REVIEW

Re-evaluation of the relationship between rodent populations and acorn masting: a review from the aspect of nutrients and defensive chemicals in acorns

Takuya Shimada · Takashi Saitoh

Abstract The responses of rodent populations to acorn masting were examined by reviewing 17 studies from the aspect of acorn nutrients and defensive chemicals. Oak species were grouped into three types based on their acorn nutritional characteristics by cluster analysis: Type 1 acorns (two North American red oaks, subgenus *Erythrobalanus*) were high in tannins and high in fat and proteins (and consequently rich in metabolizable energy); Type 2 acorns (two Japanese evergreen oaks, *Cyclobalanopsis*; three Japanese deciduous oaks, *Lepidobalanus*; one North American white oak, *Lepidobalanus*) were high in tannins but low in fat and proteins; and Type 3 acorns (one *Cyclobalanopsis* species; seven *Lepidobalanus* species) were low in tannins and had intermediate levels of fat and proteins. These three acorn groups were nutritionally, and thereby ecologically, not equivalent. Rodents, in general, responded differently to acorn masting depending on their feeding habits and the nutritional characteristics of acorns. Granivorous rodents showed positive responses to masting of Type 1 and 3 acorns, whereas rodents with feeding habits intermediate between granivory and herbivory showed positive responses to masting of Type 3 acorns. In addition, for herbivorous rodents, the responses to masting of any types of acorns have not been reported. The present findings emphasize that the relationship between ro-dents and acorn masting should not easily be general-ized, because there are large variations in characteristics of both acorns and rodents. The viewpoint presented in this review could offer more convincing interpretations to the contradictory observations, found in the studies reviewed, on the response of rodent populations to acorn masting.

Keywords Feeding habit · Nutrient composition · Population dynamics · *Quercus* · Tolerance to tannins · Total phenolics

Introduction

Acorns (seeds of the genus *Quercus*) are considered a staple resource for forest-dwelling wildlife. They are a large and potentially digestible food, thereby providing high levels of energy per seed (Vander Wall 2001). In addition, acorns are relatively rich in minerals com-pared with other vegetative parts (Vander Wall 2001). Because, in general, obtaining sufficient minerals is a difficult task for forest-dwelling herbivores (Robbins 1983), the concentrated distribution of minerals in acorns may represent a precious resource. Further-more, acorns are advantageous for consumers in being storable for extended periods compared to soft mast (seed with fresh pulp), because acorns are less subject to decay and degradation (McShea and Healy 2002). This feature is particularly important for small rodents that must survive winter without migration to warmer areas or hibernation. However, acorns are not a reli-able food source, as acorn crops fluctuate greatly from year to year (e.g., Kelly 1994). The production of such large seed crops is known as masting.

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Ecologists have studied the fluctuation of acorn crops as a key factor in the population dynamics of small rodents (e.g., Jensen 1982; McShea 2000). Several reports found positive effects of acorn masting on rodent population dynamics, including an increase in overwinter survival (Watts 1969; Hansen and Batzli 1979), reproduction extending into winter (Smyth 1966; Jensen 1982; Wolff 1996), and an increase in population density (e.g., Hansen and Batzli 1979; Elkinton et al. 1996; McShea 2000). A not negligible number of studies, however, reported cases in which no positive responses were observed (McCracken et al. 1999; Schnurr et al. 2002; Selås et al. 2002; Hoshizaki and Miguchi 2005).

In the relationship between acorn masting and rodent population dynamics, various confounding factors, including climate, alternative food availability, synchrony and geographic scale of masting, and the nutritional characteristics of acorns, may be involved. In most studies, however, the interaction between acorn masting and rodent populations has been investigated without considering these confounding factors. The rough and implicit assumption that acorns are a good resource for rodents has been widely accepted without in-depth consideration of the nutritional value of acorns as a diet, and the palatability and digestibility of acorns to consumers. Contrary to this assumption, it was shown that feeding wood mice with *Quercus crispula* acorns, which contain high levels of tannins, causes severe negative effects, including a steep reduction in body weight, endogenous nitrogen loss, and consequent high mortality (Shimada and Saitoh 2003).

Tannins, a diverse group of water-soluble phenolics with high affinity for proteins, are widely distributed in various parts of plants. They have several detrimental effects on plant consumers, including mammals: reduction in protein digestibility (Robbins et al. 1987; Chung-MacCoubrey et al. 1997), damage to the gastrointestinal mucosa and epithelia (Bernays et al. 1989), kidney or liver failure (Fowler and Richards 1965), and endogenous nitrogen loss (Blytt et al. 1988; Bernays et al. 1989). Notable differences in acorn tannin content, from 2 to nearly 10%, are known to exist among oak species (Chung-MacCoubrey et al. 1997; Shimada and Saitoh 2003). Nonetheless, Wolff (1996) and McShea (2000), for instance, investigated the response of rodent population dynamics to acorn masting without distinguishing acorns of *Q. alba* and *Q. rubra*, which differ greatly in tannin and fat contents (Wainio and Forbes 1941; Chung-MacCoubrey et al. 1997). It is not reasonable to assume that resources with such different qualities would cause the same effects on population dynamics in acorn consumers.

