

The evolutionary ecology of mast seeding in trees

JONATHAN W. SILVERTOWN

*Department of Biology, Open University,
Walton Hall, Milton Keynes MK7 6AA, U.K.*

Accepted for publication May 1980

The hypothesis that masting by trees is a defensive strategy which satiates seed predators in mast years and starves them in the intervening periods is tested in 59 sets of data on the seed production and pre-dispersal seed-predation of 25 tree species. Twenty-four of the 59 data-sets support the hypothesis and show a statistically significant positive relationship between the proportion of seeds surviving the pre-dispersal stage and the \log_{10} of the crop size for the same year. Evidence that pre-dispersal seed survival increases with the length of the mast interval is poor.

A positive relationship between the strength of the masting habit and the maximum observed pre-dispersal seed mortality in a sample of 15 tree species suggests that the masting habit is best developed in predator-prone species. A survey of seed crop frequencies in the woody plant flora of North America shows masting species to be under-represented amongst shrubs and amongst trees which disperse their seeds in fleshy dispersal units. The selection pressures and evolutionary constraints which operate on the evolution of masting plants and their seed predators are discussed.

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INTRODUCTION

Many forest tree populations produce seed crops synchronously at irregular intervals but with an average periodicity characteristic of the species (Fowells,

1965). Other things being equal, reproductively mature organisms which skip potential breeding seasons will have a lower fitness than those which reproduce at every opportunity (Bull & Shine, 1979; Waller, 1979). This consideration and the synchrony of reproduction within populations of trees has led to the suggestion that this masting behaviour is of positive survival value to the individuals which exhibit it (Janzen, 1971). It has been suggested that the masting habit in plants is an anti-predator adaptation which satiates predators with more seeds than they can consume in mast years and prevents predator populations building up on these occasional bonanzas by starving them of seeds in the intervening periods. An explanation of this kind has been put forward for the evolution of periodical reproduction in semelparous bamboos (Janzen, 1976) and periodical Cicadas (Lloyd & Dybas, 1966a; Dybas & Lloyd 1974; Hoppensteadt & Keller, 1976; Bulmer, 1977).

The predator satiation hypothesis for the evolution of masting in trees is examined in this paper by means of a review of quantitative data of seed production and pre-dispersal seed predation. This is the first use of quantitative data in this way to answer two crucial questions: (1) Is the supposed predator satiation mechanism effective in reducing seed predation in mast years? and (2) Why do some trees exhibit the masting habit whilst others do not?

ANALYSIS OF THE DATA

Does predator satiation work?

There are three interdependent elements in the hypothetical defensive strategy of periodical reproduction. The first simply involves the production of enough seeds to satiate predators, thus ensuring that some seeds escape. The second element involves timing the interval between mast years so that any increase in a predator population caused by one period of prey surfeit has had time to decay before the next large crop is produced. The third element in the strategy is synchronous seed production between individuals in the same population and between populations of sympatric species sharing the same seed predators. This synchrony increases the effectiveness of the first two elements in the strategy in reducing predation upon individual trees' seeds. These three elements are examined in turn.

The relationship between seed crop size and seed survival

The diverse literature of forest entomology, forest genetics, forest management, primary production and energy flow in woodlands contains a number of studies where the seed production of species and the pre-dispersal mortality of seeds has been measured on an annual basis.

Fifty-nine sets of data covering 25 species were selected from the available literature (Appendix 1). Studies providing less than five years data and the very few accounts of post-dispersal seed mortality have not been used. A large insect fauna of cone predators and seed parasitoids is associated with many forest trees (e.g. Keen, 1958; Janzen, 1971) and seeds also form a more or less important part of the diet of many vertebrates (reviewed by Van Dersal, 1940; Smith & Aldous, 1947; Martin, Zim & Nelson, 1968; Janzen, 1971; Corbet, 1974). Not all sources of data used specify the exact cause of pre-dispersal seed mortality and a number

of authors use only the term 'viability' or 'soundness' to indicate the proportion of viable seeds dispersed after pre-dispersal mortality has operated. These cases are indicated by an appropriate entry under 'predator' in Appendix 1.

Two possible additional sources of reduced seed 'viability' or 'soundness' not due to predators are pollination failure (Sarvas, 1968) and embryo death following self pollination (Bramlett & Popham, 1971). Pollination failure will generally cause the abortion of seeds before seed crop size can be estimated and it is unlikely that total seed crop size has been overestimated due to the inclusion of unfertilized seeds. Complete gymnosperm fruits may develop after the death of self-fertilized embryos and this is a more likely source of error in estimating total seed crop size and the proportion of seeds surviving pre-dispersal mortality in cases where predation is not explicitly stated to be the cause.

Crop size itself was generally measured as either the number of cones or seeds per unit area. Details are given in the key to Appendix 1. A correlation coefficient (r) of \log_{10} (crop size) and the proportion of seeds surviving predation or other pre-dispersal mortality was computed and gives a measure of the survival value of increased crop size for individual trees in the population.

