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Nutritional Ecology of Wood-Feeding Coleoptera, Lepidoptera, and Hymenoptera

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15.1 INTRODUCTION

Woody tissues are produced by each of the approximately 44,000 species of trees, shrubs, and woody vines found worldwide (Hickin, 1975). Most woody tissues are tougher, drier, and nutritionally poorer than leaf tissue when considered as a substrate for insect growth and development (Slansky and Scriber, 1985). Nevertheless, many insects have evolved to live and feed in woody environments; some species inhabit the relatively soft and nutritionally rich inner bark (phloem), whereas others are found in the harder and more nutrient-deficient sapwood and heartwood. Other species are xylomycetophagous, feeding primarily on symbiotic fungi that grow within their galleries. Certain wood feeders inhabit living trees, some occur in recently dead trees or decaying logs, and others live within structural timbers and furniture.

This chapter reviews the evidence that the major woody tissues, by their chemical and physical nature, provide wood-feeding insects with distinct and often relatively harsh environments and that, in response to selection pressures imposed by woody environments, these insects have evolved specific morphological, physiological, and behavioral adaptations. Our coverage is limited to the principal families of phloem, sapwood, and heartwood feeders listed in Table 15.1. Additional information relevant to wood feeders is presented by Waller and La Fage in Chapter 16 (termites), Kukor and Martin in Chapter 26 (fungus-feeding arthropods), and Anderson and Cargill in Chapter 30 (aquatic detritivorous insects).

15.2 FOOD CHARACTERISTICS

15.2.1 Anatomy of the Woody Stem

Trees are generally classified as hardwoods (angiosperms—e.g., oak, ash, and maple) or softwoods (gymnosperms or conifers—e.g., pine, spruce, and fir). Proceeding inwardly through a transverse section of a "typical" tree (Fig. 15.1) is first the protective outer bark, followed by the relatively thin, food-conducting inner bark. Next is the cambium, the meristematic sheath of cells that produces phloem to the outside and xylem to the inside. The xylem (wood) comprises the bulk of the woody tissues and is divided into sapwood, the outer, water-conducting, and usually lighter-colored portion; and heartwood, the inner, physiologically inactive, and usually darker portion (Kramer and Kozlowski, 1979). At the center of the stem is the relatively soft pith.

Table 15.1. Principal Families of Coleoptera, Hymenoptera, and Lepidoptera That Inhabit the Inner Bark (IB), Sapwood (SW), and Heartwood (HW) of Woody Angiosperms (A) and Gymnosperms (G)

Order Family	Approx. No. of species: World	Approx. No. of species: N. Am.	Hosts	Principal tissues utilized[a]	Condition of woody material commonly inhabited[b]
Coleoptera					
Anobiidae	911	250	A, G	SW, HW	Dead, lumber
Bostrichidae	455	62	A	IB, SW	Live, dead, lumber
Buprestidae	11,391	662	A, G	IB, SW, HW	Live, dead
Cerambycidae	20,000	1,200	A, G	IB, SW, HW	Live, dead, lumber
Lyctidae	65	19	A	SW	Lumber
Platypodidae	1,000	7	A, G	SW, HW	Live, dead
Scolytidae	6,000	566	A, G	IB, SW, HW	Live, dead
Hymenoptera					
Siricidae	85	18	A, G	SW, HW	Live, dead
Xiphydriidae	82	6	A	SW	Dead
Lepidoptera					
Cossidae	650	45	A	IB, SW, HW	Live
Sesiidae	1,063	115	A, G	IB, SW	Live

Sources: von Dalla Torre (1923), Linsley (1959), Anderson (1960), Arnett (1971), Baker (1972), Hickin (1975), Smith (1976; 1979), Furniss and Carolin (1977), Heppner and Duckworth (1981), S. L. Wood (1982), Hodges et al. (1983).

[a] Most wood feeders consume the woody tissues that they inhabit; however, some scolytids and probably all platypodids, siricids, and xiphydriids are xylomycetophagous (see text).

[b] Live = living and healthy, weakened, or dying trees; dead = recently killed or felled trees to well-decayed logs; lumber = partially or fully seasoned timber in any stage of processing.

Woody plants add consecutive layers (growth rings) of xylem and phloem to the stem throughout their lives; xylem accumulates over time, whereas old phloem is eventually sloughed off. Within a single xylem growth ring, a transition occurs from relatively thin-walled cells produced early in the growing season (earlywood) to thick-walled cells produced later (latewood) (Fig. 15.1; Zimmermann and Brown, 1971).

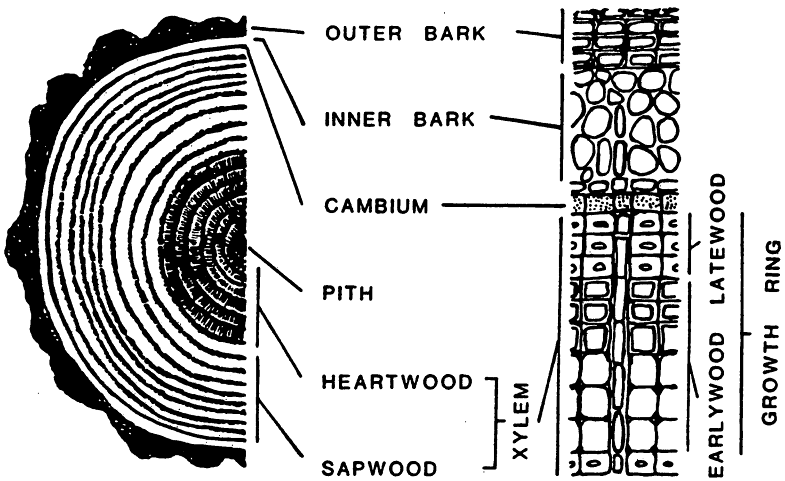

Fig. 15.1. Pictured on the left is a transverse section of a tree stem showing the major tissues, which are, proceeding inwardly, outer bark, inner bark (phloem), cambium, xylem (composed of sapwood to the outside and heartwood to the inside), and pith. On the right is a transverse section of dormant pine stem tissue showing the cellular nature of the outer and inner bark, cambium, and one growth ring of xylem that is differentiated into latewood (thick-walled cells) and earlywood (thin-walled cells). (Drawing on right adapted from Zimmermann and Brown, 1971, by permission.)

15.2.2 Nutritional and Physical Nature of Woody Tissues

Woody-tissue characteristics of potential relevance to wood-feeder performance include nutritional substances (cell wall components, starch, sugars, nitrogen-containing compounds, lipids, minerals, water, pH, and gases), secondary compounds, and structural/toughness features (Table 15.2).

Walls of woody cells are highly fibrous and consist primarily of three polymers: cellulose, hemicellulose, and lignin. A new cell wall is mostly pectic materials (polysaccharidelike compounds that serve as intercellular cement). Cellulose and hemicellulose are deposited during secondary wall formation, followed by deposition of lignin. Cellulose is deposited as rather insoluble crystalline microfibrils, and it serves as the main structural component of cell walls. The hemicelluloses (noncellulosic polysaccharides) and lignin (a highly complex polymer of phenylpropane units) further strengthen cell walls (Browning, 1963; Timell, 1965; Panshin and de Zeeuw, 1980).

Outer bark is dead, relatively dense, corky tissue that protects the underlying vascular layers from mechanical damage and desiccation. For wood feeders, it is a comparatively poor food, containing low concentrations of most nutrients and water (Table 15.2). Outer bark is highly suberized (waxy) and may contain high levels of tannins, phenolics, and alkaloids (Chang, 1954; Jensen et al., 1963).