The aims of the present review are: (1) to examine the nutritional characteristics of acorns, such as nutrient and tannin contents, distributed in North America, Europe, and Japan; (2) to re-evaluate the responses of rodent populations to acorn masting, taking acorn nutritional characteristics into consideration; and (3) to review the variation in the response to acorn masting between granivorous and herbivorous rodents, as sensitivity to tannins may differ between rodent species with different feeding habits. By doing so, we hope to resolve the inconsistencies found in previous studies on the response of rodent populations to acorn masting.

Nutritional characteristics of acorns

The genus *Quercus* includes approximately 500 species worldwide, which are classified into three subgenera: *Lepidobalanus*, *Erythrobalanus*, and *Cyclobalanopsis* (Krüssmann 1986). *Lepidobalanus* and *Erythrobalanus* in North America are known as white oaks and red oaks, respectively. *Lepidobalanus* is also distributed in Europe and Asia. *Cyclobalanopsis* is the group known as evergreen oaks.

There is no report that acorns contain defensive chemicals other than (poly)phenols, including tannins. Thus, in this section, we summarize the contents of major nutrients and tannins in acorns of various oak species, then group the species based on their nutritional characteristics.

Literature treatment and methods

Information about the nutritional characteristics of acorns was collected both from the literature and from our own analyses. We excluded reports in which the analytical methods were not explicitly shown, and thus obtained data on 24 oak species from 11 articles (Table 1). In addition, we analyzed nutrient and tannin contents of three Japanese oak species (*Q. acutissima*, *Q. aliena*, and *Q. variabilis*) and two European oak species (*Q. petraea* and *Q. robur*). Acorns of the Japanese and European oaks were collected in Shiga, central Japan, in October 2001, and in Switzerland, in October 2003, respectively. Items measured were crude protein, crude fat, crude fibre, crude ash, total phenolics (the Folin–Denis method; Waterman and Mole 1994), and protein-precipitating ability (PPA) (the radial diffusion method; Hagerman 1987). We

entrusted the measurements of crude fat and crude fibre to the Japan Food Research Laboratories in Osaka, Japan. Details of the analyses are provided in Shimada (2001).

Because many methods are used to quantify tannins (Waterman and Mole 1994), we standardized the analysis method by primarily using total phenolics measured by the Folin–Denis method and related techniques. Total phenolics are generally accepted as an index of tannins, although this measure contains both tannic and non-tannic phenolics (Waterman and Mole 1994). The Folin–Denis method and related techniques (the Folin–Ciocalteu method and the Singleton–Rossi method) and the Price–Butler method (Price and Butler 1977) are the most popular techniques for quantifying total phenolics. In addition to total phenolics, we list two other tannin indices: PPA measured by the radial diffusion method and the index of Ofcarcik and Burns (1971). The radial diffusion method (Hagerman 1987) for tannin assay was developed recently and is now widely applied in ecological studies owing to its technical simplicity. The tannin index developed by Ofcarcik and Burns (1971), which measures the amount of tannins precipitated with lead, has not been applied in other studies and thus its reliability has not been examined sufficiently. However, their article covered many oak species in North America and it has been cited frequently in subsequent ecological studies. Thus, we list this index for reference.

In addition to nutrient and tannin content, we estimated metabolizable energy (ME, kJ/g) of acorns as an indicator of food quality using the following equations (Pike and Brown 1984):

$$ME = \text{metabolizable energy coefficient } (0.969) \times DE \tag{1}$$

and

$$DE = \text{apparent digestible energy coefficient } (0.896) \times GE, \tag{2}$$

where DE and GE represent digestible energy and gross energy of food, respectively. According to Robbins (1983), the values of the two coefficients were an average of estimations for rodents fed grains or nuts. In general, GE should be determined based on the mean chemical energy content of proteins (23.7 kJ/g), fats (39.5 kJ/g), and carbohydrates (17.2 kJ/g). Because carbohydrate contents are calculated as the total minus the other nutrients, this portion includes the fraction of tannins. Thus, in the present study modified gross energy (MGE) and modified metabolizable energy (MME) were defined as follows:

$$MGE = (23.7 \times \text{protein\%}) + (39.5 \times \text{fat\%}) + [17.2 \times (\text{carbohydrate\%} - \text{totalphenolics\%})] \tag{3}$$

and

$$MME = 0.969 \times 0.896 \times MGE. \tag{4}$$

The effects of tannins on ME are twofold: their presence reduces the metabolizable fraction, and they reduce the digestibility of nutrients, thereby decreasing ME. The use of MGE and MME can overcome at least the first effect of tannins and thus may yield more realistic results in this study. However, the realized metabolized energy of acorns will be further decreased from MME according to the tannin content, due to the digestion-inhibiting effect of tannins.

We also listed the size of acorns of each species in Table 1 for the purpose of reference. The size was represented by the length of the major axis of acorns. Because the sizes of sample acorns were not mentioned in most of the references from which the nutrient and tannin content were cited, information on acorn size was obtained from the different sources.

