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BODY SIZE AND DIET QUALITY IN THE GENUS *CYDIA* (TORTRICIDAE)

WILLIAM E. MILLER

Department of Entomology, University of Minnesota,
St. Paul, Minnesota 55108

ABSTRACT. I examine forewing length, a body-size index, relative to three quality classes of larval diet for more than 75 *Cydia* species. Quality of diet refers to protein concentration in the part of the food plant consumed. Mean crude protein percentages are near 25 in the high class, near 12 in the medium, and near 6 in the low. All data are from published sources. Forewings range in length from 4.0 to 10.5 mm among study taxa, and are longest in the high food-quality class, intermediate in the medium, and shortest in the low. The high food-quality class consists entirely of seed predators whose body sizes correlate positively with food-plant seed sizes. Medium and low food-quality classes consist mostly of nonseed feeders. Results imply that as *Cydia* colonize new food plants and plant parts of differing diet quality, body sizes evolve to those for which larvae can obtain sufficient nourishment. This interpretation withstands cladistic testing against an independent *Cydia* phylogeny.

Additional key words: Olethreutinae, evolution, cladistics, seed predation, food plants.

For organisms generally, body size is thought to be a quantitative adaptive trait (Bonner 1965, Calder 1984, Roff 1981). Much interest in body size derives from consequences of allometric relations among body components (Peters 1983). Body-size physiology and ecology are more tractable and better understood than body-size evolution, one facet of which is genesis of body-size diversity. Body size usually varies somewhat within species, but it does so around a genetically controlled norm. The norm represents an adaptive and fitness compromise in a given environment; analysis of norms and environments can yield evolutionary insights (Fisher 1930, Ridley 1983, Williams 1966).

Lepidopteran body-size diversity has just begun to be studied. Dietary factors are natural choices for independent variables: food quantity and quality are potent determinants. Among examined lepidopteran families, individual and population biomass correlate with density, size, and diet quality of food plants (Mattson 1977, 1980, Mattson & Scriber

1987, Niemelä et al. 1981). Within examined lepidopteran genera, subfamilies, and families, body size correlates also with breadth of diet (Niemelä et al. 1981, Wasserman & Mitter 1978). Within lepidopteran families that mine leaves of *Quercus* (Fagaceae), body size correlates with leaf persistence, smaller-bodied species occurring on deciduous species (Opler 1978). If body size is viewed as an effect, then in evolutionary time it would seem to shift positively with diet breadth, food-plant size, and leaf persistence, and negatively with diet quality, although diet quality and plant size themselves correlate positively. Information is still too scant to yield well integrated generalizations about the genesis of lepidopteran body size diversity.

In this paper I examine body-size diversity relative to quality of larval diet in a large, worldwide sample of *Cydia* species (Tortricidae, Olethreutinae), defining food quality as protein concentration and testing analytical results cladistically.

For species of the subfamily Olethreutinae, a commonly available measure of body size is forewing length (L), values of which range from 4 to 20 mm (Miller 1987). Single genera cover large portions of this range. *Cydia* occupies more than half of it. Forewing length closely estimates dry body weight (W) of olethreutines by a power function summarized as $W = 0.0085L^3$ (Miller 1977). This function reveals that small differences in forewing length denote larger differences in body mass. The low standard error of estimate of this function justifies using forewing length as an index of body size.

Cydia in the strict sense consists of ca. 250 species. Many species are important economically, a fact responsible for much information about the genus. The most famous species is the codling moth, *C. pomonella* (L.). The generic name is in flux; I follow Brown (1979) in using *Cydia*, but others argue for using *Laspeyresia* (Kuznetsov & Kerzhner 1984).

MATERIALS AND METHODS

I devise three larval food-quality classes based on concentration of crude protein in the part of the food plant eaten, place each *Cydia* in an appropriate food-quality class, analyze inter- and intraclass differences in forewing length, and compare results with an existing phylogeny.

I include only taxa conforming to the strict *Cydia* concepts of Obraztsov (1959) and Danilevsky and Kuznetsov (1968). Using broader generic concepts, some authors refer species to *Cydia* that are more strictly referable to *Grapholita*, *Pammene*, and other genera. Strict interpretation focuses and simplifies the study by limiting genetic heterogeneity to that of *Cydia* monophyly. In classification and nomenclature of *Cydia* subgenera, sections, species, and subspecies, I follow

Danilevsky and Kuznetsov (1968) for taxa treated by them; for other taxa I apply their classification as far as I can do so confidently.

Wing measure of *Cydia* species is usually published as a range. I therefore use midrange, a statistic approximating the mean. Wingspan (S), the maximum distance between tips of spread wings, more often appears in the literature than forewing length (L). I convert span to length by the proportionality constant L = 0.458S (Miller 1977). All midranges are from published sources, mostly detailed faunal works (Appendix). Where forewing-length sample sizes are small, and a best source unavailable, I combine data from several sources. When midrange could not be based on at least two individuals, I excluded the taxon. Using standard approximate methods, I estimate standard deviation (SD) of the midrange for all taxa where explicit sample sizes are nine or more individuals. I work with midranges expressed to three decimal places, but record them here to only one place (Appendix and elsewhere).

Food-plant parts eaten by *Cydia* larvae differ in food quality. Protein is a major component of food quality (Mattson 1980, Mattson & Scriber 1987, Scriber & Slansky 1981). "Crude protein", a standard food-science term, refers to the mathematical product of Kjeldahl nitrogen percentage and a multiplier, usually 6.25 (Crisan & Sands 1978, Williams 1984, and others). Crude protein percentage of food-plant parts used by *Cydia* forms a continuum. Below, I divide this continuum for study purposes into three food-quality classes: high, medium, and low. The letter n (or N) denotes number of analyses in this section of the text, number of observations in later sections.

High (mean near 25%)—seeds of Leguminosae; *Pinus, Picea, Abies* (Pinaceae); *Malus* and *Pyrus* (Rosaceae). Nutritional superiority of seeds for seed eaters over other plant parts is evident in the survey by Mattson (1980). It may be further documented with Leguminosae, one of the two plant families most used by *Cydia*: in forage species (6n), mean percentage crude protein is 24 in seeds, 16 in foliage, and 7 in pod husks (Skerman 1977). In other surveys, percentage crude protein in seeds ranges from 4 to 62 in Leguminosae (>1000n), 6 to 38 in *Pinus* and *Picea* (21n), and 18 to 49 in *Malus* and *Pyrus* (6n) (Barclay & Earle 1974, Dickmann & Kozlowski 1969, Earle & Jones 1962, Haut 1938, Jones & Earle 1966, Katsuta & Satoo 1964, McCarthy & Matthews 1984, NAS 1979, Pulliainen & Lajunen 1984, Räder-Roitzsch 1957, Short & Epps 1976, Skerman 1977, Winton & Winton 1932, 1935, Yoon et al. 1983).

Medium (mean near 12%)—inner bark, fungus-infected woody parts, photosynthesizing bark, foliage, flowers; seeds of *Acer* (Aceraceae), *Corylus* (Betulaceae), *Cryptomeria* (Taxodiaceae), and *Quercus*. Fungi are equally as proteinaceous as the seeds comprising the high food-quality class (Crisan & Sands 1978, Mattson 1980), but fungi only supplement *Cydia* underbark diets. Photosynthesizing bark occurs in the food-plant genus *Populus* (Salicaceae) (Shepard 1975). Percentage crude protein in seeds is 7 to 32 for *Acer* (11n), 4 to 32 for *Quercus* (21n), and 11 to 26 for *Corylus* (5n) and *Cryptomeria* (1n) (Anderson & Kulp 1921, Barclay & Earle 1974, Earle & Jones 1962, Jones & Earle 1966, McCarthy & Meredith 1988, Schmidt-Hebbel & Pennacciotti M. 1979, Short & Epps 1976, Wainio 1941, Winton & Winton 1932).

Low (mean near 6%)—habitations of other insects, fruits or other seed-containing parts, sapwood, outer bark; seeds of *Araucaria* (Araucariaceae), *Castanea, Fagus* (Fagaceae), and Palmae. Wood and seed-containing parts are among the plant parts lowest in protein (Mattson 1980, Skerman 1977). Percentage crude protein in seeds is 4 to 16 in *Araucaria* (2n), *Castanea* (8n), *Fagus* (3n), and Palmae (20n) (Barclay & Earle 1974, Cardemil & Reinero 1982, Earle & Jones 1962, Jones & Earle 1966, McCarthy & Meredith 1988, Schmidt-Hebbel & Pennacciotti M. 1979, Wainio 1941, Winton & Winton 1932).

In intraclass analyses, I examine *Cydia* forewing length relative to food-plant seed size measured as weight of one seed. Mean seed weights for a given plant species do not vary much (Harper et al. 1970). I take most seed weights from published sources (Appendix, Table 2), using sample means and midranges in that order of preference. Where reported weights are few, I combine data from several sources if available. For seeds also consumed by man, I use seed weights of wild-type food plants if known. For other domesticated seeds, I use the smallest values reported. Because such plants have long been cultivated or bred for large seeds (Smartt 1980), the lowest weights are probably nearer to wild-type values. For those few species for which only seed dimensions are available, I estimate weights from one or more relatives of known seed weight and similar seed dimensions. Where one main food-plant species is not apparent, I use the mean of available seed weights for the appropriate number of food-plant species. In botanical nomenclature, I give only original authors (Appendix), following Schopmeyer (1974) and Krüssmann (1978) in that order for food plants treated by them, and following source authors for others. I work with seed weights expressed to four significant figures, but report them here to three figures (Appendix, Table 2).

