Chapter 7
Adaptations to Pollen feeding

Behavior is often manifested in the physiological structure and function of an organism. Pollen has nutritional and structural features that are unique from prey, and consequently predators and parasitoids that are suited to consuming insects may not necessarily possess the means to efficiently consume and digest pollen. If pollen feeding is important to the fitness of predators and parasitoids, one should expect physiological and morphological adaptations that facilitate pollen feeding. This is indeed the case for many natural enemies, and the pollen-feeding specializations in arthropod structure and function are characterized as being sensory, morphological, or digestive in nature. Clearly the specific modifications observed in certain species are not ubiquitous in all entomophages, but documenting the adaptations allows us to have a search image for identifying pollinivory in other species.

7.1   The Pollen-Feeding Process in Entomophages

The process of pollen-feeding by entomophagous arthropods is detailed in at least two cases, with syrphid adults and phytoseiid mites. These thorough studies of how pollen is consumed are useful for identifying exact sensory and morphological features used specifically for manipulating and extracting nutrients from pollen grains. Furthermore, studying the process of pollen feeding can elucidate how individual adaptations interact with others to extract the nutrients from pollen.

   The feeding process has been recorded in the adults of several syrphids, and species-specific behaviors reveal different tactics employed during pollen consumption. Müller (1883) was the first to provide a detailed description of pollen consumption in syrphids, focusing on adults of *Eristalis*, *Episyrphus*, and *Rhingia*. Modern optical technology has greatly improved our understanding of this process. Gilbert (1981, and references therein) gave a good account of the different roles of the mouthparts in pollinivory. First, the flies needed to dislodge the pollen grains from the anthers, which was accomplished either with the laciniae or with prostomal teeth. How the nutrients were then extracted from within the pollen exine

differed among species. In some species, the labella grasped the pollen grains and lacerated them to relieve their contents. Other species consumed the grains whole and crushed them with a bristle like structure in the crop (Haslett, 1983, and references therein). However, in the majority of species it appeared that the entire pollen grain was consumed through the labrum and was left intact until it reached the midgut, where either enzymes worked to degrade the exine, or the pollen became solubilized in the fluids of the midgut (Gilbert, 1981; Haslett, 1983). The pollen exine thus remained visible throughout the digestion process. In summary, a number of morphological adaptations of the mouthparts and digestive tracts in syrphids assist them in extracting nutrients from pollen, and the heterogeneity in gastrointestinal structure has potentially resulted in multiple pollen-feeding tactics in this family.

Flechtmann and McMurtry (1992b) give a detailed account of how omnivorous phytoseiids (*Euseius stipulatus* and *Amblyseius similoides*) consume pollen. First, pollen grains are grasped singly by the chelicerae, and are brought intact toward the mouth. The pollen grain is then lacerated with several back and forth movements of the chelicerae. The fluid that escapes from the collapsing grain is ingested. This entire process is predicated on the morphology of the chelicerae, which are shaped to give them a 'side bite' so that they can pick up and hold the pollen grain without lacerating it. In another study involving electron microscopy, Flechtmann and McMurtry (1992a) note that the most pollinivorous of phytoseiids have a spoonlike surface on the inner side of the fixed digit of the chelicerae, presumably to aid in holding the pollen grains. Furthermore, these species have a relatively enlarged deutosternal groove relative to strictly predaceous phytoseiids, which may allow them to funnel the liquid contents of the lacerated pollen grains into the oral cavity (Fig. 7.1).

7.2 Sensory Adaptations for Detecting Pollen

One of the first events that must occur in pollinivory is that the entomophage must recognize pollen as food. Exact chemical and visual stimulants for pollen-feeding are not well known for most natural enemies. Nevertheless, some chemical and visual cues for feeding responses in natural enemies have been isolated from pollen, laying the groundwork for future research in this area.

