

Building rigid networks with prestress and selective pruning

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Biopolymer networks from the intracellular to tissue scale display high rigidity and tensile stress while having coordinations well below the normal threshold for mechanical rigidity. The elastic filaments in these networks are often severed by enzymes in a tension-inhibited manner. The effects of such pruning on the mechanics of prestressed networks have not been studied. We show that networks pruned by a tension-inhibited method remain rigid at much lower coordinations than randomly pruned ones. These findings suggest a possible reason for the repeated evolution of tension-inhibited filament-severing proteins.

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Biopolymer networks such as the actomyosin cell cortex, collagen extracellular matrix, and fibrin blood clots play the critical role of maintaining rigidity in cells and tissues under large and often dynamically changing mechanical stresses. These living networks are remarkably stiff; the actomyosin cortex [1–6] is far stiffer than one would expect from existing models of stressed networks [7–16]. A key difference between the living and model networks is that the living ones exist in a dynamic steady state, with filament “edges” between nodes, as well as the nodes themselves, constantly being added and removed with the help of many proteins [17–19]. Most notably, there are proteases (cofilin for actin [20–24], collagenase for collagen [25–27], and plasmin for fibrin [28]) that preferentially sever and depolymerize low-tension filaments. These proteases have evolved independently in actin, collagen, and fibrin networks, respectively, suggesting that they give the networks mechanical properties that confer important advantages.

Severing (pruning) confers on each edge a binary adaptive degree of freedom, namely, the possibility of being there or not there. Preferential pruning of low-tension filaments can be considered a “local rule” [29] for adjusting these degrees of freedom. Here we ask why this local rule might be so useful. We show that prestrained 3D central-force spring networks formed by tension-inhibited pruning are stiffer and display a narrower filament tension distribution at biologically relevant coordinations than randomly pruned networks. This allows the selectively pruned networks to achieve cortex-like stiffness for biophysically plausible tensile stresses and filament tensions, while comparable randomly pruned networks do not. These results help rationalize why tension-inhibited pruning

has evolved independently in the three different filamentous networks.

Central-force spring networks exhibit a transition from a rigid to a floppy state as a function of their coordination z . In the absence of edge tension this transition happens at the isostatic value $z_{\text{iso}} = 6$ (in 3D). Such networks can remain rigid below $z = 6$, however, if they are under prestress [7–16]. We generate our networks from jammed packings of bidisperse particles with initial $z > 6$ by placing $N = 1024$ soft repulsive particles at random in a three-dimensional box at a volume fraction above jamming and minimizing the total energy. We then use the geometry of the jammed state to generate unstressed networks by placing nodes at the centers of particles and relaxed springs, with rest length equal to the spring length, between nodes. We use periodic boundary conditions throughout the simulations. We next apply an initial prestrain by changing the rest lengths of all of the springs in one of three ways: isotropic tension, pure shear, or Gaussian random strains. Changes in rest lengths r_0 are given by

$$r_0 \rightarrow \begin{cases} (1 - \epsilon)r_0 & \text{isotropic tension} \\ (1 - \epsilon[\hat{r}_y^2 - \hat{r}_x^2])r_0 & \text{pure shear} \\ (1 - \eta)r_0 & \text{Gaussian random} \end{cases} \quad (1)$$

where $\epsilon \ll 1$ is a small prestrain, $\hat{r}_i$ is the i th component of the unit vector that points along the edge, and η is a Gaussian random variable with zero mean and standard deviation ϵ . In the isotropic tension case, all edges are tensed. In the pure shear and random cases, some edges are under compression while some are under tension. While the simulation box is kept fixed during our simulations, the edge strains induced by the change in the rest lengths are equal to lowest order to the strains induced by an equivalent deformation of the simulation box for the isotropic and pure shear cases. The Gaussian random prestress cannot be directly mapped to a box strain. After changing the rest lengths the nodes are not at rest, so we use FIRE [30] to minimize the network to a force-balanced state and obtain the energy E_i stored in each edge.

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We study the effects on these networks of sequential pruning according to two different protocols: random pruning and pruning only the edge with the lowest E_i , “min E_i ” pruning. To avoid generating twofold coordinated nodes we prune only edges connected to nodes that have coordinations ≥ 4 . It is interesting to note that strategies based on pruning edges with maximal E_i lead to fracture of the networks for all types of prestrain.