I use both nonparametric and parametric statistics because sample sizes are sometimes unequal, and distributions are sometimes more important than parametric values. Nonparametric methods treat data by ranks rather than by values. Hence differences between means may actually refer to differences between underlying rank distributions.

Because forewing-length equations involve dimensions, I use nonlinear power functions for them (Peters 1983) solved by ordinary least squares.

For one-third of *Cydia* taxa, the part of the food plant eaten is known, thus enabling estimation of the quality of larval diet. This fraction of the genus comprises the study sample. There are 82 observations in all, one each for 78 species, 2 other than nominotypical subspecies, and 2 additional populations that behave like separate taxa in using food plants different from those of allopatric sister populations. Observations are grouped into high, medium, and low food-quality classes within which they appear alphabetically by *Cydia* species-level taxon in the Appendix. The 34 taxa and populations in the high food-quality class, all of which are seed predators, are from six continents; the 34 in the medium class feed mostly on nonseed parts, and are from three continents; and the 14 in the low class feed mostly on nonseed parts, and are from five continents. Corresponding numbers of food-plant families are 3, 12, and 9, respectively. Food-plant families and percentages of *Cydia* study species using them are, for the high class: Pinaceae—47%, Leguminosae—47%, Rosaceae—6%; for the medium class: Pinaceae—35%, Fagaceae—16%, Aceraceae—10%, Leguminosae—9%, Salicaceae—9%, others—21%; for the low class: Pinaceae—21%, Salicaceae—21%, Fagaceae—14%, others—44%.

I provisionally include five *Cydia* species whose strict generic affinities are unconfirmed: *araucariae* (Pastrana), *palmetum* (Heinrich), *staphiditis* (Meyrick), *stirpicola* (Meyrick), and *tonosticha* (Meyrick). Some species whose strict generic affinities require exclusion are *Fulcrifera torostoma* (Clarke), *F. tricentra* (Meyrick), *Grapholita deshaisiana* (Lucas), *Leguminivora glycinivorella* (Matsumura), *L. ptychora* (Meyrick), *Matsumuraeses critica* (Meyrick), and *M. fabivora* (Meyrick).

RESULTS

Forewing lengths range from 4.0 to 10.5 mm (Appendix, Table 1). The main assumption in this study is that body-size diversity really exists in this sample range. If such diversity is present, variance (SD^2) in forewing length among taxa should exceed that within taxa; if it is absent, the two variances should not differ. Comparison shows that variance among taxa (1.611, 82n) exceeds weighted average variance within taxa (0.156, 38n) (1.611/0.156 = 10.3, $P < 0.001$, variance ratio test), thus confirming the presence of diversity.

Body-size and Food Quality

Forewings are longest in the high food-quality class (6.8 mm), intermediate in the medium class (6.4 mm), and shortest in the low class

TABLE 1. Body size of *Cydia* taxa and populations relative to quality of larval diet.

Food-quality class	N	Forewing-length midrange (F) (mm) Mean ± SD[a]	Range	Estimated mean dry wt. (W) (mg)[b]
High	34	6.8 ± 1.4	4.0–10.5	2.6
Medium	34	6.4 ± 0.9	4.8–8.2	2.2
Low	14	5.8 ± 1.3	4.4–8.5	1.7

[a] Means differ statistically (F-test, $P < 0.05$); their rank distributions differ in all possible comparisons (Kruskal-Wallis and Mann-Whitney tests, $P < 0.001$).
[b] $W = 0.0085\ F^3$.

(5.8 mm) (Table 1). Estimates of body weight (Table 1) differ more markedly among the classes because forewing length is being multiplied by a power function. On average, members of the high class are 1.16 times heavier than those of the medium class, and 1.57 times heavier than those of the low; members of the medium class are 1.35 times heavier than those of the low.

Members of the high food-quality class have the greatest range and variability in forewing length (Table 1). Further scrutiny and analysis of this group reveals a major source of intraclass body-size variation. In this class, forewing length correlates with food-plant seed size; the larger the seeds, the longer the forewings in both the pinaceous and leguminous subsets (Fig. 1). In a control analysis of nonseed-feeders from the medium and low food-quality classes, no such correlation appears between forewing length and food-plant seed size (Fig. 2: line A).

Size is only part of the seed factor accounting for body-size variation in the high class. Food-plant seed weight in this class traverses three orders of magnitude; the smaller the seed, the greater the number required to nourish a larva, the number increasing from 2 to more than 30 in taxa for which such data are available (Fig. 3, Table 2). Thus the product of seed size and number required underlies the correlation of forewing length and seed size shown in Fig. 1.

In the medium and low food-quality classes, range and variability of forewing length are narrower than in the high class (Table 1), and sources of intraclass body-size variation are less evident. In pooled medium and low classes, mean forewing length of seed predators (7.2 mm) is greater than that of nonseed feeders (5.9 mm) ($P < 0.001$, Student *t*- and Mann-Whitney tests). Forewing length of seed predators in these classes also correlates with seed size (Fig. 2: line B). Secondary plant chemistry could be a factor in intraclass variation in the medium and low food-quality classes because a greater diversity of food plants is involved: 12 and 9 food-plant families, respectively, compared with 3 in the high class.

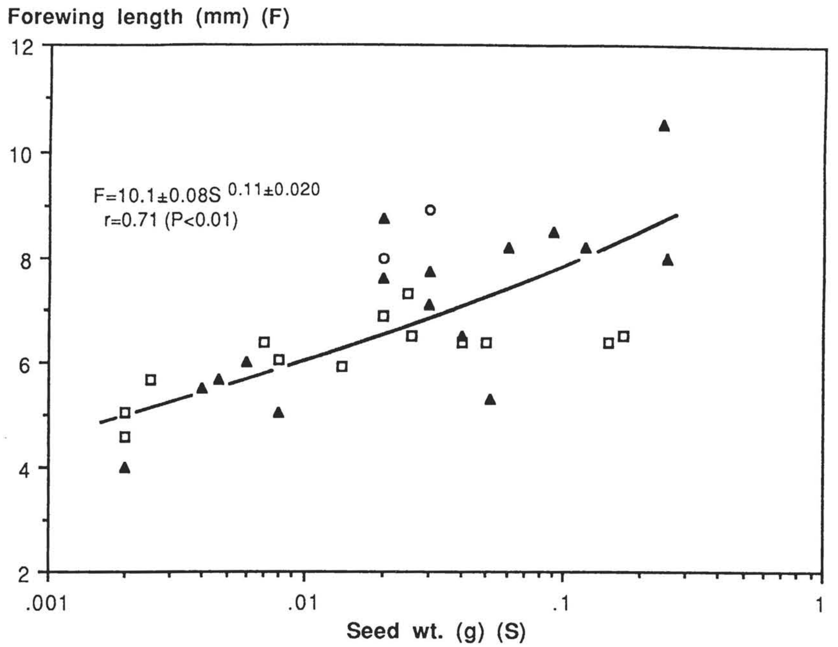

FIG. 1. *Cydia* body size as related to food-plant seed size in the high food-quality class. Each point represents a *Cydia* taxon or population enumerated in the Appendix. Solid triangles depict the pinaceous subset; open squares, the leguminous subset; open circles, others. The symbol ± denotes standard error.

TABLE 2. Number of seeds eaten or destroyed per *Cydia* larva in the high food-quality class. (Ditto is abbreviated do.)

Species of *Cydia*	Food plant	Mean seed wt. (g)[a]	Mean no. seeds/ larva	References
anaranjada	*Pinus elliottii*	0.0314	6	Merkel 1967
conicolana	*P. sylvestris*	0.00605	7	Gibb in Betts 1958
ingens	*P. elliottii*	0.0314	12	Coyne 1968
do.	*P. palustris*	0.0926	4	do.
montezuma	*P. montezumae*	0.0198	9	Cibrián-Tovar et al. 1986
n. nigricana	*Pisum sativum*	[0.178]	2.6	Stenmark 1971
piperana	*Pinus p. ponderosa*	0.0589	4	Hedlin 1967
do.	*P. p. scopulorum* Engelm.	[0.0346]	5	Kinzer et al. 1972
pomonella	*Malus pumila*	0.0227	8	Crandall 1917, Denno & Harwood 1973, Heriot & Waddel 1942
toreuta	*Pinus banksiana*	[0.00346]	10	Kraft 1968
do.	*P. resinosa*	[0.00872]	7	Lyons 1957
strobilella	*Picea abies*	0.00709	17	Andersson 1965, Györfi 1956
do.	*P. glauca*	0.00201	31	Tripp & Hedlin 1956

[a] Brackets denote weights absent or different in the Appendix. Bracketed weights for *Pinus* from Krugman & Jenkinson (1974).

