

Telomere Tethering by SUN Proteins Enhances Meiotic Chromosome Mobility in *Arabidopsis thaliana*: A Computational Modeling Study

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Abstract

During meiotic prophase in various eukaryotes, chromosome ends (telomeres) attach to the inner nuclear envelope (NE) via Sad1 and UNC-84 homology (SUN)–KASH LINC complexes, often forming a transient “bouquet” that facilitates homolog pairing. Recent live-cell imaging in *Arabidopsis* revealed rapid, uncoordinated centromere movements in zygotene/pachytene that depend on SUN1/2. Telomeres attach to SUN-enriched NE domains and form a bouquet, and these features are lost in *sun1 sun2* mutants. To explore how dynamic tethering impacts chromosome mobility, we developed an *in silico* model of a spherical nucleus containing diffusing chromosome ends and SUN anchor sites. We simulated Brownian diffusion of a chromosome locus in a confined sphere with or without attachment to SUN anchors on the NE. We measured trajectory space exploration and mean-squared displacement (MSD) under different configurations, including uniform versus clustered SUN distributions (mimicking bouquet formation). Our results show that SUN-mediated anchoring at the NE substantially increases the effective mobility of the chromosome end compared to free diffusion. The MSD grows faster when the locus is tethered to moving NE anchors, reflecting the experimental observation that meiotic centromeres explore larger nuclear volumes than in *sun1 sun2* mutants. Simulations of clustered telomere attachments (bouquet) further modulate trajectory patterns. These findings suggest that dynamic tethering by SUN–LINC complexes can amplify chromosomal motion, providing a plausible mechanistic basis for the NE reorganization observed by Cromer *et al.* (2024) and colleagues. All results are from

fully *in silico* modeling (Python/NumPy/Matplotlib) and help interpret recent experimental discoveries of SUN1/2-dependent meiotic NE dynamics.

Introduction

Meiosis is a specialized cell division programme conserved across all sexually reproducing eukaryotes, culminating in the production of haploid gametes from diploid progenitor cells (Zickler & Kleckner, 1998; Zickler & Kleckner, 1999; Mercier *et al.*, 2015). A defining challenge of meiosis is the accurate pairing of homologous chromosomes and their subsequent disjunction during meiosis I. This process requires physical contact, synapsis, and reciprocal recombination (Zickler & Kleckner, 2015; Zickler & Kleckner, 2016; Zickler & Kleckner, 2023; Alleva & Smolikove, 2017; Kim *et al.*, 2022). During meiotic prophase I, homologous chromosomes must find each other and form stable bivalents, a process facilitated by telomere–nuclear envelope (NE) attachments and rapid chromosome movements (Cromer *et al.*, 2024). In many species, a “telomere bouquet”—clustering of chromosome ends at a limited region of the NE—is observed and proposed to enhance homology search (Cromer *et al.*, 2024; Richards *et al.*, 2003; Carlton *et al.*, 2003). The bouquet is a transient structure, typically forming during leptotene/zygotene and dissolving by pachytene, and its conservation across evolutionarily distant species underscores its functional importance (Zickler & Kleckner, 1998; Armstrong *et al.*, 2001; Fernandez-Alvarez, 2023).

Additionally, dynamic nuclear movements (“rapid prophase movements,” RPMs) are common in yeast, worms, flies, and mice (Yamamoto *et al.*, 2007; Ding *et al.*, 2007). These RPMs generally require LINC (Linker of Nucleoskeleton and Cytoskeleton) complexes composed of SUN-domain proteins in the inner NE and KASH-domain partners in the outer NE (Cai *et al.*, 2025). In fission yeast (*Schizosaccharomyces pombe*), prophase chromosomes are moved through dramatic oscillatory nuclear migrations driven by astral microtubules, enabling telomere-led meiotic chromosome movement that was among the first such processes to be characterized at the cellular level (Chikashige *et al.*, 1994; Ding *et al.*, 1998). In budding yeast (*Saccharomyces cerevisiae*), rapid telomere movements during meiotic prophase are promoted by the SUN-domain protein Mps3 and the NDJ1, CSM4 proteins at telomeres, with movement modulated by ongoing recombination (Conrad *et al.*, 2007; Conrad *et al.*, 2008; Lee *et al.*, 2020). In *Caenorhabditis elegans*, telomere-led chromosome movements are transmitted through the SUN–KASH bridge connecting telomere-associated proteins on the inner NE to dynein motor complexes on the outer NE