There are 24 statistically significant positive correlations of seed survival with \log_{10} (crop size) and two statistically significant negative correlations in the sample of 59 cases analyzed. Eleven of the 24 cases do not refer to specific predators as the cause of seed mortality. Predation is the most likely factor to produce correlations between crop size and mortality though such a correlation might also be the result of embryo-lethality due to selfing if the selfing rate was inversely proportional to crop size. Even assuming the latter explanation to be the correct one, the sample contains 13 instances in which a selection pressure in favour of large crops is exerted by predators.

The relationship between mast interval and seed survival

If a minimum interval between mast crops is an important factor in preventing predator populations increasing steadily after every large crop, we may expect to find that seed survival in the crops following mast years is lower than that predicted by the relationship between seed survival and crop size in the same year. Data for 14 of the 24 cases of a significant relationship between crop size and seed survival are complete enough to provide six consecutive years' of information and thus five comparisons of the effect of the size of one years' seed crop on the following years' seed survival. In only three of these populations is there any relationship between the residual variance in seed survival for a year and the size of the seed crop the previous year. In populations 30 (*Pinus ponderosa*) and 40 (*P. resinosa*) there is significantly decreased seed survival in years following large crops ($r = -0.86$, $P < 0.01$; $r = -0.87$, $P < 0.05$ respectively) but in population 32 (*P. ponderosa*) seed survival is significantly greater in years following large crops ($r = +0.62$, $P < 0.05$).

Seed crop synchrony

Synchronous seed production by individuals in the same population is implied by most of the primary sources of data used in this study and is evident in the seed crop data for individual trees given by Gysel (1956) and McNeill (1954). Correlation matrices for the seed production of sympatric populations of different species in seven localities are given in Table 1. All localities except one show synchrony in seed production between some species.

Table 1. Correlation coefficients for annual seed crops of mixed-species forest stands

Source	N	t	CV	Correlation coefficients	Location
Hagner (1965)	9	2	59	<i>Pinus sylvestris</i>	Sweden
	9	1	83	-0.56 <i>Picea abies</i>	
Haig, Davis & Weidmann (1941)	7	2	132	<i>Pinus monticola</i>	N.W. North America
	7	1	191	-0.02 <i>Larix occidentalis</i>	
	7	1	69	0.71* 0.55 <i>Pseudotsuga menziesii</i>	
	7	1	151	0.16 0.94*** 0.72* <i>Abies grandis</i>	
	7	1	151	0.21 -0.24 0.12 0.04 <i>Thuja plicata</i>	
	7	1	66	-0.02 -0.43 0.04 -0.26 0.56 <i>Tsuga heterophylla</i>	
Fowells & Schubert (1956)	16	2	102	<i>Pinus ponderosa</i>	Sierra Nevada, California, USA
	16	2	137	0.76*** <i>P. lambertiana</i>	
	16	1	201	-0.01 0.15 <i>Abies concolor</i>	
Flores Calderon (1969)	15	2	89	<i>Pinus engelmannii</i>	Chihuahua, Mexico
	15	2	82	0.67** <i>P. arizonica</i>	
	15	2	78	0.70** 0.42 <i>P. durangensis</i>	
Sarvas (1954)	5	1	42	<i>Betula verrucosa</i>	Finland
	5	1	67	0.96** <i>B. pubescens</i>	
Downs & McQuilkin (1944)	7	2	100	<i>Quercus borealis</i>	Georgia, USA
	7	2	90	0.71* <i>Q. velutina</i>	
	7	2	106	0.97** 0.59 <i>Q. coccinea</i>	
	7	1	131	0.32 0.26 0.49 <i>Q. alba</i>	
	7	1	92	0.73* 0.21 0.84** 0.86** <i>Q. montana</i>	
Burns, Christisen & Nichols (1954)	6	2	98	<i>Quercus nigra</i>	Missouri, USA
	6	2	74	0.78* <i>Q. marilandica</i>	
	5	2	212	0.98*** 0.53 <i>Q. coccinea</i>	
	6	1	22	-0.02 0.47 -0.43 <i>Q. stellata</i>	
	6	1	55	0.18 0.15 -0.06 0.55 <i>Q. alba</i>	

Which species exhibit the masting habit?

The predator satiation hypothesis leads us to two predictions about the occurrence of masting in tree populations. Firstly we may expect the masting habit to be most pronounced in populations suffering the heaviest seed predation. Secondly we may expect the habit to be absent from species which produce animal dispersed fruit with protected seeds since satiation of dispersal agents would be a poor strategy.

Masting and the intensity of predation

The intensity of the masting habit is measured by the coefficient of variation (*CV*) of crop size which is tabulated for each population in Appendix 1. The highest observed value of predation loss (*m*) for each case is also recorded in the Appendix as an indication of the potential annual seed mortality a tree could suffer. Figure 1 is a scatter diagram of *CV* plotted against *m* for all statistically significant cases of positive correlation between \log_{10} (crop size) and seed survival. Mean values of *CV* and *m* have been used where more than one population of a species shows a significant correlation. In cases where more than one factor caused seed loss in a population, only the largest identified cause of

seed mortality is plotted. Axes have been drawn through the median values of CV and m and show that there is an under representation of cases in the quadrant with high CV and low m in the sample. The mast seeding habit therefore appears to be most highly developed in those tree populations which experience high levels of pre-dispersal seed mortality in years of low seed production.

