low seed mass, high frequency of large seed crops, and short time spent as a juvenile were traits found in the weedy pine species. These traits follow Grime's (1979) ruderal classification. Rejmánek and Richardson (1996) then showed that a discriminant function based on these characteristics was highly effective for correctly identifying non-pine species as invasive or non-invasive (38 of 40 species). This analysis included numerous weedy vines problematic in North America (*Lonicera japonica, Pueraria lobata, Passiflora mollissima,* and *Rosa multiflora*). It appears that life history characters can successfully be applied to predict weediness and invasive ability (Rejmánek & Richardson, 1996).

The frequency at which exotic species become weeds has been generalized in the "tens rule" of Williamson and Fitter (1996). For simplification, the invasion process can be broken into stages: arrival, establishment, and integration (Vermeij 1996). In short, one in ten of those species "imported" will appear in the wild, one in ten of those appearing in the wild will become established, and one in ten of those established will become a pest. This means that 1 in 1000 species introduced will have a negative economic effect as a pest. The tens rule is a generalization that works for a large number of organism groups (Williamson & Fitter 1996). Possible reasons for exotic species to succeed as weeds are the lack of their native pests, diseases, and competitors. At the same time, a lack of pollinators and dispersal agents can be problematic for exotic plant species (Crawley 1987). The rule of tens demonstrates that most species introductions fail.

Characteristics of exotic lianas leading to invasion

The defining characteristics of vines may indicate why they can potentially be weeds. They are "mechanical parasites," meaning they depend on external support for vertical growth (Stevens 1987). A liana is a woody vine with secondary growth. The liana stem is characteristically narrow, with long and wide vessels, providing lots of conductive vessel area, and often has anomalous secondary growth patterns, making for flexible stems. There is often a high ratio of leaf to stem area. These characters combine to make lianas highly effective at water transport with a minimal investment in structural support (Ewers et al. 1991, Fisher & Ewers 1991).

Lianas native to North America, e.g., *Parthenocissus, Vitis,* and *Toxicodendron*, are capable of reaching the tops of tall trees and shading out their hosts. These vines rarely develop into thick monospecific stands to the exclusion of other species (except see Trimble & Tryon 1974, Siccama et al. 1976). However, three exotic lianas are particular problems in North America: *Pueraria lobata* (kudzu), *Celastrus orbiculatus* (oriental bittersweet) and *Lonicera japonica* (Japanese honeysuckle)(Wechsler 1977, Patterson 1974, Slezak 1976). Comparisons of *C. orbiculatus* and *L. japonica* with their far less prevalent native sympatric congeners may offer insight into some of the basic traits of weedy exotics (Schierenbeck et al. 1994).

Pueraria lobata, C. orbiculatus and *L. japonica* are native to Japan, Korea and eastern China. *Celastrus orbiculatus* and *L. japonica* thrive even where freezing conditions are common. All three were introduced to North America on purpose, yet the outcomes were unanticipated though even Darwin (1859) was aware of the potential response of species released from their native constraints. The introduction of *C. orbiculatus* can be taken as an example. *Celastrus orbiculatus* was introduced to the US from Asia in 1860 as a control measure against erosion and as an ornamental plant. During the period of 1966 and 1967 the National Arboretum sent seeds of *C. orbiculatus* to nurseries in 30 states. By 1970, *C. orbiculatus* was planted as an ornamental in 33 states and was reported to be naturalized in 21 states. (Patterson 1974). By the 1980s, *C. orbiculatus* was considered a problem weed (Dreyer et al. 1987, Robinson et al. 1994, Goslee 1998).

The weedy nature of *C. orbiculatus* may be related to its reproductive success. Dreyer et al. (1987) compared pollen viability and seed germination in *C. orbiculatus* and *C. scandens*. The native *C. scandens* has decreased in abundance in part due to overcollecting by hobbyists (Rabeler 1998). At the same time, *C. orbiculatus* has been increasing in distribution. It would be valuable to know if this decrease has in part been influenced by or is merely concomitant with the invasion of the exotic species. Dreyer et al. (1987) found that the pollen of *C. orbiculatus* had higher viability than *C. scandens* (67% and 48%, respectively). Additionally, the seed germination rate of *C. orbiculatus* was greater than *C. scandens* (71% and 27%, respectively). Much of the success of *C. orbiculatus* over *C. scandens* can be understood using reproductive explanations.

A species newly established in a community may be too foreign to the local fauna to be recognized as a resource. This may lead to lower herbivory compared to that experienced by the native species, thereby giving the exotic species an advantage. Schierenbeck et al. (1994) found this to be the case with the exotic liana *L. japonica* and its native sympatric congener *L. sempervirens*. *Lonicera sempervirens* suffered greater damage due to herbivory and had lower total biomass accumulation than *L. japonica*. *Lonicera japonica* not only suffered less herbivory but it demonstrated a compensatory response to the low levels it experienced. This favors the growth and spread of *L. japonica* where the two species grow in sympatry (Schierenbeck et al., 1994).

Vines use a variety of different mechanisms to climb, including twining up stems and specialized tendrils. The mechanism utilized in part dictates the size of the substrate that the liana can successfully climb, and therefore also determines the light available to the growing vine. Carter and Teramura (1988) compared climbing mechanism and vine photosynthesis. They found that the exotic twiner *P. lobata* was best suited to full light, but performed poorly in low light. The exotic twiner *Lonicera japonica*, native tendril climbers (*Parthenocissus quinquefolia, Vitis vulpina, Smilax rotundifolia*) and adhesive root climbers (*Hedera helix, Rhus radicans*) were better suited to the low light levels of the understory. However, under full sunlight *Parthenocissus quinquefolia, Vitis vulpina,* and *Smilax rotundifolia* increased photosynthetic capacities. Since *L. japonica* is evergreen in the southeastern US and can utilize sun flecks, it may be problematic in low light environments. *Celastrus orbiculatus* also has been shown to have a wide tolerance of light levels and increased response to high light (Patterson 1974). These findings indicate that exotic lianas utilize different light-use strategies; that there is not one single key to success, and that there is a range of physiological plasticity in some liana species. (Carter & Teramura 1988).

Carter et al. (1989) further established that simple high photosynthetic capacity is not responsible for the success of exotic lianas. They demonstrated that under field conditions, the steady-state photosynthesis was similar between exotic *Pueraria lobata* and *Lonicera japonica* and native *Parthenocissus quinquefolia*, *Vitis vulpina* and *Clematis virginiana*. Additionally, under high leaf-air water vapor pressure differences common at high temperatures, photosynthetic rates decreased more in the exotic lianas than several of the natives (Carter et al. 1989). Their results indicate that steady-state photosynthesis is not the simple answer explaining the weedy nature of these exotic lianas. However, mechanisms such as maintaining optimal leaf temperature through conductance and transpiration may give exotics like *P. lobata* an advantage over native species(Forseth & Teramura 1987).

Case Studies: Community invasions by exotic lianas

Robertson et al. (1994) examined the colonization dynamics of exotic species on a northern piedmont in Pennsylvania. Included in their study were two true climbing lianas (*L. japonica* and *C. orbiculatus*) and one scrambling vine (*Rosa multiflora*). Density and frequency data were collected for each species in different successional communities. *Lonicera japonica* was by far the most frequent invader, present in 75% of all plots. *Rosa multiflora* was the second most frequent, though it was less successful in mature forest and old field plots. *Celastrus orbiculatus* presence did not differ between seral stages (Robertson et al. 1994). The mature forest had the lowest frequency and density of exotic species. Only *C. orbiculatus* and *L. japonica* were found in the mature forest to any degree (39% and 48% of plots, respectively). This is probably due to the ability of *C. orbiculatus* to germinate under low light conditions (Patterson 1974, Dryer et al. 1987) and *L. japonica* to remain somewhat evergreen (Carter & Teramura 1988). Additionally, this study may be evidence that mature forest tends to be relatively exotic free because it suffers less physical disturbance (Robertson et al. 1994).

When a community is subjected to high levels of disturbance, the native flora can be significantly altered, making room for invasion. Robinson et al. (1994) looked at the change in flora of Staten Island over 112 years. During this time 443 native species were lost and more than 100 alien species were naturalized. The only traits correlated to the loss of native species were that herbaceous and uncommon species were more likely to be lost. Among the naturalized aliens were the exotic lianas *C. orbiculatus, P. lobata* and *L. japonica*.

The New Zealand flora is already largely comprised of alien species. Each wave of human settlers brought with them their favorite plant species, including agronomic and ornamental plants. The introduced species often escaped and became naturalized. By the tens rule, approximately 146,300 species introductions have occurred in New Zealand in the last 133 years! Baars and Kelly (1996) compared growth responses to light availability in introduced and native vines. Two of the introduced vines (*Clematis vitalba* and *Lonicera japonica*) displayed low light compensation points as well as high relative growth rates in the presence of high light availability. The third introduced vine (*Passiflora mollissima*) was more similar to a native vine (*Muehlenbeckia australis*): higher light compensation point and higher requirement of light availability for maximum growth rate. A final native vine (*Parsonsia heterophylla*) had the lowest light compensation point and also the lowest maximum growth rate. This study demonstrates the wide variety of strategies for exotic lianas in varying light environments. It may be that for every community, there is a corresponding invader.

Conclusion

Any community is theoretically invadable, since all communities have at least some probability of disturbance. Whether an invasion occurs depends on the timing of disturbance and dispersal of the invader. Human activities have increased the frequency of disturbance as well as the relative rates of species introductions through global travel, so high invasion rates would not be surprising.

Exotic lianas pose a real threat to temperate communities because there are fewer native lianas with which to compete. The native Michigan flora may be at particular risk from exotic lianas, since only 1% of the native flora are lianas. This suggests that the climbing strategy is currently underutilized in Michigan. Historically, the depauperate Michigan liana flora may relate to habitat resistance to lianas and therefore little opportunity to diversify. Currently, however, exotic lianas have the potential to proliferate through disturbed habitats with open liana niches. The ruderal traits outlined by Grime (1979) are a good start for characterizing these weedy pests. However, further studies comparing exotic weedy and native non-weedy congeners will help define more traits common among pests. These traits will be essential for modeling forest community

CHAPTER 2

Celastrus orbiculatus (Oriental bittersweet) natural history and presence in Michigan

Introduction

The spread of exotic, invasive plant species continues to threaten native floras (Groves & Burdon 1986, Mooney and Drake 1986, Drake et al. 1989, Cronk and Fuller 1995, Pysek et al. 1995). *Celastrus orbiculatus* is one such species becoming a problem weed in Michigan (Voss 1985, Tibbetts and Ewers 2000). This liana (woody vine) may be locally more abundant than the native congener *C. scandens*. Reliable identification can be made based upon inflorescence position: terminal panicles in *C. scandens*, axillary cymes in *C. orbiculatus* (Voss 1985). An understanding of the natural history and invasion history of *C. orbiculatus* may help us combat such threats.

Taxonomy

Celastrus orbiculatus Thunb. (Oriental bittersweet) is a woody twining vine native to north and central Japan, Korea, and China (Hou 1955). It is a member of the Celastraceae, the Bittersweet or Staff Tree Family. The most recent revision of the genus *Celastrus* is by Hou (1955). The generic name traces back to Theophrastos, who assigned the name Kelastros to an evergreen tree (*Phyllyrea* = *Phillyrea*, Hooker and Jackson 1895). This tree is not a member of the Celastraceae, but instead is found in the Oleaceae, its members distributed around the Mediterranean (Mabberly 1997). In his designation of the name Kelastros, Theophrastos used the feminine gender. Linnaeus founded the genus *Celastrus* as it is now understood in his Genera Plantarum (1960), changing the gender from feminine as it applied to *Phyllyrea* to masculine for his circumscription. The International Code of Botanical Nomenclature (ICBN) requires that such borrowed Greek or Roman names revert to their classical gender for authors following Linnaeus. However, some authors (e.g., Voss 1985) have used the feminine *Celastrus orbiculata* over *C. orbiculatus* following its assignation by Theophrastos. This helps explain some of the synonymy and confusion over species names within the genus.

There is additional confusion regarding the correct name of the species *Celastrus orbiculatus*. Thunberg (1784) described this species in his Flora of Japan. Apparently Thunberg assigned the name *C. orbiculatus* in his manuscript and figures, but a printer's error substituted *C. articulatus* in its place (Maximowicz 1881). However, *C. articulatus* was already widely accepted, and not easily replaced with the correct *C. orbiculatus*. Now, *C. orbiculatus* has generally replaced *C. articulatus*, probably aided by the fact that the epithet *orbiculatus* descriptively refers to the leaf shape. However, there is still evidence of nomenclatural inertia as demonstrated by some recent publications (e.g., Osipova 1982, Shokova and Belinskaya 1987).

Distribution of the Genus

The 31 recognized species of *Celastrus* are currently found in eastern Asia, Oceania, North and South America, and Madagascar (Hou 1955). They are predominately tropical and subtropical. Berry (1919) indicates that the fossil evidence points to a widespread, abundant cosmopolitan distribution during the Tertiary. Considering the present distribution patterns, Hou (1955) suggests two centers of dispersal: Yunnan-Burma-eastern India (Asiatic center), and Central America, corresponding to subgenus *Celastrus* and subgenus *Racemocelastrus*, respectively. The one North American native member of the genus, *Celastrus scandens* L. (American bittersweet), apparently has closer affinity to the eastern Asiatic center of dispersal, and falls in subgenus *Celastrus*. The subgenera differ in diversity, with subgenus *Celastrus* including 24 species and subgenus *Racemocelastrus* only 7 species. Species of subgenus *Celastrus* have two ovules per ovary cell and is dioecious, while subgenus *Racemocelastrus* has one ovule per ovary cell and is bisexual (Hou 1955).

The distribution of the species of *Celastrus* appears to be an example of the disjunct distribution between eastern Asia and eastern North America seen in numerous taxa: *e.g. Rhododendron* (Kron 1993), *Panax* (Wen and Zimmer 1996), *Trillium* (Fukuda 1990), *Acer* (Hasebe, Ando and Iwatsuki 1998). Li (1952) describes the disjunction as the loss of a continuous mesophytic forest spanning the northern hemisphere during the Tertiary, and subsequent diversification within each region. However, the biogeographic pattern of some taxa (e.g., *Liquidambar* and *Staphylea*) may be due to exchange along contiguous land bridges (Wen 1998).

Biology

Morphologically, *C. orbiculatus* and *C. scandens*, both of subgenus *Celastrus*, are very similar. The leaf form and margin crenulation intergrade between the species. The main difference used to distinguish the two is the inflorescence: axillary cymes for *C. orbiculatus* and terminal panicles for *C. scandens*. Both species are dioecious to polygamodioecious. The gynoecium is usually 3 carpellate (sometimes 4), 3-locular, with 2 (1) ovules per locule. The fruit is a small (1 cm) orange to yellow subglobular leathery capsule. It is incompletely 3-locular, 3 valved, with 2 (1) seeds per locule. Seeds of both species have copious endosperm, and 2n = 46 for each (Brizicky 1964, Gleason and Cronquist 1991).

Viable hybrids between the two species have been produced; these resemble *C. orbiculatus* in morphology but are of lower vigor (White and Bowden 1947). The seeds are enclosed in a fleshy red aril that is exposed upon reflexing of the valves in autumn, and birds disperse the seeds of both species. Both species are also capable of vegetative propagation from root sprouts.

Ecology in native range

There is little ecological information regarding *C. orbiculatus* in its native range. Ohwi (1965) characterizes the habitat as "thickets and grassy slopes in lowlands and mountains," and the abundance as "common and often planted as a hedge." Patterson (1974) reports that *C. orbiculatus* is not a weed in Japan. A report of vine infestation of a *Chamaecyparis obtusa* plantation in Japan found *C. orbiculatus* climbing the planted trees in only one of seven stands, though it was present on the forest floor in five other stands (Suzuki 1984). This may be considered analogous to the situation with *C. scandens* which has been found to create only occasional problems in North American silviculture (Lutz 1943).

Celastrus orbiculatus is a plant used in traditional Chinese medicine. Screening for central nervous system activity of plant extracts has shown that *C. orbiculatus* has some strong binding to receptors in radioligand receptor binding assays, perhaps indicating the functional action for its traditional use (Zhu et al. 1996, Phillipson 1999). Additionally, in the search for substitutes to calf rennet for cheese making, milk-clotting activity has been found in leaf extracts of *C. orbiculatus* (Otani, Iwagaki and Hosono 1991).

Both *C. orbiculatus* and *C. scandens* have been used in decorative arts. Each species produces bright yellow-orange capsules that open to reveal red-aril covered seeds. In Japan, *C. orbiculatus* is collected and sold in autumn (Sargent 1893). Michigan Public Act 182 of 1962, also known as the "Christmas-tree law," includes *C. scandens* in the list of species protected from over-collection by avid decorators (Rabeler 1998).

There is sparse information regarding either pests or diseases affecting *C. orbiculatus*, either in its native range or in North America. There is evidence that insect herbivores utilize *C. orbiculatus*. Cotton aphids, *Aphis gossypii* Glover, feeding on *C. orbiculatus* in Japan were found to have lower resistance to organophosphorus insecticide (Saito 1989). In Michigan, Kiss (1984) reported a phloem-feeding membracid nymph of the *Enchenopa binotata* (Say) complex that feeds on several host species including *C. orbiculatus*, *C. scandens*, *Juglans nigra*, *J. cinerea*, and several species of *Viburnum*.

No mention of mortality related to feeding on *Celastrus* is mentioned (Kiss 1984). Tomato black ring virus (TBRV) was reported to spontaneously occur on *C. orbiculatus* (Schmelzer 1974).

Introduction to North America

Celastrus orbiculatus was introduced to North America as an ornamental vine around 1860 (Patterson 1974). The exact date of introduction remains confused by several different accounts and records. Seedlings of *C. orbiculatus* were being cultivated at the Arnold Arboretum and the New York Botanical Garden and had become quite popular in landscaping by the 1890s (Sargent 1890, Nash 1919, Wyman 1949; for a synopsis see Patterson 1974).

From the initial plantings, it was observed that the plant grew rapidly, aggressively, was hardy, and was therefore desirable as a cover plant (Jack 1989, Sargent 1890). The greatest concentration of early *C. orbiculatus* appears to be in the northeastern United States (Patterson 1974). Naturalized populations are noted from 1912 (Maryland) and 1916 (Pennsylvania and Connecticut) (Mehrhoff 1986, Patterson 1974). A survey of herbaria by Patterson (1974) demonstrated that *C. orbiculatus* had become naturalized in at least 21 of 33 states where it had been planted. *Celastrus orbiculatus* was planted along highways in New Jersey, Rhode Island and Massachusetts, and seeds were distributed to 30 states by the National Arboretum in 1966-1967 (Patterson 1974).

Celastrus orbiculatus has also spread to other parts of the world. Collections have been reported in Berlin and Seeheim, Germany (Bolle 1894, Hillesheim-Kimmel 1995). In Russia, *C. orbiculatus* has been noted as well-suited to the hot and arid climate of Kazakhstan, and is not negatively impacted by the high sulphur dioxide pollution levels (Shokova and Belinskaya 1987).

Status in Michigan

The earliest floras of Michigan, particularly the southern Lower Peninsula, indicate that *C. orbiculatus* was not present, but its native congener *C. scandens* was (Beal and Wheeler 1892, Beal 1904, Gleason 1939, Walpole 1924, Hanes and Hanes 1947). *Celastrus scandens* is considered native to North America (Hou 1955), and is reported as occurring frequently in these early floras. Throughout Michigan this species is present in 52 counties including both the Upper and Lower Peninsulas (Voss 1985). However, it has decreased in abundance in part due to overcollecting by hobbyists (Rabeler 1998).

At the time of Patterson's (1974) survey, *C. orbiculatus* was being cultivated in Michigan but had not been reported to have escaped. Voss (1985) noted *C. orbiculatus* as present in three counties of southern Michigan (Figure 2-1, Berrien, St. Joseph, Washtenaw). However, it has been collected further north since Voss' publication (Figure 2-2, Lenawee, Kalamazoo, Barry, Ingham, pers. obs.; Kent, Wayne, Voss, pers. com.) and is probably grossly undercollected (Voss, pers. com.). The increase in distribution over 15 years is notable, particularly the expansion to the north. This species is reported as hardy in Zone 4 (Wyman 1949). While Patterson (1974) reported that *C. orbiculatus* had spread to most of the states in its potential range east of the Mississippi, it is clearly still spreading within these states. Careful identification, monitoring, and swift removal are recommended in dealing with this species (McNab 1988). For landscaping purposes, use of the native *C. scandens* is highly preferred.

Species used in the research

Direct comparison of the ecology of the exotic *C. orbiculatus* and the native *C. scandens* would be the ideal approach to elucidating explanations for the invasive nature of *C. orbiculatus*. The habitat ranges for both species overlap, so theoretically they should be found naturally co-occurring. However, in numerous field examinations of reported *C. scandens* collection sites, this species was not found. In some instances, *C. orbiculatus* was present instead of the reported *C. scandens*, suggesting misidentification of the herbarium specimen. Replacement of *C. scandens* by *C. orbiculatus* is another possibility. In many other instances, neither species was present, sugesting local extinction of the native *C. scandens*. *Celastrus scandens* and *C. orbiculatus* were never found naturally co-occurring in the field. Investigation by Patterson (1974) into the potential of allelopathy by *C. orbiculatus* failed to detect any such interaction. Overall, *C. scandens* sites were infrequent at best and limited in extent.