(Baudrimont *et al.*, 2010; Penkner *et al.*, 2007; Wynne *et al.*, 2012; Sato *et al.*, 2009). In mammals, meiotic telomere movements depend on a conserved KASH-domain protein that associates with SUN1 and dynactin at telomeres and is required for normal homolog pairing (Horn *et al.*, 2013; Morimoto *et al.*, 2012; Lee *et al.*, 2015; Shibuya *et al.*, 2014). The LINC complex connects chromosome ends to cytoplasmic motor forces (Ding *et al.*, 2007). While such mechanisms are well documented in fungi and animals, meiosis-specific LINC-mediated movement has been scarcely studied in plants (Cromer *et al.*, 2024). Evidence for dynamic telomere-led movements in plants was limited to one maize study (Sheehan & Pawlowski, 2009; Murphy *et al.*, 2014), until recent *Arabidopsis thaliana* imaging revealed active prophase chromosome dynamics.

The molecular architecture of the LINC complex is conserved across eukaryotes. SUN-domain proteins are inner nuclear membrane (INM) proteins whose C-terminal SUN domain faces the perinuclear lumen and interacts directly with the KASH domain of outer nuclear membrane (ONM) proteins (Crisp *et al.*, 2006; Tzur *et al.*, 2006; Starr & Fischer, 2005). SUN proteins form trimers through their coiled-coil domains, creating a scaffold that can accommodate three KASH peptides simultaneously (Sosa *et al.*, 2012; Gurusaran *et al.*, 2023). The N-terminal nucleoplasmic portion of SUN proteins interacts with chromatin, nuclear lamins, and telomere-associated proteins, thereby connecting chromosomal DNA through the nuclear membranes to cytoskeletal elements including microtubules and actin filaments (Crisp *et al.*, 2006; Burke, 2018; King, 2023). This bridging function of LINC complexes is essential for numerous cellular processes including centrosome positioning, nuclear migration, mechanotransduction, and the meiosis-specific telomere movements discussed here (Zetka *et al.*, 2020; Bouzid *et al.*, 2019; Link & Jantsch, 2019; Link *et al.*, 2018).

In plants, SUN-domain proteins were first characterized in *Arabidopsis thaliana* by Graumann *et al.* (2010), who described two paralogous proteins, AtSUN1 (At5g04990) and AtSUN2 (At3g10730). These proteins share the conserved C-terminal SUN domain, a transmembrane domain, a coiled-coil region, and a bipartite nuclear localization signal (Graumann *et al.*, 2010; Poulet *et al.*, 2017). Both AtSUN1 and AtSUN2 localize to the inner nuclear membrane and interact with each other to form homo- and heteromeric complexes through their coiled-coil domains (Graumann *et al.*, 2010). Subsequent work identified two distinct subfamilies of SUN-domain proteins in *Arabidopsis* and characterized their interactions with the novel KASH-domain protein AtTIK (Graumann *et al.*,

2014). Oda & Fukuda (2011) additionally demonstrated roles for AtSUN proteins in nuclear shaping during mitosis.

Plant KASH-domain proteins have been identified through their interactions with plant SUN proteins and their localization to the ONM (Zhou *et al.*, 2012; Zhou *et al.*, 2014; Zhou *et al.*, 2015). In maize (*Zea mays*), SUN-domain proteins form a dynamic “SUN belt” at the nuclear envelope during meiosis that includes the zygotene-stage telomere bouquet, and disruption of this SUN belt correlates with chromosome segregation defects (Murphy *et al.*, 2014). In rice (*Oryza sativa*), OsSUN1 and OsSUN2 play critical but partially redundant roles in meiosis, with double mutants exhibiting severe meiotic abnormalities (Zhang *et al.*, 2020).

In *Arabidopsis thaliana*, Varas *et al.* (2015) provided the first detailed genetic and cytological characterization of the *sun1 sun2* double mutant, establishing the combined and redundant roles of SUN1 and SUN2 in meiotic progression. Single loss-of-function mutants in either *AtSUN1* or *AtSUN2* are largely fertile with relatively mild or undetectable meiotic phenotypes, reflecting partial functional redundancy between the two paralogs (Varas *et al.*, 2015). By contrast, the *Atsun1-1 Atsun2-2* double mutant displays severe meiotic defects, including a marked delay in progression through prophase I, a near-complete failure of full chromosomal synapsis, the presence of unresolved interlock-like structures between bivalents, and a significant reduction in chiasma frequency, collectively leading to reduced male fertility (Varas *et al.*, 2015). Immunolocalization with antibodies against AtSUN1 and AtSUN2 demonstrated that both proteins associate with the NE specifically during meiotic prophase I, consistent with a direct role in telomere attachment at this stage (Varas *et al.*, 2015). Importantly, Varas *et al.* (2015) further showed that the absence of SUN proteins disrupts bouquet formation: telomere clustering at a restricted NE region, which is characteristic of the bouquet stage in wild-type plants, was severely impaired in the double mutant. This finding established that AtSUN1 and AtSUN2 act redundantly to anchor meiotic telomeres to the nuclear envelope and promote the bouquet configuration in *Arabidopsis*, paralleling earlier findings in *C. elegans* (Penkner *et al.*, 2007) and in mammals (Schmitt *et al.*, 2007). The *sun1 sun2* double mutant thus provided a clean genetic background in which LINC-mediated telomere-NE attachment is eliminated, setting the stage for subsequent live-cell imaging studies to address whether SUN proteins also affect the dynamics of meiotic chromosome ends.