Masting and the dispersal of fruits and seeds

All the species considered so far and listed in Appendix 1 have non-fleshy fruits, most of which are dispersed by wind. In those non-fleshy species dispersed by animals (*Quercus* spp.) the dispersal agents consume a part of the seed crop and so behave like any other predator. Only those seeds cached for later use but not subsequently eaten by these vertebrate predators are genuinely dispersed. An effectively different kind of animal dispersal occurs in species with seeds borne in fleshy dispersal units. In these cases all seeds usually pass through the gut of the dispersal agent unharmed.

Data on the type of dispersal unit, the periodicity of large seed crops and the growth habit of 63 genera in 27 families of woody plants native to North America are tabulated in Appendix 2 (Schopmeyer, 1974; U.S.D.A., 1948). These data have been used to identify 77 independent cases of woody plants with a combination (syndrome) consisting of one of two types of dispersal unit (fleshy or non-fleshy), one of two types of seeds crop periodicity (masting plants with a mean intercrop interval > 1.5 years, non-masting plants with a mean intercrop

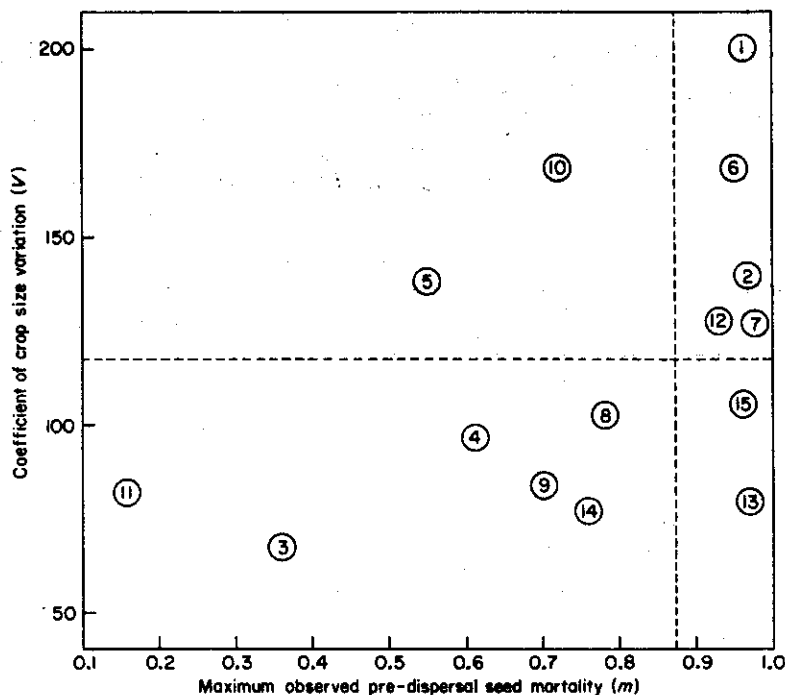


Figure 1. The relationship between CV and m for 15 tree species. Median lines are shown dashed. $P = 0.01$ (Fisher's exact test, one tail). The species are: 1, *Abies concolor*; 2, *Acer saccharum*; 3, *Betula pubescens*; 4, *Fagus grandifolia*; 5, *F. sylvatica*; 6, *Larix occidentalis*; 7, *Picea abies*; 8, *Pinus banksiana*; 9, *P. contorta*; 10, *P. lambertiana*; 11, *P. palustris*; 12, *P. ponderosa*; 13, *P. resinosa*; 14, *P. taeda*; 15, *Pseudotsuga menziesii*.

interval ≤ 1.5 years) and one of two types of growth habit (shrub or tree). Three editorial rules were applied to the data to avoid the spurious multiplication of particular syndromes in the sample due to phylogenetic inertia in large taxa (Stebbins, 1970; Clutton-Brock & Harvey, 1979). Different species in the same genus and with the same syndrome were counted as a single case, large genera (*Quercus* and *Pinus*) containing a single predominant syndrome but with one or two exceptional species were scored for the predominant syndrome only, different genera in the same family and with the same syndrome were counted as a single case. Table 2 shows the distribution of taxa by dispersal type and seed crop frequency in shrubs and trees.

A comparison of the frequency of different syndromes in these taxa shows that masting occurs significantly more often in trees than shrubs and in trees with non-fleshy dispersal units as compared with trees with fleshy dispersal units. *G* test: $G = 7.15$, $P < 0.01$, and $G = 16.9$, $P < 0.001$, respectively (Sokal & Rohlf, 1969).