7.2.1 Vision

Vision is important for identifying habitats where pollen can be found, and for eliciting a feeding response to pollen-meals. Color preferences are reported for a wide range of predators and parasitoids, and may be used to identify plants with floral resources that are suitable for natural enemies. For example, the attractiveness of specific floral color may play a role in plant fidelity, as demonstrated with syrphids like *Eriozona syrphoides*, which prefers to feed at mauve flowers (Haslett and Entwistle, 1980a).
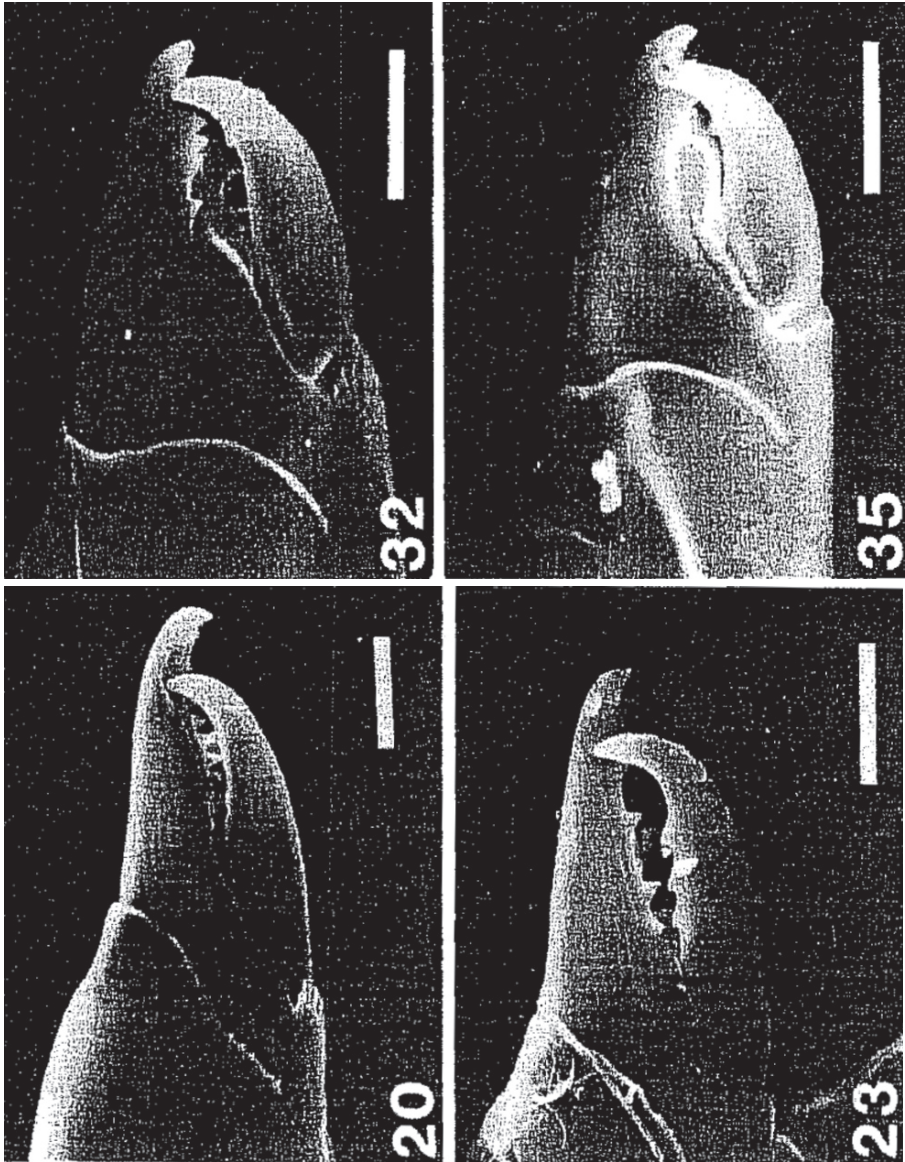
Fig. 7.1 Female cheliceral paraxial aspect for predatory (*left*) and pollinivorous (*right*) Phytoseiidae. Note the spoon-like surface of the top chelicerae in the pollinivorous taxa, presumably to aid in manipulating pollen grains (Reproduced from Flechtmann and McMurtry, 1992b. With permission from Indira Publishing House)

The physiology of color reception and subsequent feeding responses from hoverflies has revealed that specific wavelengths must be received from a food source before many syrphids will begin to feed, and that these wavelengths correspond to the color of some pollens (Lunau and Wacht, 1994; Wacht et al., 1996). The spectral wavelengths that most frequently elicited an extension of the proboscis range from 520–600 nm (green-yellow wavebands), and this same proboscis elongation behavior was observed when the flies fed at yellow anthers or floral guides (Lunau and Wacht, 1994).