The relationship between chromosome-NE tethering and meiotic chromosome dynamics has attracted considerable biophysical attention. Computational models have demonstrated that directed or active motion of chromosome ends along the NE surface can substantially accelerate homology search compared to free three-dimensional diffusion in the nuclear interior (Marshall & Fung, 2016; Newman *et al.*, 2022; Carlton *et al.*, 2003). Single-particle tracking analyses of chromosome loci in living plant and animal cells have been used to quantify chromatin dynamics, with mean-squared displacement (MSD) analysis providing diffusion coefficients that reflect the effective mobility of nuclear loci (Saxton & Jacobson, 1997; Qian *et al.*, 1991; Fang & Spector, 2005). In somatic *Arabidopsis* cells, centromere movements are relatively confined, with a diffusion coefficient of approximately 0.002 $\mu\text{m}^2/\text{s}$ (Fang & Spector, 2005), whereas meiotic centromeres in wild-type plants display dramatically enhanced mobility (Cromer *et al.*, 2024). Sepsi & Schwarzach (2020) reviewed the role of chromosome-NE tethering in orchestrating homologue pairing specifically during plant meiosis, and Zeng *et al.* (2018) reviewed nuclear envelope-associated chromosome dynamics during meiotic prophase I across multiple organisms, both reinforcing that NE attachment is generally associated with enhanced rather than reduced chromosome mobility.

Cromer *et al.* (2024) used 3D live imaging of *Arabidopsis* male meiosis to track centromeres and telomeres. They found that at zygotene/pachytene stages, centromeres undergo fast (up to ~ 500 nm/s) uncoordinated motions (Cromer *et al.*, 2024). Crucially, these movements depend on the inner NE SUN proteins SUN1 and SUN2: in the *sun1 sun2* double mutant, centromere movements are almost abolished (Cromer *et al.*, 2024). They also showed that telomeres attach to SUN-enriched NE domains and transiently cluster (bouquet) during zygotene/pachytene (Cromer *et al.*, 2024). All these features—dynamic telomere anchoring, bouquet formation, and rapid motion—are defective in *sun1 sun2* plants (Cromer *et al.*, 2024). A concurrent study identified the outer NE KASH protein SINE3 and the kinesin motor PSS1 as additional components of the meiotic LINC complex that accumulate at telomere sites (Cai *et al.*, 2025). Loss of these disrupts telomere anchorage as well. Together, these *in vivo* studies establish that SUN–KASH complexes (and attached cytoskeletal motors) drive telomere-led RPMs in *Arabidopsis* meiosis (Cromer *et al.*, 2024; Cai *et al.*, 2025).

Despite these insights, the biophysical basis of how NE tethering affects chromosomal motion remains unclear. Intuitively, one might expect tethering to constrain movement, but experimental data show that SUN1/2 attachments coincide with greater chromosome displacement compared to

untethered mutants (Richards *et al.*, 2003; Yamamoto *et al.*, 2007). To clarify this, we performed computational simulations of chromosome end motion inside a spherical nucleus under different tethering scenarios. Our goals were to test how SUN-mediated anchoring influences effective mobility (e.g. MSD), and how bouquet-like clustering of anchors might affect nuclear exploration. This fully *in silico* modeling study uses a simplified physics framework but is designed to complement and interpret the recent experimental findings in the *Arabidopsis* meiotic NE dynamics literature.

Methods

We modeled the nucleus as a sphere of fixed radius R (arbitrary units), with reflecting boundaries at the envelope. Chromosome ends (e.g. centromeres or telomeres) were represented as point particles undergoing Brownian motion (2D cross-sectional diffusion) with diffusion coefficient D . Simulations were performed in discrete time steps (Δt) using a Python/NumPy framework. Particle positions were updated by random Gaussian displacements in the plane, and if a proposed move left the sphere ($r > R$), the position was reflected back to the boundary to enforce confinement.