Table 15.2. Chemical, Nutritional, and Physical Characteristics of the Major Stem Tissues of Temperate-Zone Trees

	Percent composition by tissue				
Component[a]	Outer bark	Inner bark	Cambium	Sapwood	Heartwood
Cell wall constituents					
Cellulose	20–30 n[b]	21–37 yz	20–43 ayz	40–45 y	43–44 y
Hemicellulose	No data	9–30 yz	30–45 yz	23–35 y	25–34 y
Lignin	27–58 bnx	4–53 bnxyz	2–20 abxyz	21–30 bxy	23–30 bxy
Pectin	No data	3–18 xyz	3–22 xyz	1–4 xy	0.3–1 y
Suberin	2–40 n	—	—	—	—
Nutritional components					
Starch + sugar	No data	4–23 lmw	3–37 abx	1–5 ceo	—
Nitrogen	0.2–0.6 bkrxy	0.2–2 bfkrxy	1–5 abhkxy	0.05–0.3 bhkrxy	0.03–0.1 bhkrxy
Lipid	1–38 dn	0.3–4 n	No data	0.1–7 s	0.2–20 s
Mineral ash	0.2–3 bcxy	1–10 bcxy	3–22 abcxy	0.2–0.7 abcjxy	0.2–0.8 bcjxy
Water	17–28 qy	38–71 qy	84–94 ay	28–71 fguvy	23–62 fguvy
Density	0.4–0.7 pq	0.3–0.5 p	No data	0.3–0.8 it	0.3–0.8 it

[a] Cellulose, hemicellulose, lignin, and pectin values calculated on an extractive-free dry-weight basis; suberin, carbohydrate, nitrogen, lipid, and ash values calculated on an unextracted dry-weight basis; water content presented on a fresh-weight basis. Density = oven-dry weight of sample/weight of water displaced by the sample when in the green (fresh) condition.

[b] References: a, Allsopp and Misra (1940); b, Anderson and Pigman (1947); c, Basham and Cowling (1976); d, Browning and Bublitz (1953); e, Buchanan (1963); f, Cameron and Appleman (1933); g, Clark and Gibbs (1957); h, Cowling and Merrill (1966); i, Elliott (1970); j, Ellis (1965); k, Grozdits and Ifju (1973); l, Hepting (1945); m, Hodges and Lorio (1969); n, Jensen et al. (1963); o, Jones and Bradlee (1933); p, Koch (1971); q, Martin (1969); r, Merrill and Cowling (1966); s, Mutton (1962); t, Panshin and de Zeeuw (1980); u, Parker (1954); v, Peck (1955); w, Siminovitch et al. (1953); x, Stewart (1957); y, Thornber and Northcote (1961); z, Thornber and Northcote (1962).

Among the stem tissues, inner bark (phloem) ranks second behind cambium in nutritional quality (Table 15.2). It is relatively soft, comprising mostly living, thin-walled cells. In addition to having relatively high levels of nutrients and water, phloem may contain tannins and resins (Howard, 1971). Photosynthate transport usually occurs in the thin layer of phloem (0.2–1.0 mm thick) nearest the cambium; hence, phloem nutrients are most concentrated in these cells (Kramer and Kozlowski, 1979).

Because the cambium is an active meristematic tissue and is almost entirely living, it has the highest water content and nutrient levels of any woody tissue (Table 15.2). Although the cambium is the most nutritious tissue for wood feeders, it comprises the smallest fraction of all the major stem tissues (Kramer and Kozlowski, 1979).

Sapwood is a less nutritious environment for wood feeders than phloem (Table 15.2). The walls of most xylem cells are heavily lignified (woody), thus making the tissue hard and dense. About 10% of the sapwood is living parenchyma; the remainder consists mostly of dead, open-ended, water-conducting cells. Resins may occur in high concentrations in sapwood, especially in conifers (Hillis, 1962). Sapwood mineral levels are highest in the outer (newest) growth rings (Basham and Cowling, 1976) but are lower than those of the cambium and phloem (Table 15.2). Only a small portion of the sapwood actively conducts water: the outermost one or two growth rings in ring–porous hardwoods (e.g., ash, chestnut, and oak), and several of the outermost rings in diffuse–porous hardwoods (e.g., aspen, birch, and maple) and conifers (Kozlowski and Winget, 1963; Kramer and Kozlowski, 1979). These patterns of water conduction explain in part why ring–porous hardwoods are generally more vulnerable to wilt diseases (e.g., chestnut blight, Dutch elm disease, and oak wilt; Kramer and Kozlowski, 1979) and girdling insects (e.g., the buprestid *Agrilus bilineatus* on oaks; Haack and Benjamin, 1982), than diffuse–porous hardwoods or conifers.

Although heartwood is similar to sapwood in density, it is nutritionally poorer (Table 15.2). Because heartwood lacks living cells, N levels are typically very low; values exceeding 0.3% (dw) usually reflect the presence of alkaloids (Cowling and Merrill, 1966). Many secondary compounds are deposited in the heartwood, including resins, polyphenols (tannins, stilbenes, glycosides, and lignans), tropolones (phenollike substances with fungicidal and bactericidal properties), and alkaloids (Hillis, 1962; Shigo and Hillis, 1973). Heartwood water content is generally less than that of sapwood in conifers, but they are similar in hardwoods (Peck, 1953; Skaar, 1972). Concentrations of P and K are usually lower in heartwood than sapwood, whereas the reverse is generally true for Ca, Mg, Mn, and Zn; Cu and Fe levels are generally low in all woody tissues (Basham and Cowling, 1976).

Pith is mostly parenchyma and usually occurs as a narrow cylinder along the central axis of branches, stems, and roots (Esau, 1977). In twigs and young branches, pith cells are mostly living and function in food storage, but they are usually dead in older branches and stems, especially in regions where heartwood formation has occurred. In heartwood, the central region (near the pith) has higher N levels than the outer portions (Merrill and Cowling, 1966). Although nutritional data for the pith are mostly lacking, its nutritional quality would probably be higher than sapwood but lower than phloem. More information concerning chemistry, morphology, and physiology of woody tissues is presented in Wise and Jahn (1952), Hillis (1962), Browning (1963), Zimmermann and Brown (1971), Esau (1977), and Kramer and Kozlowski (1979).

Little is known about the pH of woody tissues. In general, phloem sap is alkaline (pH 7–8) whereas xylem sap is acidic (pH 4–6; Kramer and Kozlowski, 1979; Raven, 1983). McNamara et al. (1970) reported that heartwood is more acidic than sapwood in oaks, but in birch, beech, maple, hemlock, and pine they are of similar pH. They observed no consistent seasonal trends in xylem pH but did report that sapwood becomes more acidic as it dries.

Few studies have been conducted on the composition of gases in woody tissues (Scarth and Gibbs, 1930; Chase, 1934). Chase (1934) reported that (1) CO_2 levels are higher and O_2 levels are lower in wood than in the atmosphere, (2) wood O_2 levels are lowest in summer and highest in winter with the converse being true for CO_2, (3) O_2 levels are higher in ring–porous wood than in diffuse–porous or conifer wood, and (4) O_2 levels are higher in sapwood than heartwood. Reports are lacking on the air composition within wood-feeder galleries; however, it is probably similar to the atmosphere, because most galleries originate near or contact the bark surface.

In summary, the woody environment poses many physical and nutritional obstacles to wood feeders. Among these are (1) restriction of the physiologically active (and thus most nutritious) stem tissues to a very narrow band of phloem and sapwood on either side of the cambium, (2) protection of this nutrient-rich band using dense, high-fiber, nutrient-poor, and allelochemical-rich tissues (bark and wood), and (3) construction of cell walls using complex, highly digestion-resistant polymers.