To overcome the lack of *C. scandens* sites, and to avoid further threatening this protected species, another native liana species was used as a substitute for several of the following investigations. *Vitis riparia* Michaux (riverbank grape) was utilized in studies requiring destructive sampling and pairwise comparisons with *C. orbiculatus,* since both species could be found co-occurring. This substitution was felt to be relevant because *V. riparia* and *C. scandens* are commonly found in similar habitats and share a similar distribution throughout Michigan (Figures 2-3, 2-4)(Voss 1985).

Figure 2-1. *Celastrus orbiculatus* distribution, 1985 (after Voss 1985).

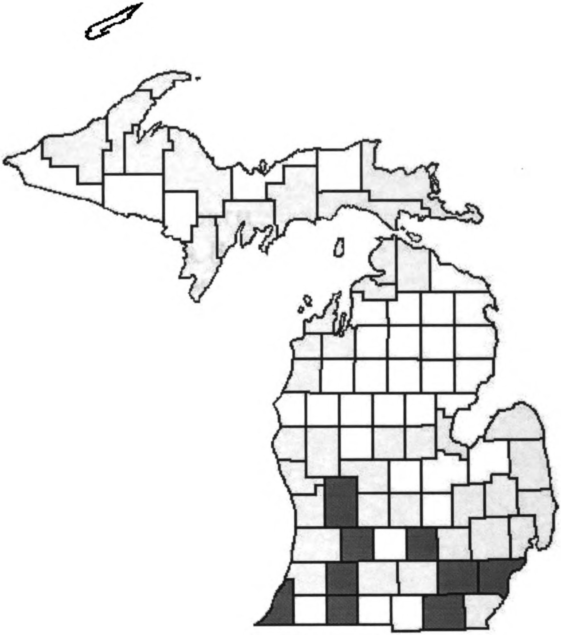


Figure 2-2. *Celastrus orbiculatus* distribution, 2000.

Figure 2-3. *Celastrus scandens* distribution (after Voss 1985).

Figure 2-4. *Vitis riparia* distribution, (after Voss 1985).

CHAPTER 3

Root pressure and specific conductivity in temperate lianas: exotic *Celastrus orbiculatus* (Celastraceae) vs. native *Vitis riparia* (Vitaceae)

Introduction

Lianas (woody vines) comprise ~1% of the Michigan flora (29 species of a total of 2465 as reported by Voss 1972, 1985, 1996). Native lianas, e.g., *Parthenocissus, Vitis,* and *Toxicodendron*, are capable of reaching the tops of tall trees and shading out their hosts. These vines rarely develop into thick monospecific stands that exclude other non-tree species. However, some exotic vines have become weeds, capable of extensive infestations that may affect community structure (Penfound 1966). *Pueraria lobata* (kudzu) is one such vine common in the southeastern United States (Wechsler 1977), while another, *Celastrus orbiculatus* (Oriental bittersweet), appears as far north as Michigan and Connecticut (Patterson 1974). *Celastrus orbiculatus* is native to China, Japan and Korea (Hou 1955). Exotic species may proliferate for various reasons such as escape from their native herbivores, pathogens, and seed predators, as well as enhanced growth in novel environments. I was interested in examining whether water transport properties could be implicated in the success of *Celastrus orbiculatus* over *Vitis riparia* in Michigan.

Lianas are much more prevalent in tropical than in temperate ecosystems, both in terms of biomass and as a percentage of species in the flora (Gentry 1991). It has been suggested (Ewers 1985, Sperry and Sullivan 1992) that low temperature limits the distribution of lianas, possibly via freeze-induced air bubble formation in xylem vessels. When the water in the vessels freezes, the solubility of dissolved gases decreases and bubbles form. If thawing occurs more rapidly than the air can redissolve, the bubbles remain and may increase in size due to the tension of the transpiration stream (Zimmermann 1983). These air bubbles (emboli) occlude the vessels and prevent further conductance of water. The likelihood of embolism occurring due to freezing increases with vessel diameter (Sperry and Sullivan 1992, Davis and Sperry 1999), and vines characteristically have wide vessels.

Embolism may also be caused by water stress. Air may enter conductive vessels through intervessel pit membranes as the xylem pressure decreases (Sperry and Tyree 1988). This relationship can be expressed as a vulnerability curve, showing an increase in embolism as xylem pressure decreases. This vulnerability curve has been shown to be characteristic for given species and can be informative regarding likely species response to the xylem pressures typically experienced by the species under field conditions (Sperry, Tyree, and Donnelly 1988; Davis et al. 1999).

Root pressure may be a repair mechanism of plants with wide vessels, such as lianas, that are at high risk of winter embolism. Without a mechanism to remove emboli, vessels will remain permanently dysfunctional. Root pressure is one manner by which conductance can be restored in embolized vessels. Water is taken into the roots osmotically and then forced up through the plant. Emboli may be quickly pushed out by the water, pushed through dry pit membranes, or more slowly dissolved when pit membranes are wetted (Sperry et al. 1987). Examples of positive root pressure include the exudation of water through hydathodes (guttation) and the "bleeding" of severed stems. These occurrences are generally limited to conditions of minimal transpiration, such as before dawn, when the stomata are closed, and during periods when relative humidity is at or near 100%, such as during rain. Positive root pressure has been observed in many plants, such as *Vitis* (Sperry et al. 1987), *Acer* (Sperry, Donnelly, and Tyree 1988b), and many tropical species (Ewers, Cochard, and Tyree 1997; Fisher et al. 1997).

The risk of dysfunction may be balanced by a high hydraulic conductivity in stems with xylem dominated by wide vessels (Chiu and Ewers 1992; Ewers, Cochard, and Tyree 1997). Hydraulic conductivity (k_h) is measured as the volume of water transported through a unit length of stem per unit time divided by the pressure gradient. Specific conductivity (k_s) is k_h per unit cross-sectional area of the xylem and reflects the efficiency of water transport (Tyree and Ewers 1996). Liana stems provide little mechanical support, are generally narrow with respect to the leaf area they supply (Ewers 1985, Ewers and Fisher 1991), contain wide vessels, and are primarily committed to water transport; therefore they typically have high k_s values.

The wide vessels of lianas should be prone to dysfunction when temperatures fall below 0°C, yet some lianas thrive in temperate climates and persist despite freezing. The best studied temperate lianas in this regard are *Vitis riparia* and *Vitis labrusca* L., and several authors have suggested that the success of wide-vesseled temperate lianas may depend upon root pressures (Sperry et al. 1987; Sperry, Donnelly, and Tyree 1988b; Ewers, Cochard, and Tyree 1997; Fisher et al. 1997). The objective of this study was to investigate whether differences in water transport characteristics were sufficient to explain the differences in growth patterns of *C. orbiculatus* vs. *V. riparia*. I hypothesized that in co-occurring species, plants of *C. orbiculatus* would have: (1) stronger or more persistent root pressures, (2) higher k_s values through much of the season, and (3) would be less vulnerable to embolism caused by water stress than the co-occurring native species *V. riparia*.

Methods and Materials

Site-- Field sites were chosen based on their proximity to laboratory facilities and the presence of both *V. riparia* Michaux and *C. orbiculatus* Thunb. at each site. Plant specimens were selected based on healthy appearance and stem diameters between 1 and 3 cm. Four sites were used, which were all within a 130-km radius of the Michigan State University (MSU) campus, where all laboratory measurements were made. Site locations are described in Table 3-1.

Root pressure-- Root pressure was measured on individual specimens at two sites with bubble manometers (Sperry 1983; Ewers, Cochard, and Tyree 1997; Fisher et al. 1997). Five healthy individuals for each species were selected, with stem diameters between 1 and 3 cm. The day prior to measurement, stems were cut and manometers containing distilled water and a distal air bubble were attached. The next day, air bubble length pre- and post- attachment to the severed stems was recorded just before sunrise to avoid the effects of transpiration. Root pressure in kiloPascals was calculated using the formula (Fisher et al. 1997):

Table 3-1. Site descriptions. Names, locations, and descriptions of the forest types and soils present in each of the study sites in Michigan.

site/location	description/soil
Petrides farm	Derelict Pinus sylvestris plantation
Williamston	Coarse-loamy, mixed, mesic Typic Hapludalfs
T4N R1E S23 NW1/4 W1/2	
Herner farm	Old successional field, with Rhus
Williamston	Fine-loamy, mixed, mesic Glossoboric Hapludalfs
T4N R1E S23 SW1/4 SW1/4	
Michigan State University (MSU)	Old successional field, with Rhamnus and Populus
East Lansing	Fine-loamy, mixed, mesic Aeric Ochraqualfs
T4N R1W S19 NW1/4 SE1/4	
Hidden Lake Gardens (HLG)	
Tipton	Beech-Maple forest
T5S R3E S21	Fine-loamy over sandy, mixed, mesic Typic Hapluda

$$P_x = 100[(L_{atm}/L_{pd}) - 1]$$

where P_x = xylem water pressure, L_{atm} = bubble length in manometer at atmospheric pressure, and L_{pd} = bubble length prior to dawn.

Specific conductivity-- Specific conductivity of both species was measured in 1996 and 1997, on stems collected from each of the four sites on a revolving schedule. Each site was sampled at least once a month in the spring and summer, and less frequently in the winter. On each collection date, stems of five individuals for each species were severed under distilled water in the field. Measurements were made in the laboratory following the method of Sperry et al. (1988a) and modified according to Chiu and Ewers (1992). Field condition k_h was measured on 10-cm-long segments with a pressure head always less than 1.5 kPa. Stem segments were then flushed at 172 kPa for 20 min, and final k_h (=maximum) was determined when repeated flushing yielded no increase in conductivity.

Following the conductivity measurements, all stems were perfused with a 0.5% crystal violet dye solution to mark the conductive vessels. A 5-cm column of dye of the same diameter as the stem was allowed to perfuse through the flushed segments. The time required for dye to reach the distal end of the stem segments was noted. Stem segments adjacent to those used for conductivity measurements served as field condition controls for dye descents. All the field condition control stems were then perfused with the dye eight times longer to insure that even some of the smaller vessels could potentially pass the dye. After perfusion with dye, the stems were perfused with distilled water a minimum of 15 min to prevent bleeding of dye from conductive to nonconductive vessels.

After perfusion and drying, each stem segment was severed 2 cm from the proximal end (perfusion port) and shaved smooth with a razor blade. The dyed growth rings and total growth rings were counted using a dissecting microscope. A growth ring was considered conductive if it had five or more stained vessels.

Sapwood area, as demarcated by the dyes in transverse view, was measured using a caliper with a digital micrometer. Bark was removed, and the maximum and minimum xylem diameters were averaged and used to calculate the xylem cross-sectional area. The pith and heartwood area, demarcated by a lack of dye, was also measured and subtracted from the xylem area to obtain the area of conductive xylem. The field condition and maximum k_{h} values calculated above were divided by the conductive xylem area to obtain k_{s} values. The percentage embolism was taken as the difference between maximum k_S and initial k_S, and standardized by dividing by the maximum k_S.

The conductivity data obtained were plotted against date and phenological data collected throughout the year to determine whether the relationship varied between the two species. Phenological data were summarized for all sites and included date of bud break, leaf out (first leaf fully expanded), flowering, and first leaf drop.

Vessel diameter measurements-- Two stems for each species were used to determine the distribution of vessel diameters. The tangential diameters of all vessels in four equivalent quadrants per stem were measured in transverse view with an optical micrometer. Quadrants were bounded by rays. Vessel diameter distributions were compared with an unpaired, two-tailed *t* test. Theoretical conductivity was calculated for each vessel diameter class using the Hagen-Poiseuille equation following Chiu and Ewers (1992).

The maximum tangential diameter in transverse view was recorded for the ten largest vessels in these distributions. Maximum vessel diameter between the two species was compared with an unpaired, two-tailed *t* test.

Vulnerability curves-- Stems were cut in the field between July and October 1997, transported to the laboratory, and allowed to dehydrate for various lengths of time (N = 30 for *C. orbiculatus*, *N* = 5 for *V. riparia*). The stems were then bagged and allowed to equilibrate in the bags overnight following Sperry, Donnelly, and Tyree (1988a). Stem segments were cut to be longer than the maximum vessel lengths. The mean xylem pressure was determined using a pressure bomb on five shoots from each stem after equilibration. The stem segments were then severed under water into ten 10-cm lengths. Specific conductivity and percentage embolism were determined as described above.

Results

In undertaking this study I expected to find differences between the two species that would relate to the success of *C. orbiculatus* as an invasive weed. I found that only *V. riparia* frequently demonstrated measurable root pressure during both 1996 and 1997 (Figure 3-1). Root pressure was greatest early in the spring, then declined into summer.

Celastrus orbiculatus had almost no measurable root pressures (Figure 3-1). Positive, but minor root pressures were observed on a very few occasions. Large air bubbles were frequently observed in the manometers, indicating negative pressure. However, the bubble manometer method is not reliable for negative pressures, so these values were considered no different from zero (Ewers et al. 1997).

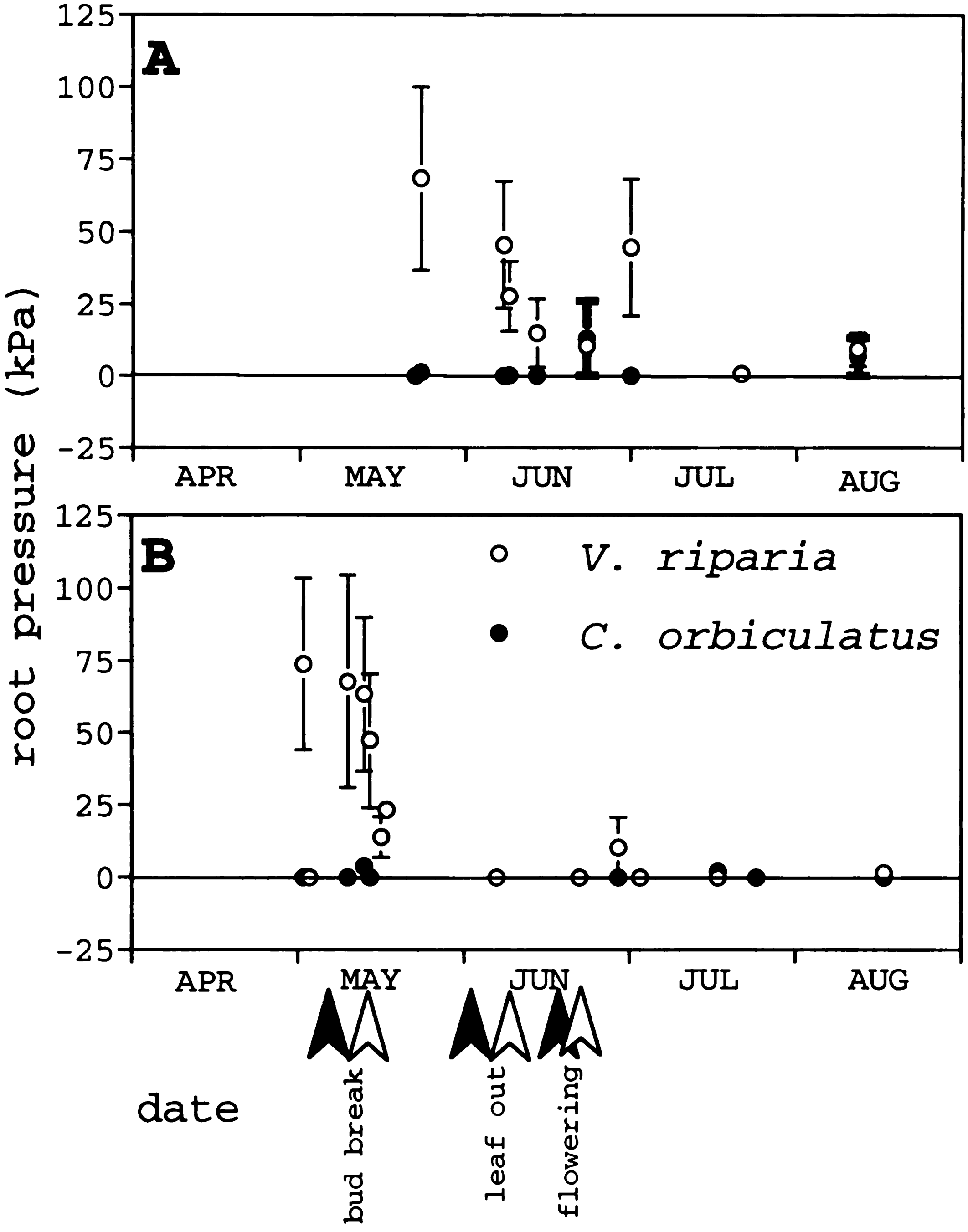


Figure 3-1. Root pressure. (A) 1996. (B) 1997. Each symbol represents the mean for five stems. The range for *V. riparia* is 0-145kPa. Error bars represent +/- 1 SE. Where error bars are not visible, they are smaller than the plotted symbol. Relative phenological events are indicated by arrows (white arrows = *V. riparia* and black arrows = *C. orbiculatus*).

Despite differences in site characteristics, the trends in conductivity were relatively uniform across sites for both species. In 1996, *V. riparia* reached its minimum percentage embolism sooner than *C. orbiculatus* (Figure 3-2A). The minimum percentage embolism in *V. riparia* (37%) was reached by the beginning of June, whereas in *C. orbiculatus* the minimum (50%) occurred at the end of August. The reduction in embolism began prior to leaf out in *V. riparia*, but it did not occur until after leaf out and after maturation of new vessels in *C. orbiculatus*.

Both species produced flowers and fruit at roughly the same time. Leaf fall in *V. riparia* roughly coincided with increased embolism and the first daily minimum temperatures below 0°C. The leaves of *C. orbiculatus* remained green at some sites for over a month beyond the first frost. During the winter of 1996-1997, embolism reached 100% in both species.

The same general patterns were observed in 1997. *Vitis riparia* reached its minimum percentage embolism sooner than *C. orbiculatus* (Figure 3-2B), however, for both species the period of reduced embolism began about one month earlier than in 1996, and therefore the total period of reduced embolism lasted longer than in 1996. In both species minimum embolism was slightly lower in 1997 than in 1996, and did not occur until one month later. The minimum percentage embolism reached during 1997 for *V. riparia* was 29% during August,

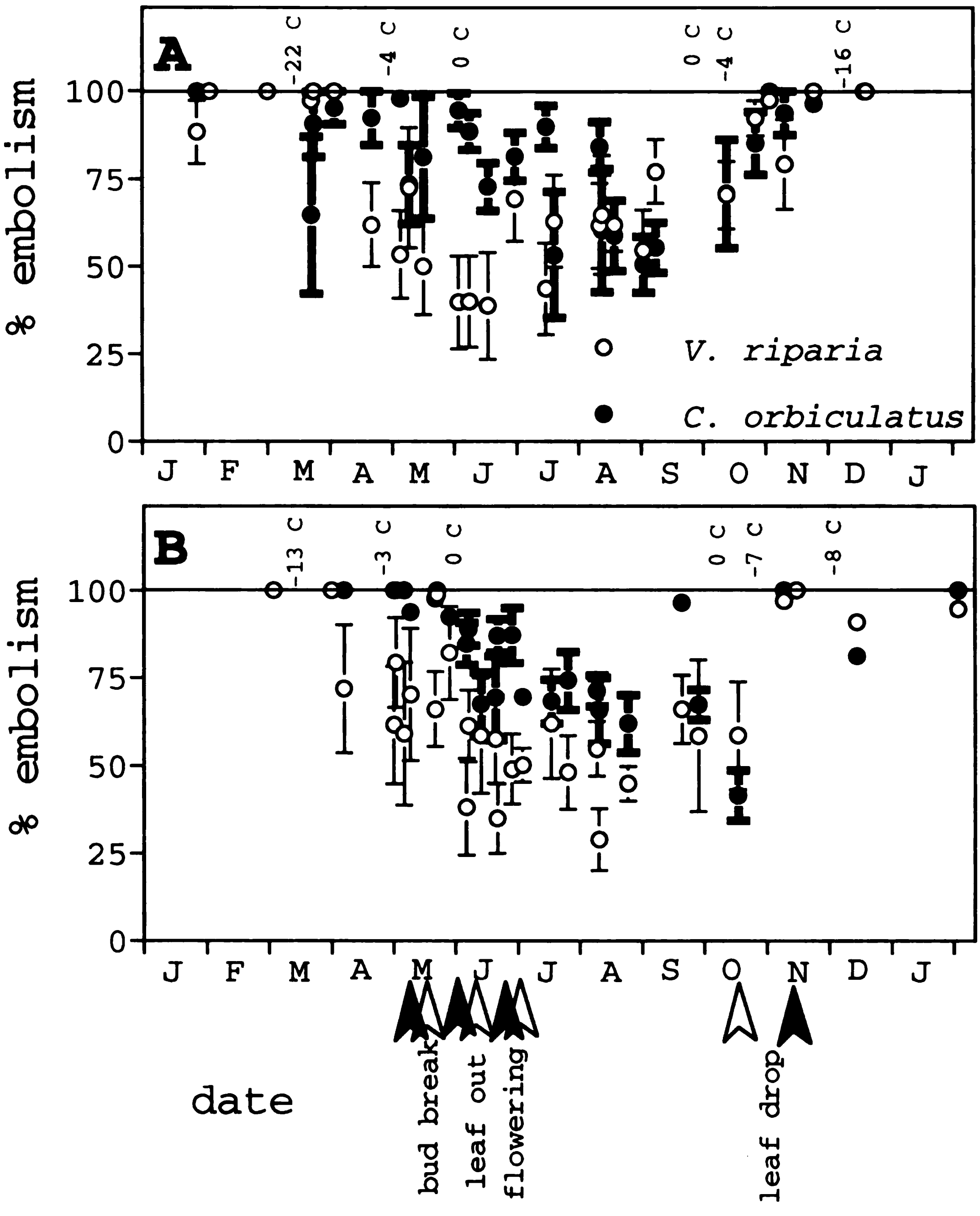


Figure 3-2. Percentage embolism. (A) 1996. (B) 1997. Each symbol represents the mean for five stems. Error bars represent +/- 1 SE. Where error bars are not visible, they are smaller than the plotted symbol. Relative phenological events are indicated by arrows (white arrows = *V. riparia* and black arrows = *C. orbiculatus*). Some relevant minimum daily temperatures are indicated along the top.

while for *C. orbiculatus* it was 42% during October. Unlike the winter of 1996-1997, embolism failed to reach 100% during the winter of 1997-1998 and, therefore, reduced embolism persisted for a longer time.