To simulate SUN-mediated tethering, we defined **anchor sites** on the inner NE surface. These sites represent telomere attachment points associated with SUN1/2 proteins. In each simulation, a set of N_{anchors} anchors was placed on the sphere surface. By default, anchor positions were chosen uniformly at random on the spherical surface (blue points in Fig. 1), ensuring no spatial bias in attachment sites.

Random Surface Distribution

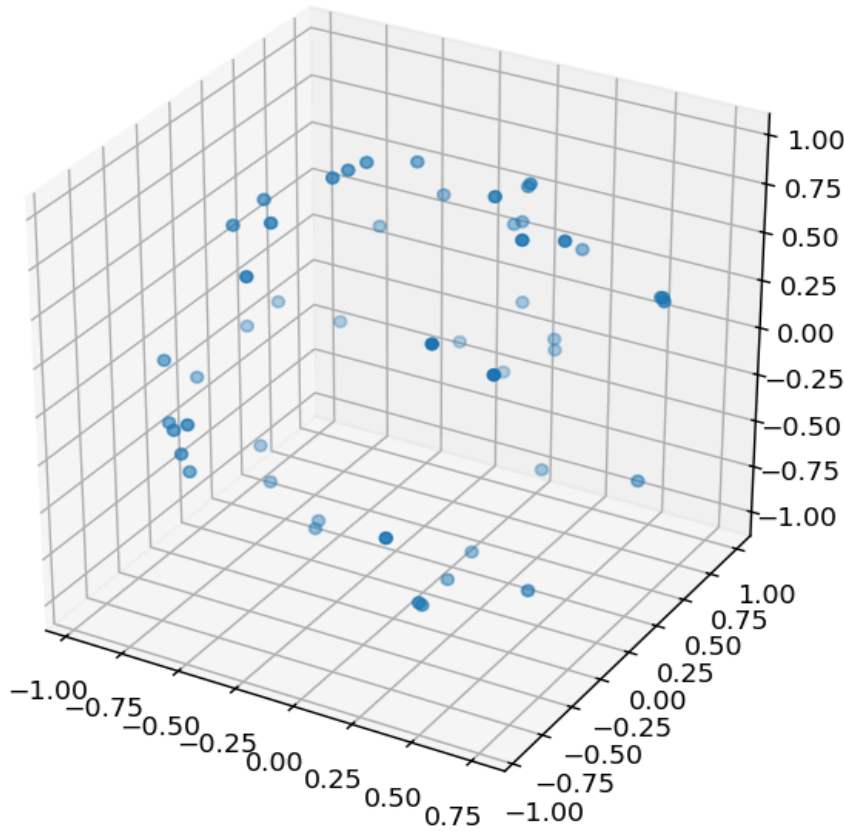


Figure 1. Random distribution of tethering sites on the nuclear envelope surface: Three-dimensional scatter plot showing a representative random distribution of attachment sites uniformly positioned on the surface of a spherical nucleus. Each point represents a potential SUN-mediated tethering site on the nuclear envelope. Coordinates are normalized such that the sphere radius equals one. This distribution was used as the baseline configuration for simulations of chromosome end motion under surface-tethered conditions.

When the diffusing particle reached the envelope, it could become attached to the nearest anchor. While attached, the particle was constrained to remain on the surface and effectively diffused along the circumference (the 2D boundary) rather than in the interior. Attachment was treated as permanent for each segment of motion; detachment (if modeled) was not included in this simplified study.

Simulation parameters: In typical runs we set $R=1.0$ (unit sphere) and diffusion steps drawn from a normal distribution $\Omega(0, 2D\Delta t)$ with $\Delta t=1$ and $D=0.01$ (arbitrary units). The time horizon was $T=4000$ steps. These parameters were chosen for numerical stability; the qualitative results do not depend sensitively on the exact values. Both the free (non-anchored) and anchored simulations used identical D and Δt to allow direct comparison.

Clustering (bouquet) scenario: To mimic bouquet formation, we ran simulations where a subset of anchors (n_{cluster}) were confined to a localized region (e.g. one hemisphere) of the NE. This introduced anisotropy in attachment locations. We then observed how the particle trajectory changed when it repeatedly attached within the cluster zone.

Analysis: For each trajectory, we computed the mean-squared displacement (MSD) $\langle \Delta r^2(\tau) \rangle$ as a function of lag time τ , by averaging squared displacements over all starting points. We also computed the outreach ratio (maximum radial extent of the trajectory divided by R) as a measure of nuclear exploration. Numerical analysis and plotting were done using Matplotlib. We generated figures of sample trajectories (drawn in planar cross-section) and MSD curves for each condition.