Nutrients and tannin content of acorns

The nutritional characteristics of acorns of 27 oak species, including those of 8 Japanese oaks, 17 North American oaks, and 2 European oaks are given in Table 1. All values are expressed as percent of acorn dry mass. Considerable variation was observed in the protein content of acorns. Those of Japanese oaks, especially subgenus *Cyclobalanopsis*, assayed low in crude protein (2.6–6.2%), whereas acorns of North American oaks generally included more protein, ranging from 3.9 to 7.6% in *Lepidobalanus* and 5.2 to 10.3% in *Erythrobalanus*, respectively. The protein content of *Lepidobalanus* acorns in Europe was intermediate (5.9–6.2%). Notable differences were also found in the crude fat content. Red oak acorns (*Erythrobalanus* in North America) were very high in fat, ranging from 10 to 30%. In contrast, acorns of Japanese and European oaks contained at most 5% fat. The fat content of white oak acorns (*Lepidobalanus* in North America) exhibited large variation, ranging from 2.6 to 11.5%. There was little difference in crude fibre and crude ash among acorns. The crude fibre content was around 2%, although red oak acorns

Table 1 Nutritional compositions and contents of phenolic compounds in acorns

Region	Subgenus	Latin name	Common name	Seed length[a] (mm)	Protein (%)	Fat (%)	Fibre (%)	Ash (%)	Total phenolic (%)	Method for total phenolics	PPA[b] (%)	Tannin index[c] (%)	MME[d] (kJ/g)	References
Japan	Lepidobalanus	Q. acutissima	–	20–23[1]	5.2	4.6	1.9	1.8	6.0	Folin–Denis	4.4	–	14.7	This study
					4.1	3.7	2.4	2.6	2.6	Folin–Denis	–	–	14.8	Matsuyama (1982)[e]
		Q. aliena	–	20[1]	5.3	2.8	1.6	1.5	6.7	Folin–Denis	4.4	–	14.3	This study
		Q. crispula[f]	–	20–30[1]	4.4	1.7	2.1	1.5	11.7	Folin–Denis	8.6	–	13.2	Shimada and Saitoh (2003)
					6.2	1.5	1.9	2.8	9.1	Folin–Denis	–	–	13.5	Matsuyama (1982)[e]
		Q. serrata	–	16–22[1]	4.5	2.5	1.9	2.8	7.3	Folin–Denis	2.7	–	13.9	Shimada and Saitoh (2003)
					4.0	2.4	1.7	2.6	6.7	Folin–Denis	–	–	14.0	Matsuyama (1982)[e]
		Q. variabilis	–	18[1]	5.1	5.3	1.8	2.3	3.2	Folin–Denis	2.4	–	15.2	This study
	Cyclobalanopsis	Q. gilva	–	10–13[1]	2.6	3.4	1.3	1.9	1.9	Folin–Denis	–	–	15.0	Matsuyama (1982)[e]
		Q. glauca	–	20[1]	3.1	3.2	1.5	2.7	7.5	Folin–Denis	–	–	14.0	Matsuyama (1982)[e]
		Q. myrsinaefolia	–	15–18[1]	3.0	3.4	1.9	2.9	7.6	Folin–Denis	–	–	13.9	Matsuyama (1982)[e]
N. America	Lepidobalanus (white oak)	Q. alba	White	19[2]	6.3	6.3	2.5	2.6	5.6	Folin–Denis	–	–	14.9	Wainio and Forbs (1941)
					7.3	8.8	–	–	3.3	Singleton–Rossi	–	–	–	Servello and Kirkpatrick (1989)
					7.2	8.8	–	–	1.4	Price–Butler	–	–	–	Chung-MacCoubrey et al. (1997)
		Q. lyrata	Overcup	17[3]	4.4	2.6	2.3	2.4	–		–	0.6	–	Ofcarcik and Burns (1971)
		Q. macrocarpa	Bur	35[3]	3.9	11.5	2.4	1.8	–		–	0.7	–	Ofcarcik and Burns (1971)
		Q. michauxii	Swamp chestnut	28[3]	–	–	–	–	–		2.4	–	–	Dixon et al. (1997)
					4.4	4.6	2.5	2.1	–		–	2.1	–	Ofcarcik and Burns (1971)
		Q. prinoides	Scrub chestnut	10–15[2]	7.6	6.3	2.4	2	4.4	Folin–Denis	–	–	15.3	Wainio and Forbs (1941)
		Q. prinus	Chestnut	20–38[2]	6.9	5.1	2.6	2.2	10.4	Folin–Denis	–	–	14.1	Wainio and Forbs (1941)
					5.9	8.8	–	–	8.1	Singleton–Rossi	–	–	–	Servello and Kirkpatrick (1989)
		Q. stellata	Post	21[3]	6.2	9.4	2.4	1.8	–		–	0.9	–	Ofcarcik and Burns (1971)
		Q. virginiana	Live	20[3]	7.4	9.4	2.5	2.1	–		–	0.9	15.8[g]	Ofcarcik and Burns (1971)
					–	–	–	–	5.0	Folin–Denis	–	–	–	Mowery et al. (1997)
	Erythrobalanus (red oak)	Q. falcate	Southern red	12[3]	6.9	31.0	3.0	2.7	–		–	8.7	–	Ofcarcik and Burns (1971)
		Q. ilicifolia	Scrub	13[2]	10.3	20.0	3.0	2.1	11.3	Folin–Denis	–	–	16.9	Wainio and Forbs (1941)
		Q. incana	Sandjack	14[3]	7.3	20.0	3.3	1.4	–		–	6.7	–	Ofcarcik and Burns (1971)
		Q. marilandica	Blackjack	22[3]	6.9	16.9	2.4	1.6	–		–	5.7	–	Ofcarcik and Burns (1971)
		Q. nigra	Water	12[3]	5.4	12.7	3.3	1.4	–		–	8.8	–	Ofcarcik and Burns (1971)
		Q. phellos	Willow	12[3]	5.2	11.1	3.4	1.3	–		–	7.2	–	Ofcarcik and Burns (1971)
		Q. rubra	Red	13–32[2]	6.6	20.8	3.1	2.4	9.8	Folin–Denis	–	–	17.1	Wainio and Forbs (1941)
					6.3	23.0	–	–	13.0	Singleton–Rossi	–	–	–	Servello and Kirkpatrick (1989)
					6.9	20.2	–	–	5.2	Price–Butler	–	–	–	Chung-MacCoubrey et al. (1997)
		Q. shumardii	Shumard	31[3]	–	–	–	–	–		7.2	–	–	Dixon et al. (1997)
					7.5	24.2	3.1	3.7	–		–	5.7	–	Ofcarcik and Burns (1971)