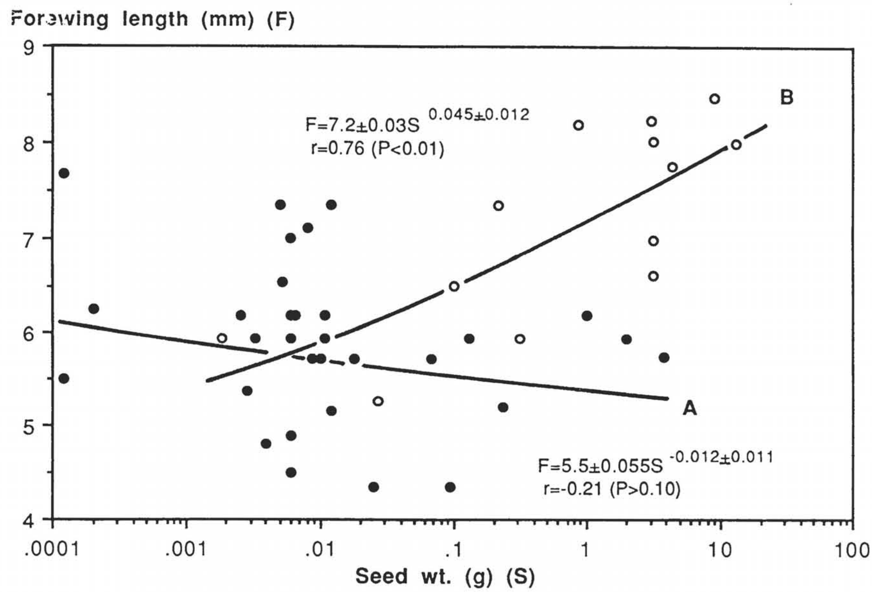

FIG. 2. *Cydia* body size as related to food-plant seed size in pooled medium and low food-quality classes. Each point represents a *Cydia* taxon or population enumerated in the Appendix. Line A (closed circles) depicts the nonseed-feeding subset; line B (open circles), the seed-predator subset. The symbol ± denotes standard error.

Cydia taxa with one recorded food plant and those with more than one are analogous to the specialist and generalist diet-breadth classes of Niemelä et al. (1981) and Wasserman and Mitter (1978). For "specialist" *Cydia* taxa, mean forewing length is 6.4 mm (37n), and for "generalist" taxa, 6.6 mm (42n). The difference, 0.2 mm, is statistically significant nonparametrically ($P < 0.001$, Mann-Whitney test), but not parametrically (Student *t*-test, $P > 0.40$). The first result matches findings of the above authors. When the high food-quality class is examined separately, however, results are reversed: mean forewing lengths are 6.9 mm (17n) for specialists and 6.6 mm (16n) for generalists. This reversal suggests that forewing length correlates more strongly with seed size than with diet breadth.

Cladistic Test of Results

Statistical analyses like the foregoing must be interpreted cautiously. Related taxa may simply inherit a given trait from a common ancestor rather than evolve it independently. If this happens, the assumption of statistical independence of observations is violated (Felsenstein 1985, Ridley 1983). It therefore seems necessary to test the assumption of independence, which is equivalent to the assumption that *Cydia* body-

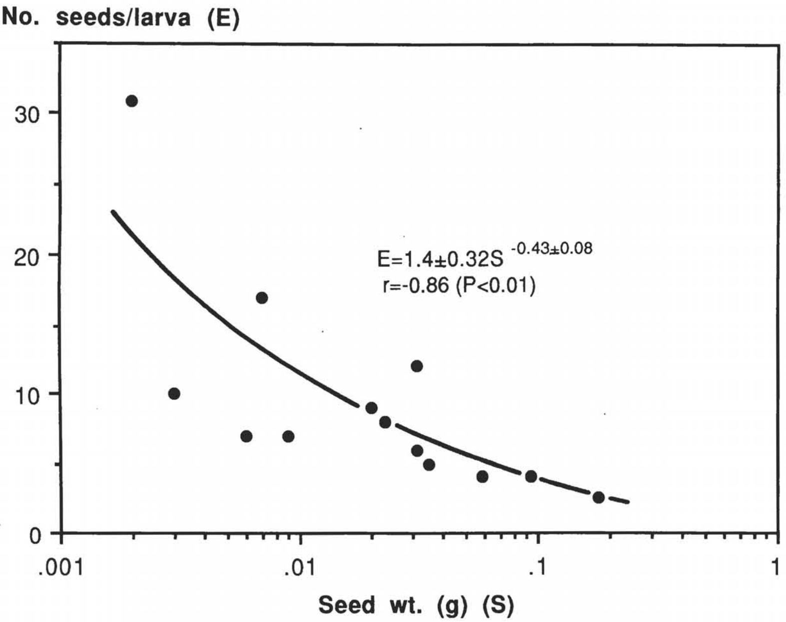

FIG. 3. Number of seeds eaten or destroyed per larva as related to food-plant seed size in the high food-quality class. Each point represents a *Cydia* taxon or population enumerated in Table 2 and the Appendix. The symbol ± denotes standard error.

size diversity represents many rather than a few evolutionary events. Below, I follow to the extent possible the test methodology advocated by Coddington (1988). I map food-quality classes indicated by the analysis on the *Cydia* phylogeny of Danilevsky and Kuznetsov (1968), then check for congruence. Congruence implies inheritance; lack of congruence, independence.

Danilevsky and Kuznetsov recognize three *Cydia* subgenera: *Cydia*, *Kenneliola*, and *Endopisa*. Their phylogeny to subgenera has the first two as sister taxa, with *Endopisa* in an outgroup position. Within each subgenus, Danilevsky and Kuznetsov further define a number of sections or species-groups, each of which represents a likely monophyletic lineage. The phylogeny to species is not resolved, but in three sections, four pairs of sister species are evident among study taxa.

Assignments to subgenus are made for 66 species in the study, 50 by Danilevsky and Kuznetsov, 16 by me. Food-quality class of each of these mapped on the phylogeny to subgenera produces the distribution in Table 3. All food-quality classes and associated body sizes occur among all subgenera, although most *Endopisa* species (12/15 = 0.80) are in the high class, and most *Kenneliola* species (13/14 = 0.93) are not. *Cydia* outgroup genera such as *Grapholita* also contain species

TABLE 3. Distribution of 66 *Cydia* species by food-quality class and subgenus.

Subgenus	Food-quality class		
	Low	Medium	High
Cydia	7	13	17
Kenneliola	3	10	1
Endopisa	1	2	12

assignable to high, medium, and low food-quality classes (Danilevsky & Kuznetsov 1968). Therefore, within *Cydia* outgroups as well as subgenera there is evidence that food-quality classes and associated body sizes evolved independently of subgeneric lineage.

Within subgenera, at the section or species-group level, the positions of 50 study species are available, almost entirely assigned by Danilevsky and Kuznetsov (1968). Two or more food-quality classes and associated body sizes occur in 7 of 15 sections overall, and in all 5 sections containing three or more species (Table 4). The detailed distribution of food-quality classes among sections shows 9 within-section shifts in food-quality class and associated body size out of 18 possible ones (Table 4). Thus evolutionary shifts in body size are likely to have occurred within sections.

TABLE 4. Distribution of 50 *Cydia* species by food-quality class and section, and inferred numbers of evolutionary shifts in food-quality class within sections.

Section	No. species in class			Minimal no. shifts	
	High	Medium	Low	Possible	Evident
Subgenus *Cydia*					
pactolanae	2	6	1	2	2
strobilellae	2	0	0	1	0
pomonellae	2	0	0	1	0
illutanae	1	1	2	2	2
servillanae	0	1	1	2	1
duplicanae	0	2	1	2	1
cosmophoranae	0	3	1	2	1
Subgenus *Kenneliola*					
splendanae	0	7	3	1	1
maackianae	1	0	0	0	0
trasias	1	0	0	0	0
exquisitanae	0	2	0	1	0
Subgenus *Endopisa*					
suceedanae	3	0	0	2	0
nigricanae	4	1	0	2	1
adenocarpae	1	0	0	0	0
semicinctanae	0	1	0	0	0
			Total	18	9

TABLE 5. Food-quality classes and associated body sizes of four *Cydia* sister-species pairs. Data are from the Appendix. (Ditto is abbreviated do.)

Pair no.	*Cydia* species	Food-quality class		Forewing length (mm)
1	*indivisa*	Medium		6.5
	cosmophorana	Low		4.9
2	*rana*	High		6.2
	laricana	do.		7.1
3	*strobilella*	do.	(Eurasia)	5.7
	do.	do.	(Midland No. America)	4.0
	ethelinda	do.		7.6
4	*pomonella*	do.		8.0
	pyrivora	do.		8.9

The four pairs of sister species mentioned earlier represent two sections (*strobilellae* and *pomonellae*) each containing only two species, and one section (*cosmophoranae*) containing four species that can be resolved into one Palearctic sister pair and one Nearctic sister pair. The four pairs, their food-quality classes, and forewing lengths are shown in Table 5. The members of the first pair belong to different food-quality classes, and differ in size by 25% ([6.5 − 4.9]/6.5 = 0.25). The remaining pairs all belong to the high class, but members of the third differ in size similarly to or more than members of the first, as expected from their differing food-plant seed sizes ([7.6 − 5.7]/7.6 = 0.25; [7.6 − 4.0]/7.6 = 0.47). Members of the second and fourth pairs differ least, from 10 to 13%; inherited similarity in their body sizes cannot be ruled out.

In sum, independence and number of degrees of freedom are no doubt overestimated, but only mildly. *Cydia* body-size evolution seems sufficiently independent of subgeneric, section, and species phylogeny to uphold rather than refute results of the statistical analysis.

DISCUSSION

Even though I consider only one independent variable, it relates well to body size (Table 1, Fig. 1). The correlation of body size and food-plant seed size among seed predators of all food-quality classes ultimately results from finite size and finite numbers of seeds. Seeds occur within seed-bearing parts of lesser food quality (Mattson 1980, Skerman 1977). The smaller the seed, the more feeding disruptions larvae experience as they finish one seed and seek another or eat seed-bearing tissue or both; the more feeding disruptions, the smaller the body size.

Potential number of seeds per fruit is reduced by frequent failure of some seeds to develop (Stephenson 1981, Tripp & Hedlin 1956) and by other seed predators. Intraspecific predation occurs in the high class (Bovey 1966, Coyne 1968, Hedlin 1967, Tripp & Hedlin 1956, Kraft 1968, Putman 1963) as well as in the medium and low classes (Bovey 1966). Intraspecific predation promotes net survival when the seed supply in one fruit or the nourishment in one large seed is not sufficient for all inhabitants.