Vitis riparia achieved rates of initial (=native) specific conductivity about two to four times higher than *C. orbiculatus* (Figure 3-3). The peak values (± 1 SE) for *V. riparia* in 1996 were 49.4 ± 10.3, and for 1997 64.8 ± 20.1 kg • s^{-1} • MPa $^{-1}$ m m^{-2}. For *C. orbiculatus*, the values were 17.9 ± 5.7 in 1996, and for 1997 21.0 ± 3.5 kg • s^{-1} • MPa $^{-1}$ m m^{-2}. Similarly, the final k_S, measured after flushing the stems, was consistently higher in *V. riparia* than in *C. orbiculatus* (Figure 3-4). These values did not show a clear seasonal trend in 1996, although in 1997 the values peaked in July for *C. orbiculatus*.

Stems sampled for conductivity measurements ranged between 5 and 12 mm in diameter. During 1997, the mean stem diameter (± 1 SE) for *V. riparia* was 7.5 ± 0.1 mm (N = 145) and for *C. orbiculatus* 8.1 ± 0.1 mm (N = 145). The difference in stem diameter was significant (two-tailed t test, P = 0.0002). However, the mean stem age (± 1 SE) for *V. riparia* was 4.2 ± 0.2 yr. (N = 140) and for *C. orbiculatus* 3.7 ± 0.1 yr. (N = 140). The difference in stem age was significant (two-tailed t test, P = 0.03).

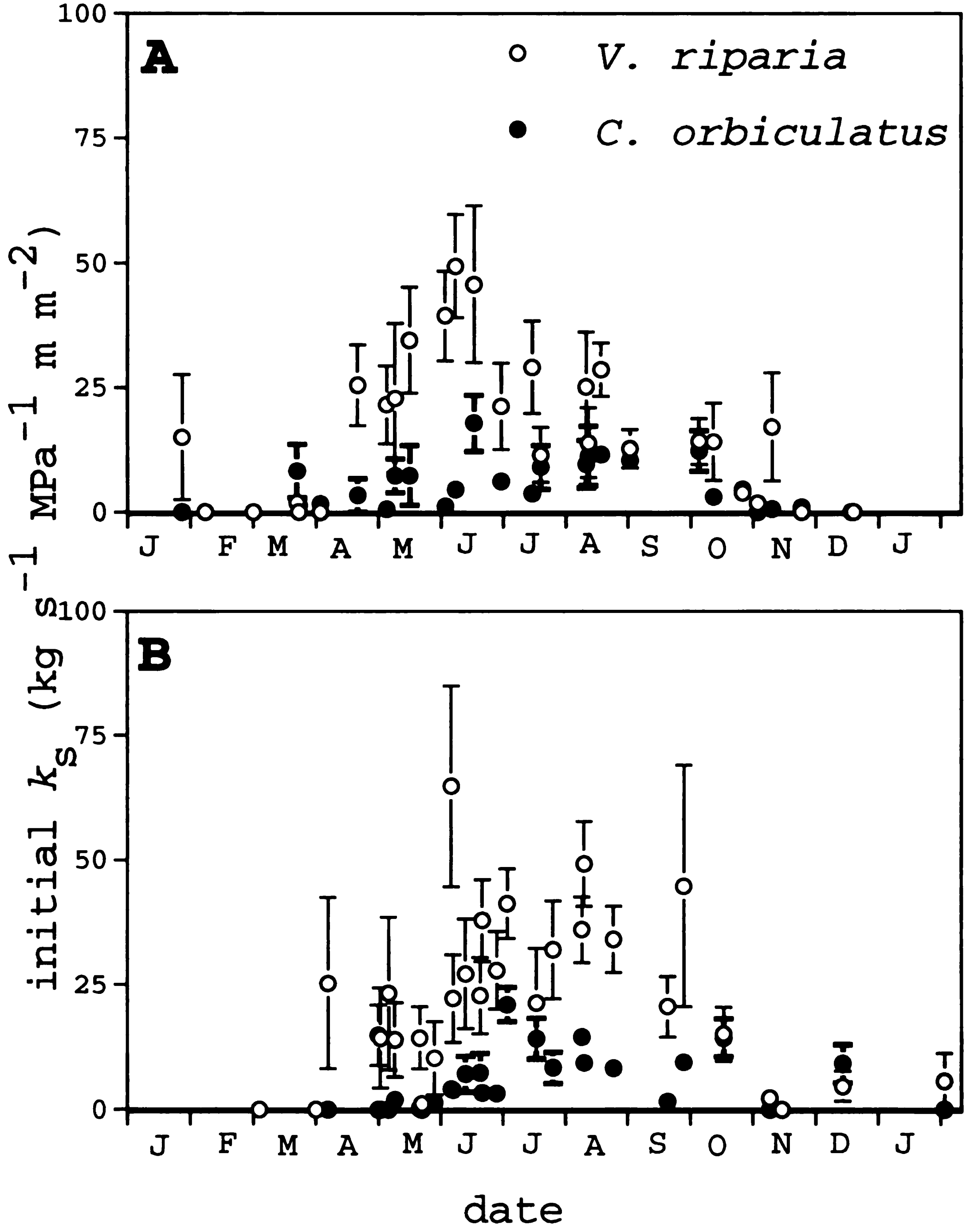


Figure 3-3. Initial (native) specific conductivity (k_S). (A) 1996. (B) 1997. Each symbol represents the mean for five stems. Error bars represent +/- 1 SE. Where error bars are not visible, they are smaller than the plotted symbol.

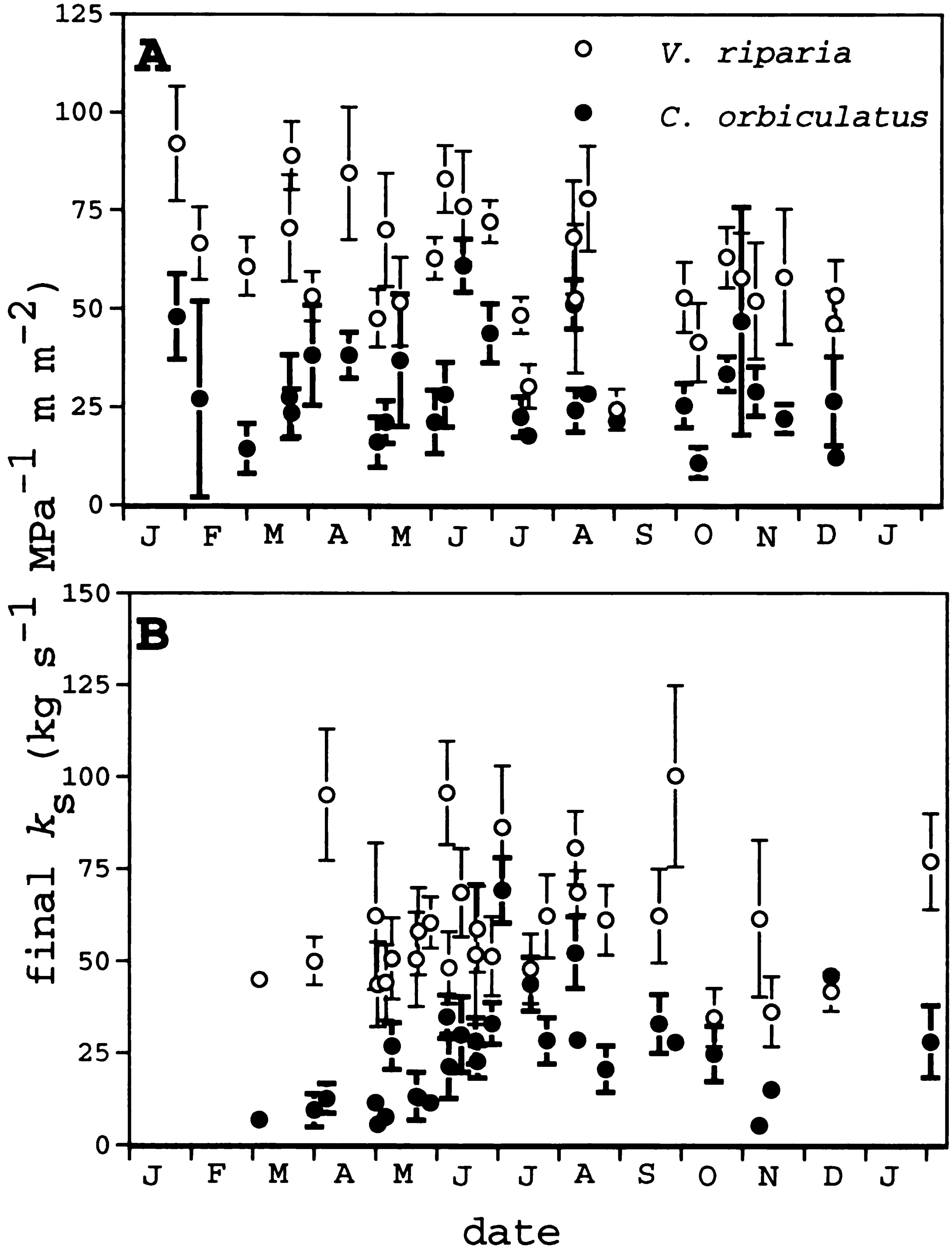


Figure 3-4. Final (maximum) specific conductivity (k_s). (A) 1996. (B) 1997. Each symbol represents the mean for five stems. Error bars represent +/- 1 SE. Where error bars are not visible, they are smaller than the plotted symbol.

The number of active growth rings differed between the two species (Figure 3-5). Stems of *V. riparia* routinely showed that in their native state (without removal of emboli), several growth rings contributed to the stem conductivity (Figures 3-7 and 3-11), with about two to four conductive growth rings by the end of April (Figure 3-7). However, for *C. orbiculatus* rarely more than one growth ring was capable of conductance (Figures 3-6 and 3-10). High pressure flushing to remove emboli induced conductance in additional growth rings in *C. orbiculatus* (Figures 3-8 and 3-12), but not in *V. riparia* (Figures 3-9 and 3-13).

The distributions of vessel diameters of the two species are remarkably similar ($P > 0.9$, Figure 3-14). Both species have a large number of narrow diameter vessels that contribute little to the theoretical conductivity. However, the four largest vessel diameter categories (<160 µm) are responsible for ~63% of the theoretical conductivity, though numerically they only represent 8% of the total vessels in the stems of each species. The average maximum vessel tangential diameter (± 1 SE) for *C. orbiculatus* was 203 ± 6 µm, and for *V. riparia* 191 ± 3 µm. This difference was not statistically significant ($P = 0.08$), despite the wood of *C. orbiculatus* being ring-porous and that of *V. riparia* diffuse-porous.

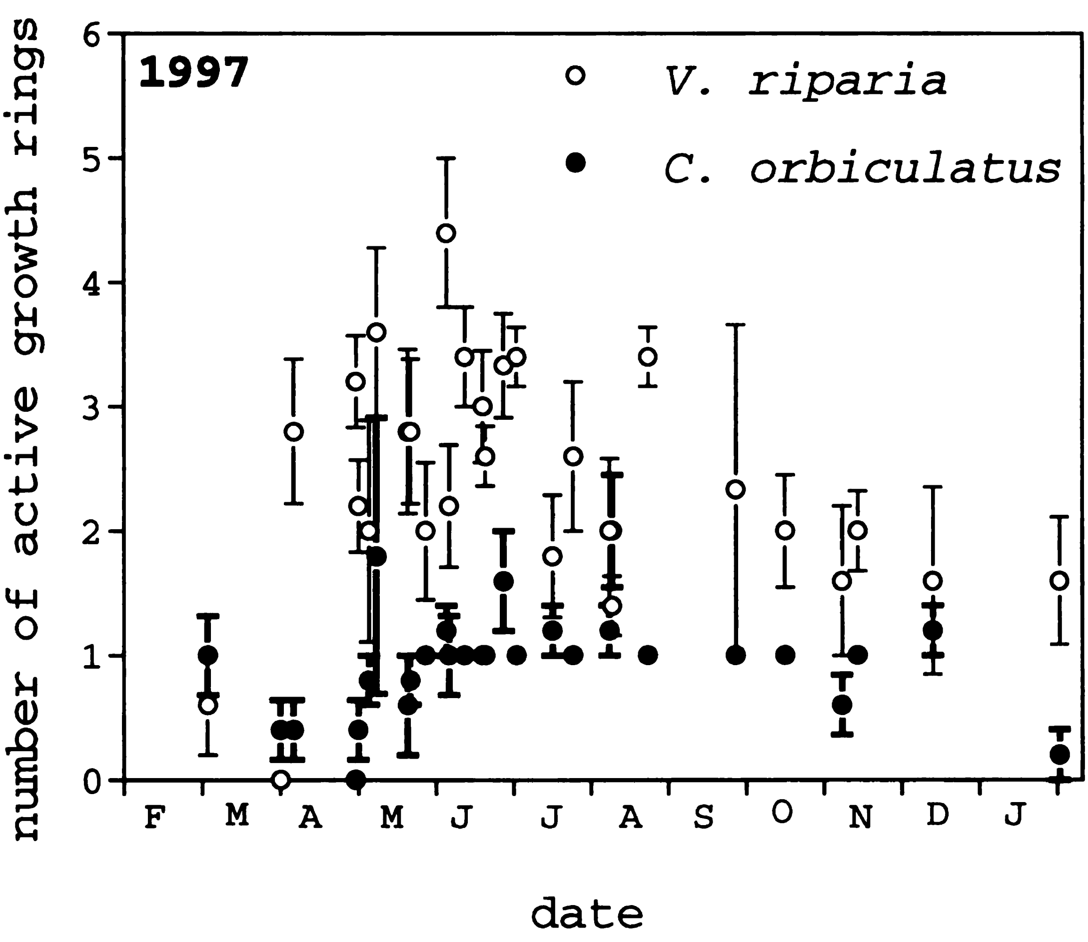
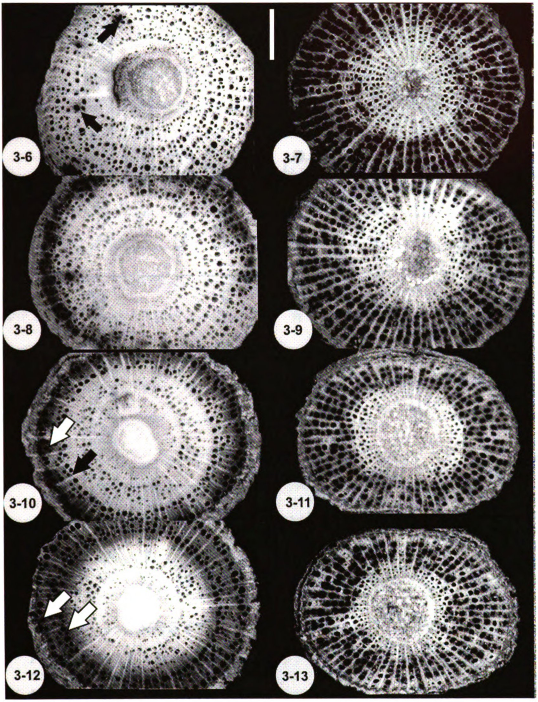


Figure 3-5. Number of active growth rings. Error bars represent +/- 1 SE. Where error bars are not visible, they are smaller than the plotted symbol.

Figures 3-6 to 3-13. Transverse view of stems. Scale bar = 200 µm and applies to all figures. Perfusion of stems with crystal-violet-marked conductive vessels. Stems were collected from the same site on two different dates. Figures 3-6 to 3-9, stems collected on 30 April 1997. **3-6.** *Celastrus orbiculatus*, native state. The arrows indicate conductive vessels. **3-7.** *Vitis riparia*, native state. **3-8.** *C. orbiculatus*, after being flushed to remove embolism. **3-9.** *V. riparia*, flushed. Figures 3-10 to 3-13, stems collected on 18 June 1997. **3-10.** *C. orbiculatus*, native state. The white arrow indicates a conductive growth ring; the black arrow indicates a nonconductive growth ring. **3-11.** *V. riparia*, native state. **3-12.** *C. orbiculatus*, flushed. The white arrows indicate conductive growth rings. **3-13.** *V. riparia*, flushed.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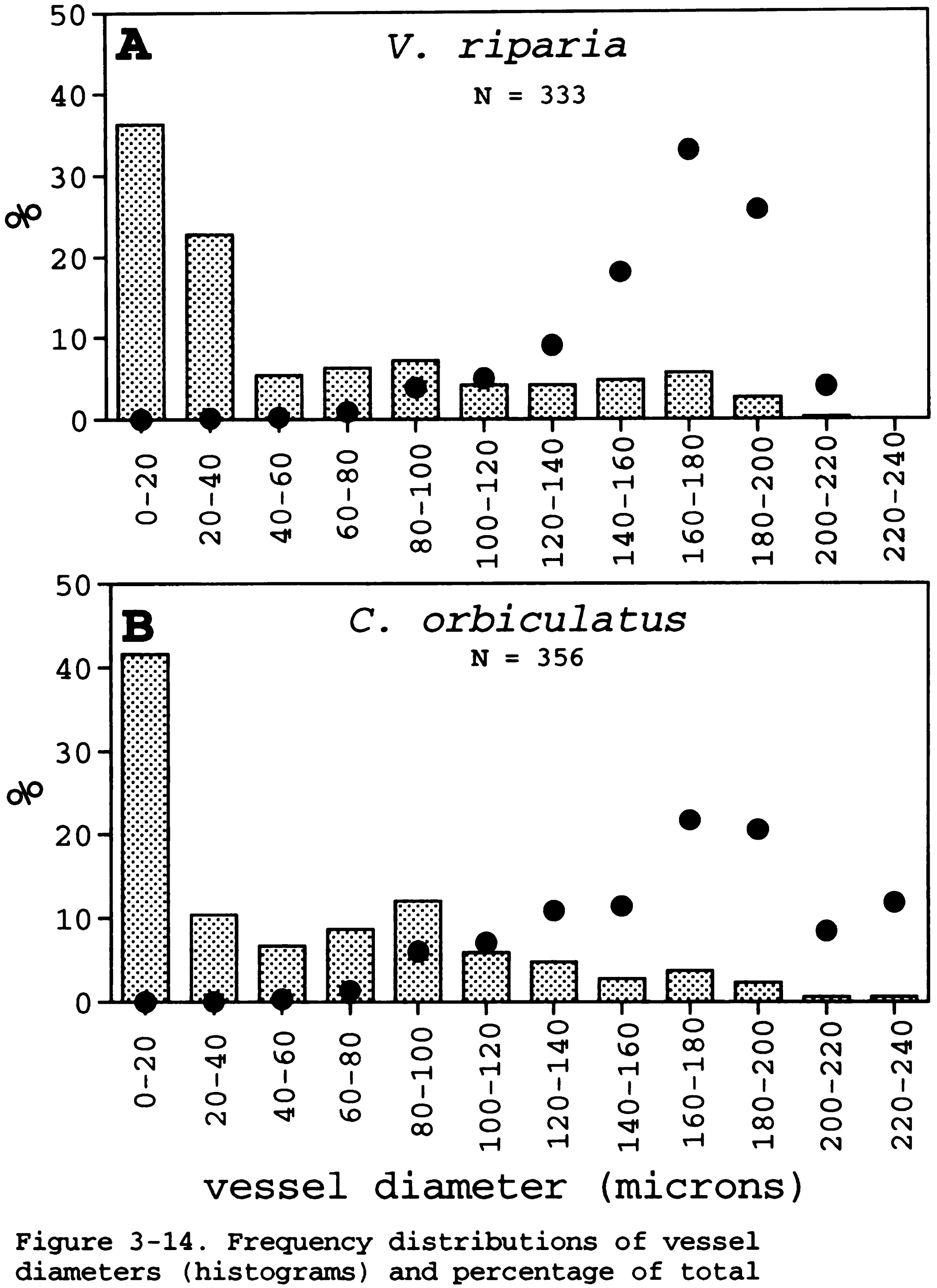

Figure 3-14. Frequency distributions of vessel diameters (histograms) and percentage of total theoretical k_h(filled circles). (A) *V. riparia* (N = 333 vessels). (B) *C. orbiculatus* (N = 356 vessels). Based upon vessels from stems shown in Figures 3-6, 3-7, 3-10, and 3-11.

Vulnerability curves were similar for *C. orbiculatus* and *V. riparia* (Figure 3-15). From the amount of scatter in the data and the high amount of native embolism, it is difficult to tell if there is any difference between the two species. If there was a difference, *C. orbiculatus* was more vulnerable to water-stress-induced embolism than *V. riparia*.

Discussion

In Michigan, *C. orbiculatus* is considered an escaped weed (Voss 1985). Its extensive and prolific growth suggests that it possesses characteristics that set it apart from native lianas. Apparently the sampled stems of *C. orbiculatus* had significantly greater rates of secondary growth than *V. riparia* since the stems of *C. orbiculatus* were, on average, a half year younger (3.7 vs. 4.2 yr) but 8% wider than for *V. riparia*.