After each pruning event we minimize the energy to maintain a force-balanced state. From this state, we calculate the moduli using linear response. We prune until we reach the critical coordination z_c , defined as where the bulk modulus drops by more than an order of magnitude within one pruning event. The linear response calculation is an extension to nonzero prestress of a previous approach [31]. Essentially, we apply an affine deformation to the network and calculate the induced nonaffine displacements due to the affine forces by using the Hessian. The resulting total displacement allows us to calculate the change in energy at each edge for a given deformation, which gives the contribution of that edge to the corresponding modulus (see the Supplemental Material, SM [32]). A representative cross-section cut from a rigid network at $z \approx 4$ is shown in Fig. 1(a).

It has been shown that pruning edges in unstressed central-force spring networks with mean coordinations $z > 6$ leads to mechanical properties that are extremely sensitive to the choice of which bonds are pruned [31,33,34]. Figures 1(b) and 1(c) show the bulk and shear moduli B and G as a function of the number of edges removed, N_r , during random or min E_i pruning of a network initially placed under isotropic tension. Curves are shown for networks prestrained with ϵ ranging from 0.0001 to 0.01, with vertical lines showing the corresponding coordination of the networks at a given N_r . Recall that pruning terminates when the network becomes floppy at z_c . We find that the behavior of G/B [Fig. 1(d)] as $z \rightarrow z_c^+$ does not depend on pruning protocol; this is because the contributions of each bond i to the bulk and shear moduli, B_i and G_i , are strongly correlated by the prestress (see the SM [32]).

In over-coordinated central-force spring networks placed under a small isotropic tension, we would expect $G/B \rightarrow 0$ for min E_i pruning and $G/B \rightarrow \text{const}$ for random pruning as $z \rightarrow z_c$ [31,33]. In contrast, in under-coordinated networks under a significant isotropic tension, we find $G/B \rightarrow 0$ for both pruning protocols [Fig. 1(d)]. [The upturn at the lowest values of Δz in Fig. 1(d) is a finite-size effect (see the SM [32]).] The result $G/B \rightarrow 0$ is consistent with earlier findings that $G \rightarrow 0$ but $B \rightarrow \text{const}$ as $z \rightarrow z_c^+$ for under-coordinated networks under isotropic tension [15,35–37].

For over-coordinated networks placed under a small pure shear, we would expect $G/B \rightarrow \infty$ for min E_i pruning but $G/B \rightarrow \text{const}$ for random pruning, as $z \rightarrow z_c$ [31,33]. By contrast, for under-coordinated networks under significant pure shear we find $G/B \rightarrow \text{const}$ for both pruning protocols [Fig. 1(d)]. This is consistent with earlier findings that G and B both approach constants as $z \rightarrow z_c^+$ for such systems under pure shear [15] (see the SM); such behavior is also observed in shear-jammed packings [38].

Since the networks are floppy when unstressed, the total tension sets the scale of the bulk and shear moduli. Different pruning methods lead to different values of z_c (Fig. 1).