DISCUSSION

Thirteen cases of a significant relationship between crop size and seed survival in the period before seed dispersal demonstrate that predators are likely to exert a selection pressure in favour of increased crop size, an important element in the predator satiation mechanism. A further 11 correlations between crop size and seed survival may also be due to the satiation of predators by mast crops. The evidence that the length of the intermast period is also an important factor in increasing the proportion of seeds which escape pre-dispersal seed predation is poor. The most important factor determining the length of the intermast period may be the time required for the accumulation of the starch and assimilates necessary to produce an eventual mast crop capable of satiating predators and with seeds to spare. Several studies have shown that seed production in forest

Table 2. The distribution of 26 shrub taxa and 41 tree taxa by dispersal unit and seed crop frequency. Shrubs and fleshy fruited trees are predominantly annual seeders ($P < 0.01$, $P < 0.001$ respectively)

		Fleshy dispersal unit	Non-fleshy dispersal unit
Shrubs	Non-masting (≤ 1.5 years)	11	9
	Seed crop frequency		
	Masting (> 1.5 years)	3	3
		14	12
Trees	Non-masting (≤ 1.5 years)	11	12
	Seed crop frequency		
	Masting (> 1.5 years)	4	14
		15	26

trees occurs at the cost of a decreased increment in tree-girth in mast years (Holmsgaard, 1956; Eis, Garman & Ebel, 1965). Clearly the cost of reproduction itself must make it physiologically impossible for seeds to be produced in large numbers every year.

The length of the intermast period itself may not be of primary importance to the predator satiation mechanism. This would be somewhat surprising in view of the fact that the abundance of tree seeds appears to be a limiting factor in the population regulation of a number of forest rodents, often operating on population size with a time delay of one year (Burns, Christisen & Nichols, 1954; Watts, 1969; Kemp & Keith, 1970; Hansson, 1971). Passerine populations which feed on tree seed also commonly fluctuate in relation to the masting behaviour of trees (Formosoff, 1933; Reinikainen, 1937; Perrins, 1966). It is possible that the length of the intermast period could be more important in the satiation of post-dispersal seed predators for which data are unfortunately scarce.

According to the predator satiation hypothesis the offspring of individuals which produce out of synchrony with others will not be protected by the satiation of predators which occurs when prey is abundant. In the light of the relationships between crop size and seed survival demonstrated above the synchrony observed in seed production within species is very likely to enhance the individual fitness of trees. Synchrony between species which share the same predators will have the same effect on seed survival as synchrony within species, though synchrony between species is quite likely to be fortuitous, unless populations have been sympatric for a considerable time. The abundant evidence that mast years are highly correlated with specific climatic conditions in nearly all species studied (Matthews, 1963; Puritch & Vyse, 1972) makes it clear that trees use environmental cues to achieve synchrony but it also lends support to the hypothesis that irregular seed production may be solely a consequence of environmental and physiological constraints on seed production. The major difficulty of this hypothesis is that it cannot readily explain why all forest tree species do not exhibit the masting habit to the same degree.

The predator satiation hypothesis predicts that masting should occur in populations subject to intense seed predation. The relationship between the coefficient of variation of crop size and maximum pre-dispersal seed mortality shown in Fig. 1 suggests that it is definitely worth pursuing predator satiation further as an explanation of masting. The necessary inclusion of data in Fig. 1 for populations where predation has not positively been identified as the cause of seed mortality makes the case employing the present state of knowledge less than conclusive. Intense seed predation is not confined to woody plants and the potential exists for predator satiation to favour the evolution of the masting habit in some herbs too. Darwin (1859) observed that birds often eat the entire crop of seed on small quantities of wheat planted in a garden but make little inroad on field acreages of the same species. Though we cannot expect annual plants to mast, a diminishing predation rate with increasing seed crop has also been observed for the infestation of *Miarus campanulae* (Coleoptera) in seed heads of the small grassland perennial herb *Campanula rotundifolia* (Morris, 1973). It is at least conceivable that mast seeding behaviour could evolve in herbaceous perennial plants and that it is apparently confined to woody species only because the seeding habits of herbs have not been sufficiently studied. What then are the constraints which may prevent the evolution of the masting habit taking place?

The comparison of seed crop frequencies in woody plants of different growth habits and seed dispersal types suggests two constraints which have operated on the evolution of masting. Masting is uncommon amongst shrubs possibly because these plants tend to be short lived (Harper & White, 1974) and therefore cannot afford barren seasons. Shrubs generally have smaller seeds borne in smaller clutches than trees (Levin & Kerster, 1974; Levin & Turner, 1977) which may be alternative defensive strategies against seed predators (Janzen, 1968). The absence of masting from shrubs because they are short-lived would suggest that a relationship between longevity and mast interval should also occur in masting trees. Such a relationship does indeed exist for North American species in the genus *Pinus* (Fig. 2) but is not repeated in another large North American genus, the Oaks (Silvertown, unpublished). An alternative explanation for a relationship between longevity and mast interval is that early death reflects the physiological cost of frequent bouts of heavy reproductive effort. This is the explanation offered for a negative relationship between adult survivorship and annual fecundity in 13 species of lizard studied by Tinkle (1969). Whatever the ultimate explanation of the relationship between seed crop frequency and adult survivorship, the presence of this constraint and of the constraint of dispersal type on the occurrence of masting in woody plants strongly suggests a corresponding advantage to masting which must prevail in the maintenance of the habit in longer lived plants with non-fleshy seeds during the course of evolutionary time.