Root pressure has been observed in many species (Sperry et al. 1987; Ewers, Cochard, and Tyree 1997; Fisher et al. 1997) and may enhance conductivity by removing emboli. Root pressure may also negate liana distribution limits imposed by freezing-induced embolism. However, root pressure is frequently too small to account for the elimination of emboli in tall plants (Ewers, Cochard, and Tyree 1997). According to my results, positive root pressures were mostly lacking in

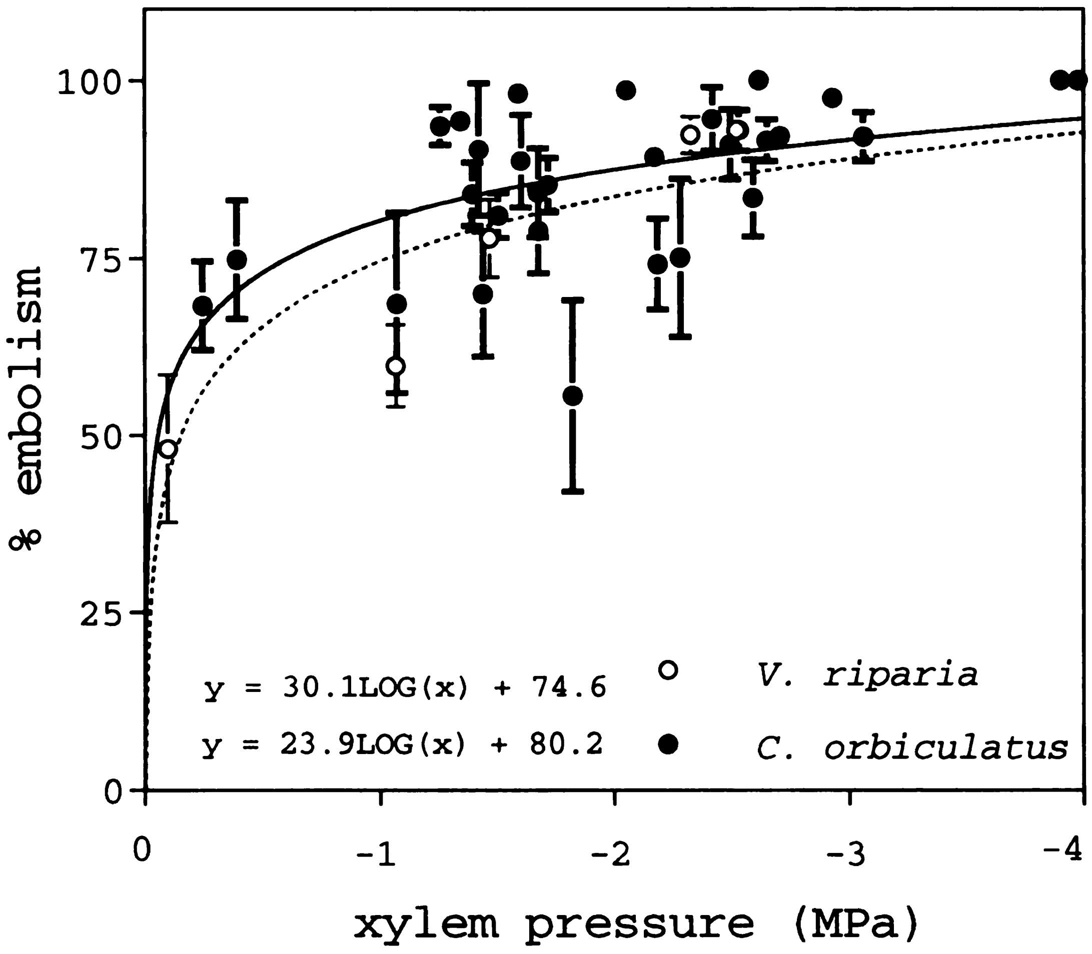

Figure 3-15. Vulnerability curves. Each symbol represents the mean for five segments from one stem. Error bars represent +/- 1 SE. Where error bars are not visible, they are smaller than the plotted symbol.

stem xylem of *C. orbiculatus* but present in *V. riparia*; thus they would not explain the weedy nature of *C. orbiculatus*.

The maximum individual root pressure measurement of 145 kPa for *V. riparia* found in this study would be sufficient, in theory, to push water 14.5 m above the ground surface. Other studies have reported root pressures for *Vitis* between 10 and 100 kPa (Sperry et al. 1987). Scholander, Love, and Kanwisher (1955) reported sap pressures of 300 - 500 kPa in *Vitis labrusca*. These measurements suggest that root pressure is an important mechanism for maintaining the conductivity of xylem vessels in this genus. The vessels remained conductive for up to 4 yr in the present study and up to 7 yr according to Smart and Coombe (1983). In *V. riparia,* increased embolism coincides with the onset of freezing conditions. Apparently, freeze-induced embolism reduces transport capability, which, in conjunction with defoliation induced by long nights, brings about winter dormancy. Since the probability of freeze-induced embolism increases with vessel diameter (Davis et al. 1999), 100% embolism may not be achieved because the narrower vessels in a stem may not become air-filled. Greater than 50% of the vessels in each species were narrower than 40 µm.

The wood of *C. orbiculatus* is ring-porous, as compared to the diffuse-porous wood of *V. riparia*, though the vessel diameter distributions are similar and both are dependent on wide vessels for most of their conductivity. *Celastrus orbiculatus* appears to rely on the production of new wood to re-establish conductivity instead of positive root pressure. In 1997, percentage embolism in *C. orbiculatus* decreased around the end of May, corresponding to the onset of conductivity by new sapwood. This dependency of *C. orbiculatus* on new wood production is similar to that reported for temperate ring-porous trees (Wang, Ives, and Lechowicz 1992; Sperry et al. 1994).

For both species the values of winter embolism were essentially 100% for 1996, but often <100% for 1997. This may be unexpected due to the different xylem anatomies of the two species, but parallels the findings of Tognetti, Longobucco, and Raschi (1998) who found the same trend looking at two species of *Quercus* that differed in anatomy. The present study may reflect the El Niño weather patterns and the lack of severe freezing during the winter of 1997-1998.

Vitis riparia had higher specific conductivity, both initial and final, than *C. orbiculatus*. This is probably explained by the fact that several growth rings were capable of contributing to conductivity in the case of *V. riparia*, but not for *C. orbiculatus*. However, using perfusion at high pressure to remove emboli, additional growth rings may become conductive in some cases. This may result in higher embolism measurements by overestimating the maximum conductivity possible. Thus the high native embolism reported here may be due to refilling of permanently nonfunctional vessels, especially for *C. orbiculatus*. Whether such embolism reversal can ever occur in intact plants of *C. orbiculatus* is unclear.

Finally, the vulnerability to desiccation curves indicate that both species are similar in their sensitivity to drought-induced embolism. Pawmmenter and Vander Willigen (1998) point out that there are numerous models for analyzing vulnerability curves. There is little agreement in the literature as to statistical tests for vulnerability curves. Our curve-fit approach represents the best fit available; however, it does not reflect coefficients of biological significance and should not be used to infer the native state of embolism for these species. Importantly, it is not possible to attribute the success of *C. orbiculatus* to greater resistance to drought-induced embolism.

Clearly, the *Vitis* root pressure paradigm (Putz 1983, Sperry et al. 1987) does not apply to all successful wide-vesseled temperate vines. *Celastrus orbiculatus* has little or no root pressure and is dependent on newly produced xylem each year, similar to temperate ring-porous trees. The weedy nature of *C. orbiculatus* cannot be explained by root pressure nor exceptional conductivity. The results of this study indicate that *V. riparia* has the advantage in the hydraulic parameters measured, although it is possible that leaf or root hydraulics, not measured in the present study, may favor *C. orbiculatus*. However, there are many alternative hypotheses not related to water relations that could explain the reality of the *C. orbiculatus* spread. Among those deserving attention are: the lack of pests and diseases afflicting the exotic species, more prolific seed production and dispersal, vegetative propagation from root sprouts, and faster growth rates.

CHAPTER 4

Seed production and germination in the invasive liana *Celastrus orbiculatus* and the native *C. scandens* (Celastraceae)

Introduction

Celastrus orbiculatus is a liana (woody vine) that is native to Japan, Korea, and China. It has become a problematic weed in eastern North America (Brizicky 1964, Patterson 1974, Dreyer 1984, Tibbetts and Ewers 2000), and it has been recognized as a threat to silviculture in the Appalachians (McNab and Meeker 1987, McNab 1988). Damage to host trees occurs from girdling, increased risk of ice damage, and death from shading of the crown (McNab 1988). In addition to silvicultural problems, exotic vines may impact plant community dynamics, slowing or arresting succession and replacing native vegetation (Penfound 1966). The native congener, *C. scandens*, is less aggressive than *C. orbiculatus* and can be supplanted by the exotic species when they co-occur (Dreyer 1984). Manual removal of *C. orbiculatus* has proven difficult due to resprouting from its extensive root system; nonselective herbicides have had some success following repeated exposures (Patterson 1974, Dreyer 1988, Hutchinson 1992).

Morphologically, the two species are very similar. The main difference used to distinguish the two is the inflorescence: axillary cymes for *C. orbiculatus* and terminal panicles for *C. scandens*. Both species are dioecious to polygamodioecious. The gynoecium is usually 3 carpellate (sometimes 4), 3-locular, with 2 (1) ovules per locule. The fruit is a small (1 cm) orange to yellow subglobular leathery capsule. It is incompletely 3-locular, 3 valved, with 2 (1) seeds per locule. Seeds of both species have copious endosperm, and 2n = 46 for each (Brizicky 1964, Gleason and Cronquist 1991). The seeds are enclosed in a fleshy red aril that is exposed upon reflexing of the valves in autumn. The attractive fruits have been overcollected in Michigan leading to the protection of *C. scandens* under Michigan Public Act 182 of 1962, the "Christmas-tree law" (Rabeler 1998). Both species are also capable of vegetative propagation from root sprouts, and birds disperse the seeds of both species. The similarity in reproductive biology between the species stands in contrast to their ecological behavior.

In Connecticut, Dreyer, Baird and Fickler (1987) found that two populations of the exotic *C. orbiculatus* had higher germination success (59% and 82%) than a population of the native *C. scandens* (27%) in a laboratory study. Whether these trends would hold true for Michigan, across several sites, was unclear, as *C. orbiculatus* may be more recently established in Michigan (Patterson 1974). Additionally, the scarcity and small populations of *C. scandens* in Michigan suggested that there may be some disruption or failure of its sexual reproduction.

I hypothesized that *C. orbiculatus* would demonstrate higher investment in sexual reproduction than *C. scandens,* based on its demographic spread. This would be demonstrated in greater number of seeds per fruit and greater seed germination.

Methods and Materials

Collection

Fruits were collected in the fall and winter of 1998-1999 and 1999-2000 from six sites in the southern Lower Peninsula of Michigan. Both species were collected on the Michigan State University (MSU) campus and from nearby sites in Williamston, Rose Lake, and Shoeman Road (Ingham county). *Celastrus orbiculatus* was also collected from Kellogg Biological Station (Kalamazoo county), and Hidden Lake Gardens (Lenawee county). Fruits were randomly selected from at least five individuals at each site, except where population size was limiting (Rose Lake). The fruits were allowed to air dry in the laboratory to make removal of the fleshy aril simpler.

Processing

Seeds were separated from the fruit. The number of mature seeds per fruit was recorded for each species and site. Seeds were weighed en masse, since they were too small to accurately weigh individually, to obtain the mean mass per seed. Finally, the seeds were stratified in screened sand in plastic film canisters at 5 °C for various periods of time. *Celastrus scandens* seeds have a demonstrated stratification requirement (USDA Forest Service, 1948) of 90 days at 33-50° F (Barton 1939). *Celastrus orbiculatus* seeds were also found to germinate better after a stratification period (Patterson 1974).

Subsamples of seeds were tested for viability using 2,3,5-triphenyl-2H-tetrazolium chloride (TTC, 1%) (Mattson et al. 1947, Castilla 1999). Seeds were imbibed in distilled water, bisected through the embryo, and incubated in the tetrazolium solution overnight. Viable embryos stained pink.

Germination

Germination trials were carried out in the laboratory. Seeds of each species were sown in separate flats in Hyponex Professional Mix Potting Soil. Seeds were planted approximately 3 mm deep and watered throughout with distilled water. No additional fertilizer or nutrient solutions were introduced. Light was provided on a 12-hour cycle controlled by electric timers. Light level was determined using an Extech Instruments model 401025 light meter, the sensor of which has its maximum sensivity at ~570 nm, range 400 to 700 nm. Light level, seed source, collection year, and stratification period differed between trials. Table 4-1 outlines the conditions in each trial. Observations were made roughly daily; the number of seeds germinated was recorded. A seed was considered to have germinated when its hypocotyl was first observed. Subsequent death of a seedling was observed on several occasions, this acted to slightly reduce the percentage germination, as only live seedlings were counted for each observation. In one trial (Trial 4) the seeds were abraded with 100-C grit gypsum sandpaper to disrupt the seed coat. The seeds were then planted as above.

Results and Discussion

Seeds per Fruit

The ovary anatomy indicates that both species had similar potential reproductive output. However, this study found significant differences in realized reproductive output. Overall, *C. orbiculatus* had significantly more seeds per fruit (3.68 ± 0.05) than *C. scandens*. (2.43 ± 0.07), with $P < 0.0001$. However, when looking at individual sites this trend was more variable (Figure 4-1). Based on population

Table 4-1. Seed germination trial condidions.

seed source	collection year	species	number of seeds	stratification period (days)	light intensity (lux)
trial 1					
MSU campus	1998	*C. scandens*	251	100	5165
MSU campus	1998	*C. orbiculatus*	251	100	5165
trial 2					
Rose Lake	1998	*C. scandens*	256	229	1948
KBS	1998	*C. orbiculatus*	256	202	1948
trial 3					
MSU campus	1998	*C. scandens*	198	125	2077
MSU campus	1998	*C. orbiculatus*	256	125	2077
trial 4					
Rose Lake	1998	*C. scandens*	234	271-287	2152
KBS	1998	*C. orbiculatus*	236	265	2152
trial 5					
Shoeman Road	1999	*C. scandens*	200	111	2070
Williamston	1999	*C. orbiculatus*	200	111	2070

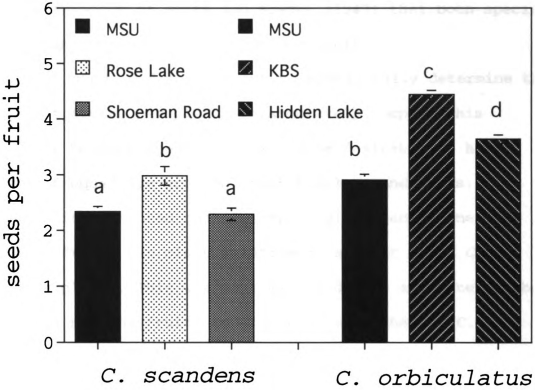

Figure 4-1. Mean seeds per fruit, +/- 1 SE. Sample sizes are as follows: *C. scandens* at MSU N = 193, Rose Lake N = 57, Shoeman Road N = 140; *C. orbiculatus* at MSU N = 312, KBS N = 336, Hidden Lake Gardens N = 355. Bars designated with different letters are significantly different from one another with $P < 0.05$.

means, *Celastrus orbiculatus* still produces more seeds per fruit than *C. scandens* (2.9-4.4 vs. 2.3-3.0). However, fruits of *C. scandens* collected at the Rose Lake site did not have significantly fewer seeds than those fruits of *C. orbiculatus* collected at the MSU site. This result quantifies the anecdotal report of White and Bowden (1947) that both species produce on average 3 to 4 seeds per fruit.

This study did not set out to specifically determine the number of fruits per plant. To accurately compare this parameter between species, it would be desirable to have plants of equal age growing under similar conditions. However, it was noted that *C. orbiculatus* plants generally had more fruits per plant relative to similar sized *C. scandens* plants. This was most likely due to a greater number of shoots bearing fruits in *C. orbiculatus* than in *C. scandens*. A post hoc analysis of shoots collected for the seeds per fruit study indicated that individual fruiting shoots of each species produced roughly similar numbers of fruits: 14.4 in *C. orbiculatus* and 13.4 in *C. scandens*. This would suggest that any advantage to *C. orbiculatus* would occur from producing more fruiting shoots, with fruits that bear more seeds per fruit than *C. scandens*.

Seed Mass

While being more numerous, *C. orbiculatus* seeds were of consistently lower mass than seeds of *C. scandens* (Figure 4-2). Mean seed mass across sites for *C. orbiculatus* was 10.3 ± 1.1 (SE) mg, while for *C. scandens* mean seed mass was 16.8 ± 0.4 mg. An unpaired t-test shows these differences are significant (P = 0.0055). This would indicate that seeds of *C. orbiculatus* would have less of the copious endosperm reported for both species than *C. scandens*. (Gleason and Cronquist 1991). Relative to one another, *C. orbiculatus* would be considered more r-selected and *C. scandens* more K-selected based on this character (MacArthur and Wilson 1967, Pianka 1970). This result is not likely to represent an aberrant year; *C. scandens* is reported to bear good seed crops almost yearly (USDA 1948), and is not prone to masting (Wyman 1950).

Seed Viability

The differences in seed viability between species were minor. Staining for vital tissues using TTC indicated that 88% (n = 140) of *C. orbiculatus* seeds were viable versus 79% (n = 138) for *C. scandens*. Floatation was not a good indicator of the absence of a viable embryo in *C. scandens*: 40% of floating seeds contained viable embryos versus 100% in *C. orbiculatus*. However, 95.7% of sinking *C. scandens* seeds

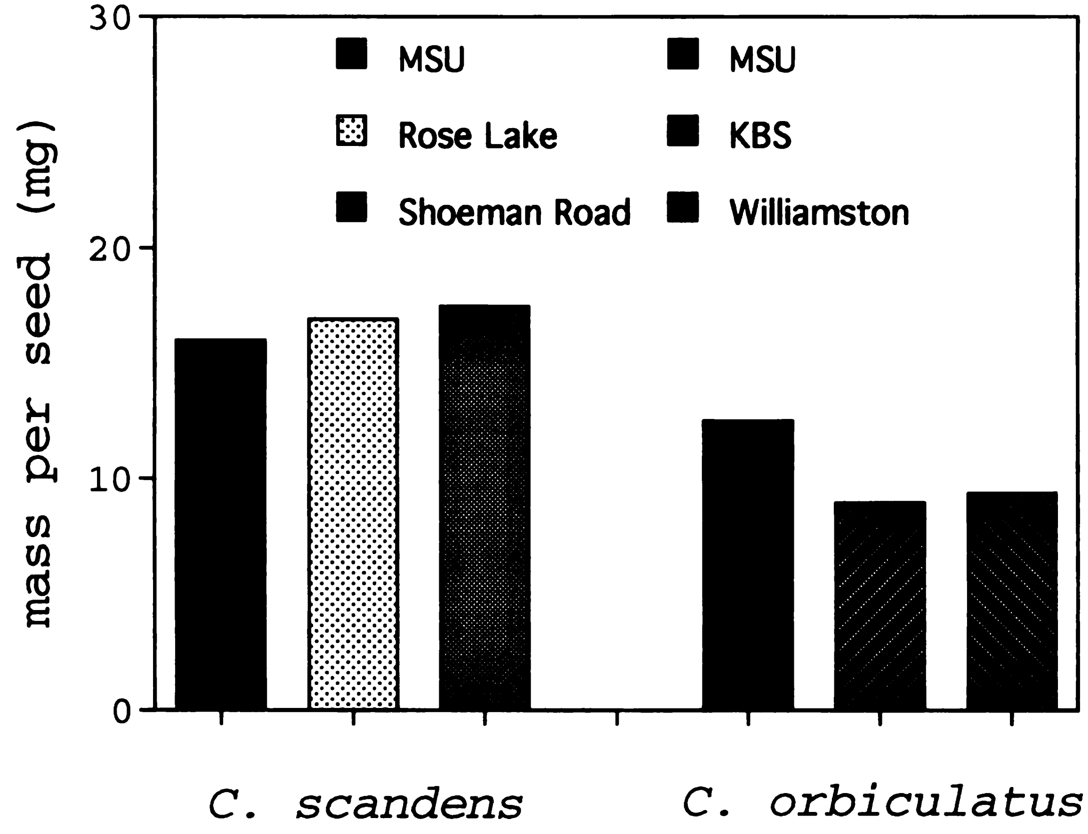

Figure 4-2. Mass per seed. Sample sizes are as follows: *C. scandens* at MSU N = 453, Rose Lake N = 234, Shoeman Road N = 376; *C. orbiculatus* at MSU N = 291, KBS N = 236, Williamston N = 624. Seeds were weighed en masse, so SE could not be calculated.

did have embryos, indicating that screening for sinking should yield potentially viable seeds.

Germination

The germination trials revealed a striking difference between the germination success of the two species (Figure 4-3). In each case the seeds of *C. orbiculatus* were more likely to germinate under controlled laboratory conditions than the seeds of *C. scandens*. The percentage germination ranged from 45 to 92% for *C. orbiculatus* and from 0 to 1.5% for *C. scandens*. Germination began one week following sowing and was largely complete by three weeks. Trial four was followed for 129 days with no increase in number of seeds of either species germinating.