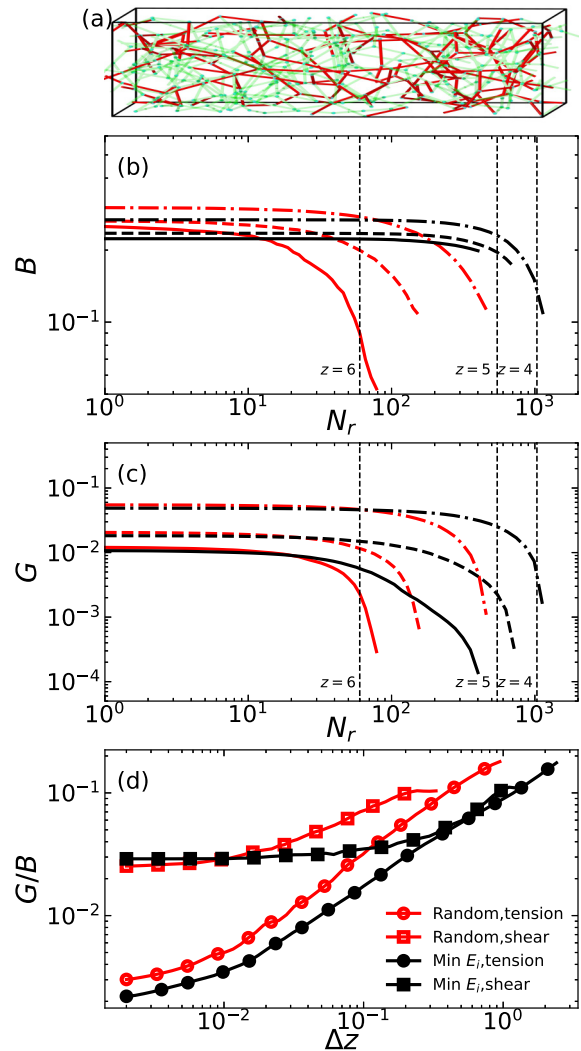


FIG. 1. (a) Cross-sectional slab cut from a 3d min E_i pruned network at coordination $z \approx 4$, initially under an isotropic tension prestrain of 0.05. Edges with tension higher than 3×10^{-9} are colored red, while lower tension edges are green and transparent. The actual simulation box is larger than the slab depicted and fully periodic. (b), (c) Bulk (b) and shear (c) moduli of networks under isotropic tension during random (red) and min E_i (black) pruning as a function of the number of bonds removed N_r . Different lines (solid, dashed, dotted) indicate different strains ϵ used to initially prestress the network (0.0001, 0.001, 0.01, respectively). (d) Ratio of shear to bulk modulus, G/B vs $\Delta z = z - z_c$, the difference from current coordination to the critical coordination, for isotropic tension (circles) and pure shear (squares) for random (red) and min E_i (black) pruning. Networks were prepared with a prestrain of 0.01.

It is possible that they might also lead to different scalings for the tension as $z \rightarrow z_c^+$. Figure 2 shows the total tensile stress or “tension” of the network, $\Pi = -Tr\sigma/3$, where $\sigma = \frac{1}{V} \sum_{ij} r_{ij} \times f_{ij}$ is the stress tensor, r_{ij} is the distance between bonded nodes and f_{ij} is the force stored in bond ij , for the case where the initial prestress has the form of isotropic tension. We plot Π as a function of $\Delta z = z - z_c$ for random and min E_i edge pruning. Close to the transition, we see that $\Pi \sim \Delta z$, independent of the pruning method. The inset to Fig. 2 shows

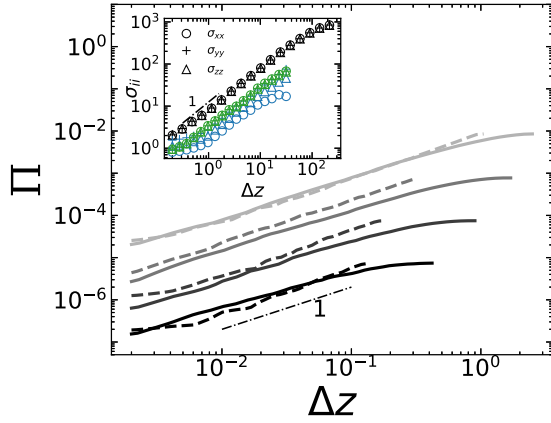


FIG. 2. Tension on randomly (dashed) or min E_i (solid) pruned isotropic tension networks as a function of Δz . The different shades represent different initial prestrains (0.00001, 0.0001, 0.001, and 0.01 from darkest to lightest). (inset) Diagonal components of stress for randomly pruned networks at 0.001 initial strain for the three different types of prestrain (black for tension, blue for shear and green for Gaussian). Different symbols correspond to different diagonal components of the stress. All networks converge to a state where the three diagonal components are positive even when compressed edges are present in the initial state.

that the same scaling holds for each of the individual diagonal components of the stress tensor σ_{ii} during random pruning for the different types of prestrains. Thus, the scaling of Π for $z \rightarrow z_c^+$ is independent of pruning method and type of initial prestrain. The pruning method then primarily affects the scaling of the bulk and shear moduli with Δz by lowering the critical coordination z_c .

