SILK

1. Introduction

Silks can be defined as externally spun fibrous protein secretions. Of all the natural fibers, silks represent the only ones that are spun. Silk fibers have been used in textiles for thousands of years, owing to their unique visual luster, tactile properties, and durability. These fibers are remarkable materials displaying unusual mechanical properties. Strong, extensible, and compressible, silks display interesting electromagnetic responses, particularly in the uv range for insect entrapment; form liquid crystalline phases related to processing; and exhibit piezoelectric properties (1). Silks were used in optical instruments as late as the mid-1900s because of their fine diameter and high strength and stability over a range of temperatures. Spider silks are reportedly used in the South Pacific for gill nets, dip nets, and fishing lures as well as in weaving and ceremonial dress (1).

2. Types of Silk

Silks are synthesized by a variety of organisms, including silkworms, spiders, scorpions, mites, and flies. Few of these silks have been characterized. Silks differ in properties, composition, and morphology, depending on the source. Silkworm cocoon silk from *Bombyx mori* is the most well characterized, owing to the extensive use of these fibers in the textile industry for over 5000 years in a practice originating in China. The dragline silk from the orb-weaving spider, *Nephila clavipes*, is the most well characterized of the different spider silks. Spider silk has not been domesticated for textile applications because spiders are more difficult to raise in large numbers owing to their solitary and predatory nature. Unlike the cocoon silk from the silkworm, orb webs are not reelable as a single fiber.

2.1. Silkworm Cocoon Silk. The cocoon silk from *B. mori* contains two structural fibroin filaments coated with a family of glue-like sericin proteins, resulting in a single thread having a diameter of 10 to 25 μm. Wild silkworms generally have larger-diameter threads, ranging up to 65 μm and displaying a variety of different cross-sectional morphologies. The life cycle of *B. mori* runs for 55 to 60 days, and the organism passes through a series of developmental stages or molts. Silk production occurs during cocoon formation around day 26 in the cycle during the fifth larval instar just before molt to the pupa. The silkworm passes through four different metamorphosizing phases: egg or embryo, larva, pupa, and moth (adult). Smaller quantities of silk are produced at all larval stages except during molts.

2.2. Spider Silk. Spider silks function in prey capture, reproduction, and as vibration receptors, safety lines, and dispersion tools. Spider silks are synthesized in glands located in the abdomen and spun through a series of orifices (spinnerets). The types and nature of the various silks are diverse and depend on the type of spider (2). Some general categories of silks and the glands responsible for their production are listed in Table 1. Methods and apparatus for spinning spider silk protein have been patented (3).

3. Structure

3.1. Composition. Table 2 summarizes the amino acid composition of various silk proteins (see AMINO ACIDS; PROTEINS). The silkworm cocoon silk contains two structural proteins, the fibroin heavy chain (mol wt ca 325,000) and fibroin light chain (mol wt ca 25,000), plus the family of sericin proteins (mol wt 20,000–310,000) to hold the fibroin chains together in the final cocoon fiber. Other silks, such as the caddis fly and aquatic midge, which spin silks underwater to form sheltered tubes, have also been characterized and consist of a family of proteins having high cysteine content and running from low to very high ($>10^6$) molecular weights (5). Some silkworm silks from wild strains have been reported to contain up to 95% alanine (1).

The consensus crystalline amino acid repeat in the B. mori silkworm cocoon silk fibroin heavy chain is the 59mer: GAGAGSGAAG[SGAGAG]$_8$Y. More detailed analysis of these repeats indicates that the fibroin contains alternate arrays of repeating GAGAGS and GAGAGY. Valine or tyrosine replacements for alanine exist in the second repeat (6). These core repeats are surrounded by homogenous nonrepetitive amorphous domains. The repetitive structures in the protein are thought to be the result of genetic level continuous unequal crossovers or genetic recombination events during evolution.

The spider dragline silk from the principal ampullate gland contains at least one protein, called MaSp1, for major ampullate silk protein, previously termed spidroin 1; mol wt is around 275,000 (7). It remains unclear whether additional proteins play a significant role in the dragline silk fiber. There is no sericin or glue-like protein associated with the dragline fiber. MaSp1 contains amino acid repeats considerably shorter than those found in the silkworm fibroin and not as highly conserved. The repeats contain polyalanine domains consisting of from six to nine residues, and a 15-amino acid region showing a GGX repeat motif, where X = alanine, tyrosine, leucine, or glutamine (7,8).

3.2. Secondary Structure. The silkworm cocoon and spider dragline silks are characterized as an antiparallel β-pleated sheet wherein the polymer chain axis is parallel to the fiber axis. Other silks are known to form α-helical (bees, wasps, ants) or cross- β-sheet (many insects) structures. The cross- β-sheets are characterized by a polymer chain axis perpendicular to the fiber axis and a higher serine content. Most silks assume a range of different secondary structures during processing from soluble protein in the glands to insoluble spun fibers.

The crystalline structure of silk was first described in the 1950s as an antiparallel, hydrogen-bonded β-sheet based on the characterization of *B. mori* fibroin (9), and further modifications to this early model have been made over the years (10,11). Two crystalline forms for silk have been characterized based on x-ray diffraction and ^{13}C-cross-polarization magic angle spinning (cp/mas) nmr spectroscopy. The random coil or silk I, ie, the prespun pseudocrystalline form of silk present in the gland in a water-soluble state, is predominant in the gland; silk II, ie, the spun form of silk which is insoluble in water, becomes predominant once the protein is spun into fiber (10,12). The unit cell parameters in the silk II structure are 940 pm (*a*, interchain), 697 pm (*b*, fiber axis), and

920 pm (*c*, intersheet). The chains run antiparallel with interchain hydrogen bonds roughly perpendicular to the chain axis between carbonyl and amine groups. Van der Waal forces stabilize intersheet interactions owing to the predominance of short side-chain amino acids (glycine, alanine, serine) in these crystalline regions. Solid-state ^{13}C-nmr studies of *N. clavipes* dragline silk have concluded that the polyalanine runs in the MaSp1 are in a β-sheet conformation (13).

The structure of silk I remains incompletely understood. This structure is unstable and upon shearing, drawing, heating, spinning, or exposure in an electric field or exposure to polar solvents, such as methanol or acetone, converts to silk II. The change in unit cell dimensions during the transition from silk I to silk II during fiber spinning is most significant in the intersheet plane, where an 18.3% decrease in distance occurs between overlying sheets (14). This change results in the exclusion of water, thus reducing solubility of the protein. Silk II is more energetically stable than silk I and the energy barrier for the transition is low, whereas the return barrier is high and considered essentially irreversible (1,15). Because the instability or metastable nature of the silk I conformation leads to difficulty in obtaining an orientated sample for fiber diffraction analysis and detailed structural characterization, different models have been proposed to describe the silk I structure (15,16).

3.3. Crystallinity. Generally, spider dragline and silkworm cocoon silks are considered semicrystalline materials having amorphous flexible chains reinforced by strong stiff crystals (4). The orb web fibers are composite materials (qv) in the sense that they are composed of crystalline regions immersed in less crystalline regions, which have estimates of 30–50% crystallinity (4,17). Earlier studies by x-ray diffraction analysis indicated 62–65% crystallinity in cocoon silk fibroin from the silkworm, 50–63% in wild-type silkworm cocoons, and lesser amounts in spider silk (18).

3.4. Structure of the Spider Orb Web. The construction of the orb web is a feat of engineering involving material tailoring, optimization of material interfaces, and conservation of resources to promote survival of the spider (2,4). In addition, the web absorbs water from the atmosphere and ingestion by the spider may provide a significant contribution to water intake needs (19). Around 70% of the energy is dissipated through viscoelastic processes upon impact by a flying insect into the web (4). Thus the web balances stiffness and strength against extensibility, both to keep the web from breaking and to keep the insect from being ejected from the web by elastic recoil (4). The ability to dissipate the kinetic energy of a flying insect impacting the web is based on the hysteresis of radial threads and also aerodynamic damping by the web (19,20). Some orb webs appear to be at least in part recycled by ingestion as a conservation tool, and some of the amino acids are reused in new webs.

4. Processing

4.1. *In Vivo* Processing. Silks are synthesized in specialized glands within the organism. Initially, some degree of self-organization or assembly occurs as a result of protein–protein interactions among the crystalline repeats

in the protein chains (14). In the spider gland, changes in physiological conditions such as pH and salt concentrations accompany the processing and, presumably, help maintain solubility, despite increasing protein concentration during passage through the various regions of the gland (1). In silkworm there are three distinct regions to the glands and two sets of these organs feeding into one final thread (21,22). The fibroin is synthesized in the posterior region of the gland and the protein moves by peristalsis to the middle region of the gland where it is stored as a viscous aqueous solution until needed for spinning. The protein concentration is 12–15% in the posterior region of the gland where fibroin chain synthesis occurs, increases to around 20–30% in the middle region of the gland where the fibroin is stored and sericin is synthesized, and is significantly higher in the anterior region of the gland where spinning is initiated (21). The two lobes of the gland join just before the spinnerets in the anterior region and the fiber is spun into air. Aside from binding together the fibroin chains in the final spun fiber, sericin in this process may function in plasticization to ease the flow through the spinneret, as a reservoir for divalent cations, or as a water-holding medium to promote plasticization of the fiber after spinning.

Rheological experiments indicate that crystallinity in the fiber correlates positively with shear and draw rates, and an extrusion rate of around 50 cm/min was found to be a minimum threshold for the appearance of birefringence and the conversion of the soluble silk solution in the gland to the β-sheet found in the spun fiber (21,23). In the posterior region of the gland, 0.4–0.8 mm in diameter, the silk solution is optically featureless, a range of secondary structures are present, including random coil and silk I, and the shear rate is low. In the middle region of the gland, the diameter is 1.2–2.5 mm, streaming birefringence is observed, and the shear rate is also low. In the anterior region of the gland, the diameter is narrow, 0.05–0.3 mm, the shear rate is high, water appears to be actively transported out of the gland, the pH decreases, and active ion exchange occurs. Viscosity also increases but presumably decreases prior to spinning as a result of the liquid crystalline phase. At this point the characteristic silk II structure forms. In the pair of major ampullate glands in the spider, which are the location of dragline protein synthesis, a similar process occurs as summarized for the silkworm. This gland is smaller, however, and there is no sericin contribution in the middle region of the gland. A lyotropic nematic liquid crystalline phase of the protein forms prior to spinning in both the spider and the silkworm, as well as in many of the different glands of the spider responsible for the different silks (24).

4.2. Commercial and Artificial Processing. Commercially, silkworm cocoons are extracted in hot soapy water to remove the sticky sericin protein. The remaining fibroin or structural silk is reeled onto spools, yielding approximately 300–1200 m of usable thread per cocoon. These threads can be dyed or modified for textile applications. Production levels of silk textiles in 1992 were 67,000 metric tons worldwide. The highest levels were in China, at 30,000 t, followed by Japan, at 17,000 t, and other Asian and Oceanian countries, at 14,000 t (25). Less than 3000 metric tons are produced annually in each of eastern Europe, western Europe, and Latin America; almost no production exists in North America, the Middle East, or Africa. 1993 projections were for a contin-

ued worldwide increase in silk textile production to 75,000 metric tons by 1997 and 90,000 metric tons by 2002 (25).

Most solvents used to solubilize globular proteins do not suffice for silks owing to extensive hydrogen bonding and van der Waals interactions, and the exclusion of water from the intersheet regions. Silks are insoluble in water, dilute acids and alkali, and most organic solvents; they are resistant to most proteolytic enzymes (7,26). Silkworm fibroin can be solubilized by first degumming or removing the sericin using boiling soap solution or boiling dilute sodium bicarbonate solution, followed by immersion of the fibroin in high concentration salt solutions such as lithium bromide, lithium thiocyanate, or calcium chloride. These salt solutions can also be used to solubilize spider silk, as can high concentrations of propionic acid–hydrochloric acid mixtures and formic acid (7). After solubilization in these aggressive solvents, dialysis into water or buffers can be used to remove the salts or acids, although premature reprecipitation is a common problem. Ternary-phase diagrams of silk, water, and chaotropic salt for processing windows have been published (27,28) for native silkworm silks and for genetically engineered versions of silkworm silk.

Films or membranes of silkworm silk have been produced by air-drying aqueous solutions prepared from the concentrated salts, followed by dialysis (12,29). The films, which are water soluble, generally contain silk in the silk I conformation with a significant content of random coil. Many different treatments have been used to modify these films to decrease their water solubility by converting silk I to silk II in a process found useful for enzyme entrapment (29). Silk membranes have also been cast from fibroin solutions and characterized for permeation properties. Oxygen and water vapor transmission rates were dependent on the exposure conditions to methanol to facilitate the conversion to silk II (30). Thin monolayer films have been formed from solubilized silkworm silk using Langmuir techniques to facilitate structural characterization of the protein (31). Resolubilized silkworm cocoon silk has been spun into fibers (32), as have recombinant silkworm silks (33).

5. Properties

5.1. Mechanical Properties. The mechanical properties of silks are an intriguing combination of high strength, extensibility, and compressibility (Table 3).

Resistance to axial compressive deformation is another interesting property of the silk fibers. Based on microscopic evaluations of knotted single fibers, no evidence of kink-band failure on the compressive side of a knot curve has been observed (34,36). Synthetic high performance fibers fail by this mode even at relatively low strain levels. This is a principal limitation of synthetic fibers in some structural applications.

5.2. Fibers. *B. mori* cocoon silk ranges from 10 to 25 μm diameter; dragline silk from *N. clavipes* from 2.5 to 4.5 μm in diameter. Web fibers from some spiders have diameters as low as 0.01 μm. A silking rate of around 1 cm/s is considered equivalent to natural spinning rates for the spider (21). Some spider silks have been observed to supercontact up to around 50% when unconstrained and

exposed to high moisture; other silks such as the silkworm cocoon silk do not contract under similar experimental conditions (37). A skin core has been reported using light microscopy and electron microscopy. However, more recent data using dragline silk from *N. clavipes* refute this finding (38).

5.3. Thermal Properties. Spider dragline silk was thermally stable to about 230°C based on thermal gravimetric analysis (tga) (34). Two thermal transitions were observed by dynamic mechanical analysis (dma), one at −75°C, presumed to represent localized mobility in the noncrystalline regions of the silk fiber, and the other at 210°C, indicative of a partial melt or a glass transition. Data from thermal studies on *B. mori* silkworm cocoon silk indicate a glass-transition temperature, T_g, of 175°C and stability to around 250°C (38). The T_g for wild silkworm cocoon silks were slightly higher, from 160 to 210°C.

6. Genetic Engineering

An understanding of the genetics of silk production in silkworms and spiders should help in developing processes for higher levels of silk expression generated by recombinant deoxyribonucleic acid (DNA) methods. The ability of the silkworm to produce large amounts of protein, around 300 μg of fibroin per epithelial cell lining the silk producing gland, has generated a great amount of interest from molecular biologists and developmental biologists in elucidating the genetic regulation of this system. Genetically engineered or recombinant DNA silkworm and spider silks have been produced using either native genes or synthetic genes (33,39,40). It is interesting to note that studies of variations in native silkworm populations indicate differences in sizes of the crystalline-encoding domains resulting from a high degree of polymorphism in length and organization of the fibroin gene and thus the encoded proteins (41,42). A significant degree of variation in protein size apparently can be tolerated in native populations of silkworms and possibly spiders. Owing to the highly repetitive nature of the genes and the encoded proteins, the deletion or addition of repeats has little impact on secondary structure and functional performance within a certain window of sizes.

7. Applications

Because of the advent of improved analytical techniques, together with the tools of biotechnology, a new generation of products is envisioned with silk. The ability to tailor polymer structure to a precise degree leads to interesting possibilities in the control of macroscopic functional properties of fibers, membranes, and coatings, as well as improved control of processing windows. Biotechnology offers the tools with which to solve limitations in spider silk production that have not been overcome with traditional domestication and breeding approaches, such as those used successfully with the silkworm. This is of interest because of the variety of silk structures available and the higher modulus and strength as compared to silkworm silk.

Hybrid silk fibers containing synthetic fiber cores having silk coextruded or grafted have been synthesized. Cosmetics (qv) and consumer products such as hair replacements and shampoos containing silk have also been marketed (see, for example, Ref. 43). Sutures, biomaterials for tissue repairs, wound coatings, artificial tendons, bone repair, and related needs may be possible applications, assuming immunological responses to the silks are controllable (see BIOMATERIALS, PROSTHETICS, AND BIOMEDICAL DEVICES). A thin-layered, endovascular silk-covered stent device has been reported (44). It is also reasonable to speculate on the use of silk webbing for tissue cell growth, nerve cell growth, and brain repair applications as temporary scaffolding during regrowth and reinfusion after surgery. Cell culture Petri plates having genetically engineered silkworm silks containing cell binding or adhesive domains have already been produced and are sold commercially. These recombinant silks are stable during injection molding with polystyrene. The demonstration of fiber spinning from resolubilized silkworm silk provides further opportunities in material fabrication using native and genetically engineered silk proteins.

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Table 1. **Function and Location of Spider Silk Glands**[a]

Silk	Gland	Function
dragline	major ampullate	orb web frame and radii construction, safety line
viscid	flagelliform	prey capture
glue-like	aggregate	prey capture, attachment
minor ampullate	minor ampullate	orb web frame construction
cocoon	cylindrical	reproduction
wrapping	aciniform	wrapping captured prey
attachment	piriform	attachment to environmental substrates

[a]Ref. 4.

Table 2. **Amino Acid Composition of Silks**

		B. mori		*P. c. ricini*[a]	*N. clavipes*
Amino acid	Abbreviation	Fibroin	Sericin	Fibroin	Dragline
glycine	G	42.9	13.5	33.2	37.1
alanine	A	30.0	5.8	48.4	21.1
serine	S	12.2	34.0	5.5	4.5
tyrosine	Y	4.8	3.6	4.5	
aspartic acid–asparagine	D, N	1.9	14.6	2.7	2.5
arginine	R	0.5	3.1	1.7	7.6
histidine	H	0.2	1.4	1.7	0.5
glutamic acid–glutamine	E, Q	1.4	6.2	0.7	9.2
lysine	K	0.4	3.5	0.2	0.5
valine	V	2.5	2.9	0.4	1.8
leucine	L	0.6	0.7	0.3	3.8
isoleucine	I	0.6	0.7	0.4	0.9
phenylalanine	F	0.7	0.4	0.2	0.7
proline	P	0.5	0.6	0.4	4.3
threonine	T	0.9	8.8	0.5	1.7
methionine	M	0.1	0.1	trace	0.4
cysteine	C	trace	0.1	trace	0.3
tryptophan	W			0.6	2.9

[a] *Philosamia cynthia ricini* = wild-type silkworm silk.

Table 3. **Mechanical Properties of Silks and Other Fibers**[a]

Fiber	Elongation, %	Modulus, GPa[b]	Strength, GPa[b]	Energy to break, J/kg[c]
		Fibroins		
B. mori	15–35	5	0.6	7×10^4
other silkworms	12–50	2–4	0.1–0.6	$(3–6) \times 10^4$
		Draglines		
N. clavipes				
quasistatic[d]	9–11	22–60	1.1–2.9	$(3.7–12) \times 10^4$
high strain[e]	10	20		
other spiders	10–39	2–24	0.2–1.8	$(1–10) \times 10^4$
		Other fibers		
nylon	18–26	3	0.5	8×10^4
cotton	5–7	6–11	0.3–0.7	$(5–15) \times 10^3$
Kevlar	4	100	4	3×10^4
steel	8	200	2	2×10^3

[a] Refs. (1, 26, 34), and 35.
[b] 1 GPa = 10^9 N/m^2. To convert GPa to psi, multiply by 145,000.
[c] To convert J to cal, divide by 4.184.
[d] Instron tensile test rates of 10%/s.
[e] Rates of >500,000%/s.