

1 **Are Maize Stalks Efficiently Tapered to Withstand Wind Induced Bending**
2 **Stresses?**

3

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15 **Word Count:** 4539

16 **Figures:** 8

17 **Tables:** 0

18 **Keywords:** bending, efficiency, lodging, maize, morphology, optimization, stalk, stem, stress,
19 structural

20 **Highlight:** Maize stem morphology was investigated through an optimization algorithm to
21 determine how efficiently their structural tissues are allocated to withstand wind induced bending
22 stresses that cause stalk lodging.

23 **Running Title:** Structural Efficiency of Maize Stalks

24 **Abstract**

25 Stalk lodging (breaking of agricultural plant stalks prior to harvest) results in millions of
26 dollars in lost revenue each year. Despite a growing body of literature on the topic of stalk lodging,
27 the structural efficiency of maize stalks has not been investigated previously. In this study, we
28 investigate the morphology of mature maize stalks to determine if rind tissues, which are the major
29 load bearing component of corn stalks, are efficiently organized to withstand wind induced
30 bending stresses that cause stalk lodging.

31 945 fully mature, dried commercial hybrid maize stem specimens (48 hybrids, ~2
32 replicates, ~10 samples per plot) were subjected to: (1) three-point-bending tests to measure their
33 bending strength and (2) rind penetration tests to measure the cross-sectional morphology at each
34 internode. The data were analyzed through an engineering optimization algorithm to determine the
35 structural efficiency of the specimens.

36 Hybrids with higher average bending strengths were found to allocate rind tissue more
37 efficiently than weaker hybrids. However, even strong hybrids were structurally suboptimal.
38 There remains significant room for improving the structural efficiency of maize stalks. Results
39 also indicated that stalks are morphologically organized to resist wind loading that occurs primarily
40 above the ear. Results are applicable to selective breeding and crop management studies seeking
41 to reduce stalk lodging rates.

42 **Introduction**

43 Stalk lodging (permanent displacement of plants from their vertical orientation) severely
44 reduces agronomic yields of several vital crop species including maize. Yield losses due to stalk
45 lodging are estimated to range from 5-20% annually (Flint-Garcia *et al.*, 2003; Berry *et al.*, 2007).
46 Several internal and external factors contribute to a plant's propensity to stalk lodge. External
47 factors include wind speed (Wen *et al.*, 2019), pest damage (Echezona, 2007), and disease (Dudley,
48 1994; Holbert *et al.*, 1923). Internal factors include the plant's morphology and material properties
49 (Esechie, 1985; Robertson *et al.*, 2017; Stubbs *et al.*, 2018). Despite a growing body of literature
50 surrounding the topic of maize stalk lodging, a detailed morphological investigation of the taper
51 of maize stalks has not been reported. The purpose of this paper is to quantify changes in diameter
52 and rind thickness of maize stalks as a function of plant height (i.e., taper) and to determine the
53 structural efficiency of the taper of maize stalks. This study investigates stalk taper from a purely
54 structural standpoint and other abiotic and biotic considerations that may affect stalk morphology
55 (i.e., taper) of maize stalks are not considered.

56 To determine the structural efficiency of maize stalks one must both quantify the stalk taper
57 and define probable wind loading scenarios. An efficiently tapered stalk is defined as one in which
58 uniform mechanical stresses are produced when the plant is subjected to probable wind loading
59 scenarios. In other words, the shape of the stalk is optimal, meaning that loads are supported with
60 as little tissue as possible. An inefficient taper is one in which non-uniform mechanical stresses
61 are produced. Inefficient stalks utilize more structural tissue than is necessary in some areas and
62 less structural tissue than is necessary in other areas to withstand the loads to which they are
63 subjected. In other words, for inefficient stalks the amount of structural tissue could be reduced
64 without affecting the load bearing capacity of the stalk. The structural efficiency of maize stalks is
65 of interest because efficient stalks would theoretically have more available biomass and bioenergy
66 to devote to grain filling as compared to inefficient stalks (i.e., efficient stalks would have a higher
67 harvest index).

68 As mentioned previously, both the taper and probable wind loading scenarios must be
69 defined to determine the structural efficiency of maize stalks. The wind load exerted on a plant
70 stalk, known as the drag force (D_f), can be approximated as (Niklas, 2000):

71
$$D_f = 0.5\rho u^2 A_p C_D \quad (1)$$

72 where ρ is the density of air, u is the local wind speed, A_p is the projected area of the structure, and
73 C_D is the drag coefficient. While this equation appears fairly simple at first glance, it is
74 complicated by the fact that the variables on the right hand side of the equation are functions that
75 can vary both temporally and spatially. For example, the drag coefficient changes spatially along
76 the length of the stalk and is also a function of the local wind speed. As the local wind speed
77 increases, the angle of the leaf blades and tassel change (known as flagging), which alters the drag
78 coefficient.

79 The strong interrelationships between the factors of Equation 1 complicate attempts to
80 directly measure wind forces on maize stalks. Direct measurements of wind speeds have
81 successfully been used to estimate drag forces in past studies of trees (Niklas and Spatz, 1999;
82 Niklas, 2000). However, the large ratio of leaf area to stalk area, close proximity of maize plants
83 to one another in commercial fields, and other confounding factors imply that a direct measurement
84 of the wind speed near a maize stalk is not necessarily a good predictor of the drag force
85 experienced by the stalk. Detailed computational engineering models that capture the interplay
86 between fluid dynamics and structural deformations (i.e. fluid-structure interaction models
87 (Zienkiewicz *et al.*, 2014)) could potentially be used to calculate the drag force experienced by
88 maize stalks over time. However, such models are computationally expensive and time-
89 consuming to run. In summary, accurately measuring drag forces in crop canopies is challenging
90 and remains an active area of research. An overview of this topic is given by Finnigan (Finnigan,
91 2000).