Our discussion up to now has been confined to the factors which favour and disfavour masting as a habit which has already evolved. Bulmer (1977) has raised the question of what initial conditions are necessary for the *de novo* evolution of periodical reproduction in insects and similar arguments apply here. Mutant individuals which delay their reproduction in a hypothetical ancestral population where all other individuals reproduce annually will not benefit from the effects of predator satiation since such benefits only arise when periodical reproduction is already established throughout the prey population. Non-periodical reproduction is an evolutionary stable strategy (Maynard Smith, 1976). If, however, there are environmentally induced fluctuations in the size of seed crops, then predation and the operation of the predator satiation mechanism would ensure the evolution of synchrony in seed production between individuals. The

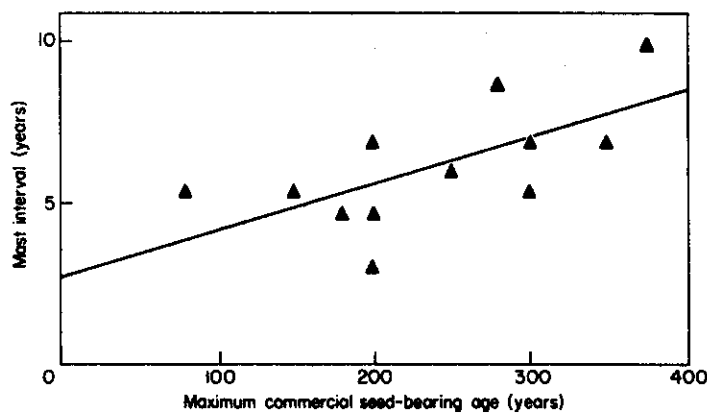


Figure 2. The relationship between length of reproductive life (maximum commercial seed bearing age) and mean mast interval for 12 North American pine species. ($F_{1, 11}=7.37$, $P<0.025$.) Data from U.S.D.A. (1948).

evidence that mast years are highly correlated with climatic conditions suggests that environmentally induced fluctuation in seed crop size did occur in ancestral populations of forest trees. If environmental cues effect a coarse tuning of fruiting synchrony and predator satiation occurs, selection may operate to tune the environmental response more finely, acting against those individuals that are deviant.

The seed predators exerting the strongest selection in favour of masting are likely to be the monophagous seed parasites found associated with most tree species (Keen, 1958). Predators in their turn may evolve tactics such as extended diapause (Kraft, 1968) to enable them to track seed production over extended periods of time. Smith (1970) has discussed the coevolution of pine squirrels and conifers and has shown that the latter have evolved morphological characteristics to reduce the predation of cones. Examples of coevolution between bird predators of seeds and trees has also recently been discussed by Ligon (1978) and Bosema (1979). It is clear that the interactions between masting trees and their invertebrate and vertebrate seed predators are strong enough to exert the kind of selection pressures necessary to accentuate environmentally induced fluctuations in crop size through evolutionary time into more pronounced, adaptive fluctuations of the kind these trees exhibit.

ACKNOWLEDGEMENTS

I should like to thank the librarians of the Forestry Library at the Commonwealth Forestry Bureau, Oxford for their help in unearthing material for this study and Beverley Simon who typed the manuscript. This paper benefited from comments made on an earlier draft by Steve Bostock, Brian Charlesworth, Alastair Ewing, Tim Halliday, Paul Harvey, John Harper, John Maynard Smith, Francis Wilkin, John Zasada and participants in the 1979 Seed Ecology Meeting at the University of Keele.

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APPENDIX I

Seed production and seed predation statistics for 25 tree species. See Key for abbreviations