I assume that food-plant seed size precedes *Cydia* body size, not the reverse. Evidence for this assumption is scant, except that many factors besides seed predation determine seed size (Harper et al. 1970).

In the medium and low food-quality classes, larvae probably eat more grams of food to support a given body size than in the high class. Smaller body size may lessen food needs of a larva. At least two members of the medium class, *C. zebeana* and *C. milleniana*, have evolved lengthened life cycles enabling their larvae to feed a second season (Kuznetsov 1987, Postner 1978). Forewing lengths of these species (7.0–7.3 mm) are greater than the class mean (6.4 mm) (Appendix, Table 1).

Among seed predators in the medium and low classes, food-plant seeds are mostly large and borne singly. Correlation between food-plant seed size and forewing length in seed predators of these classes (Fig. 2: line B) may exist because most such larvae use but one seed (Bovey 1966) through a range of seed sizes.

In conclusion, I interpret the correlation between *Cydia* body size and diet quality to reflect mechanisms whereby (a) larvae evolve body sizes for which they are able to obtain sufficient nourishment, and (b) body-size diversity arises as lineages colonize new larval food plants and plant parts of differing diet quality.

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Appendix. Enumeration of *Cydia* study taxa and populations. Asterisks denote food plants to which seed weights refer; brackets ([ ]), probable food plants; braces ({ }), seed weights estimated from relatives of similar seed dimensions; dashes, no data. Danilevsky and Kuznetsov (1968) is abbreviated D & K (1968); ditto, do.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
		High food-quality class (diet ca. 25% crude protein)			
adenocarpi (Ragonot) *Endopisa* *adenocarpi*	S Europe	*Adenocarpus* spp., *Cytisus scoparius* (L.)*	Seed (D & K 1968)	0.00789 (Gill & Pogge 1974)	6.1 (D & K 1968)
anaranjada (Miller) *Cydia* —	SE North America	*Pinus elliottii* Engelm.*	do. (Hedlin et al. 1981)	0.0314 (Krugman & Jenkinson 1974)	7.1 (Miller 1959)
blackmoreana (Walsingham) *Endopisa* *nigricanae*	N Africa	*Retama monosperma* (L.)	do. (D & K 1968)	—	6.9 (D & K 1968)
bracteatana (Fernald) *Cydia* —	W North America	*Abies bracteata* D. Don, *A. concolor* (Gord. & Gland.),* *A. magnifica* A. Murr.*	do. (Hedlin et al. 1981)	0.0518 (Franklin 1974)	5.3 (Heinrich 1926)
colorana (Kearfott) — —	SW North America	*Pinus edulis* Engelm.*	do. (do.)	0.239 (Krugman & Jenkinson 1974)	10.5 (do.)
conicolana (Heylaerts) *Cydia* *illutanae*	Britain	*P. sylvestris* L.,* *P. nigra* Arn.*	do. (Bradley et al. 1979)	0.00898 (do.)	5.0 (Bradley et al. 1979)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
dandana (Kearfott) (*nigricana* ssp.) *Endopisa* *nigricanae*	North America	*Lathyrus japonicus* Willd., *L. palustris* L., *Vicia angustifolia* L.*	Seed (Bovey 1966)	0.0135 (Barclay & Earle 1974, Hughes et al. 1962, Jones & Earle 1966)	6.0 (Heinrich 1926)
ethelinda (Meyrick) *Cydia* *strobilellae*	India	*Picea smithiana* (Wallich),* *Pinus wallichiana* A. B. Jacks*	do. (Cheema & Syed 1973)	0.0210 (Krugman & Jenkinson 1974, Safford 1974)	7.6 (Clarke 1958)
gilviciliana (Staudinger) *Endopisa* *nigricanae*	S Europe	*Pisum s. sativum* L.,* *P. s. elatius* (Bieb.)*	do. (Bovey 1966)	0.145 (Hughes et al. 1962, Makasheva 1973, Purseglove 1968, Wheeler & Hill 1957)	6.4 (Bovey 1966)
ingens (Heinrich) *Cydia* —	SE North America	*Pinus palustris* Mill.*	do. (Coyne 1968)	0.0926 (Krugman & Jenkinson 1974)	8.5 (Heinrich 1926)
injectiva (Heinrich) *Cydia* *pactolanae*	W North America	*P. jeffreyi* Grev. & Balf.*	do. (Hedlin et al. 1981)	0.123 (do.)	8.2 (do.)
latefemoris (Walsingham) *Endopisa* —	Hawaii	*Sophora chrysophylla* (Salisb.)	do. (Zimmerman 1978)	{0.0259} (Little & Skolmen 1989)	6.5 (Zimmerman 1978)
latisigna Miller *Cydia* —	Mexico	*Pinus engelmannii* Carr.,* *P. michoacana cornuta* Martinez*	do. (Cibrián-Tovar et al. 1986)	0.0305 (Patiño Valera & Villagómez Aguilar 1976)	7.8 (Miller 1986)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
maackiana (Danilevsky) *Kenneliola* *maackianae*	E Asia	*Maackia amurensis* (Rupr. & Maxim.)	Seed (D & K 1968)	{0.0204} (Zaborovsky 1962)	6.9 (D & K 1986)
malesana (Meyrick) *Endopisa* —	India	*Cassia auriculata* L., *C. corymbosa* Lam.*	do. (Beeson 1941)	0.0253 (Jones & Earle 1966, Sen Gupta 1936)	7.3 (Clarke 1958)
medicaginis (Kuznetsov) *Endopisa* *succedanae*	Eurasia	*Medicago sativa caerulea* (Less.),* *M.* spp.	do. (Bovey 1966)	{0.00200} (Lesins & Gillies 1972)	4.6 (Bovey 1966)
membrosa (Heinrich) — —	SW North America	*Prosopis juliflora velutina* (Woot.), *P. glandulosa* (Torr.)*	do. (Heinrich 1926)	0.0406 (Earle & Jones 1962, Harden & Zolfaghari 1988, Walton 1923)	6.4 (Heinrich 1926)
microgrammana (Guenée) *Endopisa* *microgrammanae*	SE Europe	*Ononis spinosa* L.	do. (D & K 1968)	{0.00247} (Brouwer & Stählin 1975)	5.0 (D & K 1968)
miscitata (Heinrich) *Cydia* —	SW North America	*Pinus ponderosa* Doug.*	do. (Hedlin et al. 1981)	0.0378 (Krugman & Jenkinson 1974)	6.5 (Heinrich 1926)
montezuma Miller *Cydia* —	Mexico	*P. montezumae* Lamb.,* *P. rudis* Endl.*	do. (Cibrián-Tovar et al. 1986)	0.0198 (Patiño Valera & Villagómez Aguilar 1976, Rafn ca. 1912)	8.8 (Miller 1986)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
nigra (Miller) *Cydia* —	Mexico	*P. ayacahuite veitchii* Shaw*	Seed (Cibrián-Tovar et al. 1986)	0.250 (Patiño Valera & Villagómez Aguilar 1976)	8.0 (Miller 1966)
n. nigricana (Fabr.) *Endopisa* *nigricanae*	Europe	*Lathyrus pratensis* L., *L. odoratus* L.,* *Vicia cracca* L.,* *V. sativa* L.*	do. (Bovey 1966)	0.0481 (Earle & Jones 1962, Hughes et al. 1962, Jones & Earle 1966, Stefferud 1961)	6.4 (Bovey 1966)
oxytropidis (Martini) *Endopisa* *nigricanae*	S Europe	*Oxytropis pilosa* (L.)	do. (D & K 1968)	—	6.5 (D & K 1968)
phyllisae Miller *Cydia* —	Mexico	*Picea chihuahuana* Martinez	do. (Cibrián-Tovar et al. 1986)	{0.00428} (Martinez 1963)	5.5 (Miller 1986)
piperana (Kearfott) *Cydia* —	SW North America	*Pinus ponderosa*,* *P. jeffreyi**	do. (Koerber 1967)	0.0589 (Krugman & Jenkinson 1974)	8.2 (Heinrich 1926)
platydryas (Meyrick) *Endopisa* —	Africa	"*Acacia*"	do. (Clarke 1958)	—	6.6 (Clarke 1958, Diakonoff 1969)
pomonella (L.) *Cydia* *pomonellae*	E North America	*Malus sylvestris* (L.), *M. pumila* Mill.*	do. (Chapman & Lienk 1971)	0.0227 (Crossley 1974)	8.0 (Chapman & Lienk 1971)
pyrivora (Danilevsky) *Cydia* *pomonellae*	S Europe	*Pyrus communis* L.*	do. (Bovey 1966)	0.0315 (Gill & Pogge 1974)	8.9 (D & K 1968)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
strobilella (L.) *Cydia* *strobilellae*	Eurasia	*Picea abies* (L.),* *P. jezoensis* (S. & C.),* *P. koyamai* Shir.,* *P.* spp.	Seed (Postner 1978)	0.00466 (Safford 1974)	5.7 (D & K 1968)
do.	Midland North America	*P. glauca* (Moench)*	do. (Tripp 1954)	0.00201 (do.)	4.0 (Miller 1987)
succedana (D. & S.) *Endopisa* *succedanae*	Britain	*Ulex europaeus* L.,* "*Genista*", "*Lotus*", *Cytisus scoparius* (L.)*	do. (Bradley et al. 1979)	0.00728 (Gill & Pogge 1974, Rudolf 1974)	6.4 (Bradley et al. 1979)
tonosticha (Meyrick) — —	South America	*Cassia fistula* L.*	do. (Becker 1971)	0.169 (Barclay & Earle 1974, Guppy 1912, Sen Gupta 1936, Swingle 1939)	6.5 (Becker 1971, Costa Lima 1952)
toreuta (Grote) *Cydia* —	Midland North America	*Pinus resinosa* Ait.,* *P. banksiana* Lamb.	do. (Miller 1987)	0.00609 (Krugman & Jenkinson 1974)	6.0 (Miller 1987)
vallesiaca (Sauter) *Endopisa* *succedanae*	S Europe	*Ononis natrix* L.	do. (Kuznetsov 1987)	{0.00247} (Heywood & Ball 1968)	5.7 (Kuznetsov 1987)
		Medium food-quality class (diet ca. 12% crude protein)			
acerivora (Danilevsky) *Endopisa* *semicinctanae*	Asia	*Acer ginnala* Maxim.,* *A.* spp.	Seed (D & K 1968)	0.0267 (Olson & Gabriel 1974)	5.3 (D & K 1968)
amplana (Hübner) *Kenneliola* *splendanae*	Europe	*Corylus avellana* L.,* *C.* spp.	do. (Postner 1978)	0.848 (Brinkman 1974a)	8.2 (do.)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
amurensis (Danilevsky) *Kenneliola* *splendanae*	Japan	*Quercus mongolica* Fisch. ex Turcz.*	Seed (D & K 1968)	3.16 (Swingle 1939, Zaborovsky 1962)	6.6 (D & K 1968)
candana (Forbes) — —	E North America	"*Acer*"	do. (MacKay 1959)	—	6.4 (Heinrich 1926)
cognatana (Barret) *Cydia* *duplicanae*	Britain	*Pinus sylvestris**	Cortex (Bradley et al. 1979)	0.00650 (Krugman & Jenkinson 1974)	6.2 (Bradley et al. 1979)
coniferana (Saxesen) *Cydia* *illutanae*	Eurasia	*P.* spp. [*sylvestris,** *nigra**], *Abies alba* Mill.,* *Picea abies**	do. (Postner 1978)	0.00859 (Franklin 1974, Krugman & Jenkinson 1974, Safford 1974)	5.7 (D & K 1968)
cornucopiae (Tengström) *Kenneliola* *splendanae*	S Asia	*Populus tremula* L.,* *Betula* spp.	do. (Kuznetsov 1986)	0.000124 (Schreiner 1974)	7.7 (D & K 1968)
cryptomeriae (Issiki) — —	Japan	*Cryptomeria japonica* (L. F.)*	Seed (Kawabe 1982)	0.00183 (Walters 1974)	6.0 (Kawabe 1982)
cupressana (Kearfott) *Cydia* *illutanae*	W North America	*Cupressus macrocarpa* Hartw.*	Cortex (Frankie & Koehler 1971)	0.00596 (Johnson 1974)	6.2 (Heinrich 1926)
danilevskii (Kuznetsov) *Kenneliola* *splendanae*	Japan	*Quercus mongolica**	Seed (Kuznetsov 1986)	3.16 (Swingle 1939, Zaborovsky 1962)	7.0 (D & K 1968)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
duplicana (Zetterstedt) *Cydia* *duplicanae*	Europe	*Abies alba,* Picea abies**	Cortex (Postner 1978)	0.0122 (Franklin 1974, Safford 1974)	7.3 (D & K 1968)
glandicolana (Danilevsky) *Kenneliola* *splendanae*	Japan	*Quercus mongolica**	Seed (D & K 1968)	3.16 (Swingle 1939, Zaborovsky 1962)	8.0 (do.)
indivisa (Danilevsky) *Cydia* *cosmophoranae*	Eurasia	*Picea* spp. [*abies,* asperata* Masters,* *jezoensis**]	Cortex (D & K 1968)	0.00527 (Safford 1974)	6.5 (do.)
inquinitana (Hübner) *Kenneliola* *splendanae*	Europe	*Acer* spp. [*campestre* L.,* *pseudoplatanus* L.*]	do. (Postner 1978)	0.0987 (Olson & Gabriel 1974)	6.5 (Hannemann 1961)
laricana (Busck) *Cydia* *cosmophoranae*	W North America	*Larix occidentalis* Nutt.,* *Pseudotsuga menziesii* (Mirb.)*	do. (Furniss & Carolin 1977)	0.00821 (Owston & Stein 1974, Rudolf 1974)	7.1 (Heinrich 1926)
laricicolana (Kuznetsov) *Cydia* *pactolanae*	Central Asia	*Larix gmelini* (Rupr.)*	do. (D & K 1968)	0.00378 (Rudolf 1974)	4.8 (D & K 1968)
latiferreana (Walsingham) — —	Midland North America	*Quercus alba* L.,* *Q. macrocarpa* Michx.,* *Q. rubra* L.,* *Q. velutina* Lam.*	Seed (Peacock et al. 1988)	4.45 (Olson 1974)	7.8 (Miller 1987)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
leguminana (Zeller) *Kenneliola* *exquisitanae*	Britain	"*Ulmus*" [*glabra* Huds.*]	Cortex (Bradley et al. 1979)	0.0113 (Brinkman 1974b)	6.2 (Bradley et al. 1979)
do.	Central Europe	*Acer*, *Fagus* spp. [*A. campestre*,* *A. platanoides* L.,* *A. pseudoplatanus*,* *F. sylvatica* L.*]	do. (D & K 1968)	0.131 (Olson & Gabriel 1974, Rudolf & Leak 1974)	6.0 (D & K 1968)
leucobasis (Busck) *Cydia* *pactolanae*	W North America	*Larix occidentalis*,* *Picea engelmannii* Parry*	do. (Furniss & Carolin 1977)	0.00333 (Rudolf 1974, Safford 1974)	6.0 (Heinrich 1926)
leucogrammana (Hofmann) *Endopisa* *nigricanae*	E Asia	*Peganum harmala* L.*	Flowers (D & K 1968)	0.00282 (Barclay & Earle 1974)	5.4 (D & K 1968)
leucostoma (Meyrick) — —	India	*Camellia sinensis* (L.)*	Foliage (Wyniger 1962)	1.97 (Purseglove 1968)	6.0 (Clarke 1958)
milleniana (Adamzewski) *Cydia* *pactolanae*	Eurasia	*Larix decidua* Mill.,* *L. gmelini*,* L. *siberica* Ledeb.*	Cortex (Kuznetsov 1987)	0.00519 (Rudolf 1974)	7.3 (Kuznetsov 1987)
p. pactolana (Zeller) *Cydia* *pactolanae*	Europe	*Picea abies**	do. (Postner 1978)	0.00594 (Safford 1974)	6.0 (D & K 1968)