Note from the inset to Fig. 2 that near the transition, all diagonal components of the stress tensor are positive, indicating the network is under tension in all directions. This is surprising since σ_{xx} is initially negative for systems initially placed under pure shear strain by expanding in the y direction and compressing in the x direction. To understand this, we note that spring networks are unstable under compression due to structural buckling [12]. The observation that σ_{xx} changes sign to become positive indicates that compressed edges are either removed or put under tension by pruning. As a result, after sufficient pruning the network eventually reverts to a state of tension for any form of the initial prestress.

We now examine the critical coordination reached by pruning in more detail. Figure 3(a) shows how z_c depends on the initial prestrain ϵ for different types of prestrain and for the two pruning methods. In general, z_c decreases with increasing ϵ . This is reminiscent of the behavior of strain stabilized subisostatic networks, where the value of the critical strain at the onset of stiffness increases as a function of Δz below the isostatic point [9,15]. As noted earlier, z_c is lower for min E_i -pruned networks than for randomly pruned networks at the same ϵ , for all types of initial prestrain. Importantly, min E_i -pruned networks under isotropic tension can reach coordination values found in biopolymer networks with initial prestrains on the order of 1–5%, while randomly pruned networks require on the order of 10% prestrain on the filaments to reach the same coordination.

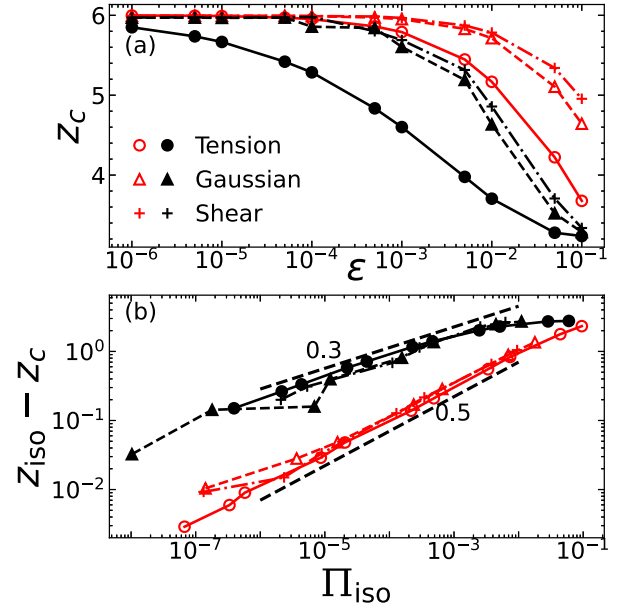


FIG. 3. (a) Critical coordination as a function of initial strain for different types of prestrain and pruning strategy. The networks under isotropic tension (solid circles) show a lower z_c than networks under pure shear (dash-dot crosses) or with Gaussian distributed disorder in rest lengths (dashed triangles). Min E_i pruning (black) leads to networks that are still rigid at lower coordinations compared to random pruning (red). (b) Difference between critical coordination and the isostatic value as a function of the trace of the total tension of the networks. Min E_i data flattens out for the highest tension values due to the constraint on pruning 3-fold coordinated nodes. Marker and line styles and colors are the same as in (a).

Note that networks prepared at different initial coordinations above z_{iso} require different prestrains to attain the same z_c from pruning. Therefore, the initial prestrain is not very useful for characterizing a network. A more useful measure is the total amount of tension at the isostatic coordination $\Pi_{iso} = \Pi|_{z=z_{iso}}$. This is the total amount of tension available to stabilize the network at the point where the network would become floppy with no stress. In Fig. 3(b) we plot $z_{iso} - z_c$ as a function of Π_{iso} .