15.2.3 Sources of Variation in Woody-Tissue Quality

15.2.3.1 Seasonal Variation. Most of the woody tissues show seasonal fluctuations in nutrient levels, especially the phloem and sapwood of temperate-zone woody plants (Kramer and Kozlowski, 1979). In these, levels of starch (Jones and Bradlee, 1933; Siminovitch et al., 1953), N (Cameron and Appleman, 1933; Tromp, 1970), and lipid (Gäumann, 1935; Arrhenius, 1942) generally peak during autumn or winter, decline sharply in spring, when rapid growth resumes, and remain low or slowly increase during summer. Concentrations of the above nutrients are thus relatively low during the summer, when warmer temperatures favor wood-feeder activity. Sapwood water content (Clark and Gibbs, 1957) and mineral levels (Bollard, 1958) are generally highest in spring and lowest in winter; however, most phloem minerals reach maximal levels in autumn and minimal levels in spring (White et al., 1972). Nutrient fluctuations are more pronounced in phloem than sapwood and in deciduous hardwoods than evergreen conifers (Kramer and Kozlowski, 1979).

15.2.3.2 Inter- and Intraspecific Variation. Almost every measurable tree characteristic varies among species as well as within a species with respect to tree age, distance from the pith, height along the stem, and position within a growth ring (Kramer and Kozlowski, 1979; Panshin and de Zeeuw, 1980). In sapwood, nutrient concentrations decline from the cambium to the heartwood (Cameron and Appleman, 1933; Murneek, 1942), probably reflecting the diminishing number of living parenchyma cells (Merrill and Cowling, 1966). Within a single growth ring of sapwood, water content and nutrient levels are greater in earlywood than latewood (Merrill and Cowling, 1966). In many trees, sapwood water content increases from the base of stems upward (Ovington, 1956). Drought stress (Mattson and Haack, 1987) and soil fertility (Stark, 1965; White et al., 1972) influence a tree's chemical composition as well as its ability to resist attack by wood-feeding insects.

15.2.3.3 Wood Seasoning. The most obvious result of seasoning timber is a reduction in water content. Wood holds about 20–23% water (fw) at fiber saturation, which theoretically is when cell walls are saturated but cell cavities are devoid of water (Panshin and de Zeeuw, 1980). In the United States, water content of lumber is about 11% after commercial drying but varies between 11 and 13% when stored outdoors under cover (Skaar, 1972; Panshin and de Zeeuw, 1980). Under heated conditions during winter, water content of interior woodwork can drop to 4–7% (Peck, 1955; Panshin and de Zeeuw, 1980). As wood dries, lipid content declines (Browning and Bublitz, 1953; Mutton, 1962) whereas soluble carbohydrates and N move with the water stream and accumulate near the outer surfaces (King et al., 1974; Long, 1978).

15.2.3.4 Decay. Logs, lumber, and dead portions of living trees are subject to decay caused by fungi and bacteria, which enzymatically degrade cell wall polymers (Kirk, 1973). Wood decay usually occurs when the water content is above fiber saturation, a common situation where wood comes in contact with soil (Panshin and de Zeeuw, 1980). As decay progresses, wood porosity and moisture-holding capacity increase whereas wood density and structural strength decline (Campbell and Bryant, 1940; Yoneda, 1975; Panshin and de Zeeuw, 1980). Close to 90% of the initial woody mass of temperate-zone trees is lost in the first 75 years following death (Lambert et al., 1980; MacMillan, 1981), but less than 10 years is required for bole wood to decay in the humid tropics (Lang and Knight, 1979). As bole wood of balsam fir decays, N, P, and H_2O levels increase whereas density, Ca, Mg, and K levels decrease (Lambert et al., 1980).

15.2.4 Predictability and Persistence of Woody Tissues

Perennial growth and the long lives of woody plants contribute to making woody tissues seemingly predictable and persistent resources. However, because wood feeders require host plants of a particular species, age, and physiological condition (Sections 15.3.4 and 15.3.5), the actual distribution of usable resources becomes spatially and temporally unpredictable (Beaver, 1984). For example, *Scolytus ventralis* colonizes only about 4%, and *Dendroctonus ponderosae* 66%, of the trees they attack (Raffa and Berryman, 1980). Such resource patchiness may have selected for widespread insect dispersal via flight and development of complex chemical communication systems (Section 15.3.5).

Once trees die, the lignified nature of most cell walls allows for their lengthy persistence. However, the degree of persistence for any woody tissue tends to be inversely correlated with its nutritional quality. Phloem and cambium deteriorate rapidly through drying, decay, and exploitation by wood feeders, whereas outer bark and xylem may persist for years (Graham, 1925; Savely, 1939; Wallace, 1953; Hamilton, 1978; Beaver, 1984).

15.3 INSECT ADAPTATIONS TO WOODY ENVIRONMENTS

15.3.1 Morphological and Anatomical Adaptations

Adaptations to the woody environment are seen in the body form, integument, mouthparts, and digestive tract of wood feeders. Body form is very similar among those insects in which both the adults and larvae actively tunnel (most Anobiidae, Bostrichidae, Lyctidae, Platypodidae, and Scolytidae). Adults are generally cylindrical, are more or less squat, and have a strongly rounded off prothorax (Browne, 1961; Cymorek, 1968). This shape is well designed for boring in wood, because these beetles, and scolytids in particular, fold their legs and walk on protibial spines while rotating along their longitudinal axes (Schmitz, 1972; Gouger et al., 1975). Larvae of the above families are mostly scarabeiform; however, first-instar larvae of some anobiids, bostrichids, and lyctids are elongate, with these usually originating from eggs deposited inside xylem cells (Cymorek, 1968).

It is primarily the larval stage that actively tunnels in the Buprestidae, Cerambycidae, and wood-feeding Hymenoptera and Lepidoptera. Larvae of these groups are elongate, but their cross-sectional shape varies with the host tissue inhabited. For example, phloem-feeding cerambycids are dorsoventrally flattened, xylem feeders are cylindrical, and some species that develop first in phloem and later in sapwood are first flattened and then cylindrical (Craighead, 1923). Similarly, phloem-feeding buprestids are dorsoventrally compressed whereas xylem-feeding Buprestidae, Hymenoptera, and Lepidoptera are cylindrical (Cymorek, 1968).

In general, wood feeders range in adult body size from small (many anobiids, bostrichids, lyctids, platypodids, and scolytids) to large (many buprestids, cerambycids, and wood-feeding Hymenoptera and Lepidoptera). However, within a specific group, body size tends to increase with decreasing food quality (Table 15.3). For example, xylem-feeding buprestids, cerambycids, and sesiids tend to be larger on average than their phloem-feeding counterparts. In the scolytid tribe Micracini, body size is distinctly related to the tissue consumed, with average elytral length (from S. L. Wood, 1982) being 1.3 for 75 phloem feeders, 1.7 for 20 pith feeders, and 2.1 mm for 65 xylem feeders (i.e., those that are actually xylophagous, not xylomycetophagous). Such evidence supports our earlier hypothesis that the nutritional quality of pith is intermediate between phloem and sapwood (Section 15.2.2). This trend in wood-feeder body size may have evolved to allow better digestion of poor-quality foods as evidenced by longer and more complex digestive systems in xylem than in phloem feeders (see below).

The legs of many wood-feeding larvae are reduced in size and number. For example, the legs of anobiids, bostrichids, and lyctids are very small and are used primarily in feeding and frass removal (Cymorek, 1968). Buprestid, platypodid, scolytid, and some cerambycid larvae are completely legless. Among cerambycid larvae, species with legs typically tunnel in decayed wood whereas legless species usually feed in solid wood (Craighead, 1923).

