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Flow-induced pruning of branched systems and brittle reconfiguration

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Abstract

Whereas most plants are flexible structures that undergo large deformations under flow, another process can occur when the plant is broken by heavy fluid-loading. We investigate here the mechanism of such possible breakage, focusing on the flow-induced pruning that can be observed in plants or aquatic vegetation when parts of the structure break under flow. By computation on an actual tree geometry, a 20-yr-old walnut tree (*Juglans Regia L.*) and comparison with simple models, we analyze the influence of geometrical and physical parameters on the occurrence of branch breakage and on the successive breaking events occurring in a tree-like structure when the flow velocity is increased. We show that both the branching pattern and the slenderness exponent, defining the branch taper, play a major role in the breakage scenario. We identify a criterion for branch breakage to occur before breakage of the trunk. In that case, we show that the successive breakage of peripheral branches allows the plant to sustain higher flow forces.

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This mechanism is therefore similar to elastic reconfiguration, and can be seen as a second strategy to overcome critical events, possibly a widespread solution in plants and benthic organisms.

Keywords: Wind-loading, Allometry, Tree-like structure, Bending stress, Branch breakage

1 **1. Introduction**

2 Most living systems are surrounded by a fluid, be it air or water. When this
3 fluid flows, it generates mechanical forces, that may have major consequences on
4 growth as well as on reproduction or survival [1, 2, 3]. Typical cases are trees
5 subjected to wind or corals subjected to water currents. In terms of flow-induced
6 deformations, two typical behaviors can be pointed out. In the most common one,
7 the solid undergoes large elastic deformations, for instance in crops or aquatic
8 vegetation. In the second type, the system breaks before any significant deforma-
9 tion can occur; this will be referred to as brittle behavior in the following. The
10 former has been abundantly studied, a key result being that of load reduction by
11 elastic reconfiguration [4, 5]. The latter has already been described in trees or
12 corals [6, 7], but to the best of our knowledge the effect of branching has never
13 been studied theoretically. Therefore, we shall focus hereafter on brittle branched
14 slender systems, which are ubiquitous in nature: trees [8], bushes, algae [6], corals
15 [9] and corallines [10], to list a few. In the following we refer mainly to trees un-
16 der wind loading, with the understanding that these results are also applicable to
17 a large variety of other biological systems under fluid-loading.

18 For a brittle branched system attached to a support, breakage under flow may
19 occur in three distinct types: (i) base breakage, Fig. 1a, when the attachment to

20 the ground is broken, as in uprooting, (ii) trunk breakage, Fig. 1b, when the main
21 element is broken, and (iii) branch breakage, Fig. 1c, when an upper element
22 breaks, as in flow-induced pruning.

23 [Figure 1 about here.]

24 In fact, the distinction between trunk and branch breakage has a biological
25 relevance, since breakage of the trunk is likely to be fatal, while re-growth is often
26 possible after branch breakage. Moreover branch breakage does reduce loads
27 on the trunk and the attachment, as in elastic reconfiguration, thereby delaying
28 their breakage [6, 11]. Finally, branch breakage can also be part of the asexual
29 reproduction process by propagation. This is observed in terrestrial plants such
30 as willows and poplars [12], and in stony corals such as *Acropora Cervicornis* or
31 *Acropora Palmata* [13, 14].

32 Breakage is the consequence of an unacceptable stress level; it is therefore
33 directly related to the stress state in the structure [11, 15]. In particular, the issue
34 of whether the stress level is uniform or not in the tree is crucial, as breakage is
35 expected to occur at the point of maximal stress. For instance, Niklas and Spatz
36 [11] showed that in a cherry tree the stress level varies by one to two orders of
37 magnitude within the tree and has a local maximum in the branches. On the other
38 hand, Bejan et al. showed that the flow-induced stress is uniform for a tapered
39 trunk when the taper is linear [16]. In fact the stem taper is an important parameter
40 regarding the stress distribution; see the discussion in [17].