Appendix. Continued.

Species / Subgenus / Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
populana (Busck) *Kenneliola* *exquisitanae*	Midland North America	*Populus tremuloides* Michx.,* *P. trichocarpa* Torr. & Gray*	Cortex (Furniss & Carolin 1977)	0.000165 (Schreiner 1974)	6.2 (Miller 1987)
pseudotsugae (Evans) *Cydia* *pactolanae*	W North America	*Pseudotsuga menziesii**	do. (Evans 1969)	0.0110 (Owston & Stein 1974)	6.0 (Evans 1969)
rana (Forbes) *Cydia* *cosmophoranae*	E North America	*Picea engelmannii,** *P. glauca**	do. (Heinrich 1926, W. E. Miller unpubl.)	0.00251 (Safford 1974)	6.2 (Heinrich 1926)
servillana (Duponchel) *Cydia* *servillanae*	Britain	*Salix caprea* L., *S. cinerea* L.	do. (Bradley et al. 1979)	—	6.0 (Bradley et al. 1979)
splendana (Hübner) *Kenneliola* *splendanae*	do.	*Quercus* spp. [*petrea* (Mattushka),* *robur* L.*]	Seed (do.)	3.02 (Olson 1974)	8.2 (do.)
staphiditis (Meyrick) — —	India	*Bauhinia purpurea* L.*	Cortex (Beeson 1941)	0.239 (Earle & Jones 1962, Sen Gupta 1936, Swingle 1939)	5.3 (Clarke 1958)
stirpicola (Meyrick) — —	do.	*Butea frondosa* Koenig*	Multiple (do.)	0.987 (Swingle 1939)	6.2 (do.)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
trasias (Meyrick) *Kenneliola* *trasias*	E Asia	*Maackia amurensis* Rupr. & Maxim.,* *Sophora japonica* L.*	Multiple (Komai & Lantoh 1984)	0.0679 (Barclay & Earle 1974, Earle & Jones 1962, Rafn ca. 1912, Swingle 1939, Zaborovsky 1962)	5.7 (Komai & Lantoh 1984)
yasudai (Oku) (*pactolana* ssp.) *Cydia* *pactolanae*	Japan	*Abies sachalinensis* Fr. Schm.*	Cortex (Kawabe 1982, Oku 1968)	0.0103 (Franklin 1974)	5.7 (Oku 1968)
zebeana (Saxesen) *Cydia* *pactolanae*	Europe	*Larix decidua*,* *L. siberica**	do. (Postner 1978)	0.00581 (Rudolf 1974)	7.0 (Hannemann 1961)
		Low food-quality class (diet ca. 6% crude protein)			
araucariae (Pastrana) — —	South America	*Araucaria angustifolia* (Bert.)*	do. (Schönherr 1987)	9.07 (Walters 1974)	8.5 (Schönherr 1987)
caryana (Fitch) — —	Midland North America	*Carya ovata* (Mill.),* *C. illinoensis* (Wangenh.),* *Juglans nigra* L.*	Seed husk (Moznette et al. 1940)	3.85 (Bonner & Maisenhelder 1974, Brinkman 1974c)	5.8 (Miller 1987)
commensalana (Danilevsky) *Kenneliola* *splendanae*	Asia	*Rosa* spp.	*Diplolepis* galls (D & K 1968)	—	6.0 (D & K 1968)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
corollana (Hübner) *Cydia* *illutanae*	Europe	*Populus tremula**	*Saperda* galls (Hannemann 1961)	0.000124 (Schreiner 1974)	5.5 (D & K 1968)
cosmophorana (Treitschke) *Cydia* *cosmophoranae*	W Europe	*Pinus sylvestris**	*Retinia* tunnels (Postner 1978)	0.00605 (Krugman & Jenkinson 1974)	4.9 (do.)
erotella (Heinrich) *Cydia* —	E North America	*P. taeda* L.*	do. (Heinrich 1926, W. E. Miller unpubl.)	0.0249 (do.)	4.4 (Heinrich 1926)
fagiglandana (Zeller) *Kenneliola* *splendanae*	Britain	*Fagus sylvatica**	Seed (Bradley et al. 1979)	0.216 (Rudolf & Leak 1974)	7.3 (Bradley et al. 1979)
gallaesaliciana (Riley) *Cydia* *servillanae*	E North America	"*Salix*"	Dipterous galls (Heinrich 1926)	—	5.5 (Heinrich 1926)
illutana (Herrich-Schäffer) *Cydia* *illutanae*	Eurasia	*Larix gmelini*,* *Picea abies*,* *Abies alba**	Cone scales (Postner 1978)	0.018 (Rudolf 1974)	5.7 (D & K 1968)
inopiosa (Heinrich) *Cydia* *pactolanae*	North America	*Pinus contorta* Doug.,* *P. resinosa**	Bark (Brown & Miller 1983, R. G. Dearborn pers. comm.)	0.00621 (Krugman & Jenkinson 1974)	4.5 (Miller 1987)

