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# BIRD-DISPERSAL OF PHYTOLACCA AMERICANA L. AND THE INFLUENCE OF FRUIT REMOVAL ON SUBSEQUENT FRUIT DEVELOPMENT[1]

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ABSTRACT

Characteristics of fruits, seeds, and ripening of *Phytolacca americana* were studied in New Jersey, USA to assess their importance in the dispersal strategy of this species. Removal by birds was directly related to the percent of ripe fruits available on a raceme. Fruit removal from a raceme resulted in lower fruit pulp and seed weights for fruits developing on the same raceme, but these differences probably do not influence probability for dispersal by birds. We demonstrate that characteristics of the fruit pulp may decrease seed availability for the primary seed predator, *Peromyscus leucopus*, and increase the time fruits are available for dispersal. We speculate on the significance of the sequential fruiting in *Phytolacca* and the relationship to availability of dispersal agents and high-lipid fruits. Sequential ripening and protection from predation result in seed dispersal from late August to early December.

THE CHARACTERISTICS of bird-disseminated fruits and fruiting patterns for individual species of native plants may aid in understanding general patterns of mutualism between birds and fruits. In the tropics Howe and co-workers (Howe, 1981; Howe and De Steven, 1979; Howe and Vande Kerckhove, 1979, 1980, 1981) have made detailed studies of species of *Virola* and *Guarea*, while in the temperate zone Herrera and Jordano (1981) have studied dispersal in *Prunus*, Jordano (1982) has evaluated dispersal patterns of *Rubus*, Moore and Willson (1982) have evaluated some aspects of *Lindera* dispersal, and Stapanian (1982) has studied dispersal in *Morus*. Several characteristics of fruits are known to influence their attractiveness to birds (Ridley, 1930; McKey, 1975) and their rates of removal. Some of these fruit characteristics include color when ripe (Willson and Thompson, 1982; Stiles, 1982), accessibility (Denslow and Moermond, 1982), number of fruits produced (Howe, 1979) and nutrient quality (McKey, 1975; Stiles, 1980; Herrera, 1982). The degree of patchiness of plants and characteristics of the habitat have also been reported to affect dispersal by birds (Thompson and Willson, 1978; Moore and Willson, 1982). In this paper we evaluate some characteristics of fruits, fruiting patterns, and seed predation of a common bird-dispersed herb, *Phytolacca americana* L. (Phytolaccaceae). These characteristics are evaluated in the context of potential advantages to be realized if seeds are disseminated by birds (Stiles, 1980). It is apparent that *Phytolacca americana* (pokeweed) has substantial economic importance (over 100 papers involving *Phytolacca* were cited in Biological Abstracts for the last 6 months of 1981), yet little is known about its natural history (Sauer, 1952). Here we address the following questions: 1) What morphological characteristics of *Phytolacca* fruits and racemes influence bird-dispersal? 2) How does dispersal of mature fruits affect development of new fruits and seeds on a raceme? 3) How are the primary seed predators deterred from eating *Phytolacca* seeds during the long persistence time of fruits on the plants? 4) What are the ecological and evolutionary implications of indeterminate fruit production on bird-dispersal of *Phytolacca*?

MATERIALS AND METHODS—*Study site*—The study was conducted at the William L. Hutcheson Memorial Forest, located on the Piedmont of New Jersey 14 km west of New Brunswick. It consists of a 28 ha mixed oak forest with adjoining fields in varying stages of succession. The soil is primarily silt loam derived from underlying red shale of the Brunswick Formation (Ugolini, 1964). Dominant overstory

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trees are white oak (*Quercus alba*), black oak (*Q. velutina*), and red oak (*Q. borealis*) along with an occasional red maple (*Acer rubrum*). Most of the oaks were severely defoliated by gypsy moths (*Porthetria dispar* (L.)) during the early part of the 1981 growing season which increased the amount of light reaching the forest floor. This apparently favored growth and establishment of *Phytolacca* in this area. In addition to *Phytolacca*, other common forest floor species include snake root (*Eupatorium rugosum*), jewelweed (*Impatiens biflora*), blackberry (*Rubus* sp.) and Japanese honeysuckle (*Lonicera japonica*).