92 While direct measurement of exact wind forces on maize stalks is challenging, defining the
93 realm of possible wind loading scenarios less so. To define the realm of possible wind loading
94 scenarios we assume the wind speed acts in the same direction along the length of the stalk. In
95 other words the wind does not blow in one direction at the bottom of the stalk and in a different
96 direction at the top of the stalk. We can also bound the degree of change in the magnitude of the
97 wind force along the length of the plant. For example, previous studies and engineering fluid
98 mechanics theory dictate that the local wind speed in crop canopies increases with height (Cionco,
99 1965; Wen *et al.*, 2019; Yi, 2008). A simple examination of corn stalks also suggest that the

100 combination of the drag coefficient and projected area increases with plant height (i.e., the leaves
101 near the bottom of mature maize plant are often dead and fall off whereas the top leaves remain
102 structurally robust). Thus both the local wind speed and the combined effect of the drag coefficient
103 and projected area can be assumed to increase with plant height. Combining these insights with
104 Equation 1, we can determine that the wind force (i.e. drag force) increases with plant height. Next,
105 we apply upper and lower bounds of probable wind loading scenarios. At the upper bound of
106 probable wind loading we assume all of the wind force acts at the top of the plant as a point load.
107 At the lower bound of probable wind loading we assume a uniform load is applied to stalk along
108 its entire length (i.e., the drag force at the top of the plant is the same as the drag force in every
109 other cross-section of the plant including the bottom of the plant). These bounds allow for all
110 probable wind loading scenarios (e.g., linear, quadratic exponential etc. increase in drag force with
111 plant height) and exclude improbable scenarios such as the drag force being higher at the base of
112 the plant than at the top of the plant. Figure 1 visually represents each of these assumptions.

113 The structural efficiency of maize stalks can be determined by using Engineering equations
114 which relate stem morphology and mechanical stress to probable wind loading scenarios presented
115 in Figure 1. In particular, the maximum stress in any cross-section (σ) due to wind-induced bending
116 is calculated as (Beer *et al.*, 2002):

117
$$\sigma = \frac{\int D_f dx}{S_x} \quad (2)$$

118 where D_f is the drag force (see Equation 1) and S_x is the section modulus at a distance x along the
119 stalk. Section modulus is an engineering term that quantifies the morphology of the cross-
120 section. Maize stalks possess elliptical cross-sections, therefore, the section modulus of each
121 cross-sections is a function of the ellipse's major diameter (D), minor diameter (d), and the
122 thickness of the rind (t) in the form (Young and Budynas, 2002):

123
$$S_x = \frac{\pi}{4}(Dd^3 - (D - t)(d - t)^3) \quad (3)$$

124 By combining Equations 2 and 3, we can calculate the drag force / section modulus that results in
125 a uniform stress along the length of the plant.

126 Figure 1 displays a visual representation of the range of possible tapers for maize stalks
127 that would produce uniform stresses during probable wind loading scenarios. The range of
128 probable wind loadings is defined with an upper bound (red curve) of a point load applied to the
129 top of the plant, and a lower bound (blue curve) of a uniform drag force applied to the entire length
130 of the specimen. The graph depicts the most efficient plant tapers (white area) from the ground (x
131 $= 0$) to the top of the plant specimen ($x = 1$), and from the section modulus at the uppermost
132 internode of the plant specimen ($y = SM_{top}$) to the section modulus at the bottommost internode of
133 the plant ($y = SM_{bottom}$). If the section modulus of an internode falls above the red curve, then that
134 internode will experience a lower maximum stress than the rest of the plant, as it has more
135 structural tissues (i.e., mass) than is necessary. If the section modulus of an internode falls below
136 the blue curve, then that internode will experience a higher maximum stress than the rest of the
137 internodes of the plant, as it has less structural tissue than is efficient. If the section modulus of an
138 internode falls between the red and blue curves (white area), then that internode will experience a
139 similar level of mechanical stress as compared to the rest of the plant, and therefore has an efficient
140 allocation of structural tissues.

141 To determine the structural efficiency of maize plants, a select group of maize stalks were
142 analyzed. Their major and minor diameters and rind thicknesses were measured at each internode
143 and compared to Figure 1. In addition, a custom optimization algorithm was employed to
144 determine the exact drag force profile for each plant that would produce the most uniform
145 mechanical stress possible for the given stalk structure. The details and results of these
146 experiments are presented in the following sections.

147

148 **Methods**

149 All maize specimens in this study were subjected to the following battery of tests. First,
150 major and minor diameters of each internode were measured with calipers and internode lengths
151 were measured with a ruler. Second, bending strength was measured in three-point
152 bending. Third, rind thickness was measured through rind penetration tests (Seegmiller *et al.*,
153 2020). Each stalk was then analyzed and an optimization algorithm was employed to determine
154 the theoretical drag force profile that would produce the most uniform stresses along the entire

155 length of the stalk. Finally, statistical analyses were performed to investigate the relationship
156 between each specimen's strength and its structural efficiency.

157

158 ***Plant materials***

159 Forty-eight maize hybrids, chosen to represent a reasonable portion of maize genetic
160 diversity, were evaluated for variation in stem morphology and structural tissue distribution. The
161 hybrids were planted at Clemson University Simpson Research and Education Center, Pendleton,
162 SC in well drained Cecil sandy loam soil. The hybrids were grown in a Random Complete Block
163 Design with two replications. In each replication, each hybrid was planted in two-row plots with
164 row length of 4.57 m and row-to-row distance of 0.76 m with a targeted planting density of 70,000
165 plant ha⁻¹. The experiment was surrounded by non-experimental maize hybrids on all four sides to
166 prevent any edge effects. To supplement nutrients, 56.7 kg ha⁻¹ nitrogen, 86.2 kg ha⁻¹ of phosphorus
167 and 108.9 kg ha⁻¹ potassium was added at the time of soil preparation, and additional 85 kg ha⁻¹
168 nitrogen was applied 30 days after emergence. Standard agronomic practices were followed for
169 crop management.

170 Stalks used for this study were harvested when all the hybrids were either at or past
171 physiological maturity (i.e., 40 days after anthesis). Ten competitive plants from each replication
172 were harvested by cutting at just above ground level, stripped of all the leaves and ears, and
173 transferred to a forced air dryer for drying at 65°C. Some plots lacked 10 competitive plants and,
174 therefore, the total number of plants evaluated for each hybrid varied slightly. In total, 945 fully
175 mature, dried commercial hybrid maize stalks were used in this study (48 hybrids, ~2 replicates,
176 ~10 samples per hybrid).

177

178 ***Three-Point-Bending Tests***

179 Specimens were tested in three-point-bending using an Instron Universal Testing System
180 (Instron Model # 5944, Norwood, MA). Specimens were supported at their bottom and top node,
181 and loaded at their middle node. Care was taken to ensure that the specimens were both loaded

182 and supported at nodes, and that the span lengths were maximized. This was done to obtain the
183 most natural possible failure modes (Robertson *et al.*, 2015; Stubbs *et al.*, 2018). Specimens were
184 loaded at a rate of 2 mm/s until structural failure. Additional details on the three-point-bending
185 test protocol were documented in a previous study (Robertson *et al.*, 2017). Short span 3-pt bend
186 tests (test of a single internode) were not employed in this study as they have been shown to
187 produce unnatural failure patterns and result in inaccurate bending strength measurements
188 (Robertson *et al.*, 2015).