Figure 3(b) shows that for all types of prestrain the results collapse onto two different curves, one for random pruning and the other for min E_i pruning. For small Π_{iso} , min E_i pruning leads to a decrease in z_c that is an order of magnitude larger than for random pruning, and the difference between pruning methods decreases with Π_{iso} . We observe the scaling

$$z_{iso} - z_c \sim \Pi_{iso}^\alpha, \quad (2)$$

where $\alpha \approx 0.5$ for random pruning and $\alpha \approx 0.3$ for min E_i pruning. With this scaling, the critical coordination for a network can be predicted from Π_{iso} for a given pruning method. Since biological filament networks have a mean coordination between three and four due to a combination of branching points and crosslinks and are rigid, model networks must have z_c in that range. Figure 2 shows that stress scales as Δz independently of stress type or pruning method, so the isostatic stress Π_{iso} can be used as a proxy for the stress

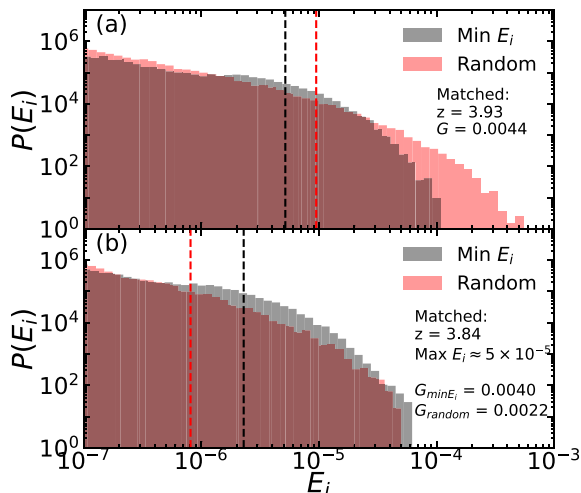


FIG. 4. (a) Distribution of edge energies E_i at same z and G for a min E_i (black) and a randomly (red) pruned network. Dashed lines show the average bond energy. The randomly pruned network requires a larger average and maximum energy to sustain the same modulus as a min E_i pruned network at same z . In our model $E_i \sim \delta_i^2$, where δ_i is the strain of edge i , so an energy of 10^{-4} corresponds to a strain of 1%. Both networks are at tension $\Pi \approx 1.7 \times 10^{-3}$. (b) Distribution of edge energies as in (a), but at a lower coordination where both networks have a similar maximum E_i . The min E_i network is at tension $\Pi \approx 1.1 \times 10^{-3}$, while the randomly pruned network is at a much lower tension of $\Pi \approx 1.6 \times 10^{-4}$.

throughout the pruning process. The smaller scaling exponent α means that biologically relevant coordinations are more easily accessible by min E_i pruning, requiring tensions up to an order of magnitude smaller than random pruning.

To examine this point in more detail, we compare the properties of networks created by each pruning method at a fixed, biologically relevant coordination. At a fixed z , the shear modulus obeys a power-law scaling with tension that is independent of z or pruning strategy (see Fig. S4 in the SM [32]). In contrast, other biologically relevant mechanical properties do depend on pruning strategy at fixed z . We compare the probability distribution of edge energies in two networks pruned by different methods at the same z and shear modulus [Fig. 4(a)] as well as at the same z and maximum edge energy [Fig. 4(b)]. We accomplish this by comparing a randomly pruned network under isotropic tension prestrain of 0.08 and a min E_i -pruned network under a prestrain of 0.01 that have similar mechanical properties at the same $z \approx 4$. Figure 4(a) shows that the min E_i -pruned network has a much narrower distribution of edge energies and also smaller mean E_i when compared to the randomly pruned network. This implies that a min E_i pruned network can achieve the same shear modulus with much less average energy stored in the edges. A similar effect has been seen in networks with catch and slip bonds [39], where catch bonds (which have smaller lifetimes at low tensions) exhibit a narrower distribution of loads per crosslinker. This suggests that narrow distributions of tension may be a universal feature of models where edges preferentially break or are removed at low tensions, and is independent of the particular failure mechanism or kinetics.

Figure 4(b) shows that the min E_i pruned network has almost double the shear modulus of a randomly pruned one when the maximum bond energies are similar. In networks where the stress is derived from the motion of the motors, stall forces function as a tension threshold for the filaments. Alternatively, the maximum filament tension could be set by a breaking limit. Figure 4(b) shows that min E_i pruning leads to stiffer networks under such filament tension-limited conditions.