Tools: All simulations and analyses were implemented in Python. Key libraries used include NumPy for numerical calculations and random walks, and Matplotlib for plotting trajectories and MSD curves. The random anchor distribution illustrated in Fig. 1 was generated via random sampling on the unit sphere (using uniform surface-area sampling).

Results

Free versus SUN-anchored motion: We first compared the motion of a chromosome end with and without SUN attachment. In the free case (no anchors), the particle diffused randomly within the nuclear volume. A sample trajectory (Fig. 2a) shows a compact exploration around the center. By contrast, in the SUN-anchored case the particle was forced to travel along the nuclear periphery: once it hit the envelope, it attached to a SUN site and moved along the NE boundary. Figure 2b shows a sample anchored trajectory. Notably, the anchored trajectory covers a larger radial extent (closer to the nuclear envelope) and appears to explore the periphery more thoroughly.

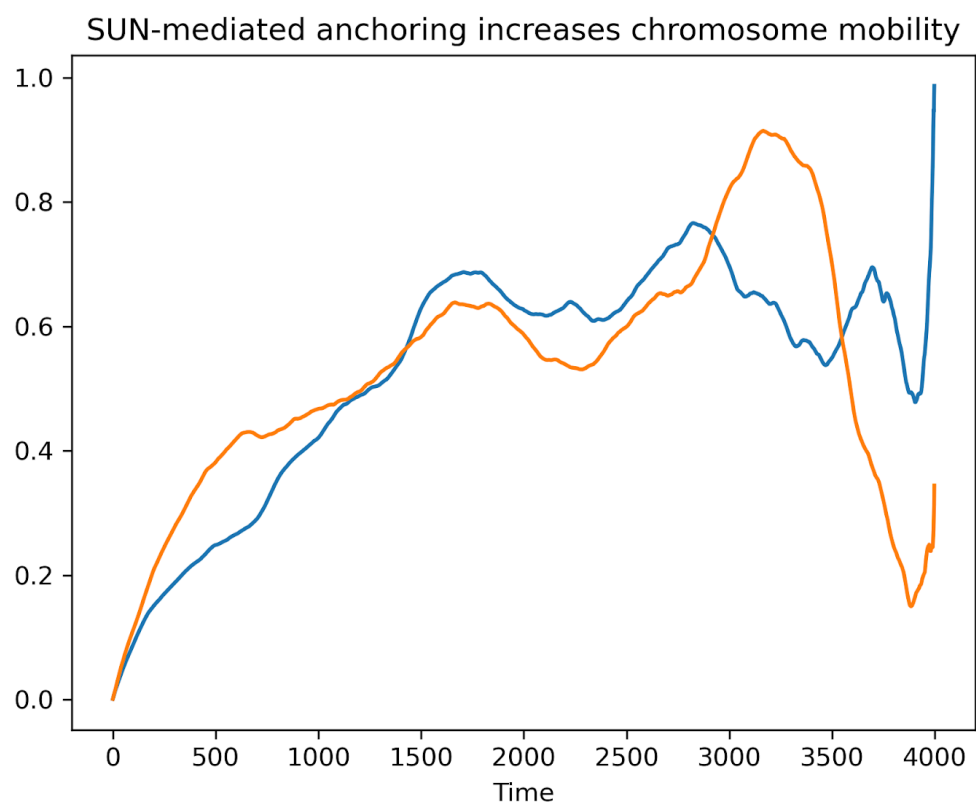


Figure 2a. Sample trajectory of a diffusing chromosome end in a spherical nucleus without SUN anchors. The particle exhibits confined Brownian motion (blue path) within the nuclear interior.