*Species characteristics*—*Phytolacca americana* is a polycarpic perennial herb which ranges from southern Quebec and Ontario to Florida and Texas (Fernald, 1950). It is usually found in open, disturbed habitats, along forest edges and in light gaps. *Phytolacca* is a relatively large herb (to 2 m) with alternate, entire leaves borne on a stem that may be up to 5.6 cm in diameter. Flowers are perfect, borne on elongate, indeterminate racemes. Fruits are round, dark purple when ripe, and are borne on red racemes. Fruits are dispersed by birds (Thompson and Willson, 1978, 1979).

Plants emerge from root stocks in late May or from previous years' seed in mid-June. Growth is rapid and flowers begin to appear in late June. Flowers are produced at apices of racemes until autumn frosts kill the meristems. Fruits begin to ripen in late August from the earliest maturing flowers and ripen sequentially through the fall. Single racemes may bear both mature fruits at the base of the raceme and developing flower buds at the apex.

*Factors affecting fruit dispersal and development*—On October 20, 1981, 25 *Phytolacca* plants of approximately equal size were marked. For each of three racemes per plant we measured raceme length, and number of missing, fully ripe, partly ripe and green fruits. Racemes were chosen to have one with missing fruits (probably removed by birds) and two with all fruits present. We presumed fruits from the first raceme had been removed by birds because flower bagging experiments (Armesto, Cheplick and McDonnell, 1983) showed that *Phytolacca* is predominantly autogamous and nearly all flowers develop into fruits. Subsamples of ten ripe fruits from the same positions on the two racemes, one with missing fruit and one with no missing fruits, were collected from 14 of the 25 plants. Wet weights of these 280 fruits were recorded; then seeds were separated from the pulp, weighed and counted. Wet pulp weight was obtained by subtraction.

On the same date all ripe fruits were removed from the one raceme that had no fruits missing (a total of from 14 to 39 ripe fruits) and the raceme was enclosed in a nylon mesh bag. The third raceme on the same plant in approximately the same stage of development was bagged leaving all fruits intact. Thirty-one days following bagging on November 20, all 50 bagged racemes were collected. Numbers of fruits were recorded and subsamples of ten ripe fruits from the distal end of each of 28 racemes from 14 of the 25 plants were evaluated for fruit and seed characteristics as described above.

*Laboratory feeding experiments*—Three live-trapped *Peromyscus leucopus* were maintained in the laboratory in individual cages (25 × 30 × 90 cm) on a diet of laboratory rat chow provided *ad libitum*. We conducted two feeding experiments with each mouse. In the first experiment five *Phytolacca* fruits containing approximately 50 seeds (9.74 seeds/fruit × 5 fruits = 48.7 seeds, see below) were placed in a 10-cm diam petri dish. Treatment of all fruits and seeds by each mouse was monitored at 10 or 20 min intervals for 120 min. In the second experiment 50 cleaned, dry seeds were placed in a 10-cm diam petri dish and again treatment of all seeds was recorded at 10- or 20-min intervals for 120 min.

*Phytolacca seedfall*—As part of a larger experiment (McDonnell, unpubl.) we measured seedfall in 54, 1-$m^2$ seedtraps placed in a 20-yr-old field adjacent to Hutcheson Memorial Forest from September 28 to December 31, 1981. Seed traps were constructed of 6-mil polyethylene sheeting stretched on a wooden frame, modified after Smith (1975) and McDonnell and Stiles (1983). Traps were cleared weekly and all seeds were counted.