Genus	Species	Site	N	u	CV	r	P	m	Predator (or equivalent)	Location	Source
1 <i>Abies</i>	<i>concolor</i>	1	6	Ca	201	0.88**	0.96		<i>Megastigmus</i> spp. (Hymenoptera)	California, USA	Fowells & Schubert, 1956
2 <i>Abies</i>	<i>concolor</i>	1	14	Ca	201	0.04	0.04		<i>Tomiascurus douglasii</i>	California, USA	Fowells & Schubert, 1956
3 <i>Acer</i>	<i>saccharum</i>	1	8	Sa	140	0.92***	0.97		'Viability'	Wisconsin, USA	Curtis, 1959
4 <i>Betula</i>	<i>pubescens</i>	1	5	St	67	0.89*	0.36		'Soundness'	Finland	Sarvas, 1954
5 <i>Betula</i>	<i>verrucosa</i>	1	6	St	42	0.28	0.57		'Soundness'	Finland	Sarvas, 1954
6 <i>Fagus</i>	<i>grandifolia</i>	1	8	St	97	0.66*	0.61		Unidentified insects	Michigan, USA	Gysel, 1971
7 <i>Fagus</i>	<i>grandifolia</i>	1	8	St	97	0.55	0.73		<i>Sciurus niger</i>	Michigan, USA	Gysel, 1971
8 <i>Fagus</i>	<i>grandifolia</i>	1	8	St	97	0.21	0.96		All sources of loss	Michigan, USA	Gysel, 1971
9 <i>Fagus</i>	<i>syriaca</i>	1	7	Sw	138	0.81*	0.55		<i>Cydias fagiglandana</i> (Lepidoptera)	Denmark	Nielsen, 1977
10 <i>Larix</i>	<i>occidentalis</i>	1	6	Sa	168	0.82*	0.95		'Soundness'	Montana, USA	Shearer, 1960
11 <i>Libocedrus</i>	<i>decurrens</i>	1	5	Sa	84	0.60	0.86		'Soundness'	California, USA	Fowells & Schubert, 1956
12 <i>Picea</i>	<i>abies</i>	1	9	Sm	162	0.60	1.00		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
13 <i>Picea</i>	<i>abies</i>	2	6	Sm	142	0.83	0.94		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
14 <i>Picea</i>	<i>abies</i>	3	8	Sm	127	0.85**	0.98		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
15 <i>Picea</i>	<i>abies</i>	4	9	Sm	122	0.09	1.00		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
16 <i>Picea</i>	<i>abies</i>	5	8	Sm	214	0.50	0.91		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
17 <i>Picea</i>	<i>abies</i>	6	9	Sm	174	0.32	1.00		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
18 <i>Picea</i>	<i>abies</i>	7	8	Sm	173	0.61	1.00		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
19 <i>Picea</i>	<i>abies</i>	8	8	Sm	153	0.43	0.99		'Seed empty (cf. Rumukainen, 1960)	Finland	Sarvas, 1968
20 <i>Picea</i>	<i>glauca</i>	1	8	Sa	170	0.64	0.98		'Soundness'	Manitoba, Canada	Waldron, 1965
21 <i>Picea</i>	<i>glauca</i>	1	5	Cr	—	0.55†	0.45		<i>Laspylepsia</i> (Lepidoptera)	Alaska, USA	Werner, 1964
22 <i>Pinus</i>	<i>banksiana</i>	1	5	Cr	102	0.92**	0.78		<i>Megastigmus</i> <i>Laspylepsia torcula</i> (Lepidoptera)	Michigan, USA	Kraft, 1968

23	<i>Pinus contorta</i>	1	10	Sa	94	0.82***	0.60	'Soundness'	Oregon, USA	Dahms & Barrett, 1975
24	<i>Pinus contorta</i>	2	15	Sa	71	0.88***	0.80	'Soundness'	Oregon, USA	Dahms & Barrett, 1975
25	<i>Pinus lambertiana</i>	1	6	Ca	168	0.95***	0.72	'Soundness'	California, USA	Fowells & Schubert, 1956
26	<i>Pinus lambertiana</i>	1	13	Ca	168	0.21	0.57	<i>Tamiascurus douglasii</i>	California, USA	Fowells & Schubert, 1956
27	<i>Pinus monticola</i>	1	6	Ct	94	-0.85°	0.56	<i>Conophorus monticolae</i> (Coleoptera)	Idaho, USA	Barnes, Bingham & Schenk, 1962
28	<i>Pinus palustris</i>	1	10	Sb	82	0.75**	0.16	<i>Lepytaria ingens</i> (Lepidoptera)	Louisiana, USA	McLenore, 1975
29	<i>Pinus palustris</i>	10	10	Sb	82	0.85***	0.75	All sources of loss	Louisiana, USA	McLenore, 1975
30	<i>Pinus ponderosa</i>	8	8	Sa	138	0.93***	0.92	'Soundness'	Montana, USA	Slicar & Schmidt, 1971
31	<i>Pinus ponderosa</i>	1	6	Sa	144	0.75*	0.90	<i>Conophorus scopulorum</i> (Coleoptera)	Arizona, USA	Larson & Schubert, 1970
32	<i>Pinus ponderosa</i>	1	10	Ca	93	0.68*	0.75	<i>Saturnia aberti aberti</i>	Arizona, USA	Schubert, 1970
33	<i>Pinus ponderosa</i>	1	12	Sa	128	0.88***	0.92	'Soundness'	Oregon, USA	Dahms & Barrett, 1975
34	<i>Pinus ponderosa</i>	1	14	Ca	102	0.60*	0.52	<i>Tamiascurus douglasii</i>	California, USA	Fowells & Schubert, 1956
35	<i>Pinus ponderosa</i>	1	5	Ca	102	0.95**	0.97	<i>Megasigma</i> spp. (Hymenoptera)	California, USA	Fowells & Schubert, 1956
36	<i>Pinus resinosa</i>	1	6	Ct	88	0.93**	1.00	Various insects (cf. Lyons, 1957a,b)	N. USA	Mattson, 1971
37	<i>Pinus resinosa</i>	2	6	Ct	90	0.38	1.00	Various insects (cf. Lyons, 1957a,b)	N. USA	Mattson, 1971
38	<i>Pinus resinosa</i>	3	6	Ct	69	0.66	1.00	Various insects (cf. Lyons, 1957a,b)	N. USA	Mattson, 1971
39	<i>Pinus resinosa</i>	4	6	Ct	70	0.78*	0.90	Various insects (cf. Lyons, 1957a,b)	N. USA	Mattson, 1971
40	<i>Pinus resinosa</i>	5	6	Ct	88	0.93**	1.00	Various insects (cf. Lyons, 1957a,b)	N. USA	Mattson, 1971
41	<i>Pinus taeda</i>	1	13	Sa	92	0.85***	0.65	'Viability' (cf. Yates & Ebel, 1978)	N. Carolina, USA	Pomeroy & Korstian, 1949
42	<i>Pinus taeda</i>	1	10	Sa	59	0.77**	0.66	'Viability' (cf. Yates & Ebel, 1978)	S. Carolina, USA	Lotti, 1956
43	<i>Pseudotsuga menziesii</i>	1	6	Ca	129	0.65	0.70	<i>Conalaria oregonensis</i> (Diptera)	British Columbia, Canada	Hedlin, 1964
44	<i>Pseudotsuga menziesii</i>	1	6	Ca	129	0.56	0.72	All sources of loss	British Columbia, Canada	Hedlin, 1964
45	<i>Pseudotsuga menziesii</i>	1	6	St	106	0.75*	0.96	'Soundness'	Oregon, USA	Gashwiler, 1970