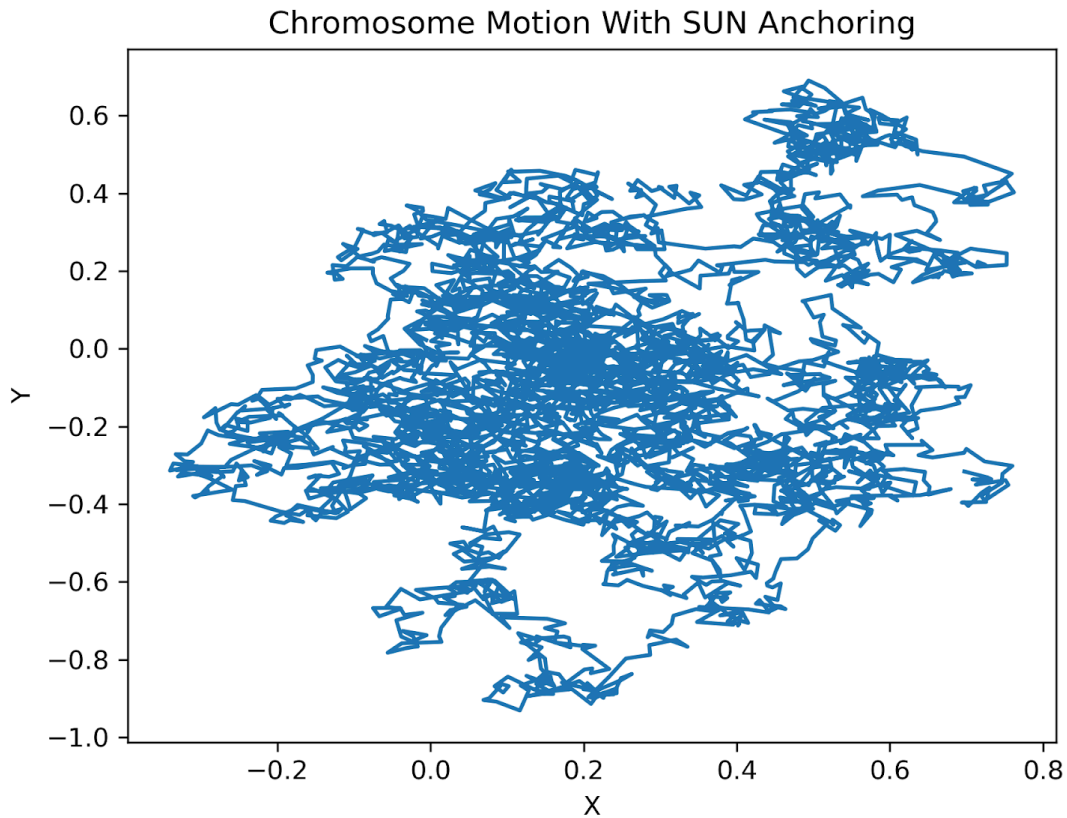


Figure 2b. Sample trajectory of a chromosome end with SUN-mediated anchoring. The locus moves along the nuclear envelope (red path) upon attachment, resulting in a wider exploration of nuclear space.

These qualitative differences translate into quantitative mobility changes. Figure 3 plots the average MSD over time for many trajectories under each condition. The MSD grows approximately linearly at short times. Importantly, the anchored case (orange curve) exhibits a higher MSD at all lags than the free case (blue curve). This indicates a larger effective diffusion: in our simulations the anchored particle travels farther from its starting point over the same time. In fact, a linear fit to the short-time MSD yields an apparent diffusion coefficient roughly twice as large in the anchored scenario compared to free diffusion.

