

for terrestrial insects. Body odor of plants and insects plays an important role in nature.

In interaction 1 (Fig. 5.6) herbivores are attracted to the host plant by volatile chemicals, and parasitoids may respond to similar compounds (interaction 16), as in Fig. 5.5. But toxic chemicals acquired from the host plant by the herbivore may be effective as defense against enemies (interaction 13). For example, Campbell and Duffey (1979) showed that increased tomatine levels in tomato plants were more deleterious to the parasitoid *Hyposoter exiguae* than to its host, *Heleothis zea*, feeding on tomato (interaction 3 was less potent than interaction 13). But when toxic chemicals are sequestered by parasitoids, as in the *Zenillia* species mentioned above, they become effective defenses against the fourth trophic level (interaction 26). As we will see later (Chapter 22), associated plants may interfere with host finding by herbivores (interaction 2) and by enemies of herbivores (interaction 19). All interactions in Fig. 5.6 are explained fully with examples in Price (1981a).

Physical characteristics of plants also mediate the herbivore–enemy interaction (Price et al., 1980). For example, trichomes on leaves may slow the searching rate of predators and parasitoids to the point where enemies become ineffective. Galls that grow relatively large provide more protection against the herbivores' enemies than do smaller galls, and galls with extrafloral nectaries attract foraging ants which interfere with attack by parasitic wasps (Washburn, 1984).

MONOPHAGY AND POLYPHAGY

If it is so advantageous to specialize in feeding on toxic plants, why are some species **monophagous** (feeding on one species of food) and others **polyphagous** (feeding on many species of food)? Also, why do some species feed on apparently innocuous hosts? There are many solutions to any given problem in nature and the evolutionary process ensures that many possible avenues are tested (Bernays and Chapman, 1994). Some species have never had the evolutionary chance to crack potent plant defenses because the gene pool has not produced the necessary combination of enzymes. Others have evolved to specialize by dealing with a few potent plant chemicals. Yet others evolved to generalize by utilization of many less toxic plants. These seem to be the two basic alternatives and both require quite an expensive metabolic commitment on the part of the insect. The monophagous species must produce large quantities of an enzyme to detoxify their food, or they must evolve storage mechanisms, as in the case of diprionid sawfly larvae. Conversely, Krieger et al. (1971) have shown that the polyphagous species of insects usually produce much more of the microsomal mixed-function oxidases in their midguts to deal with the very diverse array of plant chemicals in their potential diet.

Regarding the search for food, the monophagous species will have to search harder, but it can become highly specialized in its search and it has

those chemical markers to cue in on. The polyphagous species has a more abundant food source, but its chemical cues are less distinctive, or produced in lesser amounts, and the insect cannot afford to specialize on any one of the variety of chemicals in its diet. The monophagous species will usually have to share its food source with few other herbivores, whereas the polyphagous species may be faced with many potential competitors. There are no outright winners in nature and every avenue for adaptive gain sets rather precise limits on how far this advantage can be exploited.

It becomes clear that if either the monophagous or polyphagous feeding strategies are metabolically costly, the cost of gaining this energy must reduce the amount of energy that can be channeled into reproduction. That is, even the food source of herbivores contains an environmental resistance factor in the form of toxic chemicals. Presumably, insects fed on a bland (nontoxic) diet would show their real biotic potential and those fed on natural foods would show their biotic potential minus the environmental resistance contained in food (rather like Feeny did with winter moths on artificial diets). In the comparison of the growth parameters r and r_{\max} , this factor should be calculated (see Chapter 13).

If several evolutionary lines of insects adapt to feeding on a toxic plant, and use these toxins as cues for their behavior, as frequently happens, the result will be a unique insect fauna on each set of plants that are chemically related, a well-defined component community. This makes the study of the insect fauna of poisonous plant families very interesting and valuable for understanding community organizations (see Chapter 22).