Table 1 continued

Region	Subgenus	Latin name	Common name	Seed length[a] (mm)	Protein (%)	Fat (%)	Fibre (%)	Ash (%)	Total phenolic (%)	Method for total phenolics	PPA[b] (%)	Tannin index[c] (%)	MME[d] (kJ/g)	References
		Q. velutina	Black	13[3]	6.0	13.0	–	1.5	–	–	–	–	–	Briggs and Smith (1989)
									4.5	Folin–Ciocalteu	–	–	–	Basden and Dalvi (1987)
Europe	Lepidobalanus	Q. petraea	Sessil	10–20[4]	5.9	4.9	1.9	2.1	5.3	Folin–Denis	5.1	–	14.8	This study
									5.5	Folin–Denis	–	–	–	Kenward and Holm (1993)
		Q. robur	Common	15–25[5]	6.2	4.9	1.8	1.6	5.2	Folin–Denis	6.9	–	15.0	This study

[a] Seed size represents the length of the major axis of acorns. Superscript numerals indicate the references: 1, Kitamura and Murata (1979); 2, Brown (1938); 3, Ofcarcik and Burns (1971); 4, Mitchell (1978); 5, Rehder (1956)

[b] PPA represents protein-precipitating ability of tannins, which measured by the radial diffusion method (Hagerman 1987)

[c] Ofcarcik and Burns (1971)

[d] MME represents modified metabolizable energy. Details are in the text

[e] Transformed to percent of dry weight

[f] Synonymous with Q. mongolica var. grosseserrata

[g] Estimated using the data by Mowery et al. (1997) for total phenolics

assayed relatively high (ca. 3%). The crude ash content was around 2%, except for acorns of *Quercus shmardii* (3.7%).

The total phenolic content in acorns differed greatly among oak species even within subgenera, ranging from 1.9 to 11.7% based on the Folin–Denis method. The acorns of red oaks are well known to include more tannins than those of white oaks, but Table 1 shows that this rule is not always true. The acorns of *Quercus prinus*, which belongs to the white oak group, assayed markedly high in total phenolics (10.4%), whereas *Quercus velutina* of the red oak group contained a medium level of phenolics (4.5%). MME values were estimated to be around 15 kJ/g in most species. Red oaks had high MME (ca. 17 kJ/g) owing to their high content of fat. In contrast, the acorns of some Japanese oaks which include high tannin levels, especially *Q. crispula*, had relatively low MME.

These observations reveal that the nutritional characteristics of acorns are widely diverse even within subgenera. For instance, *Lepidobalanus* distributed in North America, Europe, and Japan showed large variation in crude fat and tannin contents. Although it was thought that acorns of red oaks contain more tannins and fat than those of white oaks, the present study reveals that there are exceptions.

Grouping of acorns

We performed a cluster analysis, based on the Ward method using MME and total phenolics measured by the Folin–Denis method, to group the acorns of different species based on nutritional characteristics. MMEs and total phenolics represent the beneficial and deleterious aspect of acorns, respectively. It should be noted that the range in variation is much greater in total phenolics than in MME. The cluster analysis was conducted for 16 oak species for which data on all five acorn characteristics (four nutrients and total phenolics) were available. When more than two datasets were available for a species, we analyzed the dataset that covered the most variables or that was obtained by our own research. In addition, for *Q. virginiana*, we merged the information from Ofcarcik and Burns (1971) with that from Mowery et al. (1997) to fill the data on total phenolics.