The higher success of *C. orbiculatus* seeds to germinate was not surprising, as others have noted similar results (Dreyer Baird and Fickler 1987). The germination success for *C. orbiculatus* appears to be in line with reported germination capacities for other temperate lianas (*Parthenocissus quinquefolia*, 69%; *Vitis riparia*, 82%; USDA Forest Service 1948). However, the extremely low success of *C. scandens* seeds to germinate, always below 2%, was surprising. The USDA Forest Service (1948) reported a mean germination success of 47%, ranging from 9 to 80% for this species. Dreyer, Baird and Fickler (1987) found germination

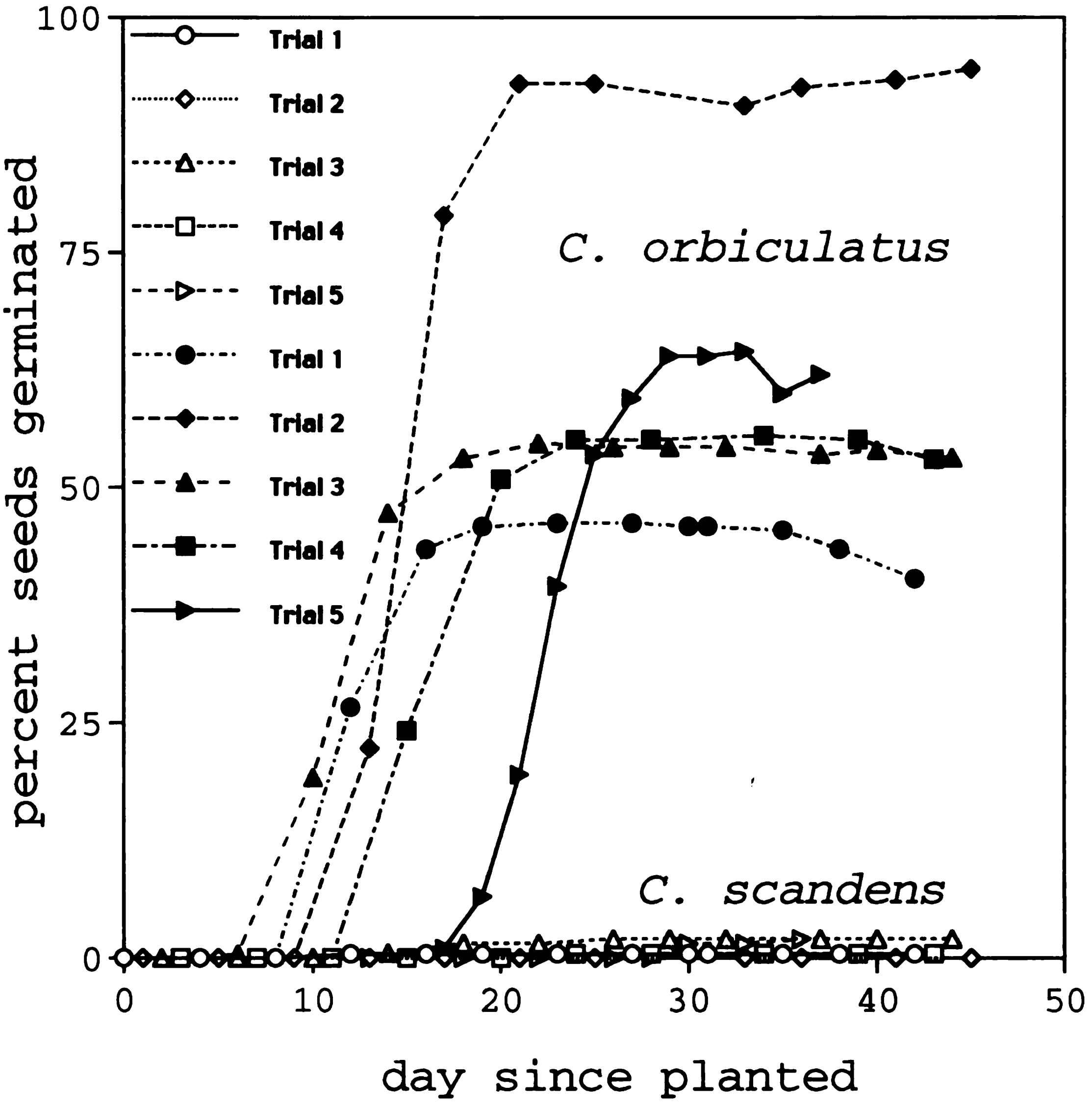

Figure 4-3. Germination trials. Open symbols for *C. scandens*, closed symbols for *C. orbiculatus*. See Table 4-1 for the conditions of each separate trial.

rates of 27%, and Joseph (1928) reported 36 to 68% germination. All of these earlier studies used similar cold stratification periods, light levels, and soil types to the methods implemented here.

Though these seed germination results do help explain the observed pattern of *C. orbiculatus* spread relative to *C. scandens*, they also beg the question: Why did the *C. scandens* seeds fail to germinate? Seed scarification was investigated, although it had not been reported as a necessary prerequisite for germination. The same results were obtained when the seed coats had been disrupted, so it is unlikely that this explains the low germination success of *C. scandens*. Likewise, the same results were found for seeds from different sites and from seeds collected in both 1998 and 1999.

I do not have a clear explanation of the low germination success of *C. scandens* in this study. Some reports (e.g., USDA 1948, White and Bowden 1947) indicate that good seed years are experienced almost annually, others (Wyman 1950) indicate that year to year trends exist and can be significant. In this light, it is possible that I have documented two bad years for *C. scandens*. However, it seems unlikely that two bad years for one species would prove to be relatively good years for a sympatric congener which might be expected to cueing on the same environmental parameters for seed production.

One possible hypothesis is that *C. scandens* is suffering from inbreeding depression. A normally outcrossing species may suffer from inbreeding depression when in small, isolated populations (Barrett and Husband 1990, Husband and Schemske 1996). Modeling has indicated the possibility for moderate amounts of selfing to lead to high inbreeding depression (Lande et al. 1994). Unfortunately, I have no information on population structure, demographics, or the frequency of selfing in *C. scandens* or *C. orbiculatus*.

Alternatively, populations of *C. scandens* may be suffering from an accumulation of deleterious somatic mutations. With reduced numbers of sexual generations through time, *C. scandens* would have fewer chances for selection to operate, purging deleterious alleles. This could eventually result in poor vigor and loss in realized sexual reproductive success (Kondrashov 1994).

Grime (1979) life history strategies would characterize both species as ruderals. One would expect that the large seeds with abundant resources should promote a high germination rate for *C. scandens*. Conversely, one would expect the many small seeds of *C. orbiculatus,* with limited resources, would demonstrate a low germination rate. This would be particularly true under field conditions, and less apparent in the laboratory. No such failure in *C. orbiculatus* or advantage to *C. scandens* seeds was observed in this study; *C. orbiculatus* is more successful as a ruderal in Michigan.

While this study found a distinct difference between the species in seed germination, it did not investigate seedling establishment or seedling survival. Differences in these characteristics could strongly enhance or negate the germination success measured in the laboratory. Additionally, both species are capable of persistence and spread by vegetative means. Whether the two species differ in this capacity was not specifically investigated, and could similarly affect the results reported here.

Predictive Theory

Much work (see Rejmanek 1996) has focused on elucidating the traits of invasive species in order to successfully predict which species will become pests. This could have direct management implications regarding which species are introduced through horticulture and agriculture. Rejmanek and Richardson (1996) developed a discriminant function based on three traits that differed between invasive and non-invasive pines: low seed mass, short juvenile period, and short interval between large seed crops. Bird dispersal of seeds also contributes positively to the invasiveness of a species (Rejmanek 1996). The discriminant function correctly identified the invasive lianas *Lonicera japonica* and *Pueraria lobata* (Rejmanek and Richardson 1996). Although the length of juvenile period has yet to be determined for *C. orbiculatus*, low seed mass, near yearly good seed crops, and bird dispersal of seeds indicate that it follows well with this predictive function for invasive species.

CHAPTER 5

Growth, phenology, and herbivory in *Celastrus orbiculatus* and *Vitis riparia*

Introduction

The invasive liana (woody vine) *Celastrus orbiculatus* is spreading through habitats that have native incumbent lianas including *Vitis riparia, Parthenocissus quinquefolia, Toxicodendron radicans* and *C. scandens*. While *C. orbiculatus* was first introduced around 1900, its localized spread into suitable habitat continues (Chapter 2). Possible explanations for the spread of an alien species into occupied habitat are enhanced growth and lower incidence of herbivory relative to the native species. Some exotic lianas (e.g., kudzu, Forseth and Teramura 1987) exhibit higher growth rates than competing vegetation. Other exotic lianas appear to benefit from escape from herbivory as proposed by Darwin (1859); for instance, *Lonicera japonica* (Schierenbeck et al. 1994).

Shoot growth is a major way by which plants expand their canopies and explore their light environment. This is especially important in lianas, where the relative amount of leaf area supplied per stem section is high (low Huber values). Liana growth rates may be enhanced since fewer resources need to be allocated to supporting stem tissue (Mooney and Gartner 1991).

Any damage to the liana stem may have growth consequences within the stem and within the whole plant. Loss of the shoot apical meristem may lead to lateral buds proliferating to replace it (Kramer and Kozlowski 1979). The loss of apical dominance may also lead to changes in the allocation of elongation between shoots (Collet, Colin and Bernier 1997).

Direct loss of leaves can also affect shoot growth. Both the position and extent of leaf loss can affect shoot elongation (Marquis 1988, 1992, Tuomi et al. 1988, Haukioja et al. 1990, Langstrom et al. 1990, Henriksson, Haukioja and Ruohomaki 1999). Additionally, timing of leaf loss can determine the extent of shoot growth response (Haukioja et al. 1990, Ruohomaki et al. 1997).

The precocious internode elongation of lianas may make their apices more susceptible to herbivory than plants with protected apices (Penalosa 1983). Additionally, tendril climbers such as *V. riparia* should have less exposed apices relative to twiners like *C. orbiculatus* (Troll 1937). There is evidence that apex predation may limit population survivorship in some vine species. Janzen (1971) found severe herbivory on the apices of *Dioclea megacarpa* (Fabaceae), ranging from 15 to 50% of shoot tips.

The recent spread of *Celastrus orbiculatus* throughout lower Michigan suggests that it may be growing unchecked by predators that hamper native lianas. There are very limited reports of herbivory on *C. orbiculatus* either in its native range (Saito 1989) or in Michigan (Kiss 1984). The native congener, *C. scandens* (American bittersweet), is reported to suffer severe winter injury from cottontail rabbit (Sweetman 1944). Herbivory on *Vitis* is well documented through viticulture, and includes insects (*Phylloxera sp.,* root louse; *Erythroneura vaiabilis*, variegated leafhopper; and *Harrisina brillians*, western grapeleaf skeletonizer) and nematodes (*Meloidogyne*, *Pratylenchus*, and *Tylenchulus*) (Mullins, Bouquet and Williams 1992).

I wished to determine whether the spread of *C. orbiculatus* was related to a lack of herbivory, greater shoot growth, or a combination of both, relative to the common native liana species *Vitis riparia.*

Methods and Materials

Thirty-four species pairs of individuals of *Celastrus orbiculatus* Thunb. and *Vitis riparia* Michaux were established in the natural regrowth forests surrounding Kellogg Biological Station, Michigan State University, Gull Lake, Michigan in 1998. One new season's shoot of each species was marked with flagging tape. The shoots were selected to be as close to one another as possible, as similar in size as possible, and experiencing the same microhabitat influences as could be discerned (e.g., same level in canopy or at ground level). Individuals were located in varying habitats, including open fields, closed canopy deciduous forest, and edges.

In 1999, thirty-seven species pairs were used. New shoots on the same stems used in 1998 were used for measurements in 1999. Several were dead and were eliminated from the subsequent year.

Measurements were made through the 1998 and 1999 growing seasons. Shoot length and leaf size at the third node were measured weekly until no change was detected. Phenological parameters of bud burst, leaf maturation, and leaf fall were monitored. Across sites, average date of leaf maturation, full shoot extension growth, and average maximum shoot length were calculated. The maximum shoot length reflected the greatest amount of growth recorded during the growing season, which was not necessarily the shoot length at the end of the season. Frequency of deer and insect herbivory, as well as likelihood of mortality, were calculated. Notes on damage by both deer and insect herbivores were made, and resprouts were followed when herbivore damage removed the initial shoot. Light level was measured with an Extech Instruments model 401025 light meter (peak sensitivity ~570 nm, range 400-700 nm) in 1999 to compare the sites. Means were compared with two-tailed t-tests, alpha = 0.05.

Results

Mean maximum shoot length differed between years, but was relatively similar in both species, and reached by the same time in the growing season (Table 5-1). Shoots in low light grew longer than shoots in high light (Figure 5-1). Leaf maturation was complete slightly earlier and leaf drop occurred slightly later in *C. orbiculatus* than in *V. riparia* in both years. Bud burst, observed in 1999, occurred slightly earlier in *C. orbiculatus* (128.1 ± 1.0) than in *V. riparia* (130.1 ± 1.2). Flowering, observed in 1998, occurred slightly earlier in *C. orbiculatus* (142 ± 0) than in *V. riparia* (145.8 ± 1.5). Overall, there was very little difference in the timing of phenological events between the two species.

Overall mortality of shoots was greater for *V. riparia* than *C. orbiculatus* in both years, but incidence of herbivory differed between species and between years (Table 5-2). In 1998, *V. riparia* was slightly more likely to be eaten by deer than *C. orbiculatus* (50 vs. 44%). However, *C. orbiculatus* was slightly more likely to be eaten by insects than *V. riparia* (82 vs. 79%). In 1999, *V. riparia* was much more likely to suffer deer browsing than *C. orbiculatus* (70 vs. 30%). Contrary to 1998, in 1999 *V. riparia* was much more prone to insect predation than *C. orbiculatus* (30 vs. 14%).

The consequences of herbivory, while correlational, suggest both species and year differences do exist. In 1998,

Table 5-1. Phenology. Julian date ± 1 SE. An asterisk below a column indicates a significant difference between between the species in a two-tailed t-test at alpha = 0.05.

	maximum shoot length (cm)		date of shoot maturation		date of leaf maturation		date of leaf fall	
species	1998	1999	1998	1999	1998	1999	1998	1999
C. orbiculatus	91.4 ± 11.5	59.5 ± 13.0	184.3 ± 5.6	175.2 ± 7.9	164.1 ± 2.3	147.8 ± 1.9	299.2 ± 2.4	292.8 ± 2.1
V. riparia	98.4 ± 11.7	58.4 ± 8.1	177.9 ± 3.8	189.9 ± 5.8	168.4 ± 2.6	158.8 ± 3.0	280.9 ± 3.7	284.0 ± 3.6
						*		*

Table 5-2. Herbivory and mortality. Percentage ± 1 SE. An asterisk below a column indicates a significant difference between the species in a two-tailed t-test at alpha = 0.05.

	% deer herbivory		% insect herbivory		% mortality	
species	1998	1999	1998	1999	1998	1999
C. orbiculatus	44.1 ± 8.6	29.7 ± 7.6	82.4 ± 6.6	13.5 ± 5.7	8.8 ± 4.9	5.4 ± 3.8
V. riparia	50.0 ± 8.7	70.3 ± 7.6	79.4 ± 7.0	29.7 ± 7.6	35.3 ± 8.3	32.4 ± 7.8
		*			*	*

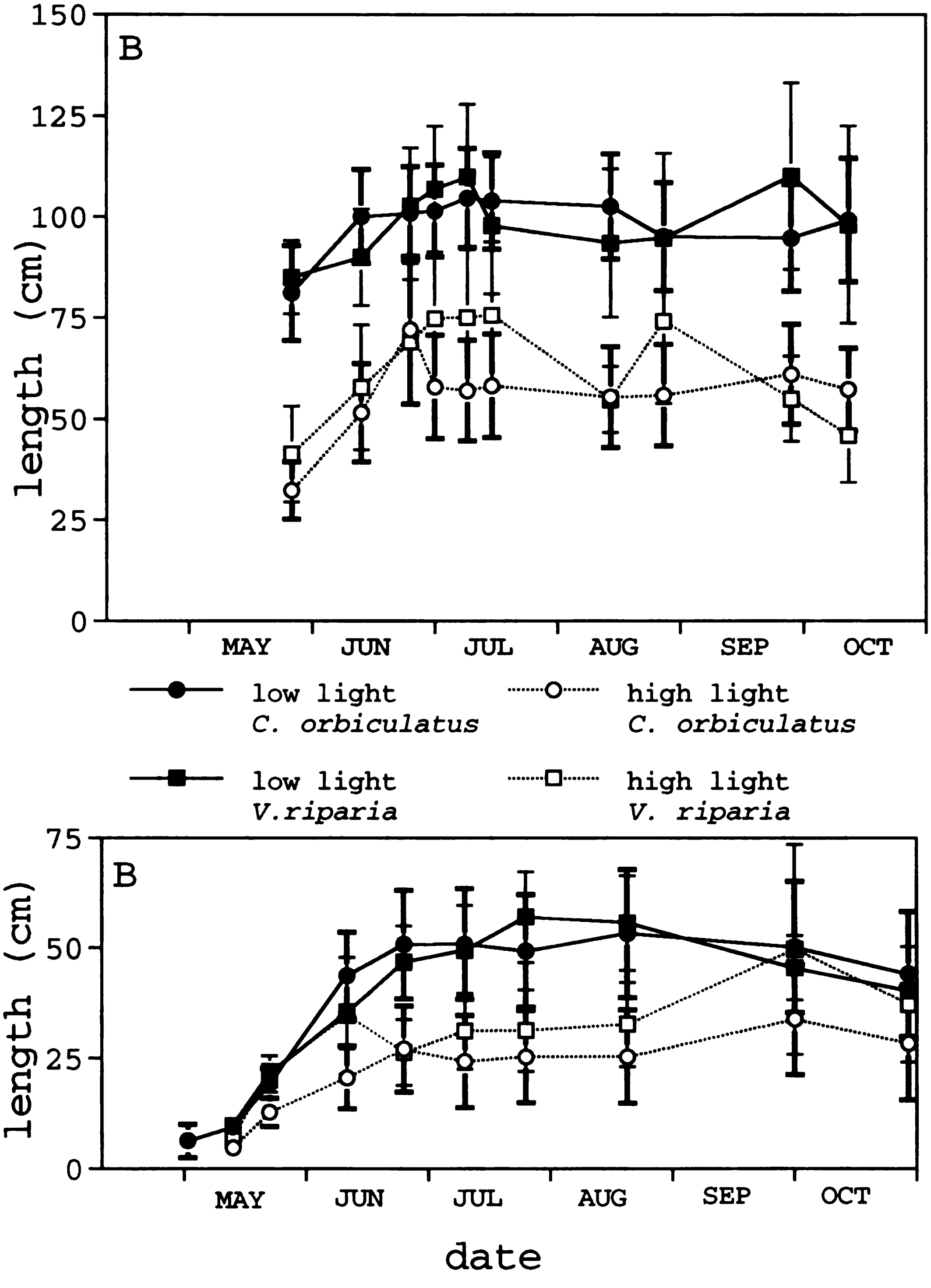

Figure 5-1. Mean shoot length, +/- 1 SE. (A) 1998. (B) 1999. Low light level < 1000 lux, high light level > 1000 lux.

most *C. orbiculatus* shoot mortality was associated with insect herbivory, while shoot mortality in *V. riparia* was associated with deer herbivory, insect and deer herbivory combined, and to a lesser extent insect herbivory alone (Figure 5-2). In 1999, most shoot mortality in both species was not associated with any observed evidence of herbivory. Deer herbivory and combined deer and insect herbivory were associated with equal portions of *V. riparia* shoot mortality.

Discussion

Celastrus orbiculatus and *V. riparia* were very similar in phenology and shoot elongation in this study. This is particularly interesting as they are from different plant families and climb by different strategies (*V. riparia* a tendril climber, *C. orbiculatus* a twiner). Timing of phenological events and overall maximum shoot elongation differed by year, but not by species. These trends are consistent with our previous experience at a different site in Michigan (Tibbetts and Ewers 2000). The year to year trends are likely related to differences in summer precipitation and temperature (Figures 5-3 and 5-4). The similarity in species responses appears to indicate that the selective pressures relative to the liana growth habit are stronger than family-specific trends.

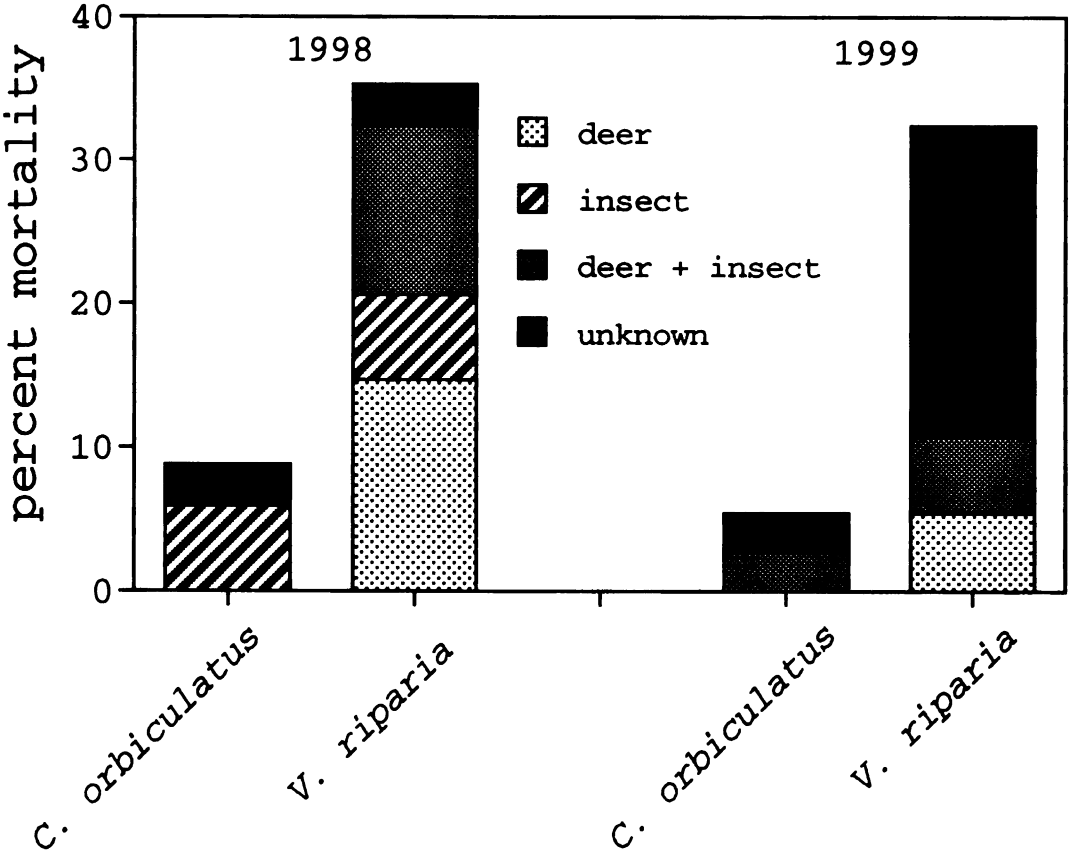

Figure 5-2. Sources of mortality, 1998 and 1999. Note that the total mortality was greater in *V. riparia* both years (see Table 5-2).