Features of the larval integument vary with the woody tissue inhabited. Cerambycid larvae inhabiting living trees possess much pubescence, which probably aids in gripping wet, sappy mines; those in decayed wood generally have a thick, glabrous integument, and those in dry wood have a few stiff setae and a thin integument (Craighead, 1923). A thin integument may allow wood feeders in dry environments to absorb water from their surroundings; this would be adaptive, because the water content of their frass is generally higher than the ingested wood (Mishra and Singh, 1977). Production of frass that is more moist than the wood inhabited may indicate a poor ability to conserve water or may serve to humidify the gallery to the benefit of associated external microorganisms. Placement and angle of body spines and setae determine in great part how and in what directions larvae can move within their galleries (Mamaev and Semenova 1961; Cymorek, 1968).

Larvae and adults of wood-feeding insects have well-developed mouthparts and associated musculature (Dorsey, 1943). Cerambycid larvae inhabiting dry wood have short, gougelike mandibles (and produce short, flaky wood chips), whereas those inhabiting living trees possess slender, toothlike mandibles (and produce fibrous shreds of wood; Craighead, 1923; Solomon, 1977a). Siricid larvae can efficiently cut and tear wood, because their mandibles are toothed along the distal edge (Cymorek, 1968).

The digestive tract of wood feeders varies according to the woody tissue consumed. For example, many anobiids and cerambycids that inhabit dry wood or heartwood possess a grinding gizzard (Mansour and Mansour-Bek, 1934; Cymorek, 1968; Chararas, 1979) that fragments ingested wood, thus

Table 15.3. Average Body Length and Developmental (Generation) Time of Families of Wood-Feeding Insects That Inhabit Various Stem Tissues of Temperate-Zone Trees

Order Family	Principal feeding zone(s)[a]	No. of spp.	Body length (mm)[b] Mean	(Range of means)	Developmental time (yr) Mean	(Range)	Ref.[c]
Coleoptera							
Anobiidae	SW, HW	6	5	(4–7)	1.8	(1–3)	bfim
Bostrichidae	SW	9	7	(3–16)	1.7	(0.5–3)	abim
Buprestidae	IB	6	9	(8–12)	1.2	(1–2)	bcilm
	IB, SW	10	10	(6–18)	1.9	(1–2)	abcim
	SW, HW	10	19	(12–30)	3.0	(2–4)	abfim
Cerambycidae	OB	2	19	(17–20)	2.3	(2–3)	bd
	IB	11	14	(6–25)	1.1	(1–2)	abdhim
	IB, SW	24	17	(11–30)	1.6	(1–2)	abdhijkmnsvxz
	IB, SW, HW	6	20	(14–24)	2.2	(1–3)	abhit
	SW, HW	3	27	(15–37)	3.1	(2–4)	bdfhmo
	HW	20	30	(14–53)	3.6	(2–5)	bdhimru
Lyctidae	SW	7	4	(3–5)	1.0	(0.5–2)	abim
Platypodidae[d]	SW, HW	4	5	(4–6)	1.0	(0.5–2)	bi
Scolytidae	IB	32	4	(2–7)	1.0	(0.5–2)	abi
	SW, HW[d]	10	3	(2–4)	0.6	(0.3–1)	abi
Hymenoptera[d]							
Siricidae	SW, HW	9	25	(16–44)	1.8	(1–3)	biqwy
Xiphydriidae	SW	8	15	(11–17)	1.2	(1–2)	befim
Lepidoptera							
Cossidae	IB, SW, HW	5	47	(37–60)	2.9	(2–4)	bfim
Sesiidae	IB	11	18	(13–27)	1.0	(1–2)	bgip
	IB, SW	10	29	(22–40)	2.3	(2–4)	bgip

[a] OB, outer bark; IB, inner bark; SW, sapwood; HW, heartwood.

[b] Values represent adult body length for Coleoptera and Hymenoptera, and larval (last instar) body length for Lepidoptera.

[c] References: a, Anderson (1960); b, Baker (1972); c, Carlson and Knight (1969); d, Craighead (1923); e, Deyrup (1984); f, Dominik and Starzyk (1983); g, Duckworth and Eichlin (1978); h, Duffy (1953); i, Furniss and Carolin (1977); j, Galford (1983); k, Gardiner (1960); l, Haack and Benjamin (1982) and Haack et al. (1983); m, Hickin (1975); n, Hosking and Bain (1977); o, Kühne (1975); p, MacKay (1968); q, Morgan (1968); r, Nord et al. (1972a); s, Nord et al. (1972b); t, Solomon (1968); u, Solomon (1972, 1974); v, Solomon (1977b); w, Spradbery and Kirk (1978); x, Starzyk (1977); y, Stillwell (1966); z, Wickman and Seminoff (1968).

[d] The platypodids, SW/HW scolytids (ambrosia beetles), and Hymenoptera are xylomycetophagous.

exposing more surface area to digestive enzymes. The sapwood-feeding lyctids and bostrichids, and certain phloem- and sapwood-feeding cerambycids, lack such a gizzard. The digestive tract, especially the midgut, is very long in certain dry wood- and heartwood-inhabiting cerambycids (Semenova and Danilevskii, 1977; Chararas, 1981), which probably allows for more efficient food breakdown and absorption.

15.3.2 Digestive Enzymes

Wood feeders enzymatically degrade sugars, starch, and structural polysaccharides to varying degrees (Table 15.4). In general, heartwood feeders degrade more classes of structural polysaccharides than sapwood feeders, and these in turn degrade more than phloem feeders. Sapwood-feeding bostrichids and lyctids are exceptions; they lack the ability to degrade hemicellulose and cellulose and must therefore derive nourishment from sapwood parenchyma. Some xylem-feeding cerambycids apparently do not digest sugars (Parkin, 1940), compounds that are often lacking in their food. Certain scolytids of the Micracini are apparently true sapwood feeders (Browne, 1961; S. L. Wood, 1982), but it is not known if they degrade cellulose, a compound that phloem-feeding scolytids do not degrade (Table 15.4; Courtois and Chararas, 1966). Lignin digestion has been recorded in a few xylem feeders (Seifert, 1962; Becker, 1977; Mishra and Singh, 1978; Mishra, 1983; Mishra et al., 1985), with certain heartwood-feeding cerambycids degrading up to 38% of the lignin present. The digestive enzymes of wood feeders may be produced by the insect itself or by gut microorganisms, or they may be acquired from ingested fungi (Chararas, 1979; Breznak, 1982; Chararas et al., 1983; Kukor and Martin, 1983; Martin, 1983; Mishra and Sen–Sarma, 1986).

The great variation in the numbers of species belonging to the families listed in Table 15.1 may reflect the abilities of wood feeders to degrade structural polysaccharides (Table 15.4). For example, cerambycids degrade all classes of structural polysaccharides and comprise the largest family, whereas the sapwood-feeding lyctids, which do not degrade cell walls, have the fewest members worldwide.

Most wood feeders are associated with internal and external symbionts (Francke–Grosmann, 1967; Breznak, 1982). Certain anobiids have gut-dwelling bacteria and yeasts that contribute vitamins and sterols and that fix atmospheric N (Becker, 1977). This latter process may explain how in studies by Baker et al. (1970) and Mishra et al. (1985), xylem feeders accumulated more N than was present in the ingested wood. Fixation of atmospheric N by hindgut bacteria is known to occur in termites (Breznak, 1982) and a wood-feeding cockroach (Breznak et al., 1974). Certain gut symbionts are involved in pheromone synthesis in scolytids (Section 15.3.5). External fungal symbionts of certain bark beetles influence phloem quality by increasing levels of total N (Hodges et al., 1968) and free fatty acid (Clark and Richmond, 1977) and by lowering the reducing sugar content (Barras and Hodges, 1969). Certain scolytids require their associated fungi for successful brood development (Barras, 1973; Norris, 1976) and for overcoming host-tree resistance (Berryman, 1972; Whitney, 1982; Lorio and Hodges, 1985).