RESULTS—*Fruiting characteristics*—A total of 75 racemes (50 with no fruit removed and 25 with ripe fruits removed by birds), three from each of 25 plants were included in the study (Table 1). Raceme length and total number of fruits did not differ among the three groups of 25 racemes; however, racemes from which birds had removed fruits had a higher percentage of fully ripe fruits, and a higher mean fruit weight, pulp weight and pulp/seed ratio, all presumably associated with fruit ripeness and especially increased water content. The number of flowers and fruits produced is

TABLE 1. *Comparison of fruit and raceme characteristics from racemes with fruits removed by birds and from complete racemes*

| Characteristic | Racemes with no fruits removed (*N*) | Racemes with fruits removed by birds (*N*) | ANOVA[a] |
|---|---|---|---|
| Raceme length (cm) | 23.0 (50) | 24.3 (25) | NS |
| Total fruits | 58.6 (50) | 56.8 (25) | NS |
| Percent fully ripe | 56.7 (50) | 81.6 (25) | * |
| Percent unripe | 43.3 (50) | 18.4 (25) | ** |
| Fruit wt. (g) | 0.37 (140) | 0.41 (140) | *** |
| Pulp wt. (g) | 0.26 (140) | 0.30 (140) | *** |
| Total seed wt. (g) | 0.11 (140) | 0.10 (140) | ** |
| Pulp/seed ratio | 2.45 (140) | 2.65 (140) | ** |
| Fruits removed by birds | 0 (50) | 14.9 (25) | |

[a] NS = no significant difference; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

TABLE 2. *Characteristics of racemes used in the fruit-removal experiment (N = 25)*

| Characteristic | Control | SD | Fruits removed | SD |
|---|---|---|---|---|
| Raceme length (cm) | 23.0 | 3.2 | 22.9 | 3.4 |
| "Fully ripe" fruits | 26.4 | 10.7 | 25.3 | 11.9 |
| Intermediate ripe fruits | 15.8 | 6.9 | 17.4 | 7.2 |
| Green fruits | 16.7 | 7.3 | 14.5 | 8.0 |
| Total fruits | 59.1 | 7.6 | 58.0 | 10.9 |

a function of the number and length of the racemes produced, which is a function of plant size (Armesto et al., 1983). The number of fruits per raceme was correlated with raceme length ($r = 0.37$, $P < 0.001$). Racemes may bear as many as 78 ripe fruits. Fresh weight of single *Phytolacca* fruits is 0.39 g (Table 1) with a mean of 9.74 seeds/fruit. Fruits are high in water content (83.6%). The dry weight lipid is 1.0%, with 38.3% carbohydrate and 9.82% protein (White and Stiles, unpubl.).

Percentage of fruits missing from a raceme was directly related to percentage of "fully ripe" fruits on a raceme (Fig. 1), but not to the number of "fully ripe" fruits or total fruits on a raceme. Very few fruits were missing from racemes with fewer than 40% "fully ripe" fruits, but the percentage missing increased linearly with increased percentage ripe from this point (Fig. 1).

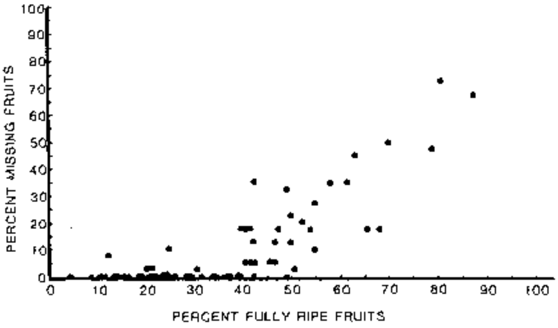


Fig. 1. The relationship between percent fully ripe fruits and the percent of the fruits that had been taken by birds for individual racemes of *Phytolacca americana*.

*Fruit removal and subsequent fruit development*—There were no significant differences between fruits from the two groups of racemes when they were bagged on October 20 for use in the experimental removal experiment (Table 2). On November 20 bagged racemes were collected. Fruits from racemes in which fruits were removed experimentally had significantly lower fruit weight, pulp weight, seed weight and pulp/seed ratio than fruits on the control racemes (Table 3).