189

190 ***Morphology Measurements***

191 Internode lengths of each specimen were measured with a ruler. Other morphology
192 measurements were taken at the midspan of each internode of every specimen. In particular,
193 caliper measurements were used to obtain the minor and major diameters of each internode. Rind
194 penetration tests were used to obtain the rind thickness of each internode. Rind penetration tests
195 were performed using an Instron universal testing machine. A probe was briefly forced through
196 the specimen at a rate of 25 mm/s, and the resulting force-displacement curve was analyzed using
197 a custom MATLAB algorithm to calculate the rind thickness (t) of the stalk cross-
198 section. Additional details on the rind penetration test protocol are documented in (Seegmiller *et*
199 *al.*, 2020).

200

201 ***Optimization of Loading Condition***

202 An optimization algorithm was employed to determine the drag force profile ($f(x)$) for each
203 stem specimen that would produce the most uniform stress along the length of the stalk. As the
204 specimens examined only spanned the bottom half of the stalk (from the ground to the ear), the
205 loading above the ear was resolved into a single positive force (F_0) and positive moment (M_0)
206 applied to the top of the specimen as described by Beer (Beer *et al.*, 2002) and shown in Figure
207 2. For the hybrids investigated, the ear was an average of 49.6% (+/- 14.3% standard deviation)
208 of the way up the stalk.

209 Based on this setup, we can now calculate the resolved force (F_0) and the loading profile
210 ($f(x)$) for each specimen that results in the most uniform stress state in each particular

211 specimen. This was accomplished through the use of an optimization algorithm. In particular, a
212 custom code was developed in Matlab to perform an *fmincon* optimization for each stem specimen
213 (Chuan et al., 2014; Han, 1977, 1977; Sreeraj et al., 2013). The objective of the optimization
214 function was to minimize the variation in mechanical stress across the length of the specimen by
215 changing the values of the input parameters F_0 and $f(x)$ (see figure 3). To accomplish this each
216 specimen was computationally partitioned into 100 cross-sections and the optimization routine
217 would then: (1) take in user-supplied initial estimations of F_0 at the top of the specimen and $f(x)$ at
218 the other 99 cross-sections (100x1 vector X), (2) calculate bending stress at every cross section
219 using Equation 2 (100x1 vector s), (3) calculate the total variance between the bending stress at
220 each cross-section and the uniform stress state (i.e. the area between the curves in Figure 3) (scalar
221 value Y), (4) iterate on X until the variance Y was minimized. The code would then give the drag
222 force profile X that produced the most uniform stress state along the specimen (s), and the total
223 variance in the bending stress (Y), which is a quantitative assessment of how efficiently the
224 specimen's structural tissues (i.e., rind) were allocated. The optimization routine was conducted
225 with several different initial starting points for each specimen (i.e., initial values for F_0 and $f(x)$)
226 to ensure the global optimal solution was found as opposed to a local minimum. Tolerances and
227 stopping criteria were set to 1E-6 (first order optimality tolerance), 1E-6 (function tolerance), and
228 1E-10 (step size tolerance).

229

230 **Results**

231 Both the three-point-bending tests and rind penetration tests yielded the expected results,
232 based on previous studies (Robertson *et al.*, 2015, 2017; Stubbs *et al.*, 2018). The three-point-
233 bending force-deflection responses were linear in nature until failure and demonstrated failure
234 patterns that occur in naturally lodged maize plants (Robertson *et al.*, 2015; Stubbs *et al.*,
235 2018). The rind penetration tests gave results characteristic of the protocol. Both test regimes
236 were found to be reliable and repeatable. The bending strength of each specimen, as well as the
237 section modulus, length, major diameter, minor diameter, and rind thickness of each specimen
238 internode is presented in Figure 4.

239

240 ***Structural Efficiency***

241 Section modulus values for each stalk were analyzed to determine structural efficiency
242 (i.e., how structurally efficient the taper of each stalk was). It was found that the median taper of
243 all stalks demonstrated an efficient allocation of structural tissues for probable wind loadings (see
244 Figure 5). However, many internodes fell well outside the range of structural efficiency (i.e.,
245 outside of the white area in Figure 5). In particular, 35% of the measured internodes in the study
246 fell within the most efficient range, 38% of measured internodes fell below the blue curve (too
247 little structural tissue), and 27% of the measured internodes fell above the red curve (too much
248 structural tissue).

249

250 ***Optimal Drag Force Profile for Each Stalk***

251 The optimization procedure was performed on all 945 stalks. The *fmincon* procedure
252 successfully determined the drag force profile (\mathbf{X}) that produced the most uniform state for each
253 specimen. Figure 6 depicts histograms of the resulting stress states of the specimens. In particular,
254 the overall average stress along the length of each specimen ($n = 945$) and the stress at every cross-
255 section of each specimen ($n = 94500$) is presented in Figure 6. To enable all specimens to be
256 plotted on the same graph the stress of each specimen / cross-section was normalized to a target
257 stress of 1.00. In other words, a stress state different than a stress of 1.00 represents a suboptimal
258 allocation of structural tissues.

259 Analysis of the drag force profiles for each specimen that would produce the most uniform
260 stress in the specimen revealed that the resolved force F_0 was far larger than the drag force profile
261 below the ear (see Figure 7). These data imply that the stalks allocate structural tissues for wind
262 loading that primarily occurs above the ear (e.g. the drag force increases exponentially with
263 height). This does not imply that there is no wind below the ear, but that the drag force (determined
264 by the local wind speed, projected stalk and leaf area, and drag coefficient) is much less below the
265 ear as compared to the drag force above the ear. Note this does not imply the bending stresses are
266 lower at the base of the stalk. Bending stresses are determined by forces (i.e., $f(x)$ and F_0) and

267 moment arms (i.e., distance at which the force is applied). Thus, bending stresses are always higher
268 at the base of the stalk even if the drag force profile is lower at the base of the stalk.