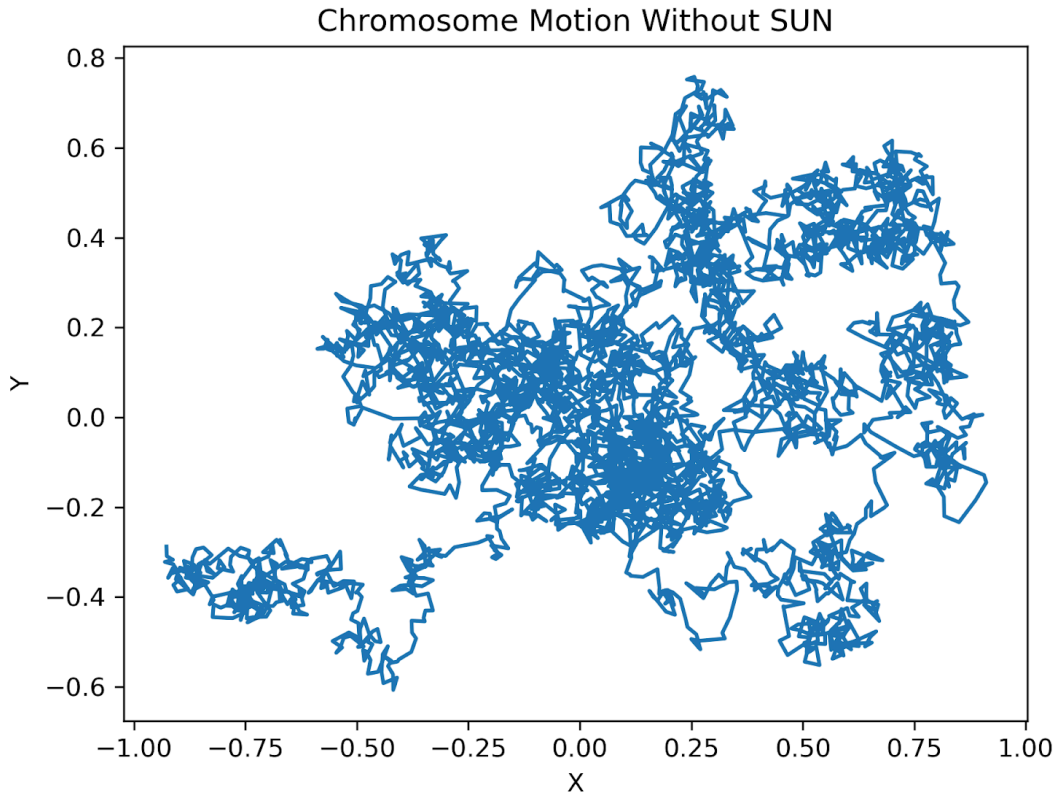


Figure 3. Mean-squared displacement (MSD) of the simulated chromosome ends as a function of time lag, for the free-diffusion (blue) and SUN-anchored (orange) models. SUN anchoring leads to a higher MSD slope, indicating enhanced mobility.

The increase in MSD with anchoring may seem counterintuitive, but it is consistent with experimental findings. In wild-type *Arabidopsis* meiosis (with SUN1/2 tethering), centromere diffusion coefficients were measured at $\sim 0.045 \mu\text{m}^2/\text{s}$ (zygotene) and ~ 0.016 at pachytene, whereas in *sun1 sun2* mutants (no functional tethering) it dropped to ~ 0.002 . Our simulation shows that allowing the particle to roam freely in the 3D volume (analogous to the mutant) constrains it to the interior, whereas attaching to moving NE anchors effectively increases the area it can sample, raising the MSD.

Effect of SUN clustering (bouquet formation). Next we examined the impact of spatial clustering of SUN anchors, as occurs during telomere bouquet formation. We created a scenario where several anchors were restricted to a localized patch of the NE. In this case, once the particle attaches, it tends to remain in the same neighborhood of the envelope. Trajectory plots (not shown) indicated

that clustering reduces isotropy: motion becomes biased toward that region. The outreach ratio (maximum radial distance) sometimes decreased because the particle lingered near the cluster zone. Thus, bouquet-like clustering can impose a more confined pattern of motion, potentially focusing homolog interactions at the bouquet pole. This effect contrasts with the uniform case, and suggests that while SUN tethering generally *increases* movement, strong clustering can locally constrain it.

Simulation of telomere bouquet dynamics. Finally, we mimicked a telomere bouquet by assuming a subset of chromosome ends rapidly attach near one NE pole. In the model, this is equivalent to initializing multiple particles at a cluster of anchors. We found that individual ends then exhibit back-and-forth motions within that cluster region. The collective density of chromosome ends at the cluster could be quantified (data not shown), reproducing a “bouquet” cluster of telomeres on the NE. This artificial bouquet stayed intact over simulated time, illustrating how NE-tethering sites can generate and maintain telomere aggregation. However, because our simulation treats each end independently, we did not capture any active pulling forces or synapsis-driven motion. Even so, the anchored cluster scenario yielded slower dispersion of ends away from the pole than the evenly distributed case, consistent with the idea that bouquet formation concentrates chromosome interactions.

Discussion

Our computational model demonstrates that SUN-mediated attachment of meiotic chromosomes to the nuclear envelope can paradoxically enhance their effective mobility. By simulating a particle confined to the NE surface (SUN-anchored) versus one free in the nuclear interior, we found that tethering greatly increases the mean-squared displacement. This arises because the NE-bound particle effectively moves along the nuclear circumference without penetrating the core, allowing it to cover larger distances. In other words, while anchored motion is geometrically constrained to a shell, the available path length along the periphery is larger than the restricted interior excursions of a free diffusing particle. This effect aligns with the key observation from Cromer *et al.* (2024) that wild-type meiotic centromeres (with SUN tethering) exhibited a roughly 20–25-fold higher diffusion coefficient than the somatic or *sun1 sun2* case (Cromer *et al.*, 2024).

