Fruiting Strategies of the Woody Vine *Parthenocissus quinquefolia*

by

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Introduction

Seeds of many temperate zone plants are dispersed by animal vectors or by inanimate agents such as wind and water. Use of inanimate agents would seem probable in communities where potential animal vectors are few or unpredictable, and where wind or water sources are consistently available. Structures adapted for wind or water dispersal are relatively inexpensive for the plant to produce and therefore enable large numbers of seeds to be dispersed in a short period of time. However the seeds are not generally carried far from the parent plant and are restricted to a relatively small range of habitats. The seeds are also necessarily small, perhaps restricting their germination chances (McKey, 1975).

Avian seed dispersal of plants bearing fleshy fruit is based on the provision of food by the plant to the bird. Fruit will be defined as discrete packages produced by plants that contain both seed or seeds and pulp or fleshy material whether developed entirely from an enlarged ovary or not. The bird ingests the fruit and then either regurgitates or defecates the seed or seeds at a site which is often suitable for germination. The advantage for the bird in this relationship is the immediate energy or specific nutrients obtained. The advantage for the plant is less tangible. The plant's benefits are related to increased gene flow, escape from predators and colonizing new habitat patches (Herrera, 1981, 1982; van der Pijl, 1982). The disadvantage to the bird is represented by the energetic cost of the digestive processing and carrying of the non-nutritional seed (Stapanian, 1982; McKey, 1975). When considering fruiting strategies and frugivores' needs, it is generally thought of as a coevolution between the plants and the birds and not merely a lucky coincidence.

A prediction as to whether inanimate or animal seed dispersers are best adapted to specific types of plant forms may be made. When considering high-climbing woody vines, one would not expect wind dispersal to be the most effective since the seeds are not in an exposed area. These vines are typically supported by the trunks and large branches of trees and are effectively hidden away behind the tree's leaves and small branches. Therefore, one would expect woody vines to use fleshy fruit to attract animal dispersers rather than using wind or other inanimate agents for seed dispersal.

Stiles (1982) used the phrase "foliar fruit flags" when referring to "contrastingly colored plant parts that are temporally or spatially associated with fruits, but are not quantitative indicators of the amount of ripe fruit available." These fruit flags could be likened to flowers which signal to pollinators the potential presence of a food supply rather than some quantitative amount. Foliar fruit flags would seem to be most advantageous for plants that 1) require quick removal of fruit 2) do not have fruit in exposed places and/or 3) have an inconspicuous structural identity. Parthenocissus quinquefolia, Virginia creeper, is a high-climbing woody vine reaching lengths of 25 meters and without a distinct plant form of its own. It would therefore seem to benefit by using fruit flags. It is found in eastern United States with its western boundary extending only to central Kansas and Nebraska (Wernert, 1982; Stephens, 1969, 1973). Its fruits ripen in the early fall. The purple glaucous berries, 5-7 mm across, occur in long clusters at the ends of red pedicels. The digestible pericarp in P. quinquefolia fruit has an energy content of 980 J per fruit. This is an intermediate value compared to the sixteen common fruiting plants of eastern Kansas studied by Stapanian (1982). The energy of the pericarp levels ranged from 2040 J per fruit for Morus rubra to 80 J for Symphoricarpos orbiculatus. Parthenocissus quinquefolia also has a relatively high lipid content of 14.5% in the pericarp. In a study of 45 species in northeastern United States, only 10 had a lipid content greater than 14% (Stiles, 1982). In spite of its apparent high food value, Willson and Thompson (1981) found that P. quinquefolia fruits were often passed over by birds and that many caged birds refused to eat the autumn-harvested berries. The fruits have been found to be poisonous to humans (Wernert 1982). Of most importance to this study is that its palmately compound leaves with 5 leaflets turn a bright red in the early autumn.

In the early fall the bright red leaves of P. quinquefolia stand out dramatically to the human eye in contrast to the green foliage of the supporting and surrounding trees. This leaf color change takes place, presumably, before the physiological limit of photosynthesis for this plant. This is assumed to be the case since most plants in this area continue to carry on photosynthesis after *P. quinquefolia* has stopped. By activating chlorophyllases the breakdown of chlorophylls occurs, unmasking the flavonoids and carotenoids which produce the reds and yellows of the autumn leaves. The breakdown of chlorophylls and cessation of photosynthesis incurs a certain loss of fitness to the plant. This loss should be less relative to the fitness gain received from increased seed dissemination due to visual attraction of dispersal agents. If red leaf color is a foliar fruit flag responsible for attracting frugivores, then several predictions may be made. First, this type of fruit flag would most benefit those plants whose seed dispersers are the migrating visitors unfamiliar with the area. Therefore, one would expect the red leaves to be coincident with peak migration numbers. Second, the plant should have its fruits ripe and a high percentage of the leaves red at the same time. Also, the red leaves should be present on the vine until the fruit is removed or until the leaves of the supporting tree have turned color or dropped. And lastly, birds should be attracted to the red leaves more than to the green leaves.