269

270 *Are Stronger Stalks More Efficient*

271 To test the hypothesis that stronger plants allocate structural tissues more efficiently (i.e.,
272 they produce uniform stresses under probable wind loading scenarios), the bending strength of
273 each stalk was compared to its taper. As discussed previously, the level of structural efficiency
274 can be determined by calculating the area between the curves shown in Figure 3 (*Y*). For example,
275 a *Y* value of zero represents a perfectly efficient structure, and the larger the *Y* value, the less
276 efficiently the stalk tissues are organized. The data demonstrated that stronger stalks more
277 structurally efficiently (have a lower *Y* value) and more consistent (lower variance of *Y* values).
278 This was found to be true when comparing individual specimens and when comparing hybrids (see
279 Figure 8).

280

281 **Discussion**

282 Improving structural efficiency in maize plants could simultaneously enhance yield and
283 lodging resistance. However, there has not been any previous investigations of structural efficiency
284 in maize stalks. Consequently, plant scientists have not directly breed or managed for plants that
285 are structurally optimized in the past. Results from this study suggest that the majority of modern
286 maize hybrids may possess suboptimal stalk structures (see figure 5). In other words, most maize
287 plants utilize bioenergy and structural biomass inefficiently. This reduces the amount of potential
288 biomass and bioenergy available for grain filling (i.e., lowers harvest index) and simultaneously
289 makes stalks more susceptible to stalk lodging. Of the 945,000 cross-sections analyzed in this
290 study 65% were structurally suboptimal with 38% having too much structural tissue and 27%
291 having too little structural tissue.

292 Further studies are needed to determine the genetic, environmental and management
293 practices that influence stalk taper and structural efficiency in maize stalks. In addition, high

294 throughput phenotyping methods capable of economically measuring stalk rind thickness are
295 needed. Most methods of measuring rind thickness require destructive sectioning and imaging
296 procedures that induce plant fatality and thus prevent measurement of other important crop
297 breeding metrics such as yield. Several nondestructive methods of measuring stalk rind thickness
298 have been developed (e.g., x-ray computed tomography) but these methods are usually limited to
299 laboratory or greenhouse settings and cannot easily be implemented in an agricultural field setting
300 (e.g., (Mairhofer *et al.*, 2012; Robertson *et al.*, 2017; Seegmiller *et al.*, 2020)).

301 Results showed that lodging resistant hybrids (i.e., those with higher average bending
302 strengths) were more structurally efficient than hybrids that were weaker. The hybrids with higher
303 average bending strengths also displayed less plant to plant variation in structural efficiency. In
304 other words, strong hybrids were more structurally optimized and more consistently optimized
305 than weaker plants (i.e., demonstrated less plant to plant variability). These same findings are
306 true when analyzing individual plants. For example, if the hybrid factor is ignored and each stalk
307 is analyzed as an individual specimen (i.e., no averaging of results across hybrids) the stronger
308 stalks were more structurally efficient than weaker stalks. These results are likely due in part to
309 breeding techniques used in the past. In particular, applied selective breeding pressure based on
310 counts of lodged stalks at harvest time is expected to produce hybrids that are both strong and
311 exhibit minimal plant to plant variance in strength. That is to say that a variety with high average
312 strength but also high standard deviation in strength will have higher lodging rates than a variety
313 with a similar average strength but a lower standard deviation in strength.

314 In this study an optimization routine was used to determine the wind loading profile that
315 would produce the most uniform mechanical stresses along the length of maize stalks. It was found
316 that maize stalks are structurally optimized for wind loadings that occur primarily above the
317 ear. This is consistent with the authors' observations in field conditions; although plants at the
318 border of the field may experience loading along the full length of the stalk, the majority of maize
319 plants appear to be primarily subjected to wind loads at or above the ear. The optimization method
320 used in this study was robust and has the potential to be applied to other plants in which the
321 structure of the plant may be predictive of its loading environment. Using optimization methods
322 to infer a plants wind loading environment has several advantages over traditional measurement
323 techniques used to determine wind loads on plants. In particular, it is computationally efficient

324 (as compared to fluid-structure interaction models) and can infer the aggregate loading over time,
325 taking into account the wind profile and fluid-structure interaction between the wind and the plant
326 stalk.

327 Three-point bending tests are the most commonly employed test to quantify bending
328 strength in plant stalks (Robertson *et al.*, 2015; Stubbs *et al.*, 2018). However, results from this
329 study highlight several shortcomings of the three-point-bending test approach. In particular, most
330 plant stalks are tapered and researchers typically opt to place the loading anvil from a three-point-
331 bending test at the same anatomical location for each stem specimen in a given study (e.g. the third
332 internode). Thus, the failure location is artificially imposed by the researcher since failure always
333 occurs near the loading anvil, whereas in nature, the failure location is determined by local material
334 weakness and imperfections (i.e., suboptimal allocation of structural tissues). By artificially
335 imposing the failure location the researcher is inducing failure in a cross-section that may have
336 more structural tissue than is optimal in some specimens and less structural tissue than is optimal
337 in other specimens. This confounds comparisons of bending strength among different specimens
338 in a given study, as the measured bending strength could vary substantially for any given specimen
339 depending on the structural optimality of the failed cross-section. A better approach is to apply
340 bending loads that replicate natural loading patterns. Such loading conditions produce natural
341 failure types and failure patterns in plant specimens (i.e., failure occurs at the cross-section with
342 the least optimal allocation of structural tissue). Several devices have been recently developed
343 which accomplish this task (Grafius and Brown, 1954; Berry *et al.*, 2003; Guo *et al.*, 2018, 2019;
344 Erndwein *et al.*, 2019; Heuschele *et al.*, 2019). In particular, they utilize the natural anchoring of
345 the maize roots and apply a point load to a cross-section near the ear (very similar to the loading
346 profile shown in Figure 7). Thus these devices simulate the loading conditions experienced by
347 plants in their natural environment and consequently produce natural failure types and patterns
348 (Cook *et al.*, 2019). These devices are therefore expected to provide more distinguishing power
349 than three-point-bending test methods.

350

351 ***Limitations***

352 The primary limitation of the current study is that the rind of the stalk was assumed to be
353 a homogeneous, isotropic, linear elastic material subjected to pure bending. The inclusion of
354 heterogeneity, anisotropy, non-linear material properties, and the addition of the pith material
355 could change the behavior of the analyzed stalks. However, previous research has shown the
356 inclusion of these effects to be small and in many cases insignificant. The authors do not believe
357 inclusion of such effects would change the overall conclusions of this paper (Von Forell *et al.*,
358 2015; Al-Zube *et al.*, 2018).