Appendix. Continued.

Species Subgenus Section	Sample area	Food plant(s)	Main part eaten (source)	Seed wt. (g) (source)	Forewing length (mm) (source)
interscindana (Möschler) *Cydia* *duplicanae*	S Europe	*Juniperus oxycedrus* L.	Sapwood (D & K 1968)	{0.0124} (Debazac 1964)	5.2 (D & K 1968)
kurokoi (Amsel) *Kenneliola* *splendanae*	E Asia	*Castanea mollissima* Blume,* *C. sequinii* Dode,* *C. crenata* Sieb. & Zucc.*	Seed (Komai & Ishikawa 1987)	13.1 (Olson 1974, Sander 1974)	8.0 (Komai & Ishikawa 1987)
palmetum (Heinrich) — —	SE North America	*Coccothrinax argentata* Jacq.	do. (Heinrich 1929)	{0.307} (Long & Lakela 1971)	6.0 (Heinrich 1928)
rufipennis (Butler) *Endopisa* —	Hawaii	*Acacia koa* Gray*	Multiple (Stein 1983)	0.0926 (Whitesell 1974)	4.4 (Zimmerman 1978)

LITERATURE CITED

ANDERSON, R. J. & W. L. KULP. 1921. An investigation of the seed of the silver maple (*Acer saccharinum*). New York Agric. Exper. Sta. Geneva Tech. Bull. 81, 20 pp.

ANDERSSON, E. 1965. Cone and seed studies in Norway spruce (*Picea abies* [L.] Karst.). Stud. Forest. Suecica 23, 214 pp.

BARCLAY, A. S. & F. R. EARLE. 1974. Chemical analysis of seeds III. Oil and protein content of 1253 species. Econ. Bot. 28:178–236.

BECKER, V. O. 1971. Microlepidópteros que vivem nas plantas cultivadas no Brasil. II. O nome correto da lagarta das favas da *Cassia fistula* L. (Lepidoptera, Tortricidae). Bol. Univ. Fed. Paraná (Zool.) 4(9):45–56.

BEESON, C. F. C. 1941. The ecology and control of the forest insects of India and the neighboring countries. Dehra Dun, India. 1007 pp.

BETTS, M. M. 1958. Notes on the life-history of *Enarmonia conicolana* (Heyl.) (Lep., Eucosmidae). Entomol. Monthl. Mag. 94:134–137.

BONNER, F. T. & L.C. MAISENHELDER. 1974. *Carya* Nutt. Hickory, pp. 269–272. *In* Schopmeyer (1974).

BONNER, J. T. 1965. Size and cycle: An essay on the structure of biology. Princeton Univ. Press, Princeton, New Jersey. 219 pp.

BOVEY, P. 1966. Super-famille des Tortricoidea, pp. 456–893. *In* Balachowsky, A. S. (ed.), Entomologie appliquée a l'agriculture. Vol. 2(1), Lepidoptères. Masson & Cie, Paris. 1057 pp.

BRADLEY, J. D., W. G. TREMEWAN & A. SMITH. 1979. British tortricoid moths. Tortricidae: Olethreutinae. Ray Society, London. 336 pp.

BRINKMAN, K. A. 1974a. *Corylus* L. Hazel, filbert, pp. 343–345. *In* Schopmeyer (1974).

——— 1974b. *Ulmus* L. Elm, pp. 829–834. *In* Schopmeyer (1974).

——— 1974c. *Juglans* L. Walnut, pp. 454–459. *In* Schopmeyer (1974).

BROUWER, W. & A. STÄHLIN. 1975. Handbuch der Samenkunde. ed. 2. DLG Verlag, Frankfurt (Main). 655 pp.

BROWN, R. L. 1979. The valid generic and tribal names for the codling moth, *Cydia pomonella* (Olethreutinae: Tortricidae). Ann. Entomol. Soc. Amer. 72:565–567.

BROWN, R. L. & W. E. MILLER. 1983. Valid names of the spruce seed moth and a related *Cydia* species (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Amer. 76:110–111.

CALDER, W. A. 1984. Size, function, and life history. Harvard Univ. Press, Cambridge, Massachusetts. 431 pp.

CARDEMIL, L. & A. REINERO. 1982. Changes of *Araucaria araucana* seed reserves during germination and early seedling growth. Can. J. Bot. 60:1629–1638.

CHAPMAN, P. J. & S. E. LIENK. 1971. Tortricid fauna of apple in New York (Lepidoptera: Tortricidae). New York Agric. Exper. Sta. Spec. Publ. 122 pp.

CHEEMA, M. A. & R. A. SYED. 1973. Seed- and cone-insects, pp. 50–60. *In* Ghani, M. A. & M. A. Cheema (eds.), Biology, ecology and behaviour of principal natural enemies of major insect pests of forest trees in Pakistan. Commonwealth Inst. of Biol. Control Misc. Publ. 4, 100 pp.

CIBRIÁN-TOVAR, D., B. H. EBEL, H. O. YATES & J. T. MENDEZ-MONTIEL. 1986. Insectos de conos y semillas de las coniferas de Mexico. U.S. Dept. Agr. Forest Service Gen. Tech. Rept. SE-40, 110 pp. (Spanish and English).

CLARKE, J. F. G. 1958. Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Vol. III. Tortricidae, Olethreutidae, Noctuidae. British Museum, London. 600 pp.

CODDINGTON, J. A. 1988. Cladistic tests of adaptational hypotheses. Cladistics 4:3–22.

COSTA LIMA, A. DA. 1952. Sôbre dois microlepidopteros (Tortricoidea, Grapholitidae). Mem. Inst. Oswaldo Cruz 50:249–257.

COYNE, J. F. 1968. *Laspeyresia ingens*, a seedworm infesting cones of longleaf pine. Ann. Entomol. Soc. Amer. 61:1116–1122.

CRANDALL, C. S. 1917. Seed production in apples. Ill. Agric. Exp. Sta. Bull. 203, [183]–213 pp.

CRISAN, E. V. & A. SANDS. 1978. Nutritional value, pp. 137–168. *In* Chang, S. T. & W. A. Hayes (eds.), The biology and cultivation of edible mushrooms. Academic Press, New York. 819 pp.

CROSSLEY, J. A. 1974. *Malus* Mill. Apple, pp. 531–534. *In* Schopmeyer (1974).

DANILEVSKY, A. C. & V. I. KUZNETSOV. 1968. [Leafroller family Tortricidae, fruit-moth tribe Laspeyresiini.] Fauna USSR. Lepidopterous insects. Vol. 5, pt. 1. Leningrad. 635 pp. (Russian).

DEBAZAC, E. F. 1964. Manuel des conifères. Nancy, France. 172 pp.

DENNO, D. N. & R. F. HARWOOD. 1973. Intraspecific larval competition by the codling moth, *Laspeyresia pomonella*. Environ. Entomol. 2:783–789.

DIAKONOFF, A. 1969. Tortricidae from the Seychelles and Aldabra (Lepidoptera). Tijd. Entomol. 112:81–100.

DICKMANN, D. I. & T. T. KOZLOWSKI. 1969. Seasonal changes in the macro- and micronutrient composition of ovulate strobili and seeds of *Pinus resinosa*. Can. J. Bot. 47:1547–1554.

EARLE, F. R. & Q. JONES. 1962. Analyses of seed samples from 113 plant families. Econ. Bot. 16:221–250.

EVANS, D. 1969. *Laspeyresia pseudotsugae* n. sp. (Lepidoptera: Olethreutidae), a bark miner in Douglas-fir. Can. Entomol. 101:955–963.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. Amer. Nat. 125:1–15.