Sixteen oak species were grouped into three clusters, thereby three types (Fig. 1): Type 1 includes two *Erythrobalanus* species (13 *Q. ilicifolia* and 14 *Q. rubra*); Type 2 does one white oak (11 *Q. prinus*), three Japanese *Lepidobalanus* (2, 3, and 4), and two *Cyclobalanopsis* species (7, 8); and Type 3 was the largest cluster, including one *Cyclobalanopsis* (6) and the rest

Fig. 1 The results of cluster analysis for the acorns of 16 oak species using total phenolic content and metabolizable energy as variables. The numbers next to the species names correspond to the numbers in Fig. 2. *Letters in parentheses* represent the subgenera; L *Lepidobalanus*, C *Cyclobalanopsis*, E *Erythrobalanus*
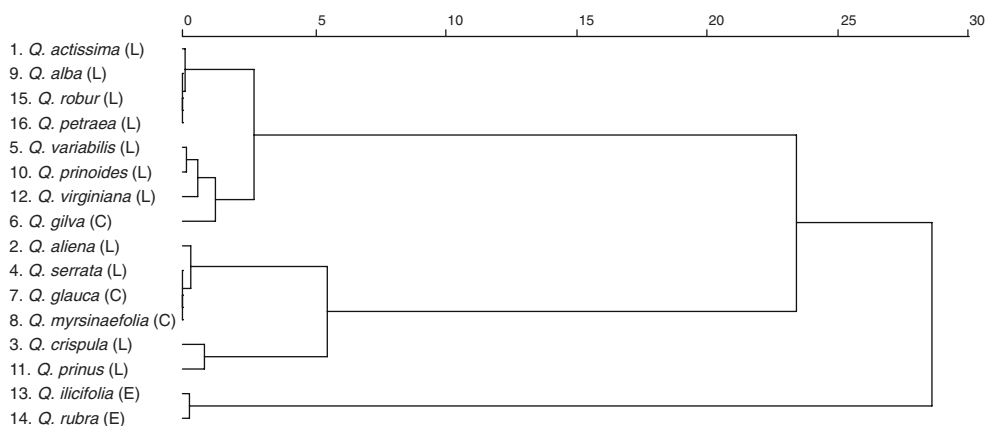
of *Lepidobalanus*. Figure 2 shows the relationship between MMEs and total phenolics. Type 1 acorns had high values of MME and total phenolics. Type 2 acorns were characterized by high total phenolics and low MME. Type 3 acorns had low phenolics and intermediate MME.

Types 1 and 3 almost correspond to the red oak group and the white oak group in North America, respectively. Type 2, whose acorns include low fat and protein contents and high tannin content, is a newly recognized category. Type 2 acorns must have the lowest nutritional value for consumers, because they are characterized not only by poor ME but also by high levels of defensive chemicals. Acorns of

Type 3 would seem to be more palatable, because they contain less tannin than Type 2 acorns, whereas the other nutrient levels are similar. Type 1 acorns contain as much tannin as Type 2 acorns, but they include much more ME than Type 2 acorns, owing to their high content of protein and fat (Table 1). Thus, these three types are not nutritionally equivalent, that is, the food value for consumers differs among acorn types.

Rodent population dynamics

Based on a review of previous studies, we summarize the responses of rodent populations to acorn masting and examine the effects of acorn nutritional characteristics on rodent responses.

Literature treatment

Seventeen studies complying with the following standards were used to review the relationship between acorn crop and rodent population dynamics: (1) the species of both oaks and consumers were specified; (2) both acorn crops and rodent population dynamics were estimated quantitatively; and (3) the study period included at least one mast year and one non-mast year (Table 2). In addition, we list the information on the rodent responses to beechnut (*Fagus* spp.) masting for the purpose of comparison. To categorize rodent species with different feeding habits separately, based on the previous studies of diet, we regarded *Apodemus* (Tatsukawa and Murakami 1976; Montgomery 1989), *Peromyscus* (Montgomery 1989), *Sciurus* (Koprowski 1994), and *Tamias* (Snyder 1982) as granivores, *Microtus* (Batzli 1985) as herbivores, and *Clethrionomys* (Merritt 1981; Hansson 1985) and *Eothenomys* (Kaneko 1992) as intermediate consumers (ones that
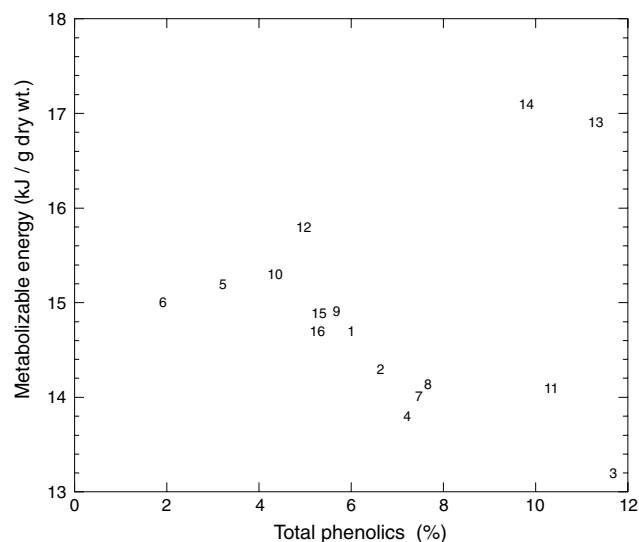

Fig. 2 The relationship between of total phenolic content and metabolizable energy in the acorns of 16 oak species. The numerals represent the following: 1, *Q. acutissima*; 2, *Q. aliena*; 3, *Q. crispula*; 4, *Q. serrata*; 5, *Q. variabilis*; 6, *Q. gilva*; 7, *Q. glauca*; 8, *Q. myrsinaefolia*; 9, *Q. alba*; 10, *Q. prinoides*; 11, *Q. prinus*; 12, *Q. virginiana*; 13, *Q. ilicifolia*; 14, *Q. rubra*; 15, *Q. petraea*; and 16, *Q. robur*