359 This study is deliberately limited in its scope to structural efficiency. Other abiotic and
360 biotic considerations can affect stalk morphology / anatomy and should be considered in future
361 studies. In addition, this study utilized three-point-bending test to measure the bending strength
362 of stem specimens. However, as mentioned in the discussion section these tests are less than
363 ideal. Unfortunately, at the time the study was conducted by the authors we were not fully aware
364 of the limitations of three-point-bending test. In particular, we did not expect to find that the
365 majority of maize stalk cross-sections are structurally suboptimal. Future studies are warranted
366 which utilize in-field phenotyping devices (Erndwein *et al.*, 2019) to assess structural efficiency
367 and its relations to stalk strength, harvest index, etc.

368

369 **Conclusions**

370 The morphology of physiological mature maize stalks was characterized, and the loading
371 environments that result in the most uniform maximum stresses along the length of maize stalk
372 were investigated. It was found that maize stalks are morphologically organized to resist wind
373 loading that occurs primarily above the ear. It was also found that plants with higher bending
374 strengths were more structurally efficient than weaker plants. However, even strong plants
375 allocated structural tissues in a suboptimal manner. There exists much room for improvement in
376 the area of structural optimization of maize stalks. These findings are relevant to crop management
377 and breeding studies seeking to improve stalk lodging resistance.

378

379 **Conflicts of Interest**

380 There are no conflicts to declare.

381

382 **Authors' Contributions**

383 All authors were fully involved in the study and preparation of the manuscript. The
384 material within has not been and will not be submitted for publication elsewhere.

385 **Acknowledgements**

386 This work was funded in part by the National Science Foundation (Award #1826715) and
387 by the United States Department of Agriculture - NIFA (#2016-67012-2381). Any opinions,
388 findings, conclusions, or recommendations are those of the author(s) and do not necessarily reflect
389 the view of the funding bodies.

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Figure Captions

Figure 1: Structural efficiency along the length of the specimen as a function of probable wind loadings (top); loading diagrams for a point load and uniform drag force (bottom).

Figure 2: A loading diagram of the wind on the plant stalk with an unknown load distribution along the length of the stalk (left); the wind loading above the ear can be resolved as an unknown positive force (F_0) and positive moment (M_0) applied to the top cross section (right) (Beer et al., 2002).

Figure 3: A typical specimen output, showing the stress state resulting from the fmincon optimization procedure, which attempts to create the most uniform possible stress state along the length of the specimen by altering values for F_0 and $f(x)$ (top); the analytical maize stalk model partitioned into 100 cross-sections along its length (bottom).

Figure 4: The geometric characterization of all 945 specimens; histograms of the specimen strengths (a) and specimen lengths (b); plots of the section modulus (c), rind thickness (d), minor diameter (e), and major diameter (f) along the lengths of each specimen.

Figure 5: The measured section moduli of the specimens as compared to the region of structural efficiency.

Figure 6: A histogram of the average stress along the length of each of the 945 specimens after optimization, $n = 945$ (left); a histogram of the average stress at all 100 cross-sections along the length of each of the 945 specimens after optimization, $n = 94500$ (right). All stress are normalized to a target stress of 1.00. Thus stress states that deviate from 1.00 represent a suboptimal structural allocation of biomass.

Figure 7: The drag force profile for all 945 specimens ($f(x)$ and F_0) (top); a loading diagram of $f(x)$ and F_0 (bottom). The 75th and 25th percentile values are generally line-on-line with the median values along the length of the specimen.

Figure 8: Strength vs. structural efficiency for each specimen (left) and the average of each hybrid (right).

Figure 1.