Figure 5-3. Precipitation. 1998 and 1999 monthly totals from the Kellogg Biological Station Long Term Ecological Research site weather station.

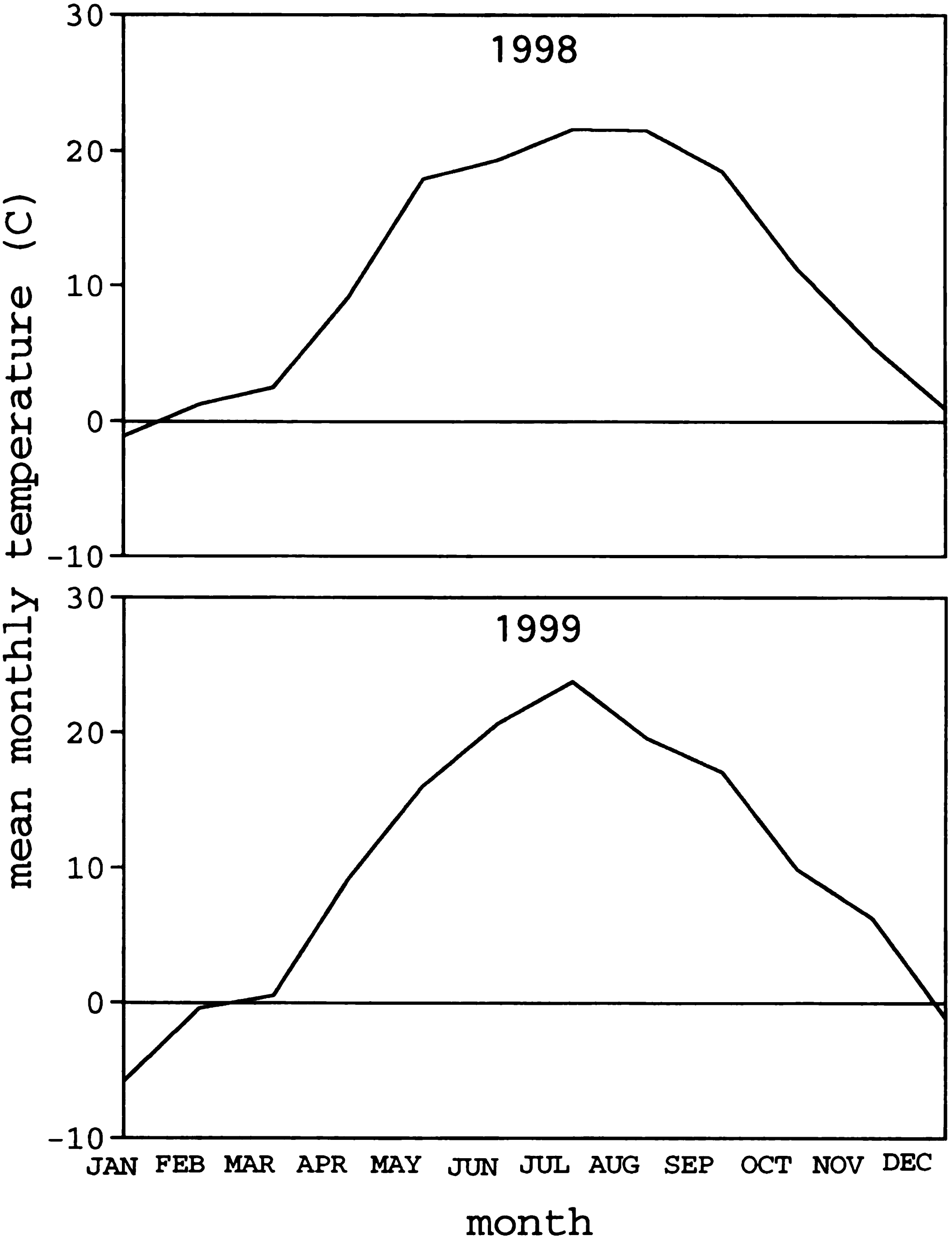

Figure 5-4. Temperature. 1998 and 1999 mean monthly temperature from the Kellogg Biological Station Long Term Ecological Research site weather station.

Herbivory damage was similar on both species in 1998, but in 1999 *V. riparia* was much more likely to show signs of herbivory. This may be related to a combination of factors. The lower overall shoot elongation seen in both species in 1999 may have resulted from lower precipitation levels than 1998 (Figure 5-3). If herbivore density in 1998 and 1999 was similar, one would expect to see greater herbivory in the year with less growth, since there would be less biomass available to the herbivores. Additionally, many herbivores may not recognize the exotic *C. orbiculatus* as a potential food item. Finally, it may be possible that *V. riparia* lacks secondary defenses while *C. orbiculatus* has such defenses.

Mortality of shoots differed between species in both years, suggesting that *V. riparia* suffers higher shoot mortality than *C. orbiculatus*. The shoot mortality difference between species also suggests a difference in shoot growth strategy. Damaged *Vitis riparia* shoots were likely to be replaced with a new sprout from the base rather than to continue growing from a lateral bud. In 1999, eleven damaged shoots were replaced by resprouts in *V. riparia*, with one shoot being replaced three times. In contrast, *C. orbiculatus* shoots that suffered damage were likely to continue growing from a released lateral bud.

The difference in shoot response to injury may relate to differences in stem architecture. *Vitis riparia* shoots typically had fewer, larger leaves relative to *C. orbiculatus* shoots. The best response to injury to *V. riparia* stems coupled with leaf damage, indicating a risky environment, may be to try a new environment. However, when in a productive environment, *V. riparia* produced numerous lateral branches ($\bar{x}$ = 4.6 ± 1.0 per stem vs. 0.8 ± 0.3 for *C. orbiculatus*, 1998). *Celastrus orbiculatus* shoots continued to elongate from lateral buds. This was further demonstrated in an simulation of herbivory in the laboratory. Eighty-four four month old *C. orbiculatus* seedlings, ranging in height from 7 to 50 cm, were cut back to 5 cm with blunt scissors, simulating herbivory. Ninety-five percent of the seedlings resprouted from lateral buds and continued to grow.

While *C. orbiculatus* does not entirely escape herbivory, it may suffer reduced rates and respond vigorously. This may be enough to explain its advantage over *V. riparia* in this study. Additionally, the reduced herbivory effect on *C. orbiculatus* may also explain its spread relative to the native congener *C. scandens*.

CHAPTER 6

Dendrochronology applied to the exotic temperate liana *Celastrus orbiculatus*

Introduction

Dendrochronology has typically been applied to tree species. However, the principles extend to any species having secondary growth with boundaries between growth increments, relatively concentric growth rings that show variability in patterns, and cross-dating within and between individuals. A multitude of species meet these requirements including, as one would expect, most temperate trees (e.g., Fritts 1976, Graumlich 1993). Non-tree species have also been examined, such as the herbaceous perennial *Bunias orientalis* L. (Dietz and Ullmann 1998). Additionally, both tree species and fish have been shown to have annual growth increments correlated to climate variables (Guyette and Rabeni 1995).

Many lianas (woody vines) have the required characteristics for dendrochronology. However, the dendrochronological literature is lacking in studies of liana growth rings. Only one dendrochronology study includes any aspect of liana growth. Birrong and Schoenwiese (1988) carried out a climatic study using European tree rings. At one site, they used the quality of grape harvest instead of tree growth as a proxy for climatic data. The growth rings of the grapevines were not evaluated. One reason for the paucity of liana dendrochronology may be the relatively short life span of lianas compared to trees. However, this shortfall may be countered by cross-dating overlapping chronologies.

Dendrochronology has been used to examine the effects of exotic species on community composition and dynamics (Russian olive and salt cedar: Howe and Knopf 1991, exotic deer: Veblen et al. 1989), to determine the establishment time of invasive trees (Butler 1986, Miller and Halpern 1998).

Celastrus orbiculatus is an exotic liana pest species in Michigan (Patterson 1974). It was desirable to understand its history at several sites, and how its growth compares to a native co-occurring liana, *Vitis riparia*. The objectives of this study were: 1) to determine if the lianas *C. orbiculatus* and *V. riparia* could be used in dendrochronology, 2) to compare annual growth increments (ring widths) in *C. orbiculatus* and *V. riparia* with precipitation data, and 3), to determine the relative age and dynamics of *C. orbiculatus* infestations at three different sites.

Methods and Materials

Vines were sampled at the Petrides farm, Hidden Lake Gardens (HLG), and the Kellogg Biological Station (KBS). Each site was chosen based on the presence of large populations of the exotic liana *C. orbiculatus* and some specimens of *V.*

riparia. The site location details and sample sizes are presented in Table 6-1. Each site was examined for C. orbiculatus specimens: all those greater than 5 cm in diameter were sampled. Stem segments were cut in the field as close to the proximal base as possible and returned to the laboratory for drying and analysis. Specimens collected included dead and apparently living stem sections approximately 20 cm in length.

Upon return to the laboratory, the stems were cut to yield discs approximately 3 cm thick. The discs were dried in a 60 °C oven for two days. Surfacing was carried out using sand paper. Chronologies were created using the skeleton plotting technique (Stokes and Smiley 1996). In this technique, representations of the narrow ring widths for each stem are made on strips of graph paper. The individual chronologies can then be compared by overlaying the graph paper strips and matching the patterns of narrow rings. Skeleton plotting was done using a dissecting microscope. Two chronologies, 180° degrees apart, were completed for each stem. This allowed me to verify consistent patterns within the stem (internal cross-dating). Stems that were alive at the time of sampling provided an anchor date to assign dates to dead stems. A master chronology for each species at each site was made by matching ring width patterns and extending the record back as far as the oldest stems.

Table 6-1. Dendrochronology site locations (Michigan).

site description/location	sample size	nearest weather stations
Petrides farm:	*C. orbiculatus* N = 18	Lansing Capital City Airport,
Pinus sylvestris plantation	*V. riparia* N = 1	Williamston
Ingham county		
T4N R1E S23 NW1/4 W1/2		
Kellogg Biological Station (KBS):	*C. orbiculatus* N = 17	Kalamazoo State Hospital,
Old field successional, Oak/Hickory	*V. riparia* N = 8	Gull Lake Bio. Stn.
Kalamazoo county		
T1S R9W S6, S8		
Hidden Lake Gardens (HLG):	*C. orbiculatus* N = 27	Jackson Reynolds Field,
Mixed Beech/Maple	*V. riparia* N = 7	Hudson, Tipton
Lenawee county		
T5S R3E S18 E1/2		

Ring width measurements were made with a Henson measuring machine. This device records the width of each growth ring in increments of 0.01 mm. Two series of measurements were made for each stem, 180° degrees apart, to calculate the mean ring width. The ring width chronologies were then aligned by year to calculate mean ring width for each species at each site.

Precipitation data for the period 1950-1999 were obtained from the NOAA weather web site (www.noaa.gov). The nearest weather stations with continuous, relatively complete records were utilized as indicated in Table 6-1. Missing values were inferred from the nearest station to provide a continuous record. Stem chronologies were aligned and ring widths were compared with precipitation data in a correlation analysis.

Results

Celastrus orbiculatus and *V. riparia* were found to produce reliable, reproducible ring width patterns. Cross-dating was achieved. Additionally, locally absent (missing) rings were noted in both species, indicating that simple ring-counting would not have produced reliable results.

Representative ring width chronologies are shown in Figures 6-1, 6-2 and 6-3. Both species demonstrate internal consistency, with the ring width chronologies 180° apart from

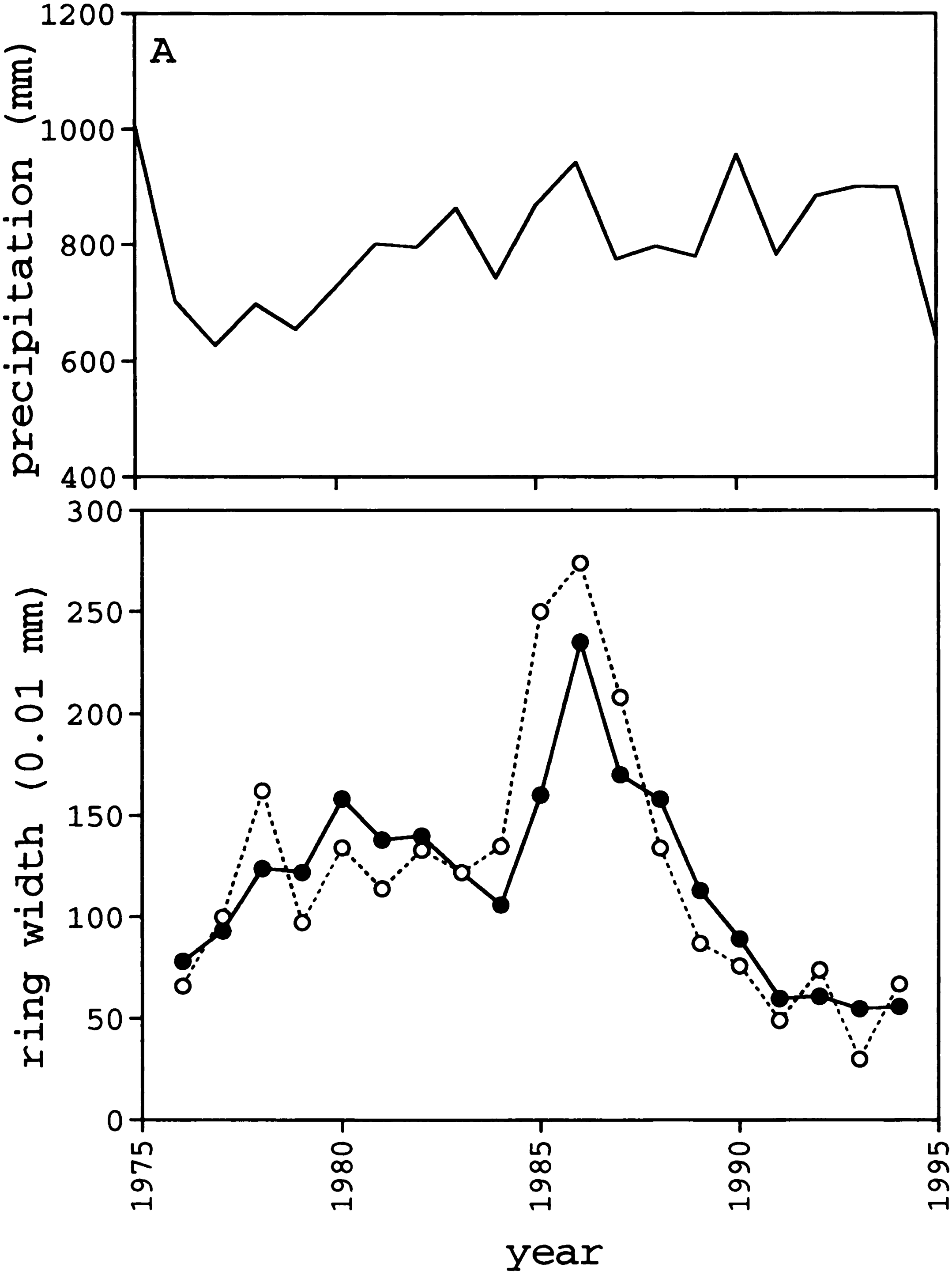

Figure 6-1. A. Annual precipitation at Petrides farm. B. *C. orbiculatus* ring width chronology. The separate lines represent two chronologies for the same individual.

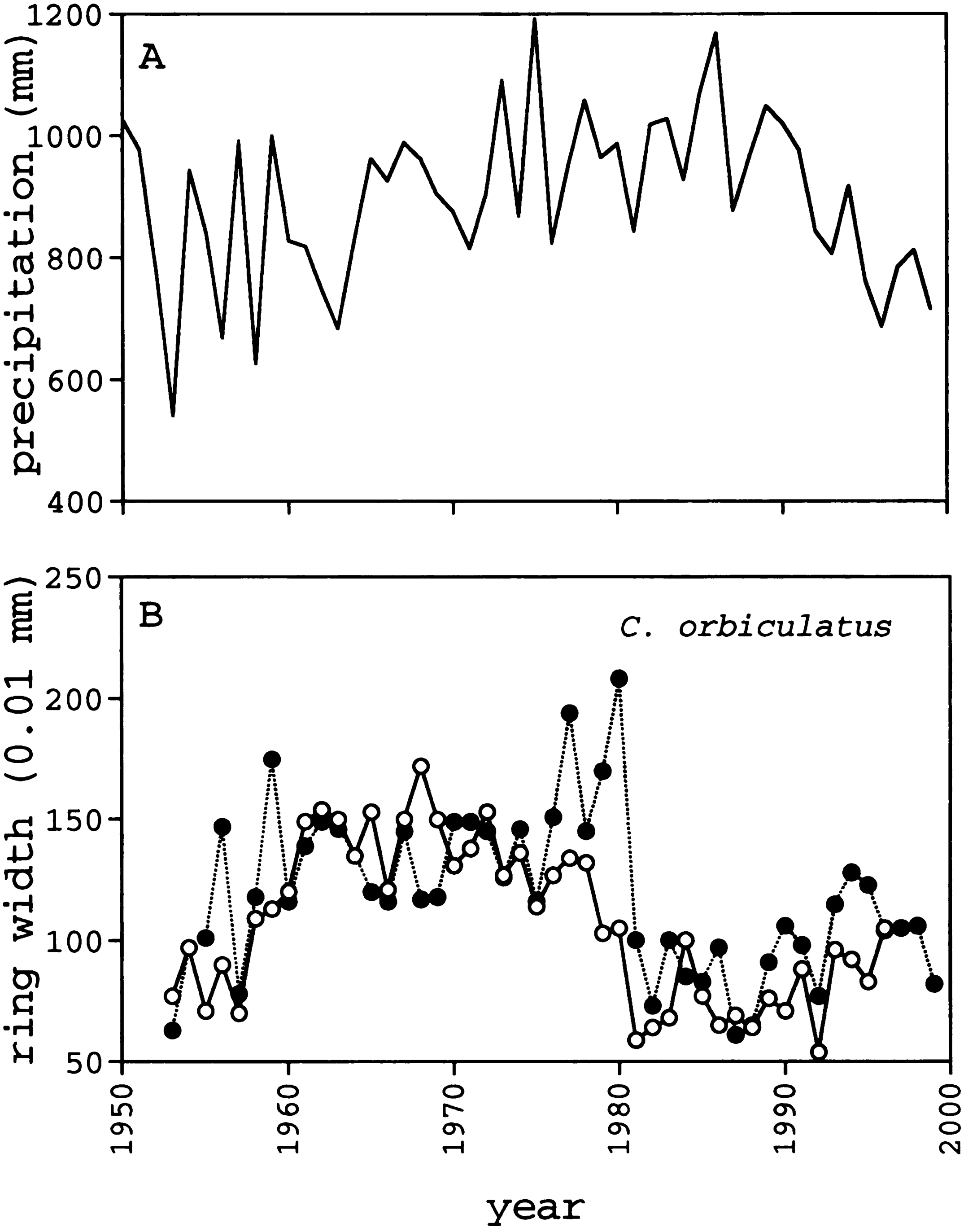

Figure 6-2. A. Annual precipitation at Kellogg Biological Station. B. *C. orbiculatus* ring width trend. The separate lines represent two chronologies for the same individual.