APPENDIX I CONTINUED

46	<i>Quercus alba</i>	1	5	Sb	55	0.40	0.80	‡ Arboreal vertebrates	Missouri, USA	Christisen & Korschgen, 1955
47	<i>Quercus alba</i>	1	5	Sb	55	-0.12	0.81	‡ Terrestrial vertebrates	Missouri, USA	Christisen & Korschgen, 1955
48	<i>Quercus alba</i>	1	5	Sb	55	-0.07	0.87	‡ All vertebrates	Missouri, USA	Christisen & Korschgen, 1955
49	<i>Quercus marilandica</i>	1	5	Sb	74	0.39	0.86	‡ Arboreal vertebrates	Missouri, USA	Christisen & Korschgen, 1955
50	<i>Quercus marilandica</i>	1	5	Sb	74	-0.04	0.87	‡ Terrestrial vertebrates	Missouri, USA	Christisen & Korschgen, 1955
51	<i>Quercus marilandica</i>	1	5	Sb	74	0.27	0.60	‡ All vertebrates	Missouri, USA	Christisen & Korschgen, 1955
52	<i>Quercus stellata</i>	1	5	Sb	22	-0.13	0.19	‡ Arboreal vertebrates	Missouri, USA	Christisen & Korschgen, 1955
53	<i>Quercus stellata</i>	1	5	Sb	22	-0.11	0.53	‡ Terrestrial vertebrates	Missouri, USA	Christisen & Korschgen, 1955
54	<i>Quercus stellata</i>	1	5	Sb	22	0.15	0.62	‡ All vertebrates	Missouri, USA	Christisen & Korschgen, 1955
55	<i>Quercus velutina</i>	1	5	Sb	97	0.23	0.24	‡ Arboreal vertebrates	Missouri, USA	Christisen & Korschgen, 1955
56	<i>Quercus velutina</i>	1	5	Sb	97	0.20	0.29	‡ Terrestrial vertebrates	Missouri, USA	Christisen & Korschgen, 1955
57	<i>Quercus velutina</i>	1	5	Sb	97	0.22	0.64	‡ All vertebrates	Missouri, USA	Christisen & Korschgen, 1955
58	<i>Thuja plicata</i>	1	6	St	142	0.05	1.00	'Soundness'	Oregon, USA	Korschgen, 1970
59	<i>Tsuga canadensis</i>	1	6	St	105	-0.75*	0.40	'Soundness'	Oregon, USA	Gashwiler, 1970

KEY

N, Sample size (years). u, Units of measurement for crop size: Ca, cones/acre; Cr, index of relative cone crop size; Ct, total cone crop; Sa, seed/acre; St, seeds trapped; Sw, seed production (g/m²); Sb, mean seeds/tree; seeds/m². CV, Coefficient of variation of crop size. r, Coefficient of correlation Log₁₀ crop size and probability of seed survival. P, Significance level of r: * = P < 0.05, ** = P < 0.01, *** = P < 0.001. m, Highest observed probability of seed mortality. †, Spearman rank correlation coefficient. ‡, Heavy predation by insects is also recorded but is not quantified.