Table 2 Summary of the responses of rodent populations to acorn (*Quercus*) or beechnut (*Fagus*) masting

References	Tree sp.[a]	Rodent sp.	Feeding habit[b]	Location	Study period	Rodent responses[c]		
						Survival during winter	Reproduction during winter	Density in next year[d]
Smyth (1966)	*Q. robur* (3)	*C. glareolus*	I	England	16		Y	
		A. sylvaticus	G				Y	
Watts (1969)[e]	*Q. robur* (3)	*A. sylvaticus*	G	England	12	Y		
Hansen and Batzli (1979)	*Q. rubra* (1)	*P. leucops*	G	N. America	2	Y		Y (Sp, Au)
Jensen (1982)	*F. sylvatica*	*C. glareolus*	I	Denmark	9		Y	Y (Sp)
		A. flavicollis	G				Y	N (Sp)
	Q. robur (3)	*C. glareolus*	I				Y	
		A. flavicollis	G				Y	
Miguchi (1988)	*F. crenata*	*A. speciosus*	G	Japan	2			Y (Su, Au)
		A. argenteus	G					N (Su, Au)
		E. andersoni	I					N (Su), Y(Au)
		M. montebelli	H					Y (Su, Au)
Elkinton et al. (1996)	*Q. rubra* (1)	*P. leucops*	G	N. America	5			Y (Su)
Miguchi (1996)	*F. crenata*	*A. speciosus*	G	Japan	5			Y (Su, Au)
		M. montebelli	H					Y (Su, Au)
Wolff (1996)	*Q. rubra* (1) and *Q. alba* (3)[f]	*P. leucops*	G	N. America	14		Y	Y (Su)
		P. maniculatus	G				Y	Y (Su)
		T. striatus	G					Y (Su)
McCracken et al. (1999)	*Q. rubra* (1)	*P. leucops*	G	N. America	10			Y (Su, Au)
		C. gapperi	I					N (Su, Au)
McShea (2000)	*Q. rubra* (1) and *Q. alba* (3)[f]	*P. leucops*	G	N. America	6–12			Y (Su, Au)
		T. striatus	G					Y (Su)
		S. carolinensis	G					Y (Sp)
Selås et. al. (2002)	*Q. petraea* (3)	*C. glareolus*	I	Norway	29	N		N (Sp)
		A. sylvaticus	G			Y		Y (Sp)
Schnurr et al. (2002)	*Q. rubra* (1)	*Peromyscus* spp.	G	N. America	3			Y (Avr)[g]
		T. striatus	G					N (Avr)[g]
		C. gapperi	I					N (Avr)[g]
Stenseth et al. (2002)	*Q. robur* (3)	*C. glareolus*	I	Poland	26	Y		Y(Sp, Au)
		A. flavicollis	G			Y		Y(Sp, Au)
Crespin et al. (2002)	*Q. robur* (3)	*C. glareolus*	I	Belgium	6	Y		
Elias et al. (2004)	*Q. rubra* (1)	*P. leucops*	G	N. America	20			Y(Su)
Hoshizaki and Miguchi (2005)	*F. crenata*	*E. andersoni*	I	Japan	8			Y (Su)
		A. speciosus	G					Y (Su)
		A. argenteus	G					Y (Su)
	Q. crispula (2)	*E. andersoni*	I					N (Su)
		A. speciosus	G					N (Su)
		A. argenteus	G					N (Su)
T. Shimada (unpublished)	*F. crenata*	*A. argenteus*	G	Japan	6	Y		Y (Sp)
	Q. crispula (2)	*A. argenteus*	G			N		N (Sp)

[a] Numerals in parentheses refer to the types of acorns. Details are in the text

[b] G, I, and H represent granivore, intermediate, and herbivore, respectively

[c] Y and N indicate whether the response was observed or not, respectively

[d] Sp, Su, and Au represent spring, summer, and autumn, respectively. These indicate the seasons in which rodent densities were estimated

[e] The data source is the same as Smyth (1966)

[f] The acorn crop was measured without distinguishing between *Q. alba* and *Q. rubra*

[g] Avr indicates that the rodent density used for analysis was the average density through the year

exhibited characteristics between granivores and herbivores). When a study included information about more than two rodent species, we treated the data for each species as a separate case.

Response to acorn masting

The relationship between acorn masting and rodent population dynamics is summarized in Table 2. Acorn

masting had three typical positive influences on rodent population dynamics: (1) an increase in overwinter survival rate; (2) induced reproductive activities during winter; and, consequently, (3) an increase in population density the next year. Because the season when rodent densities were estimated was different in each case, we listed the seasons with the presence or not of the positive responses in Table 2. There were no differences in the rodent responses among seasons in a literature, except for the case of *E. andersoni* for the beechnut masting (Miguchi 1988). When any of the above responses were observed after a mast year (and not observed after a non-mast year), we regarded it as a positive response to acorn masting.