Materials and Methods

I contrasted the manner of seed dispersal of woody vines with other woody perennials by surveying the fruit description for all plant species listed in Gleason (1963). I categorized all plant species described as to being woody vines, trees and shrubs or other (including annuals, cacti, aquatic plants, etc). Plants were also categorized as to having fleshy fruit or not. Gleason (1963) includes the flora of the area bounded by and including the states of Virginia, Kentucky and Missouri on the south, Missouri, Iowa and Minnesota on the west and Minnesota, Michigan, Lake Superior and across Ontario, Canada on the north. Gleason states that no additional plants of the deciduous forest group would be added by extending the boundary to include eastern Kansas and Nebraska. The plants of the tall-grass prairie are also almost completely represented within the range of these volumes. Only some plants of the short-grass prairie and of the arid Southwest would be added if the boundaries were so changed.

Weekly bird censuses were taken in the Manhattan, Kansas, area over a four year period. A route was set up in 1978 by Stapanian along country roads with sixteen predetermined stops for censusing. At each station, all the birds seen or heard within three minutes were recorded. These stops represented a variety of habitat, including deciduous forest areas, streams, rivers, agricultural fields, open fields and farmyards. Numbers of observers ranged from one to five, with two and three observers being the normal number. Counts made by two or more observers were reduced by an appropriate factor to put them on an equivalent basis with a single observer. The reduction factors were determined based on counts made by varying numbers of observers. These counts were taken during the birds' breeding season when bird numbers were assumed to be stable. Each weekly census was begun at, or shortly after, sunrise. The order of the stations was varied so that stops would not always be visited at the same time relative to sunrise.

Although all species of birds were recorded, only numbers of birds tending toward frugivory were important in this study. The major avian frugivores in the Manhattan, Kansas, area which I considered are listed in Table 1. Stapanian (1982) had an expanded list of potential frugivores for this same area including many species that do not concentrate on fruits to the same degree as the major frugivores. In their study in Illinois, Thompson and Willson (1979) had a list similar to Table 2, but they excluded the northern mockingbird and had the cedar waxwing included only as a minor frugivore.

Konza Prairie Research Natural Area, approximately 8 km south of Manhattan, Kansas, was the experimental site for the study of the phenology of the woody vine P. quinquefolia. This area is a natural tall-grass prairie with areas of eastern deciduous forest extending up the creek beds. In September of 1984, I selected vines growing approximately 3-5 meters up sides of trees in the Shane Creek area. At the onset of available ripe P. quinquefolia fruit in the area, seven of these vines with predominately red leaves were designated as control vines. Seven others with green leaves were selected as experimental vines. If any red leaves were present on the experimental vines, they were removed. None of these vines produced any fruit of their own. Fruit from other P. quinquefolia vines were attached in similar size bunches by stapling to the chosen vines and supporting trees at approximately breast height. Numbers of fruit were recorded at regular intervals until the fruit were removed by dispersers or were obviously dessicated. A second set of vines, ten in all, was set up in a similar manner shortly after the first run.

At the same time as these experiments I made approximately biweekly observations of surrounding trees, shrubs and vines in the same creek area for times of leaf color change. Changes in leaf color is difficult to quantify since the change is gradual both within and among individual plants.

Results and Discussion

Since environments are continually changing, often in unpredictable ways, knowledge of exact conditions responsible for an organism's evolution and adaptation is virtually impossible. However, predictions can be made as to possible reasons for the "appropriate" phenotype based on trends of other successfully adapted organisms of the area. Interspecific comparison is one important way of testing hypotheses about the significance of characteristics varying between species of plants or animals. It was hypothesized that since *P. quinquefolia* was a vine with an indistinct plant form, dispersal by frugivores would be more adaptive than wind or other types of dispersal. If this hypothesis is correct, one would expect a larger percentage of vines to bear fleshy fruit than trees or shrubs. Only woody perennials of a specific geographic area were included in an attempt to eliminate some of the confounding variables while still using an effective sample size. I then found, by using a chi-square contingency table, that a higher proportion of the species and genera of woody vines have fleshy fruit than do the trees and shrubs (Table 2). This does not necessarily prove that the differences of plant dispersal is due to their plant form. Any number of other factors may be involved. Neither can this analysis determine the direction of causation. It may be that having fleshy fruit influenced the plant form. However, a statistical tabulation such as this is still valid and useful. Many researchers have compared interspecific traits by similar quantitative methods to establish general trends and test specific hypotheses (Clutton-Brock and Harvey, 1984).

Over the four year period, the times of peaks in numbers of frugivores varied widely, from as early as late October in 1984 to as late as mid-January in 1980. When all years were averaged, the pattern showed a rapid increase in numbers of birds in October over the low summer levels with high numbers of frugivores continuing until February (Fig. 1). When the average number of frugivore species were compiled, a sharp increase occured during the time of spring migration, with a gradual decrease in species numbers over the summer months. This may have been due in part to the birds being less obvious since they were not singing. No real peak was seen in the fall (Fig. 1). During the spring, summer, and fall, the major frugivore species were the American robin, the gray catbird and the brown thrasher. Yellow rumped warblers were also fairly common. A few wood thrushes and Swainson's thrushes were recorded during spring migration but at no other time during the year. Winter species were almost entirely American robins and cedar waxwings with only a few yellow rumped warblers and a rare hermit thrush being recorded. Stapanian (1982) statistically determined that for this area, numbers of frugivores are unpredictable in both time and location in the fall. This fluctuation is mainly due to the large numbers of flocking American robins and cedar waxwings which are nomadic in behavior. These birds mainly feed on hackberry and juniper fruit which remain on the plants through the winter.

Most fall migrants such as the gray cheeked thrush and wood thrush pass east of Kansas (Robbins et al., 1966). The study by Thompson and Willson (1979) in Illinois showed a predictable and rapid increase in frugivore numbers in late August and early September. They found a second more unpredictable peak occurring in October which was mainly composed of American robins. Thompson and Willson attribute the varying numbers of American robins to the success of the hackberry crop in that area. They suggested that the October peak, although generally greater in numbers of birds, was less important than the September peak in the evolution of fruiting phenology. The peaks in September were more predictable and had a greater number of frugivore species. The larger number of species would minimize the effect of year to year fluctuations of any one species. Major frugivores in Illinois were gone by mid-November, whereas in Kansas the frugivores are at their highest numbers between November and February. Unlike Illinois, Kansas has abundant juniper as well as hackberry trees, whose fruits are heavily eaten by nomadic flocks of American robins through the winter.

Figure 2 compares dates in 1984 when P. quinquefolia and surrounding trees turned red or yellow and when they lost their leaves. It also shows times when ripe P. quinquefolia fruit could be found on the vines. The ripe berries of P. quinquefolia remain on the plant for about six weeks, well ahead of the average time for peak frugivore numbers. Stapanian also observed times of ripe P. quinquefolia fruit on the vines in this same general area in 1978. He found the ripe fruit that year from

September 17 to November 29. The peak of frugivore numbers in 1978 came in mid-November.

Numbers of frugivores must not be the only criterion for fruiting time of P. quinquefolia. In order for "foliar fruit flags" to be effective, fruiting time necessarily would be in early fall, before leaves of other plants of the area turn red or yellow. P. quinquefolia leaves were totally red ten days before the surrounding trees started to turn shades of red or yellow. As predicted, Figure 3 shows that the fruit ripened coincident with the leaves of P. quinquefolia being predominately red. The leaves, however, did not stay on the vines until the fruit dropped or were removed. There was approximately a two week period when all the leaves were gone, yet the fruit was available. This two week period was also a time of high numbers of frugivores in the area.

One would expect that P. quinquefolia vines with red leaves would attract more frugivores to remove more fruit than vines with green leaves. In this experiment, however, no real conclusions to this prediction can be made, since virtually no fruit was taken. Of all the experimental vines with attached fruit, only one-fourth of them had any fruit gone and then it was only one berry per bunch. These included both experimental and control vines. This easily could have been due to berries simply dropping off. One experimental vine with only green leaves, had seven out of its fifty five berries missing at the end of the experiment. This particular vine was close to a stand of roughleaved dogwood which had obviously had its berries removed by birds.

Several possible explanations for why the fruit was not taken can be made. _P. quinquefolia_ fruit are normally restricted to large vines growing high in trees. Although red leaves can be found low, no fruit is generally associated with these. Therefore, only inexperienced frugivores could be expected to search among low growing _P. quinquefolia_ vines. This experiment was all performed at low levels. Also, numbers of frugivores were low at the time of these experiments. One cannot rule out the possibility that the red leaves are not acting as a foliar fruit flag at all. Changing leaf color may, in fact, be due to the onset of the plant's physiological limit to photosynthesis. As stated previously, this does not seem likely since most plants of the area are still able to photosynthesize. _P. quinquefolia_ may also be a relict plant, developing this adaptation at some time in the past for some different mechanism all together. The early leaf color change may have been useful at one time, but is not being used at the present. Racoons or other mammals may also be eating the fallen fruit and therefore be responsible for some of the seed dissemination.

Another, and probably more significant explanation of why the fruit were not taken might be that _P. quinquefolia_ is at the western edge of its range in eastern Kansas. In the center of the vine's range, where it is most likely best adapted, the _P. quinquefolia_ fruit are ripe, the vine's leaves are red, and the peak of fall migrating frugivores are all at the same time. This would seem to be the ideal place to test the hypothesis that *P. quinquefolia* uses its red leaves as foliar fruit flags. It seems that in Kansas, *P. quinquefolia* is still locked into the early leaf color change even though it is not functioning effectively as a foliar fruit flag. It is interesting to speculate at *P. quinquefolia*'s success in eastern Kansas, even with its apparent loss of fitness from stopping photosynthesis early. Virginia creeper can be found, and often abundantly, in most stands of deciduous forest in this area. In Kansas, numbers of frugivores begin to rise in mid-October, the time when the vine's leaves have mostly dropped but the fruit still remains. The fruit is exposed on bright red pedicels. Although not as dramatic as the red leaves to the human eye, these pedicels may in fact be acting as another foliar fruit flag.

One would assume that by stopping photosynthesis early and incurring a certain loss of fitness that other competing plants would have an advantage. Other woody vines that can be found in Kansas include *Smilax bona-nox* (greenbriar), *Smilax hispida* (bristly greenbriar), *Aristoolchia tomentosa* (pipevine), *Cocculus carolinus* (snailseed), *Menispermum canadense* (moonseed), *Rhus radicans* (poison ivy), *Celastrus scandens* (bittersweet), *Ampelopsis cordata* (racoon grape), *Vitis riparia* (riverbank grape), *Campsis radicans* (trumpet creeper), and *Lonicera japonica* (Japanese honeysuckle) (Stephens 1969). Only two of these vines grow to heights comparible to *P. quinquefolia*: *R. radicans* and *C. radicans*.

C. radicans is not similar to the *P. quinquefolia* vine in either seed dispersal or pollination mechanisms. *C. radicans* has pods of seeds with papery wings that are dispersed by wind, not birds. It has clustered bright orange flowers which are tubular or funnel-shaped and attract hummingbirds. *P. quinquefolia* has small greenish flowers relying on insects for pollination. It does not seem likely that these two vines would be competing directly with each other.

R. radicans, on the other hand, is very similar to *P. quinquefolia*. Although *R. radicans* has male and female flowers on seperate plants, both *R. radicans* and *P. quinquefolia* flower at approximately the same time of year and have small greenish flowers. The fruit of *R. radicans* are slightly smaller, 4-5 mm in diameter but are ripe at the same time as *P.quinquefolia*. Also, both vines have bright red leaves in the early fall, presumably both incurring the same loss of fitness. Neither one could be said to be more adaptive than the other when considering these traits.

The success of *P. quinquefolia* in Kansas seems most likely to be attributed to the very large numbers of American robins and cedar waxwings in this area. It is highly likely that a vine's fruits would be found and subsequently all eaten by the flocks of frugivores at least every few years. Since the fruit of each vine are all ripe at the same time, the vine may be effectively exploiting the unpredictable pulses of these birds. It seems that the loss of fitness incurred from the early cessation of photosynthesis must not be so great as to impair the vine's ability to compete with surrounding plants.

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Table 1.-- Major frugivores in the Manhattan, Kansas area

Swainson's Thrush, *Catharus ustulatus*
Hermit Thrush, *Catharus guttatus*
Wood Thrush, *Hylocichla mustelina*
American Robin, *Turdus migratorius*
Gray Catbird, *Dumetella carolinensis*
Northern Mockingbird, *Mimus polyglottos*
Brown Thrasher, *Taxostoma rufum*
Cedar Waxwing, *Bombycilla cedrorum*
Yellow-rumped Warbler, *Dendroica coronata*

Table 2. - Comparison between woody vines and trees and shrubs with and without fleshy fruit. Probability of similarity, P, is given at the species, genus and family levels.