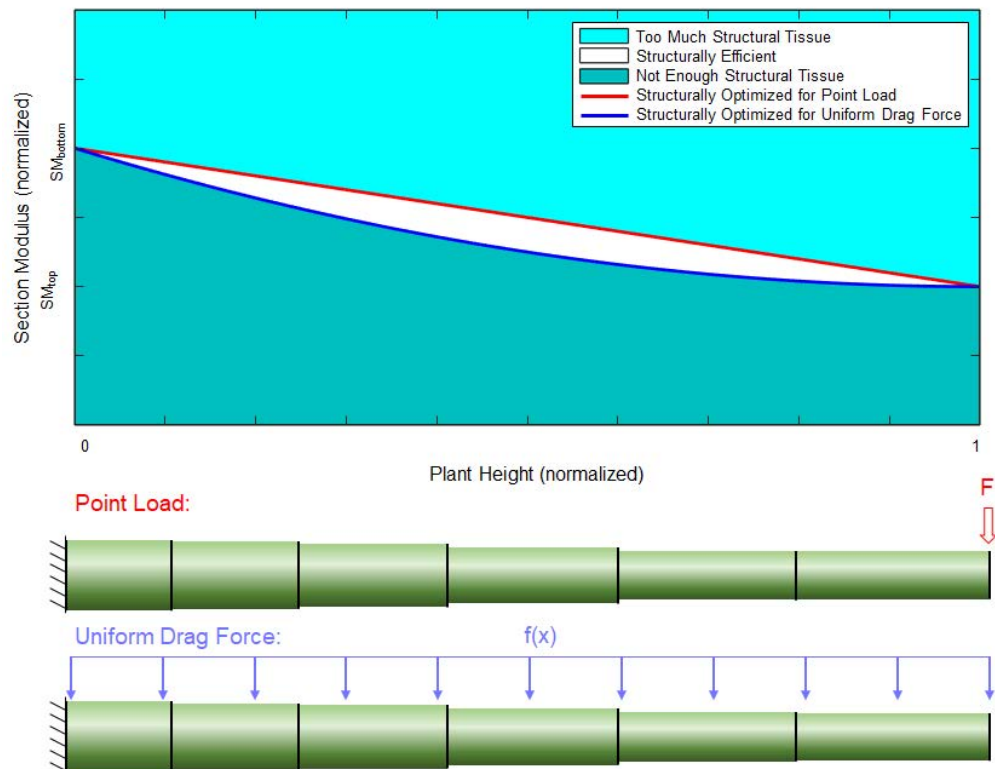


Figure 2

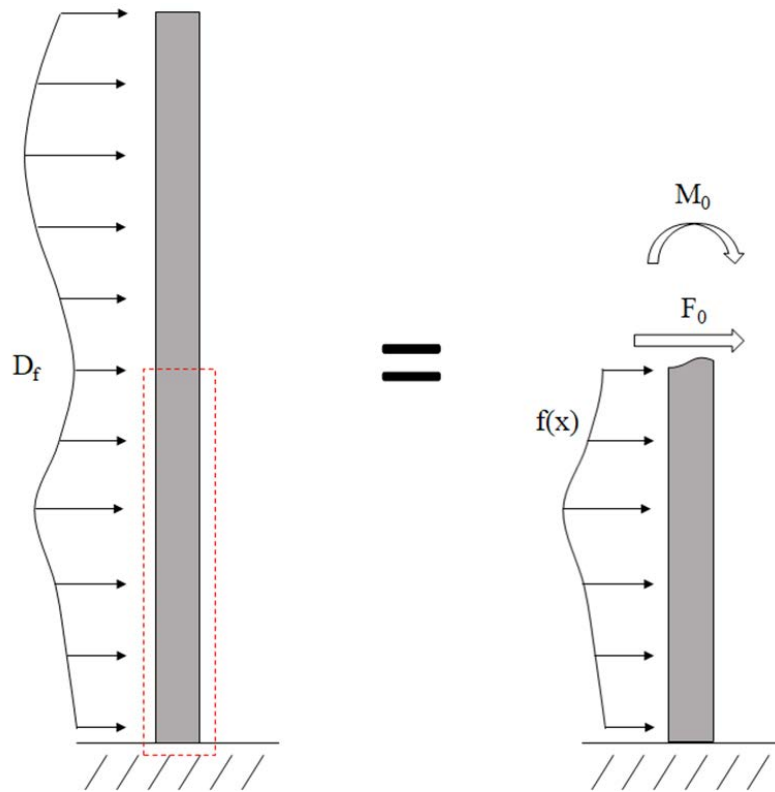


Figure 3.