7.2.2   Chemical Cues

Much of the research on chemoreception and pollinivory in natural enemies centers on the mouthparts. As an example of sensory adaptations to pollen feeding in phytophagous insects, lepidopterans that feed on pollen possess long mechanoreceptor sensillae proximally on their mouthparts, whereas these sensillae are smaller or absent in lepidopterans that do not consume pollen (Gilbert, 1972). Likewise, the mouthparts of carnivorous arthropods also possess sensory hairs that may be important in detecting non-prey foods. Cohen (1990) describes chemoreceptors in the labial tips of predatory heteropterans, and carnivorous lacewing larvae possibly detect sugarmeals with chemoreceptors in their maxillary palps (Downes, 1974). The antennae may also be important in distinguishing pollen-meals; mantids touch the pollen with their antennae before accepting it as food (Beckman and Hurd, 2003).

So what chemical cues from pollen do entomophages use to elicit feeding? It appears that the chemical elicitors used to initiate feeding are located in the pollen exine, and these chemicals are soluble in methanol or water (McMurtry et al., 1991; Wacht et al., 1996). *Euseius tularensis* aggregates to and lays eggs on leaf discs treated with extracted chemicals of *Malephora crocea* pollen; this is in contrast to untreated leaf discs, on which no eggs are laid (McMurtry et al., 1991). In *Eristalis tenax*, pollen feeding is initiated by triggering a salt receptor cell in the labellar sensory hairs (Wacht et al., 1996). In fact, proline (the predominant amino acid found in most pollens) is the only amino acid that excites this receptor, which allows the flies to identify at least five species of pollen in the laboratory (Wacht et al., 2000). Tryptophan and phenylalanine actually inhibit the salt-receptor cell. It should be noted that while most of this receptor cell work focuses on *E. tenax*, a non-predaceous syrphid, at least the results involving proline are also observed in *Episyrphus balteatus*, which has a predaceous larval stage (Wacht et al., 2000). *Orius insidiosus* is attracted to a lipophilic substance present in corn silks, and Reid and Lampman (1989) infer that these chemical cues are how this predator distinguished between silks, pollen, and leaf tissue in order to find *Helicoverpa* eggs. Thus, even in instances when the insects are thought to be primarily predaceous (e.g. lacewing larvae and mantids), there are sensory adaptations that allow them to identify non-prey foods such as pollen.

7.3   Morphological Adaptations

Structures that allow predators to collect, manipulate, and ingest pollen are pervasive throughout entomophagous arthropods. Often, these structural adaptations involve specialized morphology that is used to collect pollen from entomophilous plants, to separate pollen from liquid food sources, and to crush the hard walls of the pollen grains.

7.3.1   Setae

Pollen-collecting hairs are commonly observed on the bodies of pollinivorous natural enemies, a conspicuous example being syrphid flies. Many syrphids possess hairs that allow them to collect pollen from plants that they consume later while cleaning their bodies (Holloway, 1976; Olesen and Warncke, 1989). These hairs may be locally present in the form of a cleaning-comb (Holloway, 1976). Holloway (1976) hypothesizes that the abundance of these specialized setae may give an indication of whether specific syrphids feed on entomophilous versus anemophilous plants, since entomophilous plants produce pollen that is adapted to sticking to insect pollinators. But it should also be recognized that these hairs may have alternative functions; J. R. Haslett notes that only males of *Platycheirus* sp. have combs of dense hairs on their front femorae, but the females consume considerably more pollen than the males, which suggests that in this case the combs may serve purposes other than pollen cleaning (Gilbert, 1981). Combs are also important in mycophagy, and this topic will be revisited in Chapter 14.

7.3.2   Mouthparts

Mouthparts possess a diverse set of appendages that can be used for manipulating pollen grains or extracting their nutrients. The pollinivorous genus *Euseius* has chelicerae specialized for pollen-feeding; these chelicerae have small, convex inner surfaces with minute denticles only at the distal end of the fixed digit (McMurtry and Croft, 1997). The mandibles of pollinivorous adult lacewings are smaller than those of entomophagous species (Canard et al., 1990). Pollen rakes have been identified on the mandibles of the coccinellids, *Tytthaspis sedecimpunctata* and *T. trilineata* larvae (Hodek and Honěk, 1996; Ricci, 1982, 1986a). Pollen-feeding is correlated with larger labellums in syrphid adults, and this enlarged labellum may aid in removing pollen grains from the anthers of flowers. Dry pollen grains are grabbed and twisted with the inner labellar surface, and moved into what are termed 'food-furrows' (Gilbert and Jervis, 1998; Schuhmacher and Hoffmann, 1982). In these furrows, saliva is mixed with the grain, and the mixture is then sucked into the mouth (Schuhmacher and Hoffmann, 1982). Prestomal teeth and brush-like features on the