15.3.3 Quantitative Food Utilization

Little is known about quantitative food utilization by wood feeders, with the available data representing primarily immature Coleoptera (Tables 15.4 and 15.5). This paucity of information reflects the inherent difficulties in such studies. For example, larvae must be introduced into wood and later located and extracted for weighing, frass (feces plus wood shavings) must be collected and separated, and estimates of the volume or weight of wood consumed must be made. In many studies, frass is collected only once, often weeks or months after feeding was initiated, and analyzed without separating feces from uningested wood shavings. Values of approximate digestibility (AD) for various wood components have often been calculated on the assumption that lignin is not degraded and can thus be used as an internal standard; however, several wood feeders are known to degrade lignin (Section 15.3.2). For these and other reasons, the food utilization efficiency values presented in Tables 15.4 and 15.5 should be viewed with some caution.

Wood feeders, especially xylem feeders, exhibit low relative growth rates (RGRs), as indicated by the few available values (Table 15.5) and by the long generation times of many species (Section 15.3.6). Contributing to this slow growth are low values for AD and efficiency of conversion of digested food (ECD). Because of the dense nature of xylem, low relative consumption rates (RCRs) are expected, but the data are too limited to conclude this (Table 15.5). Nitrogen utilization efficiencies also appear to be relatively low (Tables 15.4 and 15.5). Some AD values lie within the moderate range of 30–50%, indicating that digestive adaptations of some wood feeders (Section 15.3.2) can result in relatively efficient digestion and assimilation. In general, AD values of wood-feeding termites are greater than those of wood-feeding Coleoptera (Becker, 1977). Mamaev (1961) presented several exceptionally high values for the efficiency of conversion of ingested food (ECI) for certain wood-feeding Coleoptera (exceeding 30%; Table 15.5); these imply exceptionally high AD and/or ECD values, but these were not calculated. Because these ECI values appear uncharacteristically high for wood-feeding Coleoptera, they should be confirmed.

15.3.4 Host Range

Wood feeders range from monophagous (one species or genus of host plants) to polyphagous (hosts from unrelated families). In general, monophagy is most common among wood feeders that inhabit living woody plants (early-

Table 15.4. Digestive Ability of Families of Immature Wood-Feeding Insects to Enzymatically Degrade Specific Woody-Tissue Components

Order Family	Principal feeding zone(s)[a]	No. of spp.	Component and % approx. digestibility[b] N	SG	ST	P	HC	C	Ref.[c]
Coleoptera									
Anobiidae	SW, HW	5	+[d] 22–40	+	+	No data	+ 32–40	+ 28–48	adfpqrv
Bostrichidae	SW	2	+	+	+	No data	0	0	r
Buprestidae	IB	3	+	+	+	+	±	+	et
	SW, HW	1	No data	+	+	No data	+ 31–45	+ 41–55	km
Cerambycidae	IB	8	+ 27	+	+	+	+	±	ehru
	IB, SW	4	+ 14	+	+	+	+ 36	+ 38	eior
	SW	4	+ 12	+	+ 23–55	No data	+ 25–38	+ 33–49	ckor
	SW, HW	2	No data	± 0–61	+ 10–76	+	+ 17–54	+ 31–58	en
	HW	2	+	+ 29	+ 18–39	No data	+ 30–42	+ 14–76	klmor
Lyctidae	SW	1	+ 15	+	+	No data	0	0	fr
Scolytidae	IB	12	+ 24–59	+ 25	+ 46–58	+	+ 32	0	befgr
Hymenoptera									
Siricidae	SW, HW	3	No data	+	+	+	+ 15	+ 22–31	jo
Lepidoptera									
Cossidae	IB, SW, HW	2	No data	+	+	+	±	0	es

[a] IB, inner bark; SW, sapwood; HW, heartwood.

[b] N, protein; SG, sugar; ST, starch; P, pectin; HC, hemicellulose; C, cellulose. Tests were of two types, one in which gut extracts were removed and tested for their degrative powers on various substrates, and one in which enzymatic degradation was inferred by a comparison of the relative percent of a given component in the food to that in the frass.

[c] References: a, Baker et al. (1970); b, Balogun (1969); c, Becker (1942); d, Campbell (1929); e, Chararas (1979); f, Hopf (1937); g, Hopf (1938); h, Hosking and Hutcheson (1979); i, Ikeda (1979); j, Kukor and Martin (1983); k, Mansour and Mansour-Bek (1934); l, Mishra (1983); m, Mishra and Singh (1977); n, Mishra and Singh (1978); o, Mishra et al. (1985); p, Müller (1934); q, Norman (1936); r, Parkin (1940); s, Ripper (1930); t, Rivnay (1945); u, Savely (1939); v, Spiller (1951).

[d] +, Enzymatic activity detected in all species tested; 0, no enzymatic activity detected; ±, enzymatic activity detected in some but not all species tested.

Table 15.5. Quantitative Food Utilization by Immature Wood-Feeding Insects That Inhabit Various Woody Tissues

Order Family Species	Tissue analyzed[a]	Nutritional index[b]					Re
		RGR	RCR	AD	ECD	ECI	
Coleoptera							
Anobiidae							
Anobium punctatum	SW	0.004	0.1	25.1			a
Xyletinus peltatus	SW			56.5			m
Buprestidae							
Chrysobothris affinis	IB					34.5	g
Lampra rutilans	IB					32.3	g
Buprestis geometrica	Wood			38–43			h
Cerambycidae							
Morimus verecundus	IB					6.7–28.6	g
Plagionotus detritus	IB					31.3	g
Rhagium fasciculatum	IB					9.2	g
Arhopalus ferus	IB	0.048		24.1			d
	SW	0.011					d
	SW (N)			26.8			d
Hylotrupes bajulus	SW			20–49			bkl
Phymatodes maaki	SW			3.2	35.1	1.2	f
	SW (C)			3.1	39.4	1.2	f
	SW (N)			13.6	117.6	16.0	f
Toxotus mirabilis	SW					4.5	g
Stromatium barbatum	SW, HW			20–50			i
Hoplocerambyx spinicornis	HW			37–51			hj
Scolytidae							
Hylesinus fraxini	IB			17.5			c
Scolytus carini	IB					12.3	g
Scolytus scolytus	IB					33.3	g
Pityokteines sparsus	IB (energy)			46.4			e

[a] IB, inner bark; SW, sapwood; HW, heartwood.

[b] RGR, relative growth rate (mg/mg/day); RCR, relative consumption rate (mg/mg/day); AD, approximate digestibility (%); ECD, efficiency of conversion of digested food (%); ECI, efficiency of conversion of ingested food (%).

[c] References: a, Baker et al. (1970); b, Cannon and Robinson (1981); c, Hopf (1938); d, Hosking an Hutcheson (1979); e, Hosking and Knight (1976); f, Ikeda (1979); g, Mamaev (1961); h, Mishra (1983) i, Mishra and Singh (1978); j, Mishra et al. (1985); k, Rasmussen (1967); l, Seifert (1962); m, William (1977).

succession insects) whereas polyphagy is most prevalent among those inhabiting dead tissues (late-succession insects; Beaver, 1984). This pattern has been shown for cerambycids (Craighead, 1923; Linsley, 1959), scolytids (Stark, 1982; S. L. Wood, 1982), and buprestids (based on data from Baker, 1972; Furniss and Carolin, 1977). Apparently, habitation of living trees requires higher levels of specialization that lead to monophagy, whereas the lack of active defense systems in dead woody tissues may exert less selection for dietary specialization.

Variations exist in the types of woody tissues utilized by temperate and tropical wood feeders. For example, most cerambycids inhabit dead wood in temperate regions, whereas most are live-stem borers in the tropics; the latter pattern may allow for avoidance of tropical termites, which quickly utilize dead wood (Linsley, 1959). Among scolytids and platypodids, most are phloem feeders in temperate areas (80–90%; Beaver, 1979; S. L. Wood, 1982) and dry tropical deciduous forests (58%; Atkinson and Equihua, 1986), whereas most are xylomycetophagous in the humid tropics (66–76%; Beaver, 1979). The prolonged dry season in tropical deciduous forests may select against the xylomycetophagous habit by inhibiting growth of the fungal symbionts; xylomycetophages constituted only 14% of the scolytid and platypodid fauna in the study by Atkinson and Equihua (1986).

15.3.5 Host Location and Colonization

Wood feeders locate their hosts by random search or by responding to chemical cues that are either host- (primary attraction) or insect-produced (secondary attraction; Birch, 1984). Ethanol, produced by trees under stressed conditions (Moeck, 1970; Crawford and Baines, 1977), and certain monoterpenes serve as primary attractants for some scolytids (Moeck et al., 1981) and other wood-feeding Coleoptera (Linsley, 1959; Becker, 1977; Montgomery and Wargo, 1983). In scolytids that initially locate hosts through random search (e.g., *Ips paraconfusus*; Moeck et al., 1981), host acceptance apparently occurs only after some feeding (Elkinton and Wood, 1980). Ethanol and specific products of lignin degradation serve as feeding stimulants (Norris and Baker, 1969; Meyer and Norris, 1974), whereas certain bark chemicals act as repellents or feeding deterrents for scolytids (Norris, 1977); a feeding deterrent for one scolytid species is often a phagostimulant to another.

Little is known about mechanisms of pheromone production in wood feeders other than conifer-infesting scolytids and, to a lesser degree, in some cerambycids (Iwabuchi, 1982) and sesiids (Neal, 1979). Many conifer-infesting scolytids utilize host monoterpenes to synthesize aggregation pheromones (Borden, 1982; D. L. Wood, 1982). Pheromone production occurs in the hindgut region by means of simple oxidation (Borden, 1982; Birch, 1984) and may originally have served as a detoxification mechanism (White et al., 1980; Francke and Vité, 1983). Gut-dwelling bacteria and yeasts are involved in pheromone synthesis in certain scolytids (Borden, 1982; Leufvén et al., 1984). Host quality may influence pheromone production. For example, in the scolytid *Ips calligraphus*, pheromone production is lower when feeding in thin (less resinous) than in thick (more resinous) phloem, with the resultant attack density being less in thin phloem (Vité et al., 1972). Bark beetle pheromones are used interspecifically by their parasites, predators, and associated wood-feeding invertebrates (Borden, 1982; D. L. Wood, 1982; Billings and Cameron, 1984; Birch, 1984).

Phloem feeders are usually the first to inhabit dying and recently dead trees, with sapwood feeders being the next group to colonize (Graham, 1925; Savely, 1939; Mamaev, 1961; Hamilton, 1978; Haack et al., 1983). Apparently because of selection for rapid colonization of the nutrient-rich but ephemeral phloem and cambium, phloem feeders, and especially scolytids, have evolved effective flight and chemical communication abilities. The release of pheromones by bark beetles that infest living conifers leads to further aggregation and subsequent mass attack of the host; mass attack is often required to overcome host resistance (Berryman, 1972; Raffa and Berryman, 1983; Payne and Coulson, 1985). Some bark beetles produce antiaggregation pheromones to curtail mass attack, thereby minimizing intraspecific competition (Birch, 1984). Rapid colonization by the scolytid *Dendroctonus frontalis* is important in reducing subsequent interspecific competition with phloem-feeding cerambycids (Coulson et al., 1980). Resource partitioning often occurs when two or more wood feeders share the same woody tissue within a host species (Hespenheide, 1976; Paine et al., 1981; Beaver, 1984). Changes in the wood-feeder community structure occur during forest succession (Starzyk and Witkowski, 1981) as well as within individual logs as they decay (i.e., wood feeders are replaced by fungus feeders; Wallace, 1953; Mamaev, 1961).

Lumber, although abundant and persistent, may be unsuitable to wood feeders as a result of low nutrient and water content. This restricted occurrence of suitable lumber may explain why certain anobiids and lyctids continue to reinfest the same wooden structure for several generations (Baker, 1972; Hickin, 1975).

15.3.6 Voltinism Patterns

Within a family of wood feeders, developmental times are inversely related to nutritional quality of the woody tissue inhabited (Table 15.3). For example, in temperate areas, phloem-feeding buprestids and cerambycids generally develop in 1 year, sapwood feeders in 2 years, and heartwood feeders in 3 or more. The shorter developmental times of phloem feeders probably reflect (1) the more favorable physical and nutritional qualities of phloem (Table 15.2), (2) that phloem feeders are typically smaller than xylem feeders (Table 15.3), and (3) the less persistent nature of phloem compared with xylem (Section 15.2.4).

Considering that fungus is more nutritious than wood (Martin and Kukor, 1984), the fungal diet of ambrosia beetles, siricids, and xiphydriids may explain why they have shorter generation times than those xylem-feeding anobiids, buprestids, and cerambycids that inhabit similar tissues (SW, SW/HW; Table 15.3). Similarly, the inability of wood-feeding Lepidoptera (at least in the Cossidae) to degrade most structural polysaccharides (Table 15.4) may explain their longer generation times compared with the "enzyme-rich" buprestids and cerambycids that inhabit similar tissues (IB/SW, IB/SW/HW; Table 15.3).

15.4 INSECT RESPONSES TO ENVIRONMENTAL CHANGES

15.4.1 Nutritional Quality of Wood

15.4.1.1 Effects on General Performance. Wood-feeder performance has been studied in relation to wood N, starch, and water content. Larval growth and survival are positively correlated with wood N content (Baker et al., 1970; Becker, 1977; Hosking and Hutcheson, 1979). The anobiid *Anobium punctatum* and the cerambycid *Hylotrupes bajulus* can develop in wood having as little as 0.03% N (dw) (Becker, 1963; Bletchly, 1966). Larval survival and growth rate of *A. punctatum* (Becker, 1977), *H. bajulus* (White, 1962; Becker, 1977), and the lyctid *Lyctus brunneus* (Cymorek, 1966) increase when living in N-enriched wood.

The branch-girdling behavior of adult *Onicerdes* females (Cerambycidae) improves the nutritional quality of their progeny's food (Forcella, 1982). Females girdle small branches of deciduous hardwood trees during late summer and early autumn and then oviposit in the girdled portions. Later, the girdled branches fall to the ground, where the larvae develop. Prior to leaf abscission in autumn, many nutrients (e.g., 33–66% of leaf N) are removed from the leaves and stored in the branches, trunk, and roots of deciduous trees (Kramer and Kozlowski, 1979). If girdling is timed properly, these translocated nutrients are trapped above the girdle and thereby made available to the developing larvae. Forcella (1982) reported a positive correlation between larval survival and N content of girdled branches. This girdling behavior has not evolved among conifer-inhabiting cerambycids, possibly because there is no autumn flush of translocated nutrients from needles to branches (Kramer and Kozlowski, 1979).

Starch content of wood is especially important to lyctids and bostrichids, which are unable to utilize structural polysaccharides as a carbon source (Table 15.4; Wilson, 1933; Parkin, 1936, 1940). This inability may explain why lyctids and bostrichids do not utilize heartwood, a tissue lacking in starch and sugars (Table 15.2). The minimal starch content in which *Lyctus* species develop is about 1.5% (Becker, 1977). Adult females of certain *Lyctus* species gnaw on wood prior to oviposition, possibly testing its nutritional suitability (Parkin, 1936; Cymorek and Schmidt, 1976).

Adult and larval performance of the phloem-feeding scolytid *Pityophthorus lautus* is greatly influenced by host (sumac) quality (Kirkendall, 1983). Adult female residence time (within a gallery system), egg density (eggs/unit length of gallery), and larval survival are all positively correlated with phloem N and total available carbohydrate levels.

Larval development and survival of wood feeders are also influenced by wood moisture content. Most xylem feeders require a wood moisture content above fiber saturation (>20% fw), which typically occurs in dying trees, freshly cut logs, and stumps (Becker, 1977). A few xylem feeders, especially structural lumber pests, can develop in wood with only 6–7% water (fw) (i.e., certain anobiids, bostrichids, cerambycids, and lyctids; Parkin 1943; Gerberg, 1957; Cymorek, 1966; Becker, 1977; Vongkaluang et al., 1982; Williams, 1983). The phloem-feeding buprestid *Agrilus bilineatus* typically infests stressed, but living, oak trees (Haack, 1985a) and is apparently very sensitive to changes in host moisture content. Haack and Benjamin (1980) noted that *A. bilineatus* larvae fail to complete development when infested trees are felled (and thus allowed to dry) early during larval development but that they can develop when felling occurs late in larval development.

The seasonal variation in egg density (eggs/unit length of gallery) values of the scolytid *Ips calligraphus* (Fig. 15.2) may reflect nutritional and physical changes in its host. In this study (Haack et al., 1984b), the outermost sapwood (which females etch regardless of phloem thickness) consisted of earlywood xylem cells during summer and latewood xylem during autumn. Because earlywood cells are thin-walled, less dense, and higher in water and nutrient levels than latewood (Paul, 1939; Merrill and Cowling, 1966; Ifju, 1969; Panshin and de Zeeuw, 1980), females tunneling in summer material are probably better nourished, expend less energy, and thus have more net nutrients to allocate to reproduction.

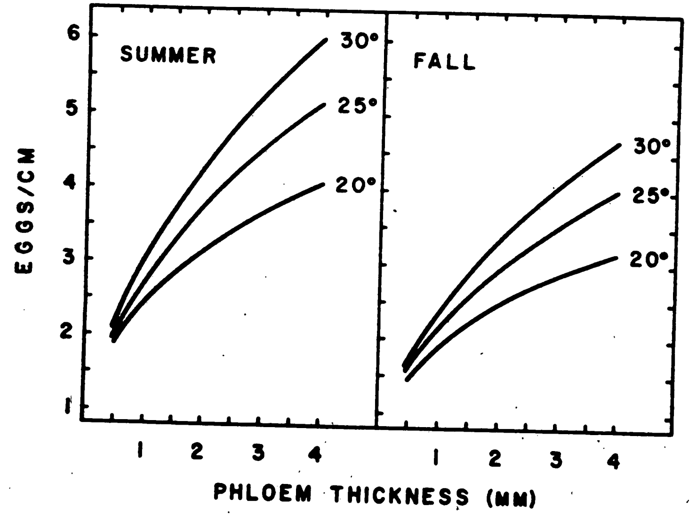

Fig. 15.2. Egg density (eggs/cm of gallery) of the scolytid *Ips calligraphus* at three temperatures in bark slabs of slash pine with phloem thicknesses ranging from 0.5 to 4.0 mm; earlywood xylem was outermost in the current-year growth ring in the summer study, whereas latewood was outermost in the autumn study. (From, and equations presented in, Haack et al., 1984b; reprinted with permission from *The Canadian Entomologist*, Vol. 116, p. 628.)

15.4.1.2 Effects on Developmental Time. As a result of protracted development, some wood feeders may be the longest-lived of all insects. Records exist indicating that certain buprestids and cerambycids have required 10–50 years to complete development (Duffy, 1953; Smith, 1962). Such situations usually occur when trees or logs are infested prior to milling, with the subsequent lumber being of such poor nutritional quality that protracted development results. The extent of wood decay also influences developmental time; generation time of the anobiid *Xestobium rufovillosum* is over 9 years in sound wood but only 1–2 years in well-decayed wood (Fisher, 1940). The ability of wood feeders to complete development under unfavorable conditions (instead of dying) may be one reason why intraspecific variation in adult size is greater in wood feeders than in free-living insects (Section 15.4.1.3; Andersen and Nilssen, 1983). Xylem feeders apparently have the "luxury" of developing over many years because of the persistent nature of wood and because they have fewer parasites and predators than free-living insects (Fiske, 1908).

The extent to which long developmental times (i.e., apparently slow RGRs) are an evolved characteristic of wood feeders rather than merely resulting from the physical and nutritional constraints of the woody environment is not clear. Improving the quality of wood by nutrient supplementation speeds development somewhat (Section 15.4.1.1), and maintaining an adequate moisture level in wood can prevent protracted development (see above). These results suggest that wood-feeder development is somewhat constrained by nutritional factors, but in spite of apparent easing of these constraints, growth rates remain relatively slow and developmental times remain relatively long. The high fiber and tannin content of woody tissues may explain in part slow wood-feeder growth. High levels of these substances are known to reduce the bioavailability of protein and minerals such as Ca, Zn, Fe, and P (see Mattson and Scriber, Chapter 3).

Further evidence suggesting that wood-feeder development is constrained by nutritional factors in nature is that wood feeders often exhibit accelerated development when reared on artificial diet (Table 15.6; Baker and Bletchly, 1966; Cymorek, 1966, 1975; Gardiner, 1970; Antonio et al., 1975; Solomon and Abrahamson, 1976; Kühne, 1981; Nielsen, 1981). However, caution must be used when viewing these data, because faster growth on diet may merely reflect higher rearing temperatures in the laboratory rather than improved nutrition per se. For example, the approximately 200-day developmental periods of the cerambycids *Chion cinctus* and *Enaphalodes rufulus* when reared on diet at 30°C (Table 15.6) may approximate the number of heat units accumulated during two growing seasons, which is the usual time required by these insects to complete development under field conditions. On the other hand, cerambycids such as *Xylotrechus colonus*, *Neoclytus acuminatus*, and *H. bajulus* do appear to develop faster, in absolute terms, when reared on diet (Table 15.6), possibly because of improved nutrition and increased rates of consumption.

Table 15.6. Developmental Times of Certain Cerambycid Species That Were Reared on Artificial Diet and under Natural Conditions

Species	Artificial conditions			Ref.[a]	Natural conditions[b]			
	Mean dev. time	Rearing data			Host feeding zone(s)	Adult body length (mm)	Mean dev. time (yr)	Typical host condition attacked
		°C	% RH					
Xylotrechus colonus	47 days	30	50	b	IB	14	1	Dead
Neoclytus acuminatus	49 days	30	50	b	IB, SW	15	1	Dying, dead
Neoclytus caprea	92 days	30	50	b	IB, SW	18	1	Recently dead
Enaphalodes rufulus	205 days	30	50	b	IB, SW, HW	26	2	Live
Megacyllene caryae	68 days	30	50	b	IB, SW, HW	20	1	Recently dead
Megacyllene robiniae	60 days	30	50	b	IB, SW, HW	18	1	Live
	80 days	27	45	c				
Chion cinctus	214 days	30	50	b	IB, SW	25	2	Dead
Hylotrupes bajulus	9–11 mo.[c]	27	75	a	SW	15	2–3	Lumber, 20–30°C

[a] References: a, Cannon and Robinson (1982); b, Galford (1969); c, Wollerman et al. (1969).