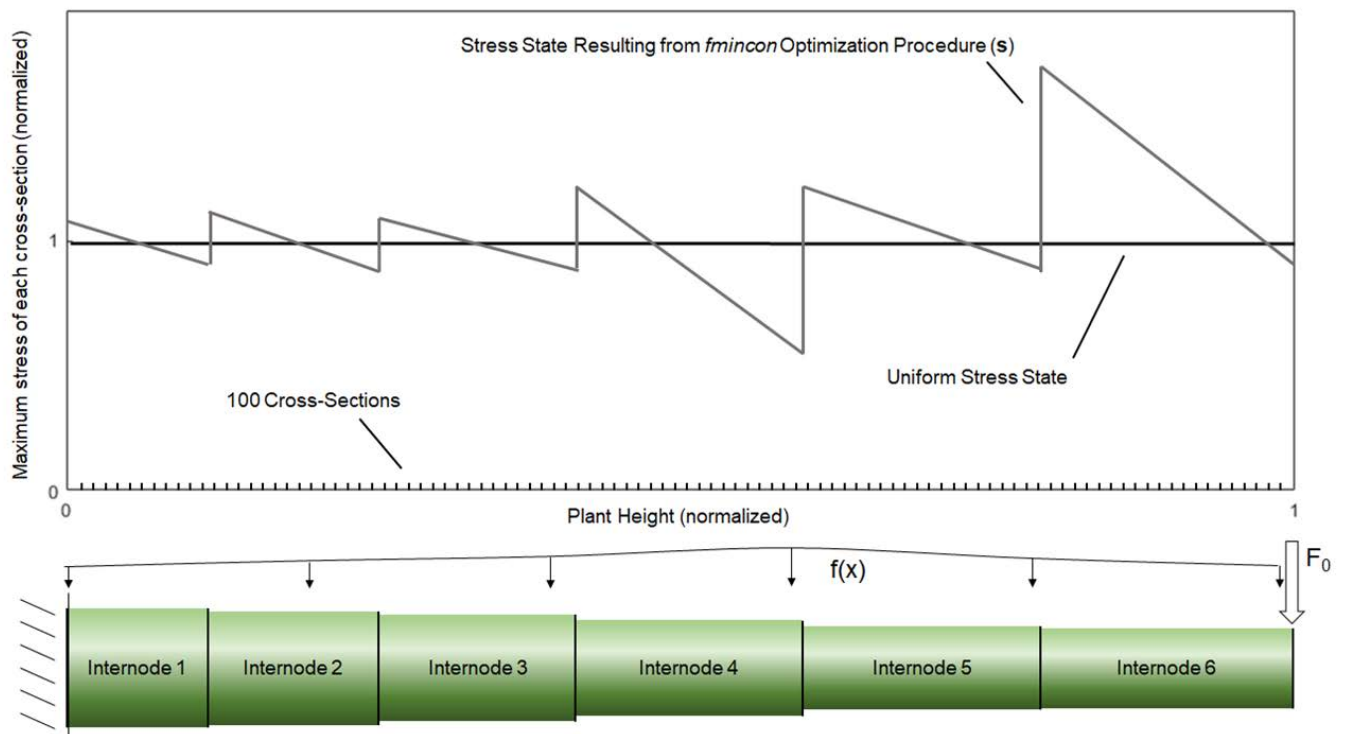


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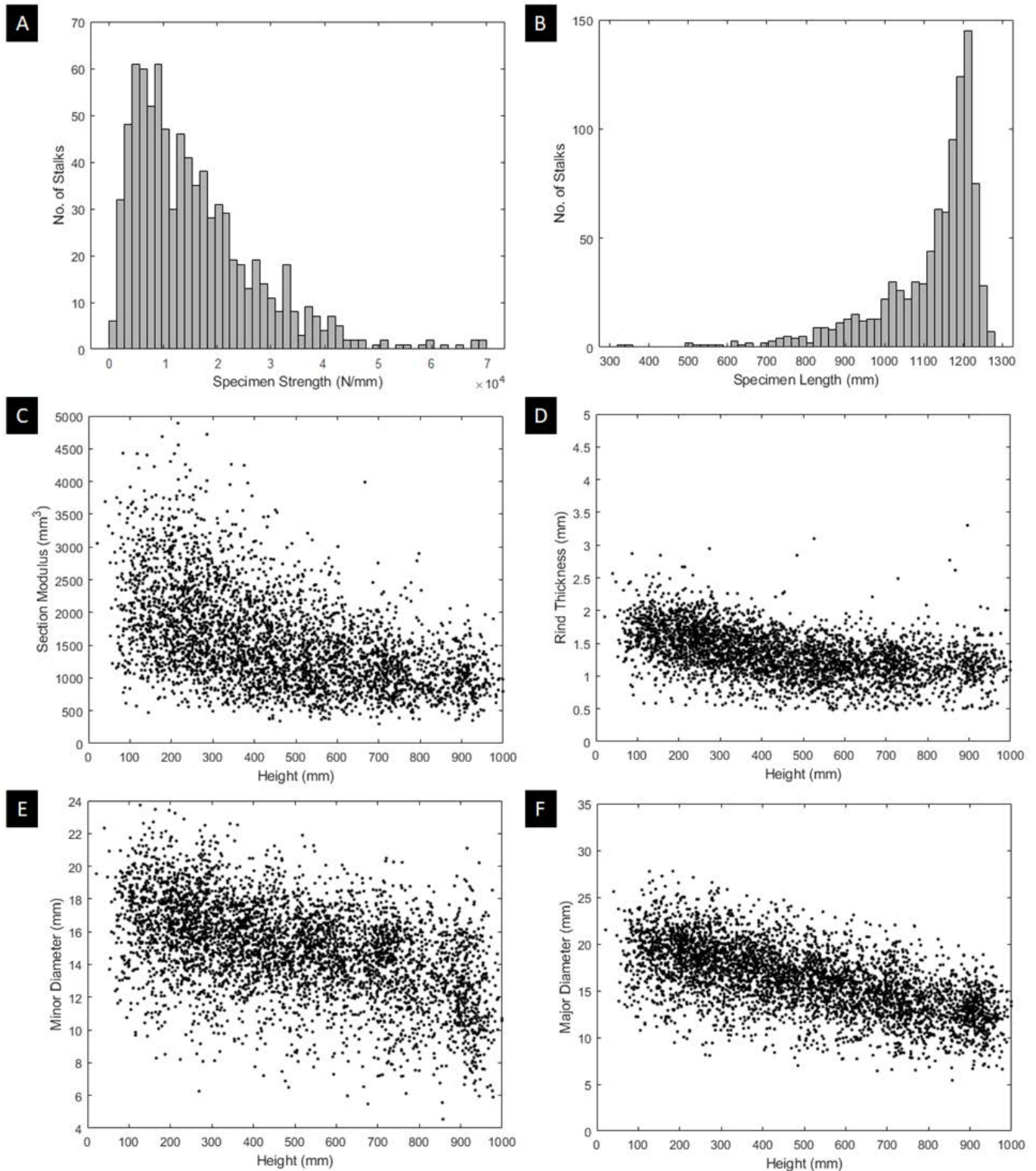


Figure 5.

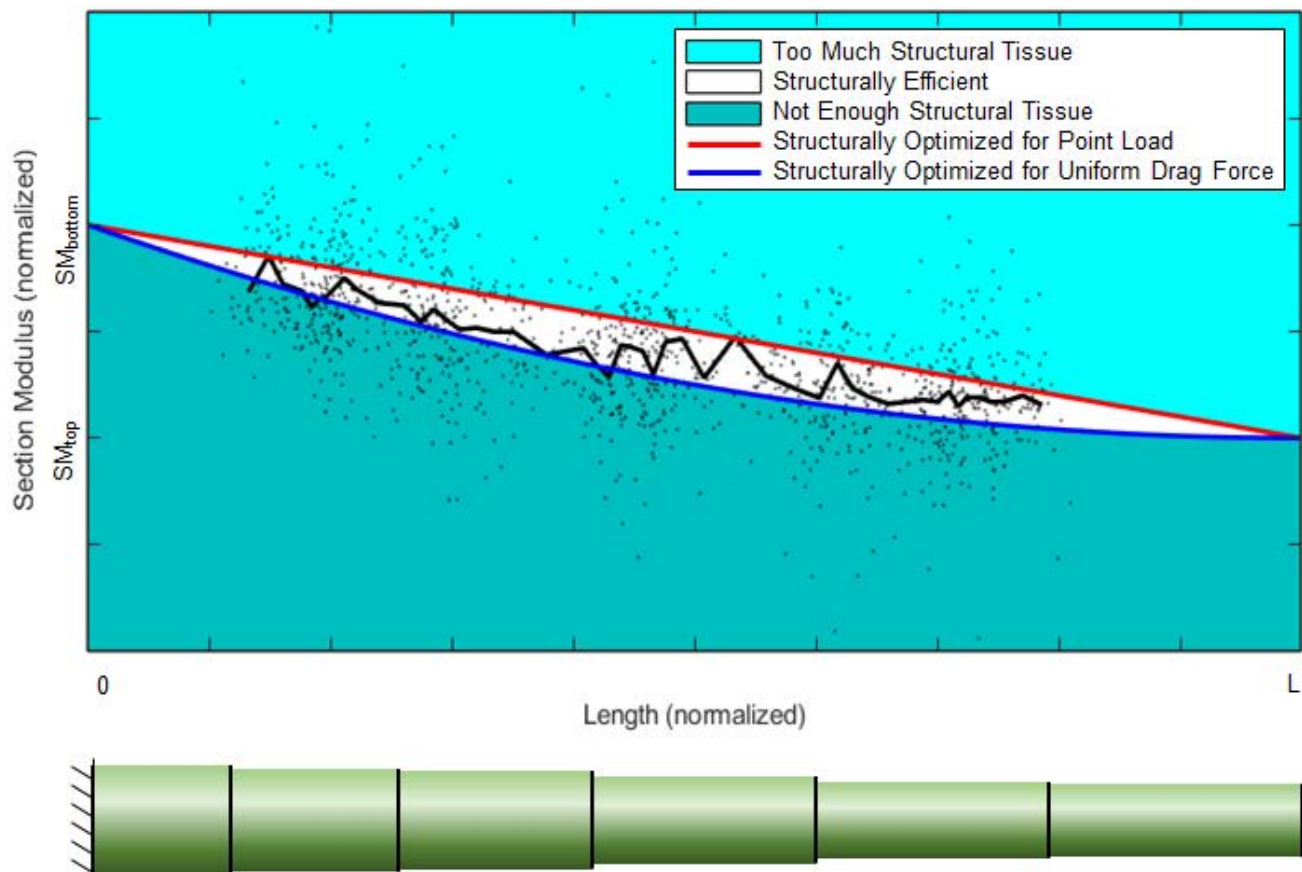


Figure 6.