tips of the labellum facilitate dislodging of pollen grains from the anthers in parasitoid Diptera, although these structures are not widespread in this group (Gilbert and Jervis, 1998). Bombiliids employ their tarsi to collect the grains and place them in the oral cavity (Gilbert and Jervis, 1998). Finally, the mouthparts of Mutellidae and Scoliidae have elongated maxillary palps that are covered in dense hairs, presumably to assist in manipulating pollen (Jervis, 1998). O'Toole observed that species in these families regurgitate liquid onto anthers, and then use their palps to collect the pollen grains that adhere to the fluid (Jervis, 1998).

Once the pollen is obtained, extracting the nutrients from within the pollen wall is accomplished using a variety of morphological adaptations. Many entomophagous arthropods prefer not to swallow the entire pollen grain, and ingest only its liquid contents. Members of Phytoseiidae and Anthocoridae pierce the grains with their stylets and extract the liquid contents (Chant, 1959; Elbadry, 1968; Elbadry and Elbenhawy, 1968a; Fauvel, 1974). In calypterate Diptera, the pollen grains are probably dissolved in saliva and then are transported in solution up the proboscis via the pseudotracheal canals of the labella (Gilbert and Jervis, 1998). A large number of pseudotracheal canals and a short labella is associated with pollinivory in flies, and the width of these canals dictates the size of pollen grain that can ultimately be consumed. Those species with a CNEA are likely entirely prohibited from directly consuming pollen (Gilbert and Jervis, 1998).

7.3.3 Internal Anatomy

For arthropods that consume the entire grain of pollen, internal anatomy may be specially adapted to dismantle the pollen wall and to ensure that maximum energy is extracted from this food. Some syrphids are believed to simply crush the grains in order to access the nutrients (Parmenter, 1953b). One way that this is accomplished is with bristle-like structures of the crop, which reportedly lacerate the grains and drain their contents into the stomach (Zimina, 1957). Other internal features may aid in swallowing pollen grains and protecting the gastrointestinal tract from damage from the tough grains. Along the oesophagus of the foregut in some syrphids there are backward-facing spines that presumably prevent pollen grains from moving anteriorly (Nayar, 1965). Also, some syrphids lack a peritrophic membrane, and possess a compensatory thickening of the midgut epithelium that reduces the risk of damage from solid pollen grains (Nayar, 1965). Finally, the length of the digestive tract is longer in phytophagous Coccinellidae than in predaceous species (Sakurai, 1968), and elongation in the gastrointestinal tracts of these and other omnivores may be a necessary adaptation that has evolved to extract nutrients from these less digestible foods.

Pollen is more difficult to digest than nectar, and so it is necessary for some insects to separate the two foods. As an example, *Apis mellifera* possesses a structure in the proventriculus that is used to separate pollen from nectar (Bailey, 1952), although in this case the insect can digest the pollen. Although the internal anatomy

of the proventriculus of granivorous carabids is known to have similar functional structures (see Chapter 10), this topic has not been well studied for pollinivory in natural enemies.

7.4   Adaptations to Digesting the Nutrients of Pollen

In order to derive energy from pollen, insects must possess a means of digesting nutrients and overcoming defensive hurdles that are unique to plants. Digesting plant nutrients poses some unique challenges for arthropods that are specialized to feeding on insects. For example, arthropods that cannot mechanically destroy the pollen wall require specialized physiological conditions that either degrade or disrupt the pollen exine (Roulston and Cane, 2000). Also, plants are composed of starches, pectin, and other polymers that are not present in animal tissues, and the most entomophagous of natural enemies may not be privy to the appropriate digestive enzymes that degrade these phytochemicals. Entomophagous arthropods use several non-mechanical strategies to access and digest pollen nutrients. First, many natural enemies produce enzymes that allow them to digest the polysaccharides in the pollen wall. Arthropods that do not produce digestive enzymes capable of breaking down plant-specific polymers may acquire the appropriate digestive peptides from the pollen itself, or from endosymbiotic relationships with microbes. Also, it may be possible for zoophagous arthropods to avoid digesting plant-specific polymers entirely, and they may access the internal nutrients within the pollen grain by producing a favorable environment within the gut that allows the pollen to germinate and exude its nutrients.