APOSEMATIC COLORATION

The family *Asclepiadaceae*, the milkweeds, contains some species that manufacture cardiac glycosides which are emetic when ingested by vertebrate predators at half their lethal dosage (e.g., Brower, 1969). This is an important point for the herbivorous insect that sequesters these glycosides because if the predator is killed, there is no chance of the predator population learning to avoid feeding on an **aposematic species** (one that advertises its distasteful nature by being brightly colored; cf. Guilford, 1990). There is only a small group of insects in four insect orders that feed consistently on *Asclepias* in temperate North America, and they are found almost exclusively on milkweed (Table 5.1 and Fig. 5.7). All but one are aposematically colored, suggesting that they all are chemically protected. Contrary to this expectation, Brower (1969) has claimed that monarch butterflies that have fed in northeastern North America are palatable because their food plants lack cardiac glycosides. However, Duffey (1970) showed that the species of milkweed mentioned by Brower do contain glycosides.

TABLE 5.1 Herbivorous Insect Community on Milkweeds (*Asclepiadaceae*) in Temperate North America which are Mostly Aposematic Species. The One Exception is Placed in Parentheses (Personal Observations). Other Insects Feed Sporadically on Milkweeds but are Not Found Predominantly on These Plants.

Order	Family	Species	Coloring
Coleoptera	Cerambycidae	<i>Tetraopes tetraophthalmus</i>	Red with black spots
		<i>Tetraopes femoratus</i>	Red with black spots
	Chrysomelidea	<i>Tetraopes quinquemaculatus</i>	Red with black spots
		<i>Labidomera clivicollis</i>	Red and black pattern
Lepidoptera	(Curculionidae)	<i>Rhyssomatus lineaticollis</i>	Black)
	Danaiidae	<i>Danaus plexippus</i>	Adult—orange and black
			Larva—black, yellow, and white stripes
	Arctiidae	<i>Euchaetias egle</i>	Adult and larva—white, yellow, and black
		<i>Cycnia inopinatus</i>	Adult—white, yellow, and black
		Larva—orange with grey hairs	
Hemiptera	Lygaeidae	<i>Oncopeltus fasciatus</i>	Red and black
Homoptera	Aphididae	<i>Lygaeus kalmii</i>	Red and black
		<i>Aphis nerii</i>	Yellow and black

PALATABILITY SPECTRUM

It now appears that there is a great variation in glycoside content in monarch butterfly populations, from zero to concentrations sufficient to cause emesis (Brower et al., 1972). Thus there exists a **palatability spectrum** for the butterfly's predators (Brower et al., 1968; Malcolm, 1991). Scudder and Duffey (1972) (see also Feir and Suen, 1971) found cardiac glycosides in aposematic lygaeids feeding on milkweeds, and these chemicals were also incorporated into the insects' defensive secretion. Beetles, such as *Tetraopes* spp., that are specific to milkweeds also contain glycosides (Duffey and Scudder, 1972). We may infer from the studies above that the majority of milkweeds of the genus *Asclepias* contain cardiac glycosides and that most insects that feed on these plants are protected by ingesting and sequestering these toxic chemicals.

COUNTERATTACK BY PLANTS

The production of sesamin in the pyrethrum flower that inhibits mixed-function oxidase activity has been mentioned. A more extensive set of



FIGURE 5.7 Two members of the milkweed fauna: (a) large milkweed bug, *Oncopeltus fasciatus*; (b) milkweed long-horn beetle, *Tetraopes femoratus*, on swamp milkweed, *Asclepias incarnata*. Both species are red on the lighter areas of the body and black on the remainder. Thus the insects contrast strikingly with the green leaves of the host plant and they sit prominently on upper foliage, a behavior that differs considerably from that of cryptic species. Drawing by Alice Prickett.

counter-responses may be seen in leguminous plants (Fabaceae) presumably in response to herbivore pressure by bruchid (pea and bean) weevils that oviposit on legume pods. A summary provided by Janzen (1969a) and Center and Johnson (1974) covers physical and chemical defense:

1. Some species produce gum when the seed pod is first penetrated by a newly hatched larva—this may push off the egg mass, or drown the larvae, or hamper their movements.
2. Pods may dehisce, fragment, or explode, scattering seeds to escape from larvae coming through the pod walls and from ovipositing females.
3. Some species have pods free of surface cracks, as some bruchids cannot glue eggs on a smooth surface.
4. Some species have indehiscent pods and thus exclude those species that oviposit only on exposed seeds.
5. Some species have a layer of material on the seed surface that swells when the pod opens and detaches the attached eggs.
6. Many species have poisonous or hallucinogenic compounds such as alkaloids, saponins, pentose sugars, and free amino acids (primary response).
7. Some are rich in endopeptidase inhibitors, making digestion of the bean by the bruchid very difficult.
8. Some have a flaking pod surface that may remove eggs laid on it.
9. In *Acacia* spp. the immature seeds remain small throughout the year and abruptly grow to maturity just before being dispersed.
10. In a species of *Cassia* the seeds are too thin to allow a bruchid to mature.
11. In many wild herbaceous legumes the seeds are so small that bruchids cannot mature in them. Janzen (1969a), Mitchell (1977), Johnson and Slobodchikoff (1979), and Johnson (1981) consider further examples.

As seen in the list above, one method of avoiding predation is to disperse seeds or fruits rapidly and extensively, with the resultant greater difficulty in discovering food for species that are seed specialists. The multitude of seed-dispersal mechanisms among plants obviously accomplish this aim. Adaptations for wind dispersal and for attaching to animals take many forms. Animals carry fruits and seeds in the mouth or gut and feed on the palatable part of the fruit or seed coat, and the seed is dispersed and may be buried by small mammals, harvester ants, and wood ants, or seed-caching beetles (see Sudd, 1967; Harper et al., 1970; Manley, 1971; Kirk, 1972, 1973; Alcock, 1973a). Many seeds have oily coats or appendages (caruncles and elaiosomes) that are eaten by ants and other insects (Sudd, 1967; Davidson and Morton, 1981; Buckley, 1982; Beattie, 1985; Huxley and Cutler, 1991), while the seed remains intact and is dispersed. Some seeds improved germination after passing through the gut of animals (Krefting and Roe, 1949; Janzen and Martin,

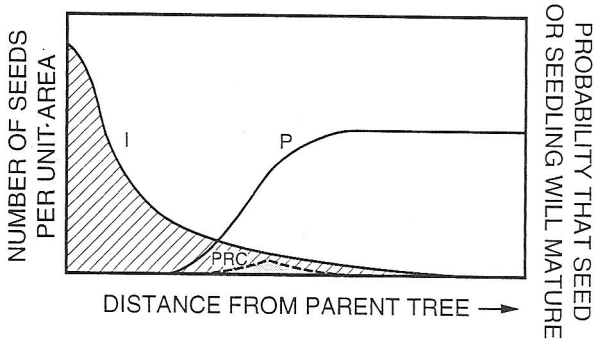


FIGURE 5.8 Relationship between density of seeds (I) and probability of escaping from a seed or seedling predator (P) relative to the distance of seeds from the parent tree. The product of I and P values gives the population recruitment curve (PRC), where progeny are most likely to survive at some distance from the parent. From D. H. Janzen, *Herbivores and the number of tree species in tropical forests*, *Am. Nat.*, 1970, **104**:501–528. Published by the University of Chicago Press. Copyright © 1970 by the University of Chicago. All rights reserved.

1982; Janzen, 1986b). This advantage can be obtained at the cost of producing a palatable fruit.

The further the seeds are dispersed, the less rewarding will predation be on these seeds, and a pattern such as that proposed by Janzen (1970) may be observed that relates seed density to the probability of survival of seed (Fig. 5.8). There is a minimum distance between parent and progeny where survival is likely. The population recruitment curve is clearly the product of seed density and probability of survival. Thus if a species does not evolve an effective dispersal mechanism to make seeds unprofitable, the only alternatives are to make them unpalatable, or very small.

PLANT APPARENCY HYPOTHESIS

Two basically different kinds of plant defense by chemicals have been mentioned in this chapter and have been recognized by Feeny (1975, 1976, 1992) and Rhoades and Cates (1976) (Rhoades, 1979). Feeny's (1976) terminology and arguments are used here. Oak leaves were seen to contain 2.4% tannins in fresh weight when old and the percentage may reach even higher levels of 5% or more. The defensive effect of tannins was dosage dependent, so as concentration of tannins increased, inhibition of larval growth increased; hence the relatively high percentage of digestibility-reducing chemicals in old oak leaves. Tannins act as **quantitative** (dosage-dependent) **barriers** to insects and are effective on insects that habitually feed on plants rich in tannins.

By contrast, the major chemical defenses of crucifers are mustard oils,