Among 26 cases of granivorous rodents, positive responses of rodent populations were observed in 21 cases (Tables 2, 3). The positive responses resulted from the masting of *Q. rubra*, the mixture of *Q. rubra* and *Q. alba*, *Q. petraea*, *Q. robur*, and two *Fagus* species. All of the oak species belong to Type 1 (*Q. rubra*) or Type 3 (*Q. alba*, *Q. petraea*, and *Q. robur*). No positive responses were found in the two reports on the masting of *Q. crispula*, which belongs to Type 2. Among 11 cases of rodents with intermediate feeding habits, positive responses were observed in 7 cases (Tables 2, 3). The positive responses were seen only in the masting of *Q. robur* (Type 3) or *Fagus* species. For herbivorous rodents, there were no reports on the responses to acorn masting, although two positive cases were observed in beechnut masting (*Microtus montebelli* in Miguchi 1988, 1996).

We compared the frequencies of the positive responses in each acorn type between granivores and intermediates using Fisher's exact probability tests. The frequencies of positive responses differed significantly between granivores and intermediates in Type 1

acorns ($P=0.035$), but did not in Type 2 and 3 acorns (Type 2: $P = 1.0$; Type 3: $P = 0.34$).

Rodent responses and nutritional characteristics of acorns

The influences of acorn masting on rodent population dynamics differed depending on the type of acorns. The positive response of rodent populations to the masting of Type 2 acorns (*Q. crispula*) were not observed in either granivorous or intermediate-type rodents (Table 3). For granivorous rodents, however, positive responses were observed in most cases after the masting of Type 1 (*Q. rubra*) or Type 3 (*Q. alba*, *Q. petraea*, and *Q. robur*) acorns. Furthermore, intermediate-type rodents responded positively only to the masting of *Q. robur* (Type 3) or *Fagus* species.

Why have not any positive responses been observed after the masting of Type 2 acorns? This phenomenon cannot be explained by the variation in acorn crop, because the magnitude of the masting did not significantly differ between Type 2 and other acorn types (e.g., *Q. crispula*, Hoshizaki and Hulme 2002; *Q. rubra*, McCracken et al. 1999). These different responses may be related to the nutritional characteristics of acorns. Different types of acorns are not nutritionally equivalent (Table 1). Traits of Type 2 acorns, namely their high tannin content and low MME, might make it difficult to generate positive responses in rodent populations even if the masting provides plentiful resources.

Tannins act as defensive chemicals against consumers. Indeed, animals that ingest food with high tannin contents suffer from impaired physical conditions (Chung-MacCoubrey et al. 1997; Shimada and Saitoh 2003). Thus, feeding on Type 2 acorns inevitably involves the physiological costs of ingesting tannins.

Table 3 Responses of rodent populations to acorn (*Quercus*) or beechnut (*Fagus*) masting

Tree sp.[a]	Location	Positive responses (no. of cases)				Statistics[b]
		Granivores		Intermediates		
		Observed	Not observed	Observed	Not observed	
Q. rubra (1)	N. America	5	1	0	2	$P = 0.035$
Q. rubra (1) and *Q. alba* (3)	N. America	6	0	0	0	–
Q. petraea (3)	Europe	1	0	0	1	$P = 0.34$
Q. robur (3)	Europe	3	0	4	0	
Q. crispula (2)	Japan	0	3	0	1	$P = 1.0$
F. sylvatica	Europe	1	0	1	0	–
F. crenata	Japan	5	1	2	0	–

[a] Numerals in parentheses refer to the types of acorns. Details are in the text

[b] Fisher's exact probability test, comparing the frequencies of the positive responses in each acorn type between granivores and intermediates

However, the masting of Type 1 acorns, which include the same level of tannins as Type 2, caused positive responses in granivorous rodent populations. This might be explained by the difference in ME: in Type 2 acorns ME is much less than that in Type 1 acorns. Although the mechanisms underlying how tannins cause physical damage to consumers are not understood fully, reduction of assimilated energy caused by the digestion-inhibiting effect of tannins may be compensated for by the additional energy intake provided by Type 1 acorns. In contrast, Type 2 acorns might have little potential to promote overwinter survival and reproductive activities in granivorous and intermediate-type rodents.

In addition, we have to notice that this hypothesis on Type 2 acorns is based on only two studies and only one oak species (*Q. crispula*). Alternatively, this situation leaves open the possibility that the positive responses to the masting of Type 2 acorns will be reported in future after further investigation. Thus, further studies on the rodent responses to the masting of Type 2 acorns, especially *Q. prinus*, are necessary to examine this hypothesis.

Rodent population responses to the masting of Type 1 acorns differed significantly between granivores and intermediate consumers. This difference is assumed to be related to the consumers' relative tolerance of tannins. In general, granivorous rodents are less sensitive to tannins than herbivorous and intermediate-type rodents (Robbins et al. 1991). Grass contains lower levels of plant secondary metabolites, whereas some kinds of seeds accumulate considerable amounts of secondary metabolites (McArthur et al. 1991; Waterman and Mole 1994). Granivores, which have had more exposure to tannins, are considered to have evolved tolerance and defence mechanisms, such as tannin-binding salivary proteins (Mehansho et al. 1987; Shimada 2006). As for rodents, these tannin-binding salivary proteins are detected mostly in granivores, such as laboratory mouse, rat (Mehansho et al. 1987), *Apodemus speciosus* (Shimada et al. 2004, 2006), and *A. argenteus* (T. Shimada, unpublished data), but not in herbivores (*Microtus pennsylvanicus*, Dietz et al. 1994; *M. ochrogaster*, Robbins et al. 1991). An exception is *M. oeconomus*, which secretes tannin-binding proteins, but this species' feeding habit is known to differ greatly from that of other *Microtus* species; tannin-rich tree bark makes up a staple part of the diet (Juntheikki et al. 1996). Thus, granivores feeding on Type 1 acorns may suffer from relatively light damage caused by tannins, while gaining the benefits of their rich ME. In contrast, intermediate-type rodents may suffer from serious damage by

feeding on Type 1 (and Type 2) acorns, outweighing the benefits of the high ME. Although it is not clear whether intermediate consumers feed on tannin-rich acorns in spite of their toxicity or avoid them, the present results indicate that the masting of Type 1 acorns may contribute little to positive responses of rodents with intermediate feeding habits.