FISHER, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford. 272 pp.

FRANKIE, G. W. & C. S. KOEHLER. 1971. Studies on the biology and seasonal history of the cypress bark moth, *Laspeyresia cupressana* (Lepidoptera: Olethreutidae). Can. Entomol. 103:947–961.

FRANKLIN, J. F. 1974. *Abies* Mill. Fir, pp. 168–183. *In* Schopmeyer (1974).

FURNISS, R. L. & V. M. CAROLIN. 1977. Western forest insects. U.S. Dept. Agric. Misc. Publ. 1339, 654 pp.

GILL, J. D. & F. L. POGGE. 1974. *Pyrus* L. Pear, pp. 689–691. *In* Schopmeyer (1974).

GUPPY, H. B. 1912. Studies in seeds and fruits. Williams & Norgate, London. 528 pp.

GYÖRFI, J. 1956. Nadelholzzapfen- und Nadelholzsamenschädlinge und ihre Parasiten. Acta Agron. Acad. Sci. Hung. 6:321–373.

HANNEMANN, H. J. 1961. Kleinschmetterlinge oder Microlepidoptera I. Die Wickler (s. str.) (Tortricidae). 236 pp. Pt. 48, Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Fischer, Jena.

HARDEN, M. L. & R. ZOLFAGHARI. 1988. Nutritive composition of green and ripe pods of honey mesquite (*Prosopis glandulosa*, Fabaceae). Econ. Bot. 42:522–532.

HARPER, J. L., R. H. LOVELL & K. G. MOORE. 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1:327–356.

HAUT, I. C. 1938. Physiological studies on after-ripening and germination of fruit-tree seeds. Md. Agric. Expt. Sta. Bull. 420, 54 pp.

HEDLIN, A. F. 1967. The pine seedworm, *Laspeyresia piperana* (Lepidoptera: Olethreutidae), in cones of ponderosa pine. Can. Entomol. 105:113–122.

HEDLIN, A. F., H. O. YATES, D. CIBRIÁN TOVAR, B. H. EBEL, T. W. KOERBER & E. P. MERKEL. 1981. Cone and seed insects of North American conifers. Canadian Forestry Service, U.S. Forest Service, Secretaría de Agric. & Recursos Hidrául. Mexico. 122 pp.

HEINRICH, C. 1926. Revision of the North American moths of the subfamilies Laspeyresiinae and Olethreutinae. U.S. Natl. Mus. Bull. 132, 216 pp.

——— 1928. A new *Laspeyresia* from Florida (Lepidoptera: Olethreutidae). Proc. Entomol. Soc. Wash. 30:109.

——— 1929. A correction. Proc. Entomol. Soc. Wash. 31:19.

HERIOT, A. D. & D. B. WADDEL. 1942. Some effects of nutrition on the development of the codling moth. Sci. Agric. 23:172–175.

HEYWOOD, V. H. & P. W. BALL (Eds.). 1968. Leguminosae, pp. 80–191. *In* Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb (eds.), Flora europaea. Vol. 2. Rosaceae to Umbelliferae. Cambridge Univ. Press, Cambridge, England. 455 pp.

HUGHES, H. D., M. E. HEATH & D. S. METCALFE. 1962. Forages: The science of grassland agriculture. Iowa State Univ. Press, Ames, Iowa. 707 pp.

JOHNSON, L. C. 1974. *Cupressus* L. Cypress, pp. 363–369. *In* Schopmeyer (1974).

JONES, Q. & F. R. EARLE. 1966. Chemical analyses of seeds II: Oil and protein content of 759 species. Econ. Bot. 20:127–155.

KATSUTA, M. & T. SATOO. 1964. Cone development in *Pinus thunbergii*. Nihon Ringakkai Shi (J. Jap. Forest. Soc.) 46:166–170.

KAWABE, A. 1982. Tortricidae, pp. 62–151. *In* Inoue, H., S. Sugi, H. Kuroko, S. Moriuti & A. Kawabe (eds.), Moths of Japan. Vol. 1. Kodansha, Tokyo. 966 pp. (Japanese).

KINZER, H. G., B. J. RIDGILL & J. G. WATTS. 1972. Seed and cone insects of ponderosa pine. New Mexico Agric. Expt. Sta. Bull. 594, 36 pp.

KOERBER, T. W. 1967. Studies of the insect complex affecting seed production of ponderosa pine in California. Ph.D. Dissertation, Univ. of California, Berkeley. 86 pp. (Diss. Abs. B 29:229 [1968]).

KOMAI, F. & K. ISHIKAWA. 1987. Infestation of chestnut fruits in China with two species of the genus *Cydia* (Lepidoptera: Tortricidae). Jap. J. Appl. Entomol. Zool. 31:55–62. (Japanese and English).

KOMAI, F. & S. LANTOH. 1984. *Cydia trasias* (Meyrick) (Lepidoptera, Tortricidae) attacking *Sophora* and *Maackia* in Japan. Tyô to Ga 35:145–151. (Japanese and English).

KRAFT, K. J. 1968. Ecology of the cone moth *Laspeyresia toreuta* in *Pinus banksiana* stands. Ann. Entomol. Soc. Amer. 61:1462–1465.

KRUGMAN, S. L. & J. L. JENKINSON. 1974. *Pinus* L. Pine, pp. 598–638. *In* Schopmeyer (1974).

KRÜSSMANN, G. 1978. Handbuch der Laubgehölze. Vol. 3. Parey, Berlin. 496 pp.

KUZNETSOV, V. I. 1986. [Review of tortricids of the subtribe Laspeyresiina (Lepidoptera, Tortricidae) from the south of the Far East], pp. 9–25. *In* Ler, P. A. (ed.), [Systematics and ecology of Lepidoptera from the Far East of the USSR.] Akad. Nauk USSR. 131 pp. (Russian).

——— 1987. Family Tortricidae (Olethreutidae, Cochylidae)—Tortricid moths, pp. 279–956. *In* Medvedev, G. S. (ed.), Keys to the insects of the European part of the USSR. U.S. Dept. Agric. & Natl. Sci. Foundation, Washington, D.C. 991 pp. (Translation).

KUZNETSOV, V. I. & I. M. KERZHNER. 1984. *Laspeyresia* Hübner, [1825], proposed conservation by the suppression of *Cydia* Hübner, [1825]. Bull. Zool. Nom. 41:110–113.

LESINS, K. & C. B. GILLIES. 1972. Taxonomy and cytogenetics of *Medicago*, pp. 53–86. *In* Hanson, C. H. (ed.), Alfalfa science and technology. Agronomy 15, 812 pp.

LITTLE, E. L. & R. G. SKOLMEN. 1989. Common forest trees of Hawaii (native and introduced). U.S. Dept. Agric. Agric. Handb. 679, 321 pp.

LONG, R. W. & O. LAKELA. 1971. A flora of tropical Florida. Univ. of Miami Press, Coral Gables, Florida. 962 pp.

LYONS, L. A. 1957. Insects affecting seed production in red pine III. *Eucosma monitorana* Heinrich, *Laspeyresia toreuta* Grote (Lepidoptera: Olethreutidae), *Rubsaamenia* sp. (Diptera: Cecidomyiidae), and other insects. Can. Entomol. 89:150–164.

MACKAY, M. R. 1959. Larvae of the North American Olethreutidae (Lepidoptera). Can. Entomol. 91, Suppl. 10, 338 pp.

MCCARTHY, M. A. & R. A. MATTHEWS (eds.). 1984. Composition of foods: Nut and seed products. U.S. Dept. Agric. Agric. Handb. 8–12, 137 pp.

MCCARTHY, M. A. & F. I. MEREDITH. 1988. Nutrient data on chestnuts consumed in the United States. Econ. Bot. 42:29–36.

MARTINEZ, M. 1963. Las Pináceas Mexicanas. ed. 3. Universidad nacional autónoma de México, México. 400 pp.

MAKASHEVA, R. K. 1973. The pea. U.S. Dept. Agric. & Natl. Sci. Foundation, Washington, D.C. 267 pp. (Translation).

MATTSON, W. J. 1977. Size and abundance of forest Lepidoptera in relation to host plant resources, pp. 429–441. *In* Labeyrie, V. (ed.), Comportement des insectes et milieu trophique. Colloq. Intern. Centre Nat. Recher. Sci. 265, 493 pp. Paris.

——— 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119–161.

MATTSON, W. J. & J. M. SCRIBER. 1987. Nutritional ecology of insect folivores of woody plants: Nitrogen, water, fiber, and mineral considerations, pp. 105–146. *In* Slansky, F. & J. G. Rodriquez (eds.), Nutritional ecology of insects, mites, and spiders. Wiley, New York. 1016 pp.

MERKEL, E. P. 1967. Life history of the slash pine seedworm, *Laspeyresia anaranjada* Miller (Lepidoptera: Olethreutidae). Fla. Entomol. 50:141–149.

MILLER, W. E. 1959. A unique new North American species of pine-cone-feeding *Laspeyresia* related to *L. ingens* Heinrich (Lepidoptera: Olethreutidae). Fla. Entomol. 42:131–134.

——— 1966. A new species of moth destructive to pine cones in Mexico (Tortricoidea). J. Lepid. Soc. 20:251–253.

——— 1977. Wing measure as a size index in Lepidoptera: The family Olethreutidae. Ann. Entomol. Soc. Amer. 70:253–256.