7.4.1   *Enzymatic Adaptations to Digesting Pollen*

Examples of nutrient polymers that do not occur in insect prey are certain polysaccharides (starch, pectin), and amylases and pectinases are necessary for the digestion of these polysaccharides (Boyd and Cohen, 2002; Cohen, 1996; Zeng and Cohen, 2000). Many entomophagous arthropods possess these enzymes, and their presence in predatory insects is an indication of phytophagy or pollinivory. Amylases are important in breaking down starch and glycogen (Amylase Research Society of Japan, 1995), and amylase is commonly reported in natural enemies. In addition to producing these enzymes in their salivary secretions, some arthropods have these enzymes in their guts. For instance, α-amylase and α-glucosidase are present in the gut of the spider, *Tegenaria atrica* (Mommsen, 1978). Although glycogen is used as a substrate in Mommsen's research, these groups of enzymes also function to cleave the amylopectin portion of starch molecules (Lehninger, 1982), and their presence in the spider gut may assist in digesting plant starches consumed with the web. Still, it should not be forgotten that amylases are used in metabolizing glycogen from

animals, and do not unequivocally indicate the digestion of starch-containing tissues, as is assumed in some literature. The coccinellid, *Exochamus flavipes*, has amylases in the guts of both larvae and adults, but larvae are supposedly strictly carnivorous (Geyer, 1947). The predatory midge, *Aphidoletes aphidimyza*, has amylase in its salivary gland secretion, and although starch is used as a substrate for this enzyme, the authors hypothesize that the amylase metabolizes glycogen in its prey (Laurema et al., 1986). Amylases are also detectable in a range of predatory Heteroptera, including *Orius insidiosus* (Zeng and Cohen, 2000) and *Podisus maculiventris*, and *Zelus renardii* tests positive for amylase in their salivas and guts (Chapman, 1998; Cohen, 1990). *Geocoris punctipes* and *Sinea confusa* have amylase only in their guts and *Nabis alternatus* only has amylase in its saliva (Cohen, 1990, 1996).

Pectins are polysaccharides that lend rigidity to the pollen wall (Roulston and Cane, 2000), and pectinases are necessary to degrade these molecules. Because pectin is only found in plants, possessing pectinases is a better indication of phytophagy than amylases. Indisputably, amylases are more commonly reported than pectinases. In part, this may be because pectins do not occur in high enough concentrations to make it nutritionally worthwhile for entomophages to harbor enzymes necessary for their degradation. Nevertheless, some predatory mirids (like *Helopeltis clavifer* and *Deraeocoris nebulosus*) possess pectinases in their saliva and midguts (Boyd and Cohen, 2002; Miles, 1972, 1987). The Miridae aside, pectinases are infrequently reported from entomophagous species.

In addition to producing enzymes specific for plant tissue, some entomophages may be able to acquire necessary enzymes from the pollen itself. Honeybees utilize pollen-derived enzymes to digest specific nutrients within the pollen, and these enzymes may also be used by entomophages to assist in pollinivory. A number of proteases can be found in pollen depending on the species, and pollen-derived chymotrypsin, trypsin, and carboxypeptidases may contribute to a substantial proportion of the protease activity in the gut of *Apis mellifera* during pollen digestion (Grogan and Hunt, 1979). Gut proteases in entomophagous arthropods are generally not limiting, but other pollen-incorporated enzymes, such as amylases and pectinases that are abundant in pollen (Stanley and Linskins, 1974) may play a role in pollen digestion. Empirical research is necessary to substantiate this hypothesis.