*Laboratory feeding experiments*—In the first experiment the three mice ate a total of 23 of an available 150 seeds (15.3%) during the 120 min of observation (Table 4). During this time the mice removed all but two fruits (13) from the petri dishes and chewed into six of them. In most cases when the fruit skin was ruptured exposing the watery flesh, the fruit was left. In the second experiment the three mice ate a total of 110 of 150 seeds (73.3%) during the 120 min of observation (Table 4). All but 18 seeds were removed from the dishes. Mice ate a significantly greater number of clean dry seeds than seeds within fruits ($\chi^2 = 31.86$, df = 1, $P < 0.001$).

*Phytolacca seedfall*—*Phytolacca* had an extended dispersal period with over 50 seeds

TABLE 3. *Comparison of fruit and seed characteristics between racemes with fruits experimentally removed and control racemes. Sample size = 140 fruits for each treatment, 10 from each of 14 racemes*

| | Control | Fruits removed | ANOVA[a] |
|---|---|---|---|
| Fruit wt. (g) | 0.401 | 0.356 | ** |
| Pulp wt. (g) | 0.297 | 0.259 | ** |
| Total seed wt. (g) | 0.104 | 0.097 | * |
| No. of seeds | 9.85 | 9.85 | NS |
| Pulp/seed ratio | 2.91 | 2.68 | ** |

[a] NS = no significant difference; * = $P < 0.01$; ** = $P < 0.001$.

TABLE 4. *Laboratory feeding experiments using* Peromyscus leucopus *feeding on* Phytolacca americana *fruits and seeds. Three mice, A, B, and C were used in the experiments*

| | Exp. 1 (5 fruits = approx. 50 seeds) | | | | | | | | | Exp. 2 (50 cleaned seeds) No. of seeds eaten | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fruits removed from dish | | | Fruit skin opened | | | No. of seeds eaten | | | | | |
| Time (min) | A | B | C | A | B | C | A | B | C | A | B | C |
| 10 | 2 | 2 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 12 | 20 | 6 |
| 20 | 5 | 2 | 3 | 0 | 4 | 0 | 0 | 0 | 0 | 13 | 37 | 9 |
| 30 | 5 | 2 | 5 | 0 | 4 | 0 | 0 | 8 | 0 | 13 | 37 | 16 |
| 50 | 5 | 3 | 5 | 0 | 5 | 0 | 0 | 15 | 0 | 17 | 39 | 18 |
| 60 | 5 | 3 | 5 | 0 | 5 | 0 | 0 | 15 | 0 | 17 | 39 | 21 |
| 80 | 5 | 3 | 5 | 0 | 5 | 0 | 0 | 15 | 0 | 19 | 39 | 25 |
| 100 | 5 | 3 | 5 | 0 | 5 | 0 | 0 | 15 | 0 | 19 | 50 | 29 |
| 120 | 5 | 3 | 5 | 0 | 5 | 1 | 0 | 15 | 8 | 23 | 50 | 37 |
| Totals | | 13/15 | | | 6/15 | | | 23/150 | | | 110/150 | |

found in the seed traps for all but two collections from the beginning of the experiment to November 23 (Fig. 2). There were two major peaks of dispersal, one in late October and one in mid-November. Figure 2 also illustrates the seedfall of flowering dogwood (*Cornus florida*) during the same period. This was the second most common species in the traps and showed a single dispersal peak in late October, coincident with the first peak in *Phytolacca* dispersal. *Cornus* fruits contain only one seed, whereas *Phytolacca* fruits contain ten seeds/fruit. The October *Cornus* seedfall peak represents a much greater number of fruits than the *Phytolacca* peak. These values may not be compared directly because although there were many *Cornus* in the field, there were no *Phytolacca* plants. We discuss the importance of these two patterns below.