41 Several questions remain however regarding the flow-induced breakage of
42 tree-like structures: (i) what are the effects of the geometrical and physical pa-
43 rameters on the occurrence of branch breakage? (ii) How do the breaking events

44 occur successively as the flow is increased? (iii) Assuming that branch break-
 45 age is favorable in biological terms, is it compatible with other constraints on the
 46 geometry? The aim of this paper is to address these questions, using simple nu-
 47 merical and analytical models for the mechanical behavior of slender and brittle
 48 structures. The modeling assumptions and framework used throughout the paper
 49 are first presented in Section 2. In Section 3, we compute the stress distribution
 50 and successive breaking events in a complex tree, using the geometry of an ac-
 51 tual walnut tree. Using an idealized branched system, we derive conditions for
 52 branch breakage in Section 4. These are further analyzed for a tapered beam, here
 53 referred to as the slender cone model, in Section 5. The corresponding three ge-
 54 ometries are sketched in Fig. 2. Finally a general discussion and conclusion are
 55 given in Section 6.

56 [Figure 2 about here.]

57 2. Mechanical model and parameters

Throughout the paper, we consider a cross flow over the entire structure, uni-
 form, as the dependence of the stress on the wind velocity profile was shown to be
 small [11]. Also, only static loads are taken into account, and the corresponding
 fluid force magnitude f per unit length reads

$$f = \frac{1}{2}\rho C_D D U^2, \quad (1)$$

58 where U is the free stream velocity, ρ its density, D the local branch diameter and
 59 C_D the drag coefficient [3, 18]. The direction is assumed to be that of the flow
 60 velocity. The fluid load is here computed on a leafless branch, and the influence
 61 of leaves will be discussed in Section 6.

62 This load is applied on the whole branched system, which is held by a perfect
 63 clamping at the base. Because of the high slenderness of the system, we use
 64 a standard linear beam theory to derive the stress state, essentially the bending
 65 moment M . The maximum stress in the cross-section resulting from this bending
 66 moment is the skin stress, defined as $\Sigma = 32M/\pi D^3$ [19, 20].

67 The brittle behavior is introduced as follows: (i) the deformations are assumed
 68 to be negligible, so the stress state is computed on the initial configuration, without
 69 elastic reconfiguration, (ii) when increasing the flow velocity U , breakage occurs
 70 when and where the local skin stress Σ reaches a critical value, Σ_c . Then, the
 71 broken branch is removed, and this results in a new flow-induced stress state.
 72 Flow velocity may then be further increased until a new breaking event occurs.

Throughout the paper, the relevant dimensionless number to scale the fluid-
 loading $\rho C_D U^2$ with respect to the critical stress Σ_c is the Cauchy number, defined
 as

$$C_Y = \frac{\rho C_D U^2}{\Sigma_c} G, \quad (2)$$

73 where G is a geometrical factor introduced for comparison purpose and defined
 74 such that $\Sigma = \Sigma_c$ at the base of the intact structure when $C_Y = 1$. Note that this
 75 Cauchy number is similar in principle but differs from that used in the analysis
 76 of flow-induced elastic deformation, namely $C_Y = \rho C_D U^2/E$ [3, 5]; the critical
 77 stress Σ_c simply replaces here the Young modulus E .

78 The non-dimensional stress is defined as $\sigma = \Sigma/\Sigma_c$ and the non-dimensional
 79 bending moment as $m = M/M_c$, with $M_c = \Sigma_c \pi D_B^3/32$, D_B being the base diameter
 80 [19]. This latter scaling is chosen so that failure occurs at the base of the trunk
 81 when $m = 1$. The non-dimensional vertical coordinate z is defined using H , the
 82 height of the structure, as a reference length scale.

