



## Mechanical Adaptations of a Giant Kelp

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# NOTES

## Mechanical adaptations of a giant kelp

**Abstract**—Unusually high extensibility of the kelp *Nereocystis luetkeana* minimizes breakage by waves and tidal currents. Cellulose fibrils in cortical cell walls have a preferred angle of  $60^\circ$  to the stipe axis; this may be the structural basis of stipe extensibility. Although undamaged plants can sustain drag due to most waves and tides, breakage of single plants occurs most often at flaws in the stipes caused by sea urchin grazing or by abrasion.

Many sessile marine organisms in areas subjected to wave action or swift currents avoid the large mechanical forces exerted by flowing water because they are short and squat or are hidden in holes and behind protrusions (Wainwright and Koehl 1976). In contrast, tall sessile organisms such as large kelp may face rapid flow ( $>0.5$  m s<sup>-1</sup>) at current-swept sites (Charters et al. 1969; Neushul 1972; Koehl in prep.). What structural and functional features of these organisms allow them to withstand waves and currents?

We studied the structure and mechanical function of stipes of the giant kelp *Nereocystis luetkeana* (Mertens) Postels and Ruprecht; these kelp thrive in beds within a few hundred meters of wave-beaten, current-swept shores from California to Alaska. Because gas-filled floats keep their fronds at or near the sea surface, large *Nereocystis* cannot avoid fast flow by bending flat against the substratum as many seaweeds do. Waves and tidal currents continually subject the stipes to tensile forces.

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**Breakage**—We expected the stipes to sus-

tain high stresses (force per cross-sectional area) or to undergo large extensions (increase in length expressed as percent original length) before breaking, either of which would increase the work (energy) required to break the stipes. Figure 1 shows the results of tensile tests on samples taken from the thinnest part of one stipe a few decimeters up from the holdfast. When whole flawless stipes were stretched, they always broke in this narrow region. The mean breaking stress of *Nereocystis* stipes was  $3.64$  MN m<sup>-2</sup> (SD = 2.2,  $n = 22$ ), an order of magnitude lower than tensile breaking stresses recorded for other structural biomaterials (Wainwright et al. 1976). Breaking extension, however, was very high (mean breaking extension = 38%, SD = 11,  $n = 10$ ). The area under a graph of force versus the distance a specimen is extended

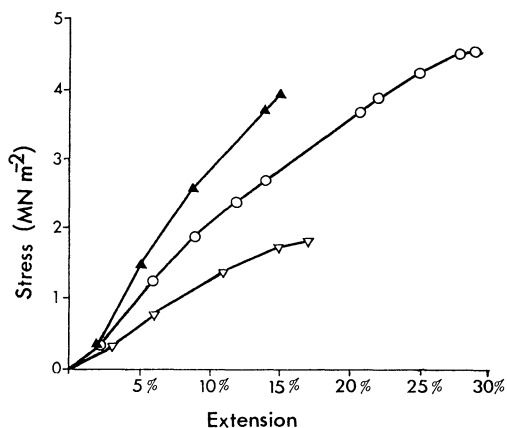


Fig. 1. Typical longitudinal stress vs. extension curves for narrow region of *Nereocystis* stipe (○), isolated inner cortex (▲), and isolated outer cortex (▽) all taken from same plant. Segments of thinnest part of stipe from plants whose stipes were 2–4 m long were pulled longitudinally in an Instron material testing machine or in a Hounsfield tensometer that simultaneously recorded force and extension.



Fig. 2. Polarized light photomicrograph of a longitudinal section of inner cortex in *Nereocystis* stipe showing continuous walls parallel to stipe axis (arrow). Scale line = 0.10 mm.

to breakage represents the work required to break the specimen. The mean work per volume required to break *Nereocystis* stipes was  $0.67 \text{ MJ m}^{-3}$  ( $SD = 0.40$ ,  $n = 6$ ) which is similar to that of wood, bone, insect cuticle, and cast iron (Wainwright et al. 1976). Hence, *Nereocystis* stipes resist breakage by being stretchy rather than by having high breaking stress.

**Structure**—The long narrow region of a stipe is circular in cross-section and consists of a thin cuticle, an epidermis, a layer of cortex 2–5 mm thick, a medulla <0.4 mm thick, and a central lumen <2 mm in diameter. Three lines of evidence lead us to conclude that the inner cortex is the main tensile load-bearing tissue of the stipe.

First, sections made with a cryostat microtome of the narrow region of the stipe show that cortical cells are uniseriate columns whose longitudinal walls are continuous. Continuous walls of the cells in the inner half of the cortex are parallel to the stipe axis (Fig. 2), whereas those of the cells in the outer half of the cortex are oriented radially in the stipe. Second, the inner cortex is stiffer, that is it requires a greater stress to extend it a given amount and has a higher breaking stress than does

the outer cortex (Fig. 1). Third, when whole stipes are stretched, before the load reaches breaking magnitude, transverse splits appear through the cuticle and into the outer cortex. These splits do not immediately propagate and cause failure of the stipe; they do so only after additional load is applied.

Walls of cylindrical plant cells are reinforced with strong, inextensible cellulose fibrils wound helically around each cell. Helical fiber arrays permit shape and volume change of cylinders according to the fiber angle (the angle between the fiber and the cylinder's long axis) by restraining the cylinder to become long and thin when pulled or to become short and wide when compressed. The mean angle of all the fibrils in a cell wall is called the preferred angle. The smaller the fiber angle, the greater the change in width of a cylinder per unit change in its length (Wainwright et al. 1976). Most mature vascular plant cell walls are wound with cellulose at  $20^\circ$  or less and can only extend a few percent in length without having the cellulose fibrils either break or slide relative to each other thus rupturing the cell wall (Wainwright et al. 1976). A similar cell wound at  $60^\circ$  could be extended by 40% simply by the helical angle decreasing to  $30^\circ$ ; no fibril breakage or slippage need occur.

We estimated the preferred fiber angle in the cellulose layers of inner and outer cortical cell walls with the polarized light microscope. From the narrowest segment in three *Nereocystis* stipes we cut, with a cryostat microtome, duplicate sections  $16 \mu\text{m}$  thick at ten different angles ( $0^\circ$ ,  $10^\circ$ , . . . ,  $90^\circ$ ) to the stipe axis. Using a quarter wave compensator and monochromatic light, we measured retardation in 20 radially oriented cell walls (10 inner and 10 outer cortex) in each section. The graph of retardation vs. section angle peaked at  $60^\circ$  for all three plants. We assume that maximum retardation coincides with the preferred angle and conclude that the preferred fiber angle in both inner and outer

cortical cell walls in *Nereocystis* is  $60^\circ$ . The fibers in a *Nereocystis* cell wall are arranged in crossed right- and left-handed helices. Given a visco-elastic gel interfibrillar matrix, perhaps of alginic acid as Andersen (1956) found in *Laminaria*, capable of allowing the extension and effecting the elastic recoil observed, we suggest that the high ( $60^\circ$ ) cellulose fiber angle of *Nereocystis* cortical cells will permit the very high breaking extensions we measured (40%) without rupture of the cell wall.

*Field*—Flowing water subjects *Nereocystis* to drag. Using an EPCO model 6130 electromagnetic flowmeter, we measured water flow velocities in *Nereocystis* beds during May and June 1975 at a current-swept site (Turn Rock) in San Juan Channel and at a less exposed site (Cantilever

Point) near Friday Harbor, Washington. The velocities of peak tidal currents at frond height (about 70% of the drag of a towed *Nereocystis* is drag on the fronds) at Turn Rock were between  $0.7$  and  $1.5 \text{ m s}^{-1}$ , and at Cantilever Point were between  $0.3$  and  $0.6 \text{ m s}^{-1}$ . By measuring (using a spring dynamometer) the drag on *Nereocystis* towed at  $1 \text{ m s}^{-1}$  by a boat, we determined that the mean tensile stress in the stipes ( $0.4 \text{ MN m}^{-2}$ ,  $\text{SD} = 0.2$ ,  $n = 11$ ) due to flow such as these kelp encounter in nonstormy weather is roughly a tenth the breaking stress of the stipes. The buoyancy of the gas-filled floats of *Nereocystis* also subject the stipes to tensile stresses. We assessed the forces due to buoyancy of the floats by hanging weights from the floats of kelp in the field during slack tide until they



Fig. 3. *Nereocystis* broken or ripped off the substratum and washed ashore (photograph by C. Vaughn).

Table 1. Modes of failure of all *Nereocystis* found on a single day washed ashore at a given site. Several sites were thus surveyed in July 1975, on Tatoosh Island, Washington (exposed coastal area with extensive nearshore *Nereocystis* beds), and near Friday Harbor Laboratories, Washington (protected area with narrow nearshore bands of *Nereocystis*).

	Holdfast detached %	Clean break, no flaws obvious %	Break at urchin bite %		Break at abrasion %	Break at flaw %	n
Plants found as solitary							
individuals: Tatoosh	3	7	51	+	39	=	74
Friday Harbor	11	3	43	+	43	=	37
Plants found tangled with others:							
Tatoosh	55	16	13	+	16	=	31
Plants in situ broken by being pulled at the float by the investigators	43	24	9	+	24	=	24

were neutrally buoyant: the mean stress ( $0.02 \text{ MN m}^{-2}$ ,  $SD = 0.005$ ,  $n = 6$ ) due to buoyancy of the float is about a hundredth of the breaking stress of the stipe. (Because the nongas-filled portion of the stipe is negatively buoyant, stresses in the lower stipe would be even smaller than calculated.)

Seaweeds withstand flowing water in a number of ways. Many are less than a half-meter tall and are very flexible so that they bend down into the slowly moving water near the substratum; these plants appear to break at low stresses and extensions (Delf 1932). Some large seaweeds such as *Eisenia arborea* have thick, strong cylindrical stipes up to a meter long that stiffly hold their fronds into the faster flow away from the substratum, thus minimizing abrasion (Charters et al. 1969). Other large kelp such as *Nereocystis* have very flexible stipes and are pushed over parallel to rapid currents as are the flexible fronds of *Eisenia* (Charters et al. 1969); drag is lower on a kelp when it is oriented parallel to the flow than when it is normal to the flow. In engineering design the flexural stiffness of a cylinder can be attained by placing rigid material toward the periphery of the cylinder (Wainwright et al. 1976). The central position of the most rigid material (inner cortex) in the long, narrow region of a

*Nereocystis* thus promotes flexibility rather than rigidity. (The upper end of a *Nereocystis* stipe, which is hollow and larger in diameter, is not flexible.)

In spite of the flexibility (which reduces drag), extensibility (which absorbs energy due to drag), and breaking stress that is greater than the stresses they normally encounter, *Nereocystis* do fail mechanically and wash up on beaches (Fig. 3). Our surveys of kelp on beaches and observations made while SCUBA diving in kelp beds revealed that 90% of detached *Nereocystis* found as solitary individuals had broken at a flaw in the stipe caused by abrasion or sea urchin feeding (Table 1). The cross-sectional area of a stipe at such a flaw is reduced; thus the stress is concentrated at the flaw and may exceed the strength of the stipe. In contrast to the detached *Nereocystis* found as solitary individuals, 55% of detached *Nereocystis* found tangled with other *Nereocystis* had been torn off the substratum at their holdfasts and 16% had been broken in the narrow region of the stipe even though no flaws were present. Broken plants in beds of *Nereocystis* frequently become entangled with their neighbors, increasing the total drag force on intact plants. Intact plants also become entangled with each other; some stipes may then be pulled more than others

when the tangled clump of plants is subjected to currents. As the process of entanglement continues, holdfasts are pulled off the substratum (as shown in Fig. 3) or the stresses in intact stipes exceed their breaking stresses and they fail.

*Summary*—*Nereocystis* reportedly grow to lengths up to 40 m (Smith 1944) and are subjected to tensile forces by the buoyancy of their floats and to predominantly tensile drag forces by waves and tidal currents. Although the strength of *Nereocystis* is low relative to other biomaterials, the stipe can absorb as much energy before breaking as can wood or bone because of its high extensibility. We suggest that the high extensibility is allowed by the crossed helical array at 60° to the stipe axis of cellulose fibrils embedded in a visco-elastic gel matrix in the cell walls of the cortical tissue. The central position of the load-bearing inner cortical tissue in the stipe is consistent with tension-resisting, bend-permitting design principles (Wainwright et al. 1976) and places this important tissue as far as possible from abrasions and from nibbling urchins whose activities ultimately lead to kelp breakage.

A *Nereocystis* is an example of a structure that can withstand flowing water not by being rigid and strong, but rather by being flexible and extensible. If a body is easily bent and stretched, the form drag of the body in flowing water may be reduced (Wainwright and Koehl 1976), and the work that moving water must perform on the body to break it may be quite high.

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### References

- ANDERSEN, G. 1956. Alginic acid and the birefringence of kelp tissue. Proc. Int. Seaweed Symp. 2: 119–124.
- CHARTERS, A. C., M. NEUSHUL, AND D. C. BARILOTTI. 1969. The functional morphology of *Eisenia arborea*. Proc. Int. Seaweed Symp. 6: 89–105.
- DELFT, E. M. 1932. Experiments with the stipes of *Fucus* and *Laminaria*. J. Exp. Biol. 9: 300–313.
- NEUSHUL, M. 1972. Functional interpretation of benthic marine algal morphology, p. 47–74. In I. A. Abbott and M. Kurogi [eds.], Contributions to the systematics of benthic marine algae of the North Pacific. Jap. Soc. Phycol.
- SMITH, G. M. 1944. Marine algae of the Monterey Peninsula. Stanford Univ.
- WAINWRIGHT, S. A., W. D. BIGGS, J. D. CURREY, AND J. M. GOSLINE. 1976. Mechanical design in organisms. Halstead.
- , AND M. A. KOEHL. 1976. The nature of flow and the reaction of benthic Cnidaria to it, p. 5–21. In G. O. Mackie [ed.], Coelenterate ecology and behavior. Plenum.

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## Observed resultant circulation of Lake Ontario

*Abstract*—Vector-averaged current data from June–October 1972 suggest that Lake Ontario's resultant circulation during the stratified period consists of a dominant counterclockwise gyre together with a small clockwise gyre in the northwest portion of the lake. Current speeds are lowest in spring and have maximum vertical shear in early autumn. Spectra comparing summer and winter winds and currents show more high frequency en-

ergy in summer winds and currents and more low frequency energy in winter winds and currents.

One of the earliest studies of Lake Ontario currents was by Harrington (1895), who deduced a mean surface drift during the stratified period. He launched drift bottles from May–October in 1892, 1893,