DISCUSSION—Numerous factors influence dispersal of fruits by birds, including attractiveness (Willson and Thompson, 1982; Herrera, 1981), accessibility (Denslow and Moermond, 1982), number (Howe, 1979; Howe and Vande Kerckhove, 1979) and display size (Moore and Willson, 1982; Stiles, 1982). Our study of *Phytolacca* concentrated on 1) morphological characteristics and development of fruit display and their influence on fruit removal and avoidance of predation, and 2) the influence of fruit removal on subsequent fruit development.

*Fruit display*—Although display size has been postulated to influence location of fruits by birds and subsequent removal by birds (Moore and Willson, 1982; Stiles, 1982), we measured total number of fruits per raceme, number of ripe fruits per raceme and raceme length and found no relationships among these factors and fruit removal. Our data indicate that over 40% of the fruits on a raceme were "fully ripe" (i.e., dark purple in color) before fruits were taken by birds (Fig. 1). This result may be influenced by two factors. First, our determination as "fully ripe" did not equal the birds' assessment of "fully ripe." As the fruits ripen sequentially over a long period, approximately 40% of the fruits on any raceme may have appeared dark purple to us before the first fruit was actually acceptable for the birds. This is consistent with our findings of a linear relationship between percent missing and percent ripe starting at 40% ripe. Second, *Phytolacca*, with sequential ripening has a constantly changing display size and our measure of display may not have been sufficient to evaluate true display. For example, Willson and Thompson (1982) note the at-

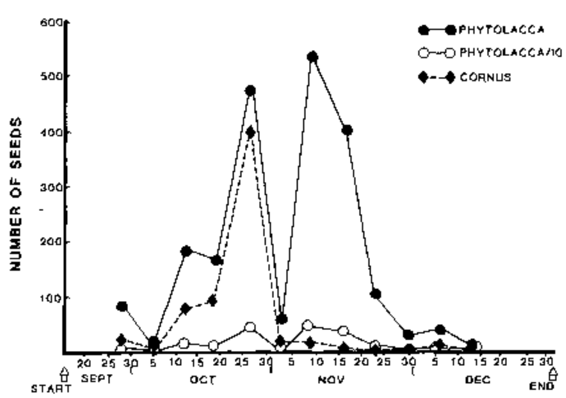


Fig. 2. The numbers of seeds of *Phytolacca americana* and of *Cornus florida* that were deposited in 54, 1-m² seed traps at the Hutcheson Memorial Forest, East Millstone, New Jersey during fall of 1981.

tractive value of color difference between the red stem of the raceme and ripe purple berries. It is possible that the display unit is larger, including either the group of racemes on a plant or even the clump of plants in an area. Because of the spreading growth habit of *Phytolacca* and the arrangement of racemes throughout the plant, racemes may also be differentially visible. We cannot rule out display size as an influence on fruit removal but our measurements did not demonstrate a relationship.

*Fruit removal and subsequent fruit development*—The lower fruit weight, pulp weight, mean seed weight and total seed weight in *Phytolacca* fruits on racemes from which fruits were removed by us was somewhat unexpected. Fruit-thinning experiments with oranges and apples produce larger fruits and seeds (Parker, 1932; Stephenson, 1981; Quinlan and Preston, 1968). After fruit thinning, plants apparently allocate some portion of the surplus resources to surviving fruits (Stephenson, 1981). However, *Phytolacca* fruits on racemes which had fruits removed had significantly smaller fruits than those on control racemes. We feel the reason for the difference lies in characteristics of the *Phytolacca* infructescence.

The amount of resources which can be translocated to fruits on a raceme may be controlled by the number, age and size of fruits on that raceme. Although the means by which substances are mobilized from other parts of a plant to developing fruits is poorly understood, it is generally agreed to be a source-to-sink phenomenon (Leopold and Kriedemann, 1975). Surrounding leaves provide food materials (source) and fruits serve as sinks. It has been shown that plant hormones, including auxins, gibberellins and cytokinins, produced by seeds strongly influence mobilization of materials from the plant to developing fruits (Leopold and Kriedemann, 1975). Nitsch (1950) showed that the size of strawberry fruit was proportional to the number of seeds developing on it. This was presumably due to the fact that the more seeds that were present, the more auxin was produced and consequently the more nutrients were mobilized. Additional data also exist showing correlations between seed number and fruit size in apples (Leopold and Kriedemann, 1975). Quinlan and Preston (1968), from a 3-yr study of apples, suggested that plants can mature fruits selectively on the basis of seed number, for they found apples with low seed numbers were selectively aborted. Stephenson (1981) suggests that fruits with low seed numbers are only matured by a plant when resources are plentiful or when fruit set is low.