	Woody Vines		Trees and Shrubs		P
	with fleshy fruit	without fleshy fruit	with fleshy fruit	without fleshy fruit	
Species	46	29	365	393	0.031
Genus	16	11	65	117	0.022
Family	11	9	32	49	0.232

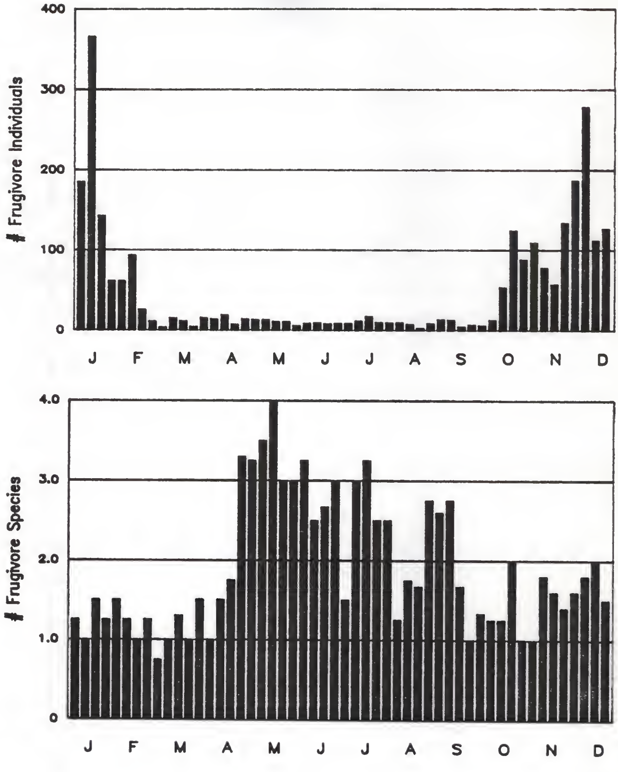

Fig. 1. - Average numbers of frugivore individuals and species observed weekly along a census route in the Manhattan, Kansas area. Data covers a period of approximately four years.

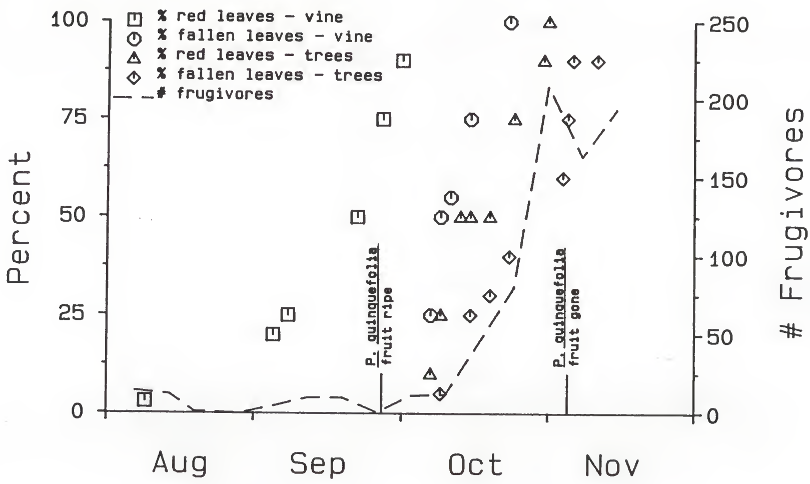

Fig. 2. - Comparison of Parthenocissus quinquefolia and surrounding trees with regard to date of leaves turning color and dropping from plants during 1984. Numbers of frugivore individuals counted along a weekly census route during the same time period are shown.

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Abstract

A greater proportion of woody vines use fleshy fruit to attract animals to disperse their seeds than do trees and shrubs. This is most likely due to the vines being hidden away behind the supporting tree's branches and leaves. *Parthenocissus quinquefolia*, Virginia creeper, is a woody vine which produces fleshy fruit in the fall. Its leaves turn a bright red earlier than most other plants of the area. Since the vine has an indistinct plant growth form, it was predicted that the red leaves acted as a foliar fruit flag to attract potential avian seed dispersers. The timing between fruiting and bird movements does not seem to be constant at the western edge of the plant's range in Kansas, where this study was conducted. East of Kansas the red leaves may be acting as an effective foliar fruit flag.