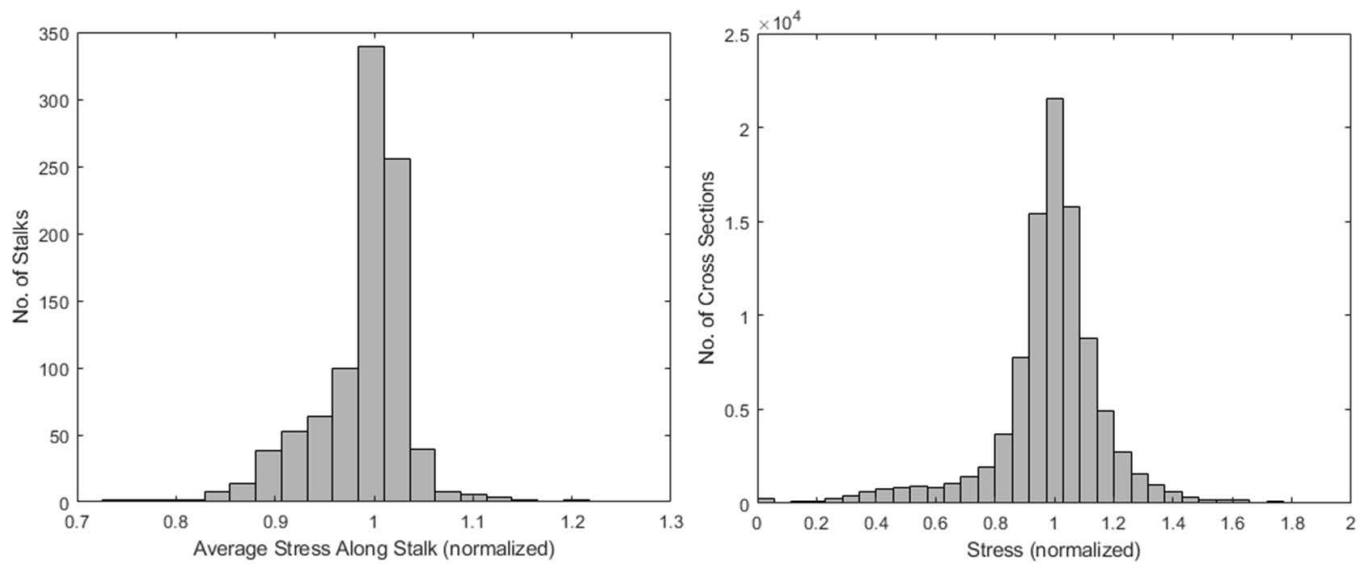


Figure 7.

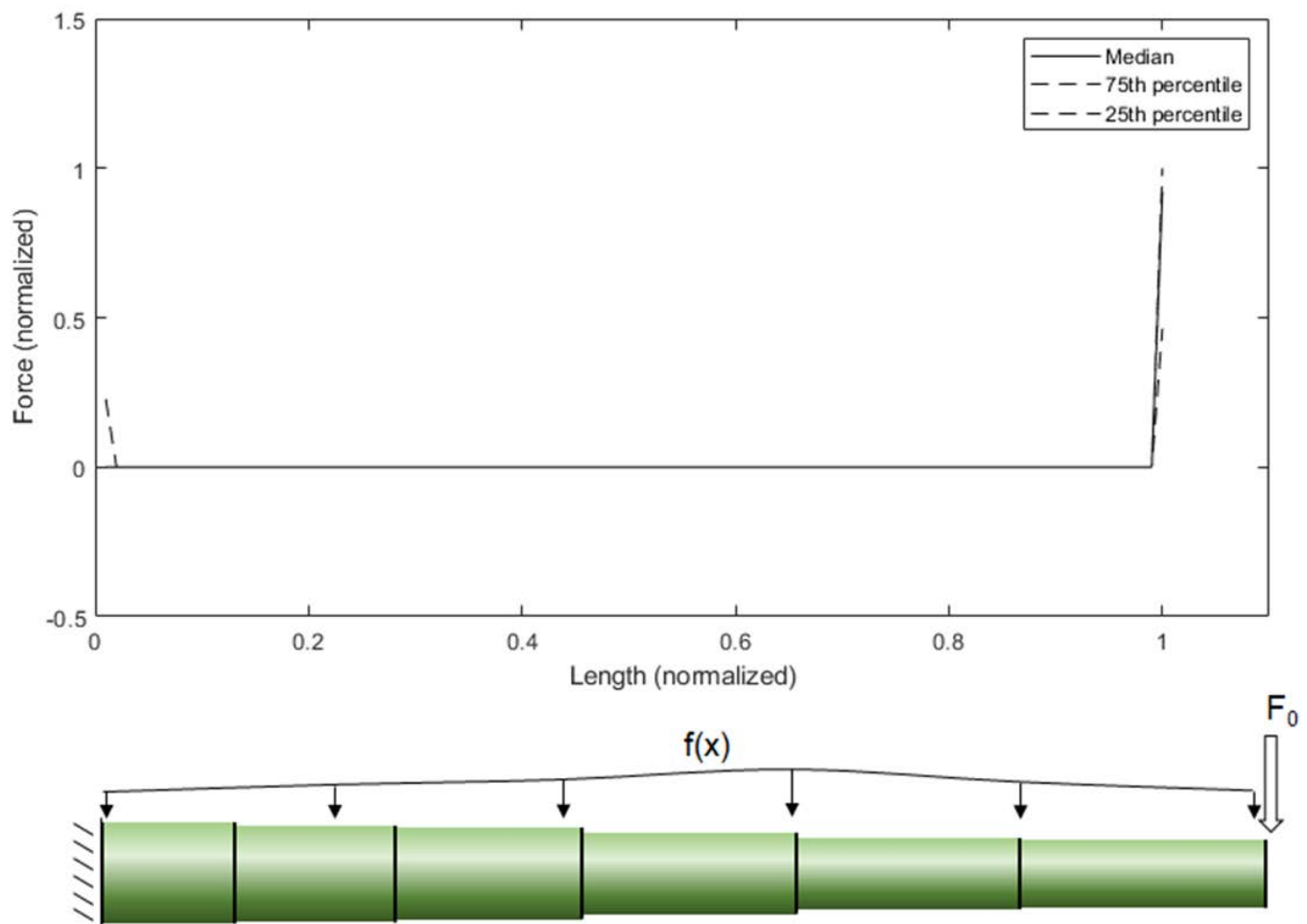


Figure 8.