Because *Phytolacca* berries all arise from a main raceme axis, hormones produced by developing fruits and seeds pass from the distal to the proximal end of the raceme into the plant body. Similarly, mobilized nutrients from the plant body move into the raceme past mature proximal fruits to developing distal fruits. Thus, the entire pokeweed raceme acts as a sink with properties similar to that of a single fruit such as an apple. We suggest that the more fruits there are on a *Phytolacca* raceme, the more seeds are present, the greater amount of hormones are produced and consequently the larger the sink is for mobilized nutrients. Such an hypothesis would explain why fruits on racemes in which we removed fruits had lower fruit weights, pulp weights, mean seed weights and total seed weights than control racemes.

The difference in fruit and seed weights (Table 3), although statistically significant, may have little or no influence on probability of dispersal. The differences are small, and we were unable to distinguish them visually. The small differences in pulp weights would have very little impact on total nutrient intake for birds, but seed weight differences could be more important in their effect on seed nutrients available for early seedling nutrition and the probability of seedling success.

*Indeterminate fruit production and dispersal in Phytolacca*—Production of fruit from an indeterminate raceme which ripens over an extended period of time in the late summer and autumn is unusual for bird-disseminated plant species in the Eastern Deciduous Forest. Many temperate species of summer fruits including the genera *Ribes*, *Amelanchier*, *Rubus*, *Vaccinium*, *Gaylusaccia*, and *Prunus* (Stiles, 1980, 1982; Willson and Thompson, 1982) as well as many tropical bird-disseminated species (see Howe and Smallwood, 1982 for review) ripen fruits over long periods of time, but almost all bird-disseminated, eastern deciduous forest species which ripen fruit in the fall, ripen their entire fruit crops over a very short period of time (usually <1 month) corresponding to the initiation of migration of frugivorous birds (Thompson and Willson, 1979; Stiles, 1980; Stiles and Meffe, unpubl.).

*Phytolacca americana* is an exception to the pattern. As noted by Thompson and Willson (1979) "*Phytolacca* exhibited characteristics intermediate between summer and other fall fruiting species in the degree of synchrony within individuals and within the population." This asynchrony is manifested by both the sequential development of fruits on the indeterminate racemes as well as the production of new racemes from the middle of August until frost. *Phytolacca* expresses a combination of fruit characteristics and a pattern of ripening which may increase seed dissemination and reduce fruit loss to microorganisms, but at the same time exposes fruit for longer periods to seed predators.

First, although similar to summer-ripening fruits in its sequential ripening, *Phytolacca* differs by having an intermediate-sized seed (90 seeds/gm) compared with summer small-seeded fruits (mean no. seeds = 1,386/gm, range 181–11,684/gm, $N = 18$) and summer large-seeded fruits (mean no. seeds = 9.9/gm, range 2.2–30.9/gm, $N = 4$) (Stiles, 1980). This places *Phytolacca* seeds in a size class that is neither so small that they would be rejected as a rodent food source nor is their seed coat extremely hard, reducing the accessibility to seed-eating rodents. Seed hulls found in the field (associated with bird defecations) as well as laboratory feeding tests with *Peromyscus* support our contention that seeds are eaten readily when available.

Second, *Phytolacca* is an herb and the supporting structures degenerate and the racemes fall to the ground in late autumn. Also the barrier to water loss, the skin of the fruit, is disrupted by freezing in late autumn causing rapid fruit drying. The first increases access to the fruits by mammalian seed predators and the second reduces fruit acceptability for birds. These two factors reduce seed dissemination substantially in late November and early December (Fig. 2).

Third, *Phytolacca* is recognized for its high numbers of toxic chemicals. Numerous toxins have been isolated from the fruits (Ogzewalla et al., 1963; Barnett, 1975; Steinmetz, 1960) as well as from other plant parts (Burque and LeQuesne, 1971; Waxdal, 1974; Steinmetz, 1960). The ecological and evolutionary significance of these toxins is unknown; however, ultimate factors selecting for some toxicity may reside in the deterrence of seed predation by mice and other mammals. Although mice readily ate *Phytolacca* seeds under laboratory conditions they rejected the seeds that were inside fruits (Table 4). The adaptive significance of the toxic nature of the fruits, whether mammal deterrents or microbial inhibitors serving to increase fruit longevity, is not yet clear. The vast majority of sequentially ripening fruits in the eastern deciduous forest, most of which are summer-ripening and utilize both birds and mammals as dispersal agents (e.g., *Amelanchier, Rubus, Ribes, Vaccinium, Gaylusaccia, Prunus*) (Stiles, 1980), are not toxic. *Phytolacca* appears to be adapted solely to bird dispersal. Characteristics of the pulp of *Phytolacca* act as a deterrent to seed predation. This is important because the large stems of *Phytolacca* may be climbed by the semi-arboreal *Peromyscus*, and because degeneration of the herbaceous stalks may allow fruiting racemes to fall to the ground where fruits would be easily accessible.

*Phytolacca* as a fall-fruiting species, ripens fruit differently from other fall-fruiting plants by continually ripening fruits from the middle of August until late autumn through fruit production on indeterminate racemes as well as through production of new racemes (Thompson and Willson, 1979; pers. observ.). During the middle of this period of availability, beginning in early to mid-September, with the ripening of lipid-rich *Lindera benzoin* (37% lipid) and continuing with ripening of *Cornus florida* (23% lipid) in early October there is competition for dispersal agents in many years, resulting in many of the low-quality fruits not getting dispersed at this time (Stiles, 1980; Stiles and Meffe, unpubl.). The fruiting season may be divided into three hypothetical periods based on presence or absence of 1) migratory frugivores, and 2) high-quality fall fruits (Stiles, 1980). The first period is from initiation of ripening until the ripening of fall high-quality fruits. Fruits are available and some seeds are dispersed in mid to late August well before the peak of fall frugivore migration (Thompson and Willson, 1979; Stiles, 1980). During this time early migrant frugivores encounter *Phytolacca* fruits when few high-quality fruits are ripe. These early fruits, however, if not taken, are subject to attack by micro-organisms until they are taken. The second period is from the ripening of fall high-quality fruits, especially *Lindera* and *Cornus*, until the high-quality fruits are depleted. The numbers of *Phytolacca* seeds dispersed at this time depend on the local abundance of high-quality fruits and of migrant frugivores. The third period is from depletion of the high-quality fruits to the time when the stems of *Phytolacca* fall to the ground or freezing and thawing rupture and dry the fruits. During this time frugivores may remain in the area, although in reduced numbers.

These three periods each yield some probability of seed dispersal for *Phytolacca*. Both migrant bird abundance and high-lipid fruit production are variable from year to year and from one location to another, so these probabilities are quite variable for any particular time period. Although the drastically changed environments in the northeastern United States over the past two centuries have probably greatly influenced the abundance and distribution of both *Phytolacca* and its dispersers (Sauer, 1952), we feel the patterns and selective pressures described here are similar to those found when *Phytolacca* occurred in scattered disturbances in primary floodplain forest. The sequential production of both racemes and fruits on racemes yields a long period of fruit availability with reduced exposure to potential rotting for later ripening fruits. The high-quantities of toxins found in these fruits are unusual, and the extension of the fruit availability through the presence of toxins and sequential fruit production certainly yields a greater total number of seeds dispersed for *Phytolacca*.

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