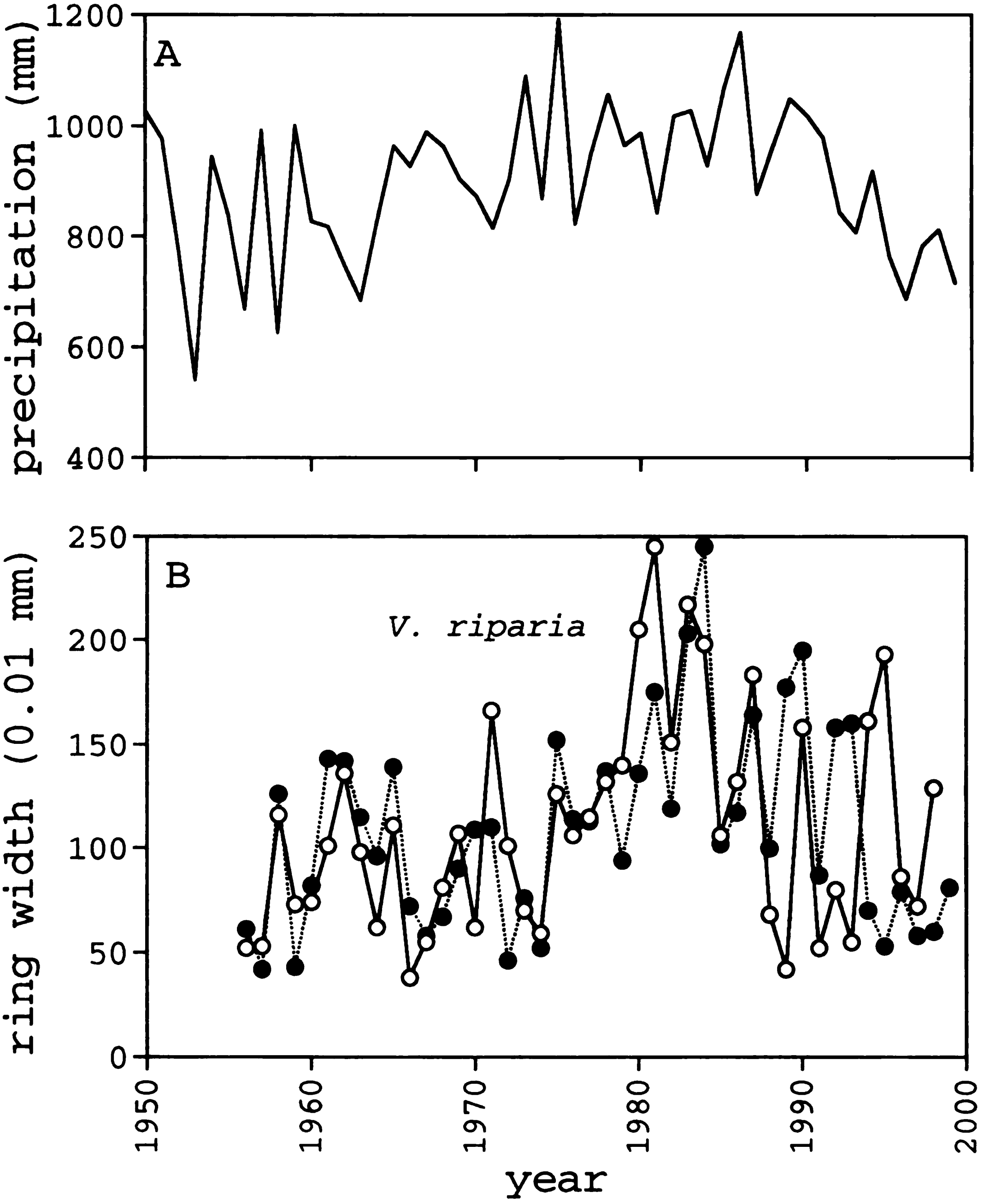

Figure 6-3. A. Annual precipitation at Kellogg Biological Station. B. *V. riparia* ring width trend. The separate lines represent two chronologies for the same individual.

the same individual matching one another relatively closely. The annual growth rings correlate with some periods of the precipitation record, but do not precisely match. Additionally, individuals of the same species at the same site show some consistency in mean ring width chronologies. *Celastrus orbiculatus* and *V. riparia* at KBS show consistent patterns of valleys and to a lesser extent peaks (Figures 6-4 and 6-5).

Mean annual ring width plots showed similar tracking of the precipitation record. At the Petrides farm (Figure 6-6), the peak at 1986 in growth ring width and the following valley in 1988 corresponded to the high precipitation in 1986 followed by the drought in 1988. Vines of both *C. orbiculatus* and *V. riparia* at KBS (Figure 6-7) showed a similar tracking of precipitation patterns. The responses of both species were very similar to one another throughout most of the chronology, though *C. orbiculatus* possessed wider growth rings during the decade 1989-1999. At HLG, a rough tracking of precipitation pattern was also observed (Figure 6-8). The mean ring width of *C. orbiculatus* increased throughout the chronology, from being narrower than *V. riparia* in the 1970's to wider in the 1990's.

While the general patterns suggest that mean annual ring width appears to be associated with precipitation, a correlation analysis failed to find strong positive

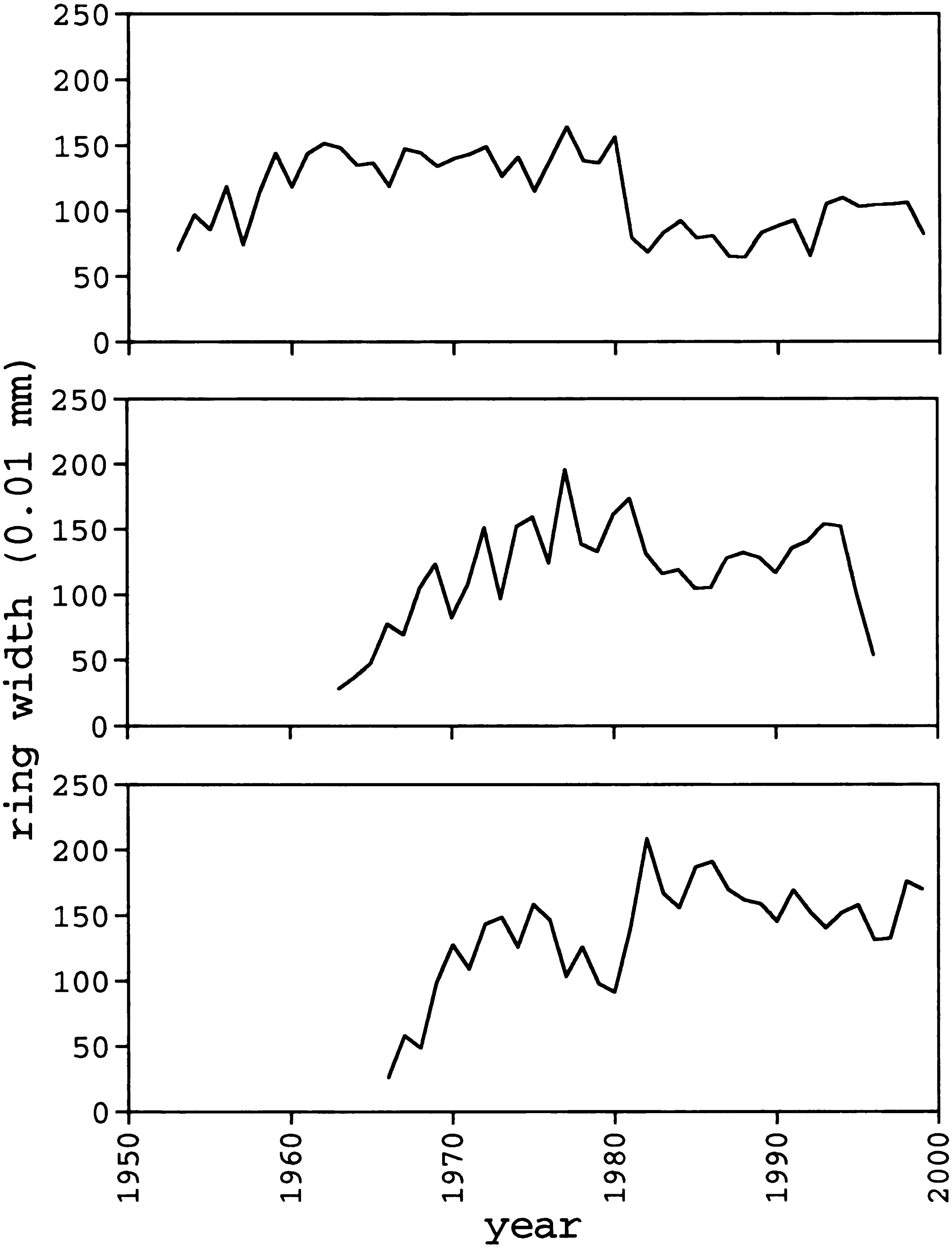

Figure 6-4. Ring width chronologies for *C. orbiculatus* at KBS. Each plot represents the mean ring width chronology for one individual. Note the consistent valley at 1979.

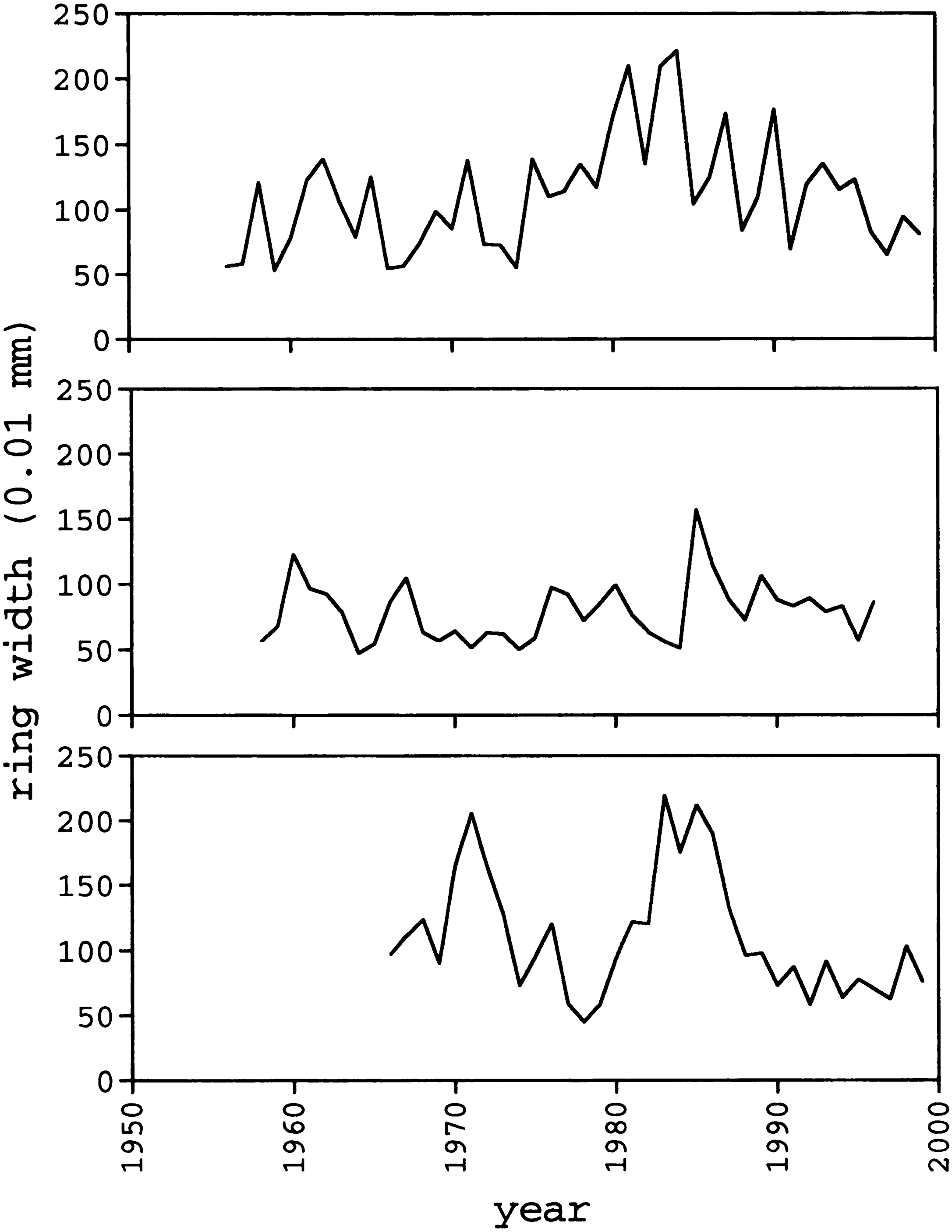

Figure 6-5. Ring width chronologies for *V. riparia* at KBS. Each plot represents the mean ring width for one individual. Note the consistent valley at 1974.

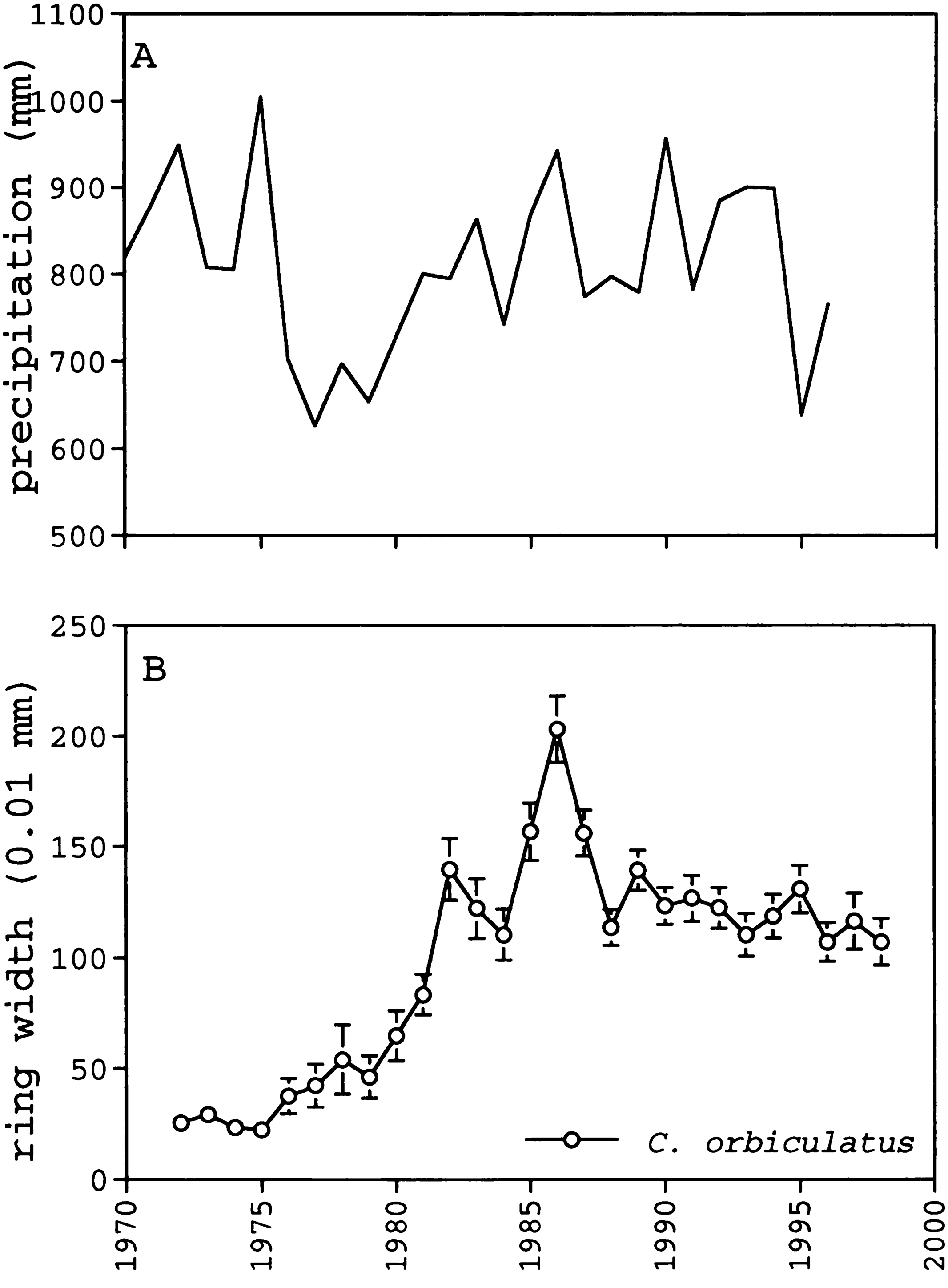

Figure 6-6. A. Annual precipitation at Petrides farm. B. Mean ring width of *C. orbiculatus*, +/- 1 SE.

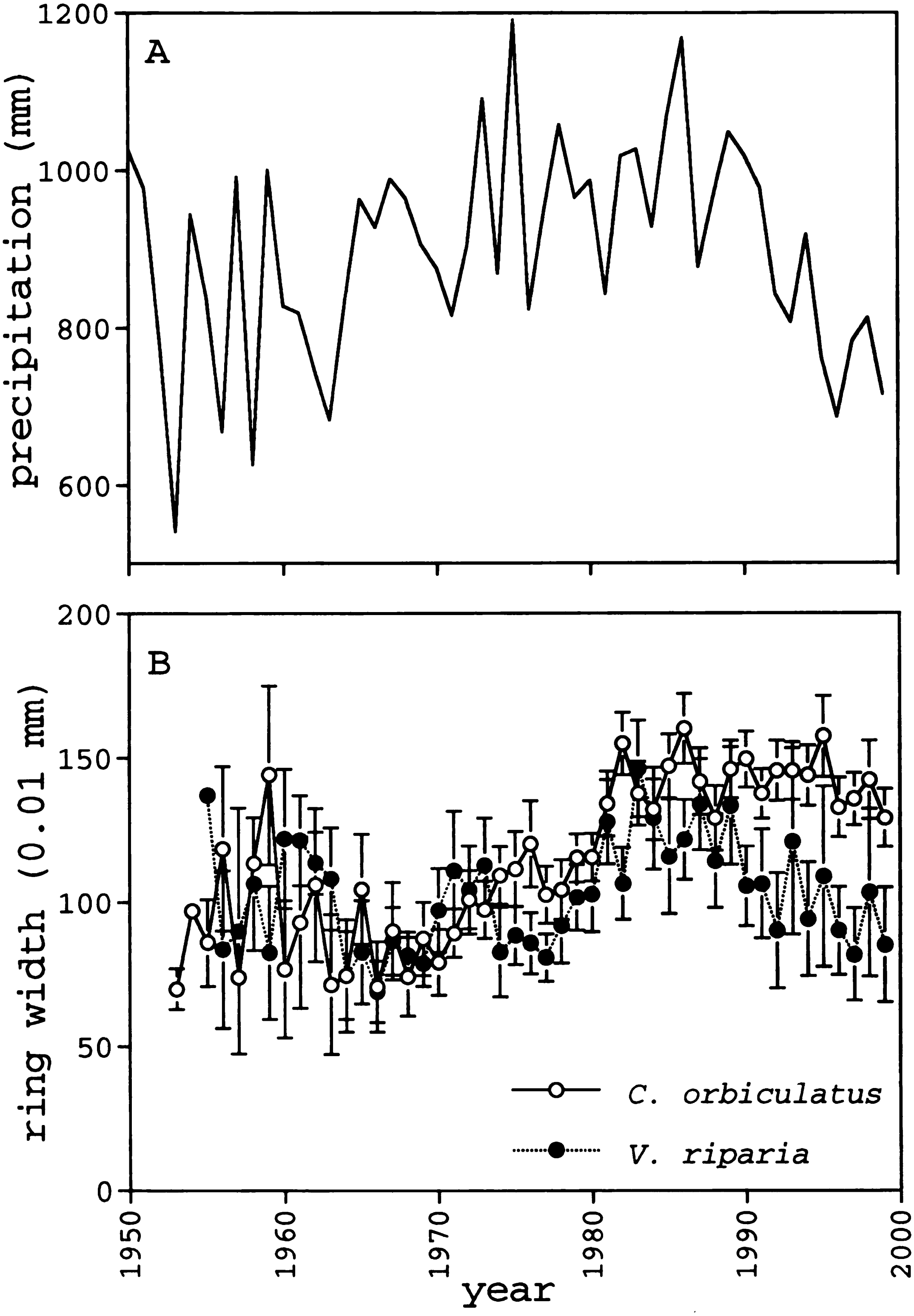

Figure 6-7. A. Annual precipitation at Kellogg Biological Station. B. Mean ring width, +/- 1 SE.

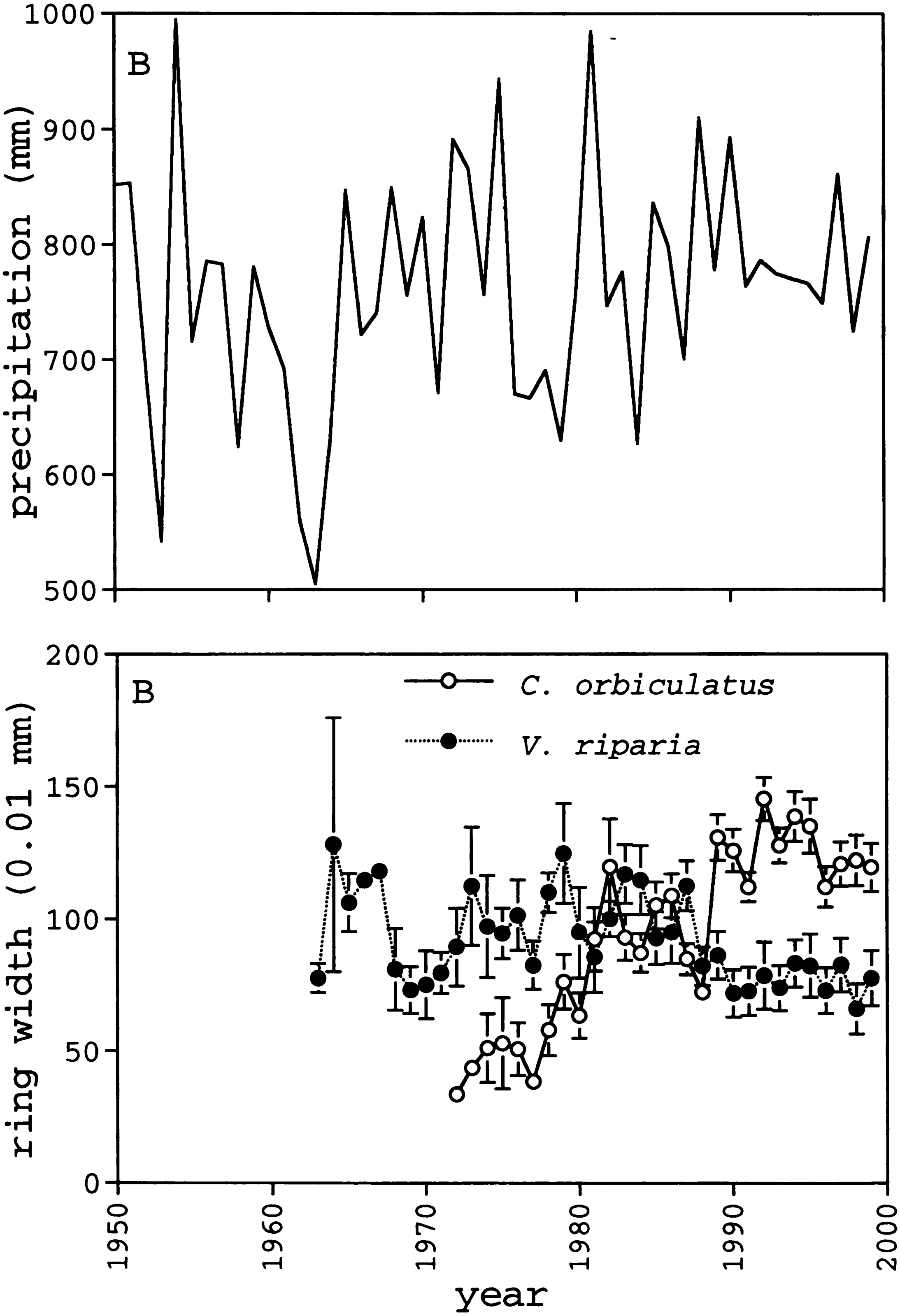

Figure 6-8. A. Annual precipitation at Hidden Lake Gardens. B. Ring width, +/- 1 SE.

relationships with various components of summer precipitation (Table 6-2). The current year's ring width of *C. orbiculatus* was slightly positively correlated with most parameters of precipitation, particularly at HLG. *Vitis riparia* current year's ring widths were not generally positively correlated with precipitation. The influence precipitation on the following year's ring width roughly followed the same trend for each species. However, at KBS, ring width of the V. riparia was positively correlated with precipitation.