APPENDIX 2

Seed crop frequency and growth habit in the woody plant flora of North America.
Seed crop interval ≤ 1.5 years (non-masting) + seed crop interval > 1.5 years
(masting). Data from Schopmeyer (1974) and U.S.D.A. (1948)

Family	Genus	Dispersal unit	Shrub	Tree
Aceraceae	<i>Acer</i>	Samara		- +
Anacardiaceae	<i>Rhus</i>	Drupe	-	--
	<i>Cotinus</i>	Drupe	-	
Annonaceae	<i>Asimina</i>	Berry		-
Berberidaceae	<i>Berberis</i>	Berry	-	
Betulaceae	<i>Alnus</i>	Nut		+
	<i>Betula</i>	Nut	-	- +
	<i>Carpinus</i>	Nut		+
	<i>Corylus</i>	Nut	+	
Bigoniaceae	<i>Catalpa</i>	Seed		+
	<i>Campsis</i>	Seed	-	
Buxaceae	<i>Simmondsia</i>	Seed	-	
Caprifoliaceae	<i>Sambucus</i>	Drupe	-	-
	<i>Symphoricarpos</i>	Drupe	-	
	<i>Viburnum</i>	Drupe	+ -	-
Celastraceae	<i>Celastris</i>	Aril + seed	-	
	<i>Euonymus</i>	Aril + seed	-	
Chenopodiaceae	<i>Atriplex</i>	Utricle	-	
	<i>Eurotia</i>	Utricle	-	
Compositae	<i>Artemisia</i>	Achene	-	
	<i>Baccharis</i>	Achene	-	
	<i>Chrysothamnus</i>	Achene	-	
	<i>Haplopappus</i>	Achene	-	
Cornaceae	<i>Cornus</i>	Drupe	-	+
	<i>Nyssa</i>	Drupe		+
Cupressaceae	<i>Chamaecyparis</i>	Seed		+
	<i>Cupressus</i>	Seed	-	-
	<i>Juniperus</i>	Fleshy strobilus		+
	<i>Libocedrus</i>	Seed		+
	<i>Thuja</i>	Seed		+
Ebenaceae	<i>Diospyros</i>	Berry		-
Elaeagnaceae	<i>Elaeagnus</i>	Drupaceous achene	-	
	<i>Spherdia</i>	Drupaceous achene	-	
Ericaceae	<i>Arbutus</i>	Berry		-
	<i>Oxydendrum</i>	Seed		-
Fagaceae	<i>Fagus</i>	Nut		+
	<i>Lithocarpus</i>	Nut		+
	<i>Quercus</i>	Nut		+
Grossulariaceae	<i>Ribes</i>	Berry	+ -	
Hamamelidaceae	<i>Liquidamber</i>	Seed		+
Hippocastanaceae	<i>Aesculus</i>	Nut		-
Juglandaceae	<i>Carya</i>	Nut		+ -
	<i>Juglans</i>	Nut		+
Lauraceae	<i>Sassafras</i>	Drupe		-
	<i>Umbellularia</i>	Drupe		-
Leguminosae	<i>Amorpha</i>	Seed	+	
	<i>Cercis</i>	Seed	+ -	
	<i>Cladrastis</i>	Seed		+
	<i>Gleditsia</i>	Seed		-
	<i>Robinia</i>	Seed		-
Magnoliaceae	<i>Liriodendron</i>	Samara		-
	<i>Magnolia</i>	Drupe		-
Moraceae	<i>Morus</i>	Berry		+
	<i>Maclura</i>	Berry		-
Oleaceae	<i>Mendora</i>	Seed	-	
	<i>Chionanthus</i>	Drupe	-	
	<i>Fraxinus</i>	Samara		+ -

APPENDIX 2 CONTINUED

Pinaceae	<i>Abies</i>	Seed		+
	<i>Tsuga</i>	Seed		+
	<i>Pseudotsuga</i>	Seed		+
	<i>Picea</i>	Seed		+
	<i>Pinus</i>	Seed		+
	<i>Larix</i>	Seed		+
Platanaceae	<i>Platanus</i>	Achene		-
Ranunculaceae	<i>Clematis</i>	Achene	-	
Rhamnaceae	<i>Ceanothus</i>	Drupe	-	
	<i>Rhamnus</i>	Drupe	-	
Rosaceae	<i>Amelanchier</i>	Pome	-	
	<i>Aronia</i>	Pome	-+	
	<i>Cerocarpus</i>	Achene	+	
	<i>Coloneaster</i>	Drupe	-	
	<i>Cowania</i>	Achene	-	
	<i>Fallugia</i>	Achene	+	
	<i>Malus</i>	Pome		+
	<i>Photina</i>	Pome	-	
	<i>Physocarpus</i>	Inflated follicle	-	
	<i>Prunus</i>	Drupe		- (+)
	<i>Purschia</i>	Achene	+ (-)	
	<i>Rosa</i>	Pome	-	
	<i>Rubus</i>	Berry	-	
	Salicaceae	<i>Populus</i>	Seed	
Sapindaceae	<i>Sapindus</i>	Drupe		-
Taxaceae	<i>Taxus</i>	Aril + Seed		-
Taxodiaceae	<i>Sequoia</i>	Seed		-
	<i>Taxodium</i>	Seed		+
Tiliaceae	<i>Tilia</i>	Woody fruit		+
Ulmaceae	<i>Ulmus</i>	Samara		+
	<i>Celtis</i>	Drupe	-	