[b] References: Craighead (1923), Duffy (1953), Baker (1972), Hickin (1975), Furniss and Carolin (1977), Cannon and Robinson (1982).

[c] During the 9- to 11-month developmental period, larvae were held at 5–10°C for 8 weeks to induce pupation.

Developmental times of some phloem-feeding scolytids (Bedard, 1966; Yearian and Wilkinson, 1967) and the root-feeding cerambycid *Prionus imbricornis* (Payne et al., 1975) are not reduced in absolute terms when reared on diet. Such results suggest that (1) developmental time in these insects may be under strong genetic control, (2) these larvae are already feeding and growing at their maximal rates in their usual food, or (3) some critical factor (whether physical or chemical) is lacking in the diet.

15.4.1.3 Effects on Body Size. Wood feeders exhibit substantial intraspecific variation in adult body size. Andersen and Nilssen (1983) concluded that size variation (calculated as the ratio I = length of longest individual/length of shortest individual) was greater in wood-feeding (range of means: I = 1.4–2.1) than in free-living (I = 1.1–1.4) Coleoptera. We found, using data from Baker (1972), Hickin (1975), Smith (1976), and Dominik and Starzyk (1983), that the xylomycetophagous Hymenoptera have even greater size variation (I = 2.8 for 12 siricids and 2.8 for 9 xiphydriids). Such extremes in size ratios suggest that wood feeders have evolved a high degree of plasticity in the critical larval body size required to molt or pupate (Slansky and Scriber, 1985). Alternately, a wide range of body sizes may indicate a high degree of genetic variability within a population. Evidence supporting a nutritional basis for size variation is seen in the phloem-feeding scolytid *I. calligraphus*, in which average-size adults produce progeny that are smaller than themselves when oviposition and development occur in thin (<beetle width) but not thick (>beetle width) phloem (Haack et al., 1987a). Moreover, the smaller progeny adults from thin phloem, when allowed to colonize thick phloem, produce a subsequent generation of adults that are larger than themselves.

According to Andersen and Nilssen (1983), wood feeders with the smallest degree of size variation are those in which there is some degree of parental care (e.g., I = 1.4 for bark beetles). Moreover, they reported that xylem feeders exhibit more size variation than phloem feeders and that among xylem-feeding Coleoptera, cerambycids have the greatest variation. Our value of I = 2.8 for the xylomycetophagous Hymenoptera is over twice that of xylomycetophagous scolytids and platypodids (I = 1.2; Andersen and Nilssen, 1983), perhaps reflecting differences in the extent of parental care (greater in the ambrosia beetles) or differences in the quality or proportion of the diet that is fungus.

15.4.2 Phloem Thickness

The thickness of the phloem layer can greatly influence the performance of phloem-feeding insects. This occurs because more outer bark and sapwood must be chewed (and possibly consumed) when the phloem layer becomes thinner than the insect. Increased consumption of these denser and less nutritious tissues (Table 15.2) would provide phloem feeders with fewer net nutrients per unit length of gallery. Evidence supporting this hypothesis is found in laboratory studies of *I. calligraphus* (Haack et al., 1984a,b, 1987a) in which (1) females live longer and lay more eggs per day, per unit length of gallery, and over their lifetime; (2) larvae develop faster; and (3) progeny adults attain a larger body size when in thick rather than thin phloem. Moreover, progeny adults that develop in thick phloem contain more lipid and fly longer (tethered flight) than those from thin phloem (Slansky and Haack, 1986; see also Atkins, 1975). Under experimental field conditions, *I. calligraphus* attack density (nuptial chambers/dm^2), egg density (eggs/dm^2), brood developmental rate, brood density (emerged brood adults/dm^2), and brood–adult body size were all positively correlated with phloem thickness (Haack et al., 1987b). These results suggest a feedback mechanism in which host quality influences both attack density and egg density and thereby minimizes intraspecific competition. Supporting evidence comes from laboratory studies in which *I. calligraphus* brood survivorship was similar in thick and thin phloem (Haack et al., 1987a). Additionally, phloem thickness is recognized as a key variable influencing performance of the scolytid *Dendroctonus ponderosae* (Amman, 1972; Amman and Pace, 1976) and development time in certain pine-infesting cerambycids (Haack and Wilkinson, 1987).

15.4.3 Temperature

Although wood feeders live in what is seemingly a well-buffered environment, they are at times subject to rapid changes in temperature. Subcortical and sapwood temperatures in trees and logs exposed to sunlight can be several degrees (5–30°C) greater than shaded portions (Graham, 1925; Savely, 1939; Wallace, 1953). Warmer temperatures experienced on the sunny versus the shaded side of logs can cause a 1- to 2-year difference in developmental time for phloem-feeding cerambycids (Graham, 1925; Hosking, 1977). However, temperatures are often so extreme on sunlit portions that few if any wood feeders exist there (Graham, 1925; Savely, 1939). Temperatures change faster in decayed wood than in sound wood (Wallace, 1953). The distribution of wood feeders within buildings may also be related to temperature. For example, the upper lethal temperatures of *A. punctatum* and *H. bajulus* are about 30 and 45°C, respectively, possibly explaining why attic and roof timbers are attacked primarily by the latter (Becker, 1977).

Voltinism patterns and developmental times are governed largely by temperature. For example, the number of generations per year completed by *I. calligraphus* varies from four in the mountains of California (Wood and Stark, 1968) to nine in northern Florida (Haack, 1985b) and to as many as 12 in Mexico (Ascencio, 1979). In northern Florida, generation times range from 27 days during the warm summer months to 81 days during the cool winter months (Haack, 1985b).

Increases in temperature are known to improve reproductive efficiency in *I. calligraphus* (Haack et al., 1984b). For a given thickness of phloem, females lay more eggs over the same length of gallery as temperatures increase from 20 to 30°C (Fig. 15.2), suggesting increased efficiencies of assimilation and conversion of ingested food with increasing temperature (Slansky and Scriber, 1985).

15.5 CONCLUSIONS

Wood feeders exhibit a number of adaptations to living and feeding within the woody environment. Their body form, digestive tract, enzymatic abilities, developmental time, adult size, and pattern of host colonization reflect the particular wood tissue they inhabit.

The many sources of variation in woody-tissue quality should be considered in biological studies of wood feeders. Researchers should provide details on when (season) and from where (site and location along and within the stem) host materials were obtained and how they were stored and treated prior to the studies or chemical analyses. Additionally, to provide the most meaningful results, researchers should use host material that is representative of that which the insect under study commonly utilizes in nature.

Much is still to be learned about (1) how wood feeders, especially non-conifer-infesting scolytids, locate their hosts and mates, (2) mechanisms of host resistance in woody plants, (3) quantitative food utilization by wood feeders in each of the various woody tissues, (4) symbiotic relationships between wood feeders and their associated microorganisms, (5) why certain wood feeders can be reared with relative ease on artificial diets (e.g., scolytids and cerambycids) while others cannot (e.g., buprestids), and (6) whether slow growth rate and long developmental time result from environmental constraints or are evolved life history attributes of wood feeders. A sound understanding of wood-feeder nutritional ecology will allow development of population dynamics models and stand hazard rating systems, insect dispersal models, and silvicultural guidelines that are sensitive to insect–host interactions (Berryman and Safranyik, 1980; Safranyik, 1985). Similarly, such knowledge will allow for improvement of current pest-related recommendations for managing, felling, storing, milling, drying, and utilizing timber and wood products (Becker and Liese, 1966, 1976).

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