Establishment dates for *C. orbiculatus* at each site, along with vine lifespan suggest dates by which each site was invaded. Petrides farm was invaded by the early 1970's, with many vines living until sampled (Figure 6-9). Numerous vines at Petrides farm died around 1996. This time corresponds to a massive manual eradication effort, carried out by cutting many vines. HLG was strongly invaded in the mid-1970's, with all vines living until sampled (Figure 6-10). KBS was invaded earliest, with a living vine found that was established by 1952 (Figure 6-11). Most of the vines sampled at KBS were still living at the time of collection. At each site, establishment of *C. orbiculatus* appears more clumped in time than for *V. riparia*.

Table 6-2. Correlation analysis of precipitation and ring width.
Summer precipitation = June + July + August precipitation.

		current year's growth ring		next year's growth ring	
site	parameter	*C. orbiculatus*	*V. riparia*	*C. orbiculatus*	*V. riparia*
Petrides farm	June precipitation	0.12		0.05	
	July precipitation	0.04		0.05	
	June + July precipitation	0.11		0.06	
	August precipitation	-0.09		0.04	
	summer precipitation	0.05		0.08	
HLG	June precipitation	0.22	-0.12	0.17	-0.18
	July precipitation	0.30	-0.22	0.08	-0.11
	June + July precipitation	0.33	-0.23	0.17	-0.19
	August precipitation	-0.23	0.16	-0.13	0.03
	summer precipitation	0.12	-0.08	0.05	-0.15
KBS	June precipitation	-0.03	-0.11	-0.03	-0.01
	July precipitation	0.14	0.09	0.13	0.28
	June + July precipitation	0.07	-0.03	0.06	0.17
	August precipitation	0.15	0.00	0.25	0.06
	summer precipitation	0.15	-0.02	0.21	0.17

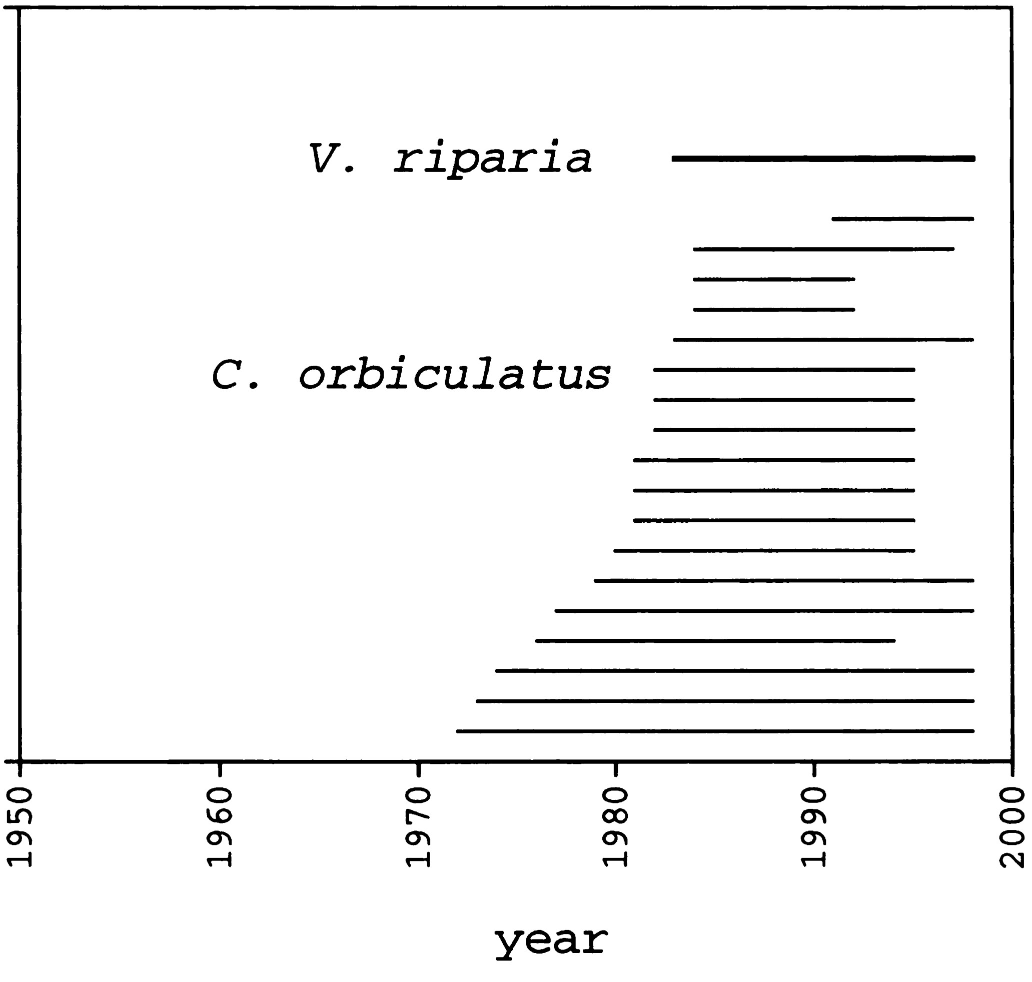

Figure 6-9. Lifespan of vines sampled at Petrides farm. Each horizontal represents one individual.

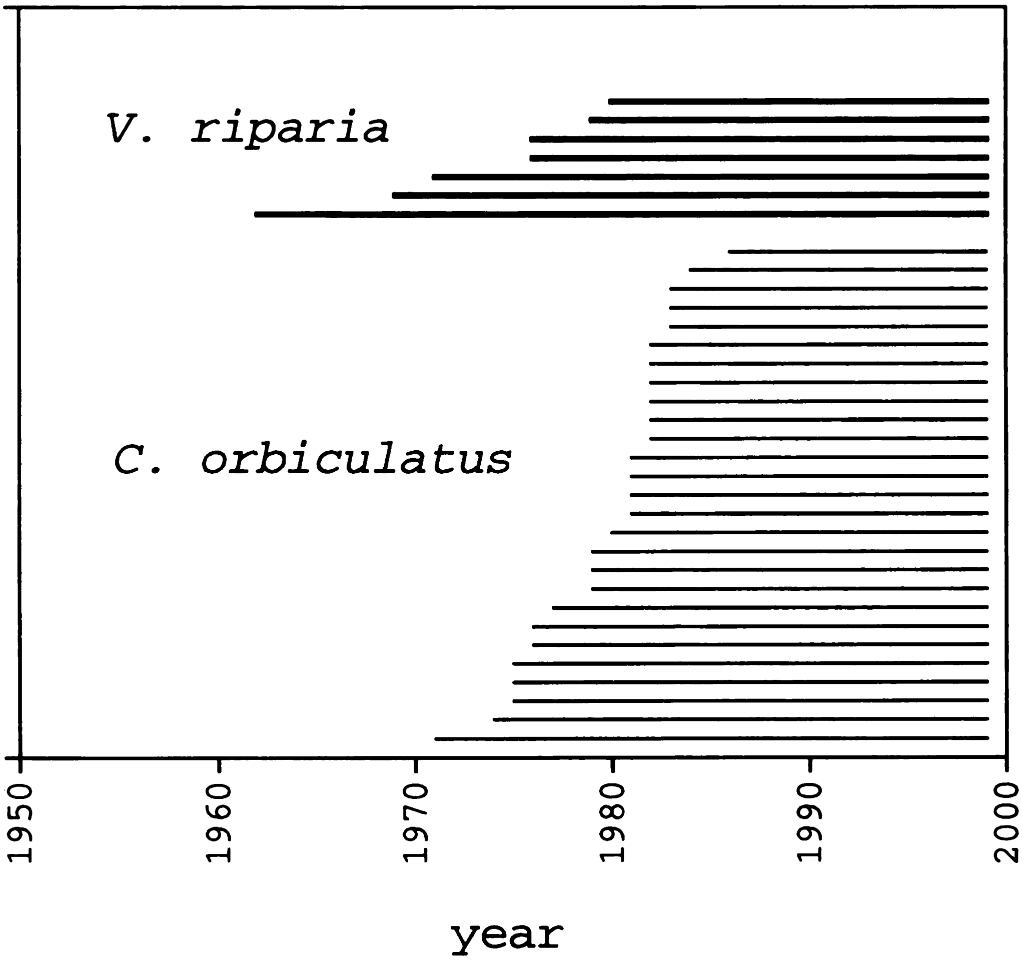

Figure 6-10. Lifespan of vines sampled at Hidden Lake Gardens. Each horizontal line represents one individual.

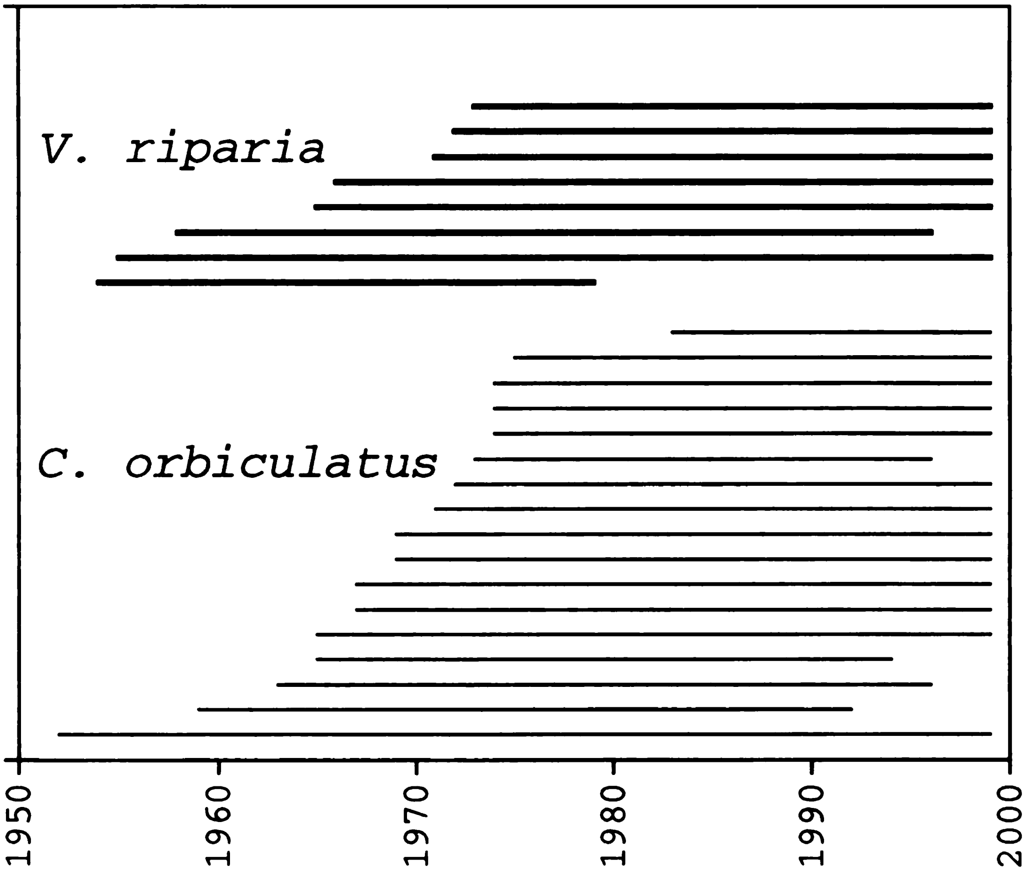

Figure 6-11. Lifespan of vines sampled at Kellogg Biological Station. Each horizontal line represents one individual.

Discussion

This study demonstrates that temperate lianas may serve as reasonable dendrochronological study species. Both *C. orbiculatus* and *V. riparia* provided cross-dated chronologies that were internally consistent for individuals. Additionally, chronologies cross-dated between individuals of the same species at the same site, though they were not perfectly aligned as indicated by noise around the trend lines. This likely represents individual variation in physiology and differential sensitivity to climate. Chronologies for each species at the same sites differed slightly, indicating that there may be species-specific differences in responses to climate. Locally absent rings were discovered in both species, indicating that simplistic ring-counting would not have been effective.

The oldest *C. orbiculatus* specimens were still living. The fact that dead material was not older raises two points. First, the young age of much of the material makes it difficult to be certain of the dating. With only a few points to work with, there are several possible dates that match the pattern. Those dates assigned in this study were subjectively the most parsimonious. Second, the ring-porous wood anatomy of *C. orbiculatus* and the fact that lianas generally provide little of their own mechanical support (hence few fibers) may mean that the dead liana debris decomposes rapidly. Thus, older material may have existed at some point in time, but is currently unavailable through loss to decomposition. This possibility is supported by the difficulty in surfacing some of the discs from dead samples, where the wood was too soft.

The apparent correspondence between chronologies and precipitation did not prove significant or consistent through correlation analysis, either the present year's precipitation or the previous year's precipitation. While precipitation is a major determinant of plant growth, it is not the only, and may have been outweighed by some other factor. Additionally, if a more discrete measure of precipitation, such as winter snowfall and consequent meltoff, was the most important, that detail would have been missed in this analysis.

The difficulty in obtaining a good, continuous climate data set reasonably close to each site is a serious problem that may hamper the detection of such relationships. However, it is important to acknowledge that spurious significant results may be detected if enough details are examined. Additionally, this study has not explicitly examined potential effects of juvenility. Strategies are available for removing juvenile growth trends in trees; however, no such strategies are available for lianas.

While the trends of ring width and precipitation have not proven significant, the chronologies themselves offer several insights into the establishment and invasion of *C.*

orbiculatus. Dendrochronology effectively indicates the date by which each site was invaded by *C. orbiculatus*. At both HLG and KBS, the ring widths of *C. orbiculatus* are initially narrower than those of *V. riparia*, but by the 1990's they were consistently wider. This may indicate that *C. orbiculatus* is enjoying a growth advantage over *V. riparia*. It may also represent an advantage of *V. riparia* over *C. orbiculatus*, since *V. riparia* may reuse xylem for conductivity through root pressure but *C. orbiculatus* does not. This has earlier been shown in the larger, younger stems of *C. orbiculatus* relative to *V. riparia* stems analyzed for hydraulic conductivity (Chapter 3).

The clumping pattern of *C. orbiculatus* establishment times suggests rapid recruitment of individuals. The long *C. orbiculatus* chronologies, (max. = 47 years, KBS), demonstrates that individuals may be long lived providing ample time for both vegetative spread and seed dispersal. Additionally, the fact that most *C. orbiculatus* individuals were living at the time of sampling indicates that the spread of *C. orbiculatus* will continue to be a serious problem in all of these sites.

Finally, it appears that of these three sites, the invasion of *C. orbiculatus* first occurred at KBS. It is possible that the bird sanctuary adjoining KBS was the source of introduction, either indirectly from migrating birds, or directly by wildlife managers at the sanctuary. There is no direct evidence of planting *C. orbiculatus* at the sanctuary, though some previous managers were fond of other exotic wildlife forage species. Hidden Lake Gardens and the Petrides farm have been invaded relatively recently by *C. orbiculatus*. This may indicate that *C. orbiculatus* is still spreading in a northward direction throughout the state.

CHAPTER 7

General Conclusions

The exotic liana *Celastrus orbiculatus* appears to thrive in Michigan for reasons understood as long ago as Darwin (1859): absence of effective predators in the form of herbivores and competitors in the form of other plant species with the same niche. Since Darwin, the characterization of species following r- or K-selected life history strategies also defines traits associated with successful invaders. Techniques such as dendrochronology provide a means of tracking and understanding invasion patterns.

Contrary to being "invisible" to herbivores, *C. orbiculatus* does suffer from herbivory. The effects of both insect and deer herbivory were observed on *C. orbiculatus*. However, its response to herbivory differs from the common native species *Vitis riparia*. In *V. riparia*, herbivory frequently translated into shoot mortality, but this was not the case in *C. orbiculatus*. While herbivory was greater on *V. riparia* in a year of relatively poor shoot elongation growth (1999), *V. riparia* did not suffer higher shoot mortality.

Competition from native lianas does not appear to affect *C. orbiculatus*. This may suggest that the liana growth habit is underrepresented in the Michigan flora, and that the niche is relatively open. The sympatric congener *Celastrus scandens* is very similar to *C. orbiculatus* in both reproductive biology and morphology. However, *C. scandens* is inferior to *C. orbiculatus* in all reproductive characters observed in this study. *Celastrus orbiculatus* produces more seeds that are smaller and have a greater chance of germinating than seeds of *C. scandens*. The smaller seed size and larger seed number indicate that *C. orbiculatus* is more r-selected than *C. scandens*. Following this argument, one would expect the species with larger seeds to have a greater germination success. But this study and others (Dreyer, Baird, and Fickler 1987) have demonstrated lower germination success in *C. scandens*. These findings imply that *C. scandens* is a poor competitor relative to *C. orbiculatus*, and that the spread of *C. orbiculatus* will continue. Further, it is possible that the historically large distribution of *C. scandens* in Michigan (52 counties) is currently dwindling and lacks recruitment through seedling establishment. At the same time, *C. orbiculatus* populations may be spreading through long range dispersal of highly successful seeds. This spread may be enhanced in disturbed sites, but the successful germination of seeds under low light conditions in the laboratory suggests that closed canopy sites may be invaded as well.

Both *C. orbiculatus* and *V. riparia* demonstrated similar patterns of shoot elongation growth. Interestingly, both species had greater shoot elongation under low light conditions in the field, apparently as a "searching" strategy. Additionally, both species were very similar in phenology. These similarities were surprising, and suggest that growth strategy overrides differences related to taxonomy. The native liana *V. riparia* does not appear to be superior to *C. orbiculatus* in terms of shoot growth. Both species demonstrated similar shoot elongation through two growing seasons.

The invasion dynamics of *C. orbiculatus* do not appear to be related to hydraulic advantages over native lianas. *Celastrus orbiculatus* lacks the root pressure mechanism seen in *V. riparia* and lacks any advantage in hydraulic conductance. These findings indicate that root pressure is not a requisite characteristic for success as a temperate liana. *Celastrus orbiculatus* manages to thrive by producing new xylem each year, even though this leads to a greater commitment of resources to hydraulic tissues and hence wider stems than *V. riparia*. It is important to note that the larger annual incremental growth does not translate into greater elongation of individual shoots. This fact is demonstrated by the equivalent maximum shoot lengths seen in *C. orbiculatus* and *V. riparia*.

Dendrochronology is a useful and novel tool for the reconstruction of liana invasion. No prior reports of dendrochronology utilizing lianas are known, but this study suggests temperate lianas should be considered as potential sources of useful dendrochronological information. Liana chronologies suggest establishment dates for *C. orbiculatus* at each site, followed by successive recruitment. The reconstruction of liana invasion events indicates that *C. orbiculatus* continues to spread northward in Michigan. A thorough sampling of *C. orbiculatus* populations throughout Michigan would further establish the invasion dynamics involved.

This study raises two important unanswered questions: what limits sexual reproduction in *C. scandens*?, and what, if anything, will limit the spread of *C. orbiculatus*? To identify the limitations of reproduction in *C. scandens*, it would be desirable to establish whether this species suffers from inbreeding depression. The populations investigated in this study produced copious amounts of seed that was apparently viable as indicated by tetrazolium staining. However, the seeds largely failed to germinate. Population genetic information would be required to establish the relatedness of individuals.

What could limit the spread of *C. orbiculatus*? Minimizing the frequent and large scale disturbances characteristic of many temperate ecosystems may help reduce the opportunities for exotic species such as *C. orbiculatus* to establish, persist, and invade. Massive eradication efforts utilizing both removal and herbicide treatment can be effective, though costly and risky to the native flora. There may be opportunity for biological control by importing natural enemies, insects or pathogens, from Asia. Realistically, however, the current perception of threat by *C. orbiculatus* invasion is too small to warrant such a reaction. I believe that *C. orbiculatus* is here to stay. At least it has attractive fruits!

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