——— 1986. New species of the genus *Cydia* that attack seeds of Mexican conifers (Lepidoptera: Tortricidae), pp. 5–7. *In* Cibrián-Tovar, D., B. H. Ebel, H. O. Yates & J. T. Mendez-Montiel (eds.), Insectos de conos y semillas de las coniferas de Mexico. U.S. Dept. Agric. Forest Service Gen. Tech. Rept. SE-40, 110 pp. (Spanish and English).

——— 1987. Guide to the olethreutine moths of Midland North America (Tortricidae). U.S. Dept. Agric. Agric. Handb. 660, 104 pp.

MOZNETTE, G. F., C. B. NICKELS, W. C. PIERCE, T. L. BISSELL, J. B. DEMAREE, J. R. COLE, H. E. PARSON & J. R. LARGE. 1940. Insects and diseases of the pecan and their control. U.S. Dept. Agric. Farm. Bull. 1829, 70 pp.

NAS (NATIONAL ACADEMY OF SCIENCES). 1979. Tropical legumes: Resources for the future. Washington, D.C. 331 pp.

NIEMELÄ, P., S. HANHIMÄKI & R. MANNILA. 1981. The relationship of adult size in noctuid moths (Lepidoptera: Noctuidae) to breadth of diet and growth form of host plants. Ann. Entomol. Fenn. 47:17–20.

OBRAZTSOV, N. S. 1959. Die Gattungen der palaearktischen Tortricidae II. Die Unterfamilie Olethreutinae, pt. 2. Tijd. Entomol. 102:175–216.

OKU, T. 1968. New or little known species of the subfamily Olethreutinae injurious to coniferous trees from Japan (Lepidoptera: Tortricidae). Kontyû 36:227–236.

OLSON, D. F. 1974. *Quercus* L. Oak, pp. 692–703. *In* Schopmeyer (1974).

OLSON, D. F. & W. J. GABRIEL. 1974. *Acer* L. Maple, pp. 187–194. *In* Schopmeyer (1974).

OPLER, P. A. 1978. Interaction of plant life history components as related to arboreal herbivory, pp. 23–31. *In* Montogomery, G. G. (ed.), The ecology of arboreal folivores. Smithsonian Institution, Washington, D.C. 574 pp.

OWSTON, P. W. & W. I. STEIN. 1974. *Pseudotsuga* Carr. Douglas-fir, pp. 674–683. *In* Schopmeyer (1974).

PATIÑO VALERA, F. & Y. VILLAGÓMEZ AGUILAR. 1976. Los analisis de semillas y su utilizacion en la propagacion de especies forestales. Inst. Nac. Invest. Forest. (Mexico). 40, 26 pp.

PEACOCK, J. W., S. L. WRIGHT & J. R. GALFORD. 1988. Attraction of acorn-infesting *Cydia latiferreana* (Lepidoptera: Tortricidae) to pheromone-baited traps. Great Lakes Entomol. 21:151–156.

PETERS, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge, England. 329 pp.

POSTNER, M. 1978. Olethreutinae. Laspeyresiini, pp. 89–109. *In* Schwenke, W. (ed.), Die Forstschädlinge europas. Vol. 3. Schmetterlinge. Parey, Hamburg. 467 pp.

PULLIAINEN, E. & L. H. J. LAJUNEN. 1984. Chemical composition of *Picea abies* and *Pinus sylvestris* seeds under subarctic conditions. Can. J. Forest. Res. 13:214–217.

PURSEGLOVE, J. W. 1968. Tropical crops. Dicotyledons 2, pp. 333–719. Wiley, New York.

PUTMAN, W. L. 1963. The codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera

Tortricidae): A review with special reference to Ontario. Proc. Entomol. Soc. Ontario 93:22–60.

RÄDER-ROITZSCH, J. E. 1957. Quantitative Stoffänderungen bei der Keimung von *Pinus silvestris* L. Forstwiss. Cbl. 76:229–245.

RAFN, J. ca. 1912. The testing of forest seeds during 25 years 1887–1912. Privately printed. 91 pp.

RIDLEY, M. 1983. The explanation of organic diversity: The comparative method and adaptations for mating. Clarendon, Oxford. 272 pp.

ROFF, D. 1981. On being the right size. Amer. Nat. 405–422.

RUDOLF, P. O. 1974. *Larix* Mill. Larch, pp. 478–485. *In* Schopmeyer (1974).

RUDOLF, P. O. & W. B. LEAK. 1974. *Fagus* L. Beech, pp. 401–405. *In* Schopmeyer (1974).

SAFFORD, L. O. 1974. *Picea* A. Dietr. Spruce, pp. 587–597. *In* Schopmeyer (1974).

SANDER, I. L. 1974. *Castanea* Mill. Chestnut, pp. 273–275. *In* Schopmeyer (1974).

SCHMIDT-HEBBEL, H. & I. PENNACCIOTTI M. (eds.). 1979. Tabla de composicion quimica de alimentos chilenos. ed. 6. Univ. Chile Facultad Ciencias Quimicas y Farmacologicas. unpaged.

SCHÖNHERR, J. 1987. Zwei neue *Cydia*-Arten aus Brasilien (Lep., Tortricidae). J. Appl. Entomol. 102:284–287.

SCHOPMEYER, C. S. (Ed.). 1974. Seeds of woody plants in the United States. U.S. Dept. Agric. Agric. Handb. 450, 883 pp.

SCHREINER, E. J. 1974. *Populus* L. Poplar, pp. 645–655. *In* Schopmeyer (1974).

SCRIBER, J. M. & F. SLANSKY. 1981. The nutritional ecology of immature insects. Ann. Rev. Entomol. 26:183–211.

SEN GUPTA, J. N. 1936. Seed weights, plant percents, etc., for forest plants in India. Indian Forest Rec. (n.s.) Silvic. 2(5):175–221.

SHEPARD, R. K. 1975. Radial distribution of corticular photosynthate in stems of bigtooth and trembling aspen. Forest Sci. 21:370–372.

SHORT, H. L. & E. A. EPPS. 1976. Nutrient quality and digestibility of seeds and fruits from southern forests. J. Wildl. Manage. 40:283–289.

SKERMAN, P. J. 1977. Tropical forage legumes. FAO Plant Prod. Prot. Ser. 2. Food and Agric. Organization of the United Nations, Rome. 609 pp.

SMARTT, J. 1980. Evolution and evolutionary problems in food legumes. Econ. Bot. 34: 219–235.

STEFFERUD, A. (Ed.). 1961. Seeds: The yearbook of agriculture, 1961. U.S. Dept. Agric., Washington, D.C. 591 pp.

STEIN, J. D. 1983. The biology, host range, parasites, and hyperparasites of koa seed insects in Hawaii: A review. Proc. Hawaiian Entomol. Soc. 24:317–326.

STENMARK, A. 1971. Studies on the pea moth (*Laspeyresia nigricana* Steph.) in central Sweden. I & II. Medd. Stat. Växtskyddsanst. 15:1–47.

STEPHENSON, A. G. 1981. Flower and fruit abortion: Proximate causes and ultimate functions. Ann. Rev. Ecol. Syst. 12:253–279.

SWINGLE, C. F. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. U.S. Dept. Agric. SCS-TP 27, 198 pp.

TRIPP, H. A. 1954. Description and habits of the spruce seedworm (*Laspeyresia youngana* (Kft.) (Lepidoptera; Olethreutidae). Can. Entomol. 86:385–402.

TRIPP, H. A. & A. F. HEDLIN. 1956. An ecological study and damage appraisal of white spruce cone insects. Forest. Chron. 32:400–410.

WAINIO, W. W. 1941. The chemical composition of forest fruits and nuts from Pennsylvania. J. Agric. Res. 62:627–635.

WALTERS, G. A. 1974. *Araucaria* (Jussieu). Araucaria, pp. 223–225. *In* Schopmeyer (1974).

WALTON, G. P. 1923. A chemical and structural study of mesquite, carob, and honey locust beans. U.S. Dept. Agric. Bull. 1194, 19 pp.

WASSERMAN, S. S. & C. MITTER. 1978. The relationship of body size to breadth of diet in some Lepidoptera. Ecol. Entomol. 3:155–160.

WHEELER, W. A. & D. D. HILL. 1957. Grassland seeds. Van Nostrand, Princeton, New Jersey. 734 pp.

WHITESELL, C. D. 1974. *Acacia* Mill. Acacia, pp. 184–186. *In* Schopmeyer (1974).

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, New Jersey. 307 pp.

WILLIAMS, S. (Ed.). 1984. Official methods of analysis of the Association of Official Analytical Chemists. 14th ed. Arlington, Virginia. 1141 pp.

WINTON, A. L. & K. B. WINTON. 1932. The structure and composition of foods. Vol. 1. Cereals, starch, oil seeds, nuts, oils, forage plants. Wiley, New York. 710 pp.

——— 1935. The structure and composition of foods. Vol. 2. Vegetables, legumes, fruits. Wiley, New York. 904 pp.

WYNIGER, R. 1962. Pests of crops in warm climates and their control. Verlag f. Recht u. Gesellschaft A.G., Basel. 555 pp.

YOON, H. S., C. CHOI & M. J. OH. 1983. Studies on the development of food resources from waste seeds II. Chemical composition of apple seed. Korean J. Food Sci. Technol. 15:128–132. (Korean and English).

ZABOROVSKY, E. P. 1962. [Fruits and seeds of trees and shrubs]. Goslesbumizdat, Moscow. 303 pp. (Russian).

ZIMMERMAN, E. C. 1978. Insects of Hawaii. Vol. 9. Microlepidoptera, pt. 1. Monotrysia, Tineoidea, Tortricoidea, Gracillarioidea, Yponomeutoidea, and Alucitoidea. Univ. Press of Hawaii, Honolulu. 881 pp.

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