7.4.2   Other Strategies for Digesting Pollen

It is possible that no digestive processes are necessary to access the nutrients of pollen. As mentioned earlier, pollen readily germinates in sucrose solutions and upon germinating the grains release their nutritional contents (Linskins and Schrauwen, 1969; Stanley and Linskins, 1965) (see Chapter 3). Some insects prompt this germination externally, by disturbing the pollen grains in nectar, and

drinking the pollen nutrients with the nectar (Gilbert, 1972; Nicolson, 1994). In 1883, Müller noted that the syrphid *Rhingia rostrata* deliberately moved pollen grains into the nectar of *Lythrum salicaria* during the feeding process in the field, likely resulting in the leaching of pollen nutrients into the nectar. Additionally, it may be possible for entomophagous arthropods to germinate the pollen grains in their stomachs, thereby accessing the nutrients. In two species of syrphids, intact grains simply rupture in the insect midgut without mechanical disruption (Haslett, 1983) (Fig. 7.2). Haslett hypothesizes that the grains ingested by the flies are yielding their contents to the sugar solutions contained within the insect gut, but does not discount that digestive enzymes may also play a role here.
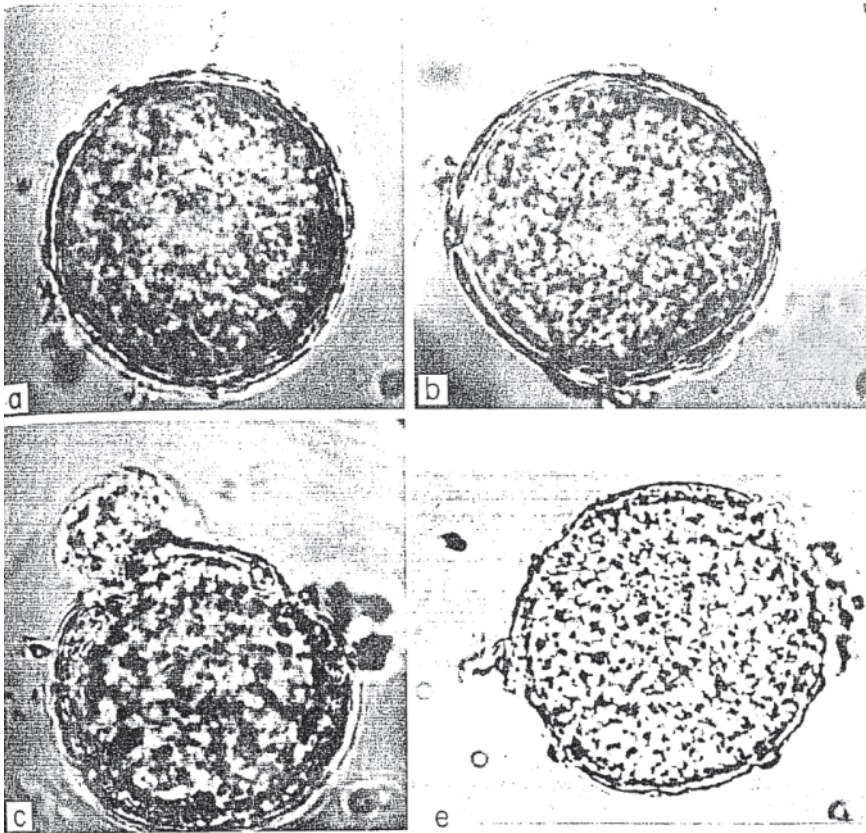

Fig. 7.2 *Ranunculus repens* pollen grains (unstained) taken from difference regions of the gut of *Cheilosia albitarsis*. (a) Pollen from the esophagus, (b) pollen from the crop, (c) pollen from the mid-gut, (d) pollen from the rectum (Reproduced from Haslett, 1983. With permission from Blackwell)

7.5   Conclusion

In summation, a range of adaptations to collecting, consuming, and digesting pollen abound within species ordinarily considered as primarily entomophagous. Indeed, the large carabid beetle, *Harpalus caliginosus*, can consume 50 mg of corn pollen per day in the laboratory (Mullin et al., 2005). Although this is a phylogenetically diverse group of organisms, analogous inventions have been put to use to collect the pollen (e.g., rakes, combs, and hairs), violate the pollen exine and gain access to the nutrients inside (e.g., crushing mandibles, internal bristles and the proventriculus, or solubilizing the grains in fluid), and catabolize the nutrients within (various digestive enzymes, some of which may be pollen-derived). The topic to be explored in the next chapter is why pollen is worth all of this fuss for natural enemies. As it turns out, this widespread plant material is a uniquely rich source of nutrients.