Type 3 acorns are the most palatable for consumers, due to their low tannin content and relatively high ME. It is noteworthy that only the masting of *Q. robur* caused positive responses in intermediate-type rodents, although some other Type 3 species (*Q. petraea*, *Q. acutissima*, and *Q. alba*) have characteristics similar to those of *Q. robur*. It remains unclear whether *Q. robur* has particular characteristics that generate positive responses or sufficient studies have not yet been conducted on other Type 3 acorns.

The above hypothesis on the relationships among responses of rodent populations, rodents' feeding habits, and nutritional types of acorns can be tested by comparing the physiological performance of captive animals via feeding experiments supplying different types of acorns. This hypothesis would generate two predictions; first, the physiological performance of rodents, including body weight change, food intake, and dry matter and protein digestibilities, would be better in animals fed Type 3 acorns than in ones fed Type 1 acorns and be the worst in Type 2 acorns. Second, the negative effects of feeding tannin-rich acorns (Type 1 and 2) would be more severe in herbivorous and intermediate rodents than granivores. The first prediction has been confirmed to be true in some previous studies. Gray squirrels (*Sciurus carolinensis*) a granivore, exhibited higher food intake and protein digestibility when feeding on acorns of *Q. alba* (Type 3) than when feeding on acorns of *Q. rubra* (Type 1) (Chung-MacCoubrey et al. 1997). Havera and Smith (1979) reported similar observations in fox squirrels (*Sciurus niger*) a granivore: individuals fed solely acorns of *Q. rubra* decreased their weight, whereas ones fed acorns of *Q. alba* increased their weight. Contrary to this, as far as we know, the second prediction has not been tested until now.

Cases in which no clear relationship was observed between rodent populations and acorn masting

The interaction between acorn masting and rodent population dynamics has been investigated mostly without considering the nutritional characteristics of acorns. The viewpoint that rodents respond differently to acorn masting depending on their feeding habits and

the nutritional characteristics of the acorns can help us understand this interaction more clearly.

For instance, the masting of *Q. rubra* did not generate positive responses in *Clethrionomys gapperi*, whereas sympatric *Peromyscus* species exhibited positive responses (McCracken et al. 1999; Schnurr et al. 2002). McCracken et al. (1999) inferred that the differences in arboreal space use and the feeding habits between *Clethrionomys* and *Peromyscus* may be responsible for the different responses to the masting of *Q. rubra*. They implied that *Peromyscus* would have a competitive advantage over *Clethrionomys* by foraging on acorns in the arboreal habitat. However, because a large number of unconsumed acorns can generally be observed in the spring after masting, it appears that intense competition for acorns did not occur. Schnurr et al. (2002) left this question unanswered, but they stressed the necessity of re-examining the feeding preferences and hoarding behaviour of *C. gapperi*.

By assuming that *C. gapperi*, an intermediate consumer, is more sensitive to tannins than *Peromyscus*, it could be easily understood why *Peromyscus* and *Clethrionomys* responded differently to the masting of *Q. rubra* (Type 1). Additional investigations, including feeding experiments using *C. gapperi* and *Q. rubra* acorns and assays for tannin-binding salivary proteins, will help to answer this question.

Selås et al. (2002) reported that the masting of *Q. petraea* caused positive responses in *Apodemus sylvaticus*, but not in *Clethrionomys glareolus*. The latter was highly dependent on the bilberry (*Vaccinium myrtillus*) crop and not on the *Q. petraea* acorn crop. Selås et al. inferred that the food and habitat selection of *C. glareolus* may be responsible for this lack of positive responses. This interpretation, however, cannot explain why *C. glareolus* would not depend on *Q. petraea* acorns when the bilberry crop is poor; like acorns, bilberry crops also show large annual fluctuations. As we have stressed in this review, detailed comparative studies focusing on the physiological performance of these two rodent species fed *Q. petraea* acorns may resolve this question.

Conclusions

First, we mention two caveats to this review: our analyses were based on a limited number of studies, and the published data we cited may be somewhat biased, as negative results are less likely to be published. However, this review revealed two significant findings: (1) acorns of different oak species are not

nutritionally, and thereby ecologically, equivalent, even within the same subgenus; and (2) rodent responses to acorn masting differ depending on the nutritional characteristics of acorns and on the feeding habits of consumers. The present findings emphasize that the relationship between rodents and acorn masting cannot easily be generalized, because there is large variation in the characteristics of both acorns and rodents. To examine acorn resources as a regulating factor of rodent populations, we must carefully consider the nutritional and secondary metabolite characteristics of acorns and consumers' feeding habits.

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