Our results shed some light on the cortical tension Π and apparent shear modulus G . Quantities in our model are expressed in terms of the network edges' spring constant κ and mean length l , which can be scaled using experimental measurements. Single actin filament stretching studies [40–42] show the stretching spring constant κ of F-actin is approximately 40 pN/nm for $l = 1 \mu\text{m}$, with stiffness scaling as $\kappa \sim 1/l$.

The stiffness and tension of our model can be compared to the typical stiffness and tension of the cortex, despite significant differences in reported values of the latter amongst different methods [3]. Careful AFM indenting measurements [6] combined with finite element modeling of the cortex as a 200 nm thick viscoelastic sheet [5] suggests a value $G \approx 15 \text{ kPa}$, orders of magnitude higher than for an unstressed actin gel. Micropipette aspiration of many cells report cortical tension of order $1 \text{ nN}/\mu\text{m}$ [43,44], corresponding to a large tensile stress of $\Pi \approx 5 \text{ kPa}$ for a 200 nm thick cortex. Scaling our values of the shear moduli and tensile stress in Fig. 4(a), with an assumed value of $l \approx 100 \text{ nm}$, yields plausible values of $G_{\text{min}E_i} \approx 4.4 \times 10^{-3} \kappa/l \approx 17.6 \text{ kPa}$, and $\Pi \approx 1.7 \times 10^{-3} \kappa/l \approx 6.8 \text{ kPa}$. Translating the edge energies to filament tensions $t_i \sim \sqrt{E_i}$ leads to an estimate for maximum tension $t_{\text{max}} = 400 \text{ pN}$ for min E_i pruning and $t_{\text{max}} = 894 \text{ pN}$ for random pruning. The breaking force of actin filaments is 600 pN [45], between the maximal filament tensions in our two model networks. That is, we find that our selectively pruned network model can reproduce the stiffness and tension of the actomyosin cortex with physically plausible filament tensions, while a randomly pruned network cannot.

It has previously been shown that for unstressed, over-coordinated networks, the scaling of the ratio of the shear to bulk modulus, G/B , depends sensitively on pruning protocol [31,33,34]. Here we have shown that pruning protocol does not affect the scaling of the ratio of the shear to bulk modulus, G/B , with Δz . This is because prestress highly correlates the changes in the bulk and shear moduli due to bond removal, in contrast to the unstressed, over-coordinated case [34]. The reason why different biopolymer networks have independently evolved the same pruning strategy is therefore not to produce a desired scaling for G/B .

Why then are biological filament networks such as the actomyosin cell cortex, collagen extracellular matrix, and fibrin blood clots, all accompanied *in vivo* by proteases that impose tension-inhibited pruning? The mean coordination of these networks is significantly lower than z_{iso} , so significant prestress must be maintained in order for the networks to be rigid. This prestress must be supported and rigidity maintained under wildly varying extreme deformation even as some filaments are being destroyed by tension-inhibited proteins

(e.g., cofilin, collagenase, plasmin) [20–28]. Our results show that selectively pruning low-tension edges leads to significantly smaller values of z_c for the same prestrain when compared to random pruning. Selective pruning also generates networks with significantly higher shear modulus when the maximum edge tension is limited. We conjecture that the functional advantage inferred by this higher stiffness may explain the repeated evolution of the motif of tension-inhibited severing proteins [20–28].

Living biological filament networks are dynamically remodeled; new filament constantly replace severed and depolymerized ones in a homeostatic state. The living cortex undergoes large strain fluctuations with a heavy-tailed distribution [46] of amplitudes, termed cytoquakes. It seems possible that the distribution of these fluctuations may be related to the tension distribution of the most tensed filaments, as we report here, via mechanisms such as filament severing, or myosin sliding or unbinding.

In the actomyosin cortex, dynamical remodeling leads to complete turnover of actin filaments every 30 seconds or so [17], with a correspondingly large expenditure of metabolic energy. Turnover introduces an adaptive degree of freedom

for each edge of the network, corresponding to whether the edge is there or not there. These adaptive degrees of freedom are adjusted by local rules, one of which is tension-inhibited pruning. Our results on tension-inhibited pruning suggest that the result of the local rules controlling turnover might be to allow the cortex to maintain the collective property of rigidity under constantly varying and complex mechanical stresses, thus “justifying” its high metabolic cost.

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