Our model thus provides a plausible explanation for why *sun1 sun2* mutants—lacking functional LINC attachment—show dramatically reduced chromosome motion (Cromer *et al.*, 2024). In *sun1*

sun2 cells, the chromosome ends are effectively “untethered” and must diffuse in the nucleus; our simulation of the free case is a simple analog. The low mobility (MSD) in the untethered condition of our model reflects the experimental diffusion coefficient $D \sim 0.002 \mu\text{m}^2/\text{s}$ measured for *sun1 sun2* centromeres (Cromer *et al.*, 2024). Conversely, with anchoring (wild type), our MSD was higher, analogous to their $D \sim 0.045 \mu\text{m}^2/\text{s}$ in zygotene (Cromer *et al.*, 2024). Thus, even without modeling explicit motor forces, the basic physical constraints of the nucleus can account for much of the SUN-dependent mobility difference.

The clustered (bouquet) scenario in our model showed that concentrating attachment sites on one side of the nucleus limits the exploration of other regions. In *Arabidopsis*, telomere bouquet formation has been observed and is SUN-dependent (Cromer *et al.*, 2024). Our results suggest bouquet clustering would locally trap chromosome ends near the cluster, which could aid homolog pairing by bringing many homologous ends into proximity. However, the trade-off is that those ends explore less of the nuclear volume. Interestingly, Cromer *et al.* noted that bouquet formation was gradually lost by diplotene as telomeres detach (Cromer *et al.*, 2024), consistent with our model expectation that later in meiosis, less tethering would eventually restore freer motion.

Recent work identified the kinesin PSS1 and the KASH protein SINE3 as meiosis-specific components linking SUN1/2 to microtubule motors (Cai *et al.*, 2025). In our model, we did not explicitly simulate active pulling by motors. Instead, we effectively treated the anchored chromosome end as undergoing Brownian motion along the NE. One can imagine that any active motor-driven movement would only augment the effect we observe. The key point is that tethering provides a medium for mechanical coupling. If SUN–KASH complexes oscillate or are driven by cytoskeletal dynamics, the chromosome end can be swept along the NE. Thus, our *in silico* results complement the *in vivo* identification of a SUN–KASH–motor chain: together they imply that the LINC complex both attaches and mobilizes chromosomes during meiosis.

Limitations

Our model is highly idealized. We used a point particle and a simple diffusive step, ignoring the internal structure of chromosomes or the three-dimensional nuclear architecture beyond a sphere. We assumed permanent attachment once the particle encounters an anchor; in reality, telomeres may attach and detach dynamically. We did not include explicit cytoskeletal forces (e.g. directional pulling) or any elastic coupling between chromosomes. Additionally, movements of the nuclear

envelope itself (such as whole-nucleus rotations or oscillations) were not modeled, although these could further enhance effective chromosome mobility. Despite these simplifications, the qualitative outcome—that tethered motion can explore more space than untethered diffusion—is robust across a wide range of parameters. Future modeling could incorporate active force terms, viscoelastic properties of the nucleoplasm, or explicit telomere attachment–detachment kinetics to more closely reproduce experimentally observed trajectories.

Our computational study provides a theoretical framework linking SUN1/2-mediated tethering to observed meiotic nuclear dynamics. It suggests a mechanistic picture in which SUN anchors at the nuclear envelope amplify chromosome-end mobility, thereby facilitating homolog recognition and pairing during meiosis. This perspective helps reconcile the counterintuitive observation that anchoring increases, rather than decreases, chromosome motion and underscores the central role of LINC complexes in shaping plant meiotic chromosome dynamics.

Conclusion

We have developed a computational simulation of meiotic chromosome end motion under different tethering scenarios. Our *in silico* results show that anchoring chromosome ends to SUN protein sites on the nuclear envelope increases effective mobility (higher MSD), compared to untethered diffusion. This finding is in agreement with recent *Arabidopsis* experiments showing that wild-type (SUN-attached) chromosomes move much more than those in *sun1 sun2* mutants (Cromer *et al.*, 2024). Prior genetic work on the *sun1 sun2* double mutant (Varas *et al.*, 2015) established the essential and overlapping roles of SUN1 and SUN2 in meiotic synapsis and recombination, providing the genetic foundation upon which the live-imaging studies of Cromer *et al.* (2024) were built. Clustering of anchors (simulating the telomere bouquet) tends to localize movement and may facilitate homolog pairing in a limited NE region. Overall, our model suggests that dynamic SUN1/2-mediated telomere tethering provides a physical mechanism for enhancing meiotic chromosomal motion, consistent with observed NE reorganization during *Arabidopsis* meiosis (Cromer *et al.*, 2024; Cai *et al.*, 2025). Future work could extend this approach by including active cytoskeletal forces and realistic genome architecture, to further integrate computational and experimental insights into meiotic chromosome dynamics.

Data availability

All the necessary data is available at
https://github.com/towardsbioscience/SUN_protien_heat_stress.git

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