83 3. Flow-induced pruning of a walnut tree

84 The geometry of the branched system is expected to have a large influence
85 on the stress state and thus on the location and timing of breaking events. We
86 therefore first apply the procedure described above using the digitized geometry of
87 an actual 20-yr-old walnut tree (*Juglans Regia L.*) described in [21] (Fig. 2a). This
88 tree is 7.9 m high, 18 cm in diameter at breast height (dbh), and has a sympodial
89 branching pattern [22] and about eight orders of branching. The stress state under
90 flow is computed using a standard finite element software (CASTEM v. 3M [23]),
91 and is presented in Fig. 3b for four different branching paths.

92 [Figure 3 about here.]

93 We observe that the stress level is not uniform but shows a maximum located
94 in the branches, which is consistent with the results of Niklas and Spatz [11] which
95 are sketched in Fig. 3a. Note that since σ varies linearly with the fluid-loading C_Y ,
96 one needs only to focus on the critical situation where $\sigma = 1$ is first reached in
97 the structure. In this tree, the criterion for breakage is satisfied first in a branch
98 and not in the trunk. This corresponds to the mechanism of branch breakage, as
99 defined in Section 1. If the fluid-loading is further increased after removal of the
100 broken parts, successive breaking events are observed, in a flow-induced pruning
101 sequence: Fig. 4a shows three states of the tree at increasing Cauchy number with
102 branches progressively removed as they break off.

103 During the sequence of breakage, the bending moment at the base of the tree,
104 m_b , evolves significantly with the Cauchy number, Fig. 4b. Up to the first break-
105 age, the moment is proportional to the fluid-loading C_Y (zone I in Fig. 4b). Then,
106 in a small range of load increase (zone II), all large branches are broken at an inter-

107 mediate level, resulting in a significant decrease of the bending moment. Breakage
108 then continues but to a much smaller extent (zone III), while the moment increases
109 almost linearly up to the value $m_b = 1$ when the trunk breaks. Note that the benefit
110 of this sequence of breaking events is that the critical value of the base moment
111 $m_b = 1$ is reached only at $C_Y \approx 10$ instead of $C_Y = 1$ if there was no branch break-
112 age. This corresponds to more than a factor of 3 on the acceptable fluid velocity.
113 For instance, for a critical stress $\Sigma_c = 40$ MPa, which is the order of magnitude of
114 maximum acceptable bending stresses measured in trees [12, 24], the maximum
115 sustainable fluid velocity before trunk breakage is increased from $U \approx 30$ m.s⁻¹
116 without branch breakage to $U \approx 100$ m.s⁻¹ with branch breakage.

117 [Figure 4 about here.]

118 To summarize, this set of computations clearly shows that branch breakage
119 can occur prior to trunk breakage, and that the sequence of flow-induced pruning
120 results in a significant reduction in the load applied on the base of the tree, or
121 equivalently, an increase in the sustainable fluid velocity. To further analyze this
122 process, we turn to a simple model in the next section.

123 **4. The ideal tree model**

124 *4.1. Infinite branched tree*

125 [Figure 5 about here.]

To establish the relation between the parameters of the system and the flow-induced pruning process, we simplify the problem to its essential elements: the branched geometry and the slenderness of branches; we disregard here the effect of branch orientation relative to the flow. Similarly to [25], we consider first

an infinitely iterated sympodial tree made of cylindrical branches (Fig. 5). Two parameters only are needed to describe this ideal tree: (i) the branching ratio λ , giving the reduction of diameter through branching, and (ii) the slenderness exponent β , giving the relationship between length and diameter in branch segments of the tree, so that

$$\lambda = \left(\frac{D_{k+1}}{D_k}\right)^2, \quad \frac{D_{k+1}}{D_k} = \left(\frac{L_{k+1}}{L_k}\right)^\beta, \quad (3)$$

126 where D_k and L_k are the diameter and length of a branch segment of order k , see
 127 Fig. 5a [25]. Typical values of these parameters are $\lambda < 1$ and $1 < \beta < 2$. Note
 128 that the number of branches emerging from a branching point is typically equal to
 129 $1/\lambda$ [26].

We use now a scaling argument similar to that of [25] for the dynamics of trees. On the ideal infinitely branched system of Fig. 5a, we can compare the stress level in branch $k = 1$ (the trunk) and in branch $k = 2$. The sub-tree labeled II in Fig. 5a is identical to the full tree, I, but for a change in length and diameter scales. All diameters (resp. lengths) in II are reduced by a factor $\lambda^{1/2}$ (resp. $\lambda^{1/2\beta}$). Let Σ_1 be the maximum skin stress in the trunk ($k = 1$) under a given fluid-loading U , and Σ_2 the maximum skin stress in the branch $k = 2$. The relations between the flow velocity and Σ_1 or Σ_2 are identical, but for the change of diameter and length scales. The dependence of the stress on diameter and length is the following: (i) Σ varies as M/D^3 , where M is the bending moment, (ii) M varies as fL^2 , where f is the norm of the local fluid force, Eq. (1), (iii) f varies as $\rho U^2 D$. Hence Σ varies as $\rho U^2 (L/D)^2$. We therefore may state that

$$\frac{\Sigma_2}{\Sigma_1} = \left(\frac{L_2}{D_2}\right)^2 \left(\frac{D_1}{L_1}\right)^2 = \lambda^{\frac{1-\beta}{\beta}}. \quad (4)$$

Since $\lambda < 1$, the condition for the stress to be higher in branches than in the trunk becomes

$$\beta > 1. \quad (5)$$

130 Here the only parameter controlling the possibility of branch breakage is the
 131 slenderness exponent, a classical parameter in the allometry of trees. As β is
 132 typically greater than 1 for trees, branch breakage is expected to occur. This
 133 simplistic approach now deserves to be improved, as the assumption of an infinite
 134 number of branching levels is very strong, and may not be compatible with the
 135 constraint that the tree area has to be finite.

136 4.2. Finite branched tree

Let us consider now the same idealized tree, but with a finite number of branching iterations (Fig. 5b). This structure has N levels, which are labeled in this section from the top to the bottom. Note that $n = N - k + 1$, where n is the label of the previous section from the base of the tree. The trunk corresponds now to the last level, N . At each level n , we define the branch diameter D_n and length L_n , which can be expressed as a function of the trunk diameter and length D_N and L_N as

$$D_n = \lambda^{\frac{N-n}{2}} D_N, \quad L_n = \lambda^{\frac{N-n}{2\beta}} L_N. \quad (6)$$

By a simple integration of the fluid force on the branches, the moment at the base of a branch of order n may be derived, as well as the corresponding skin stress, which is obtained in non-dimensional form as

$$\sigma_n = C_Y \lambda^{\frac{1-\beta}{\beta} N} \left(A \lambda^{\frac{\beta-1}{\beta} n} + B \lambda^{\frac{n}{2}} + C \lambda^{\frac{\beta-1}{2\beta} n} \right), \quad (7)$$

where the Cauchy number C_Y is defined as

$$C_Y = \left[\frac{8}{\pi} \left(\frac{L_N}{D_N} \right)^2 \right] \frac{\rho C_D U^2}{\Sigma_c}, \quad (8)$$

137 and A , B and C are functions of β and λ only. The detailed derivation of Eq. (7) as
 138 well as the expression of A , B and C can be found in Appendix A.

139 A systematic numerical exploration of the (λ, β) parameter space shows that
 140 when $\beta < 1$ the stress always increases from top to bottom. Conversely, for $\beta > 1$,
 141 the stress reaches a maximum at branch level n_c and then decreases from top to
 142 bottom, provided that $N > n_c$, where n_c depends on λ and β . This dependence is
 143 given in Fig. 6. This analysis with a finite tree model gives a criterion consistent
 144 with that of the infinite tree model, namely $\beta > 1$. Moreover, the other parameter,
 145 λ , is found to affect only the location of possible breakage. This suggests that
 146 branching is not a key factor in the occurrence of branch or trunk breakage. In the
 147 next section we explore a simpler model of the slenderness effect.

148 [Figure 6 about here.]

149 5. The slender cone model

150 5.1. Flow-induced stress

151 The simplest model that allows one to take into account a relation between
 152 diameters and lengths through a slenderness exponent is a cone. This formulation
 153 is related to MacMahon and Kronauer's equivalent geometry of a tree, a tapered
 154 beam with a rectangular cross-section of dimensions varying as power laws of
 155 height [8, 27].

The geometry considered here is a slender cone with a circular cross-section, Fig. 7a, and we follow the same mechanical approach as for the previous geometries. Let H be the cone height, $d_H = D_H/H$ the dimensionless diameter at the base and z the vertical coordinate which is orientated downwards in this section. The cone dimensionless diameter is given by

$$d(z) = d_H z^\beta. \quad (9)$$

156

[Figure 7 about here.]

Using the same formulation as in the previous section, the stress state along the cone is obtained as

$$\sigma(z) = C_Y z^{2(1-\beta)}, \quad (10)$$

where the Cauchy number is defined here as

$$C_Y = \left[\frac{16}{(1+\beta)(2+\beta)\pi d_H^2} \right] \frac{\rho C_D U^2}{\Sigma_c}. \quad (11)$$

157 From Eq. (10), we readily observe that: (i) for $\beta = 1$, the constant stress case of
 158 Bejan et al. [16] is found; (ii) for $\beta < 1$ the stress increases with z and is therefore
 159 maximum at the base, Fig. 7a; (iii) for $\beta > 1$ the stress decreases with z , and
 160 the maximum, discussed further, is not at the base, Fig. 7b-c. These results are
 161 consistent with the condition for branch breakage in the previous section.

To avoid the singular case of infinite stress at $z = 0$ for $\beta > 1$, we use a cone truncated at $z = z_0$, Fig. 7c. The truncation z_0 corresponds to the first breakage occurring as soon as $U \neq 0$, and its value is chosen arbitrarily. The corresponding stress state is then

$$\frac{\sigma(z)}{C_Y} = z^{2(1-\beta)} - (2+\beta)z_0^{1+\beta} z^{1-3\beta} + (1+\beta)z_0^{2+\beta} z^{-3\beta}, \quad (12)$$

162 which reduces to Eq. (10) when $z_0 = 0$. The detailed derivation of this equation is
 163 given in Appendix B. For $\beta > 1$, the stress shows a maximum before decreasing
 164 downwards, as illustrated in Fig. 7c. The limit case $z_0 = 0$ is in fact equivalent,
 165 in the ideal tree model of Section 4, to the limit as N goes towards infinity, which
 166 would lead to a vanishing diameter at the tip. There is therefore an analogy be-
 167 tween the cone truncation and the ideal tree with a finite number of branching
 168 levels.

169 5.2. Sequence of breaking events

170 Considering now the generic case of the truncated cone, Fig. 7c, we analyze
 171 the sequence of breaking events resulting from an increasing fluid-loading C_Y .
 172 The stress σ increases linearly with C_Y up to the point where its maximum value
 173 reaches the limit of breakage, $\sigma = 1$. This defines the first breaking event at
 174 $C_Y = C_Y^1$ occurring at $z = z_1$. It results in a new truncated cone, and the process is
 175 repeated as C_Y is further increased. Eventually, when the cone becomes truncated
 176 close to the base, the maximum stress may be reached at the base itself, resulting
 177 finally in base breakage.

178 This sequence of breaking events may be analyzed in terms of the maximum
 179 fluid-loading C_Y^{\max} that the cone can support before breaking at the base. As illus-
 180 trated in Fig. 8, this is strongly dependent on β . When $\beta < 1$, the first breaking
 181 event is at the base so that $C_Y^{\max} = 1$. Conversely when $\beta > 1$, breaking occurs
 182 progressively as C_Y is increased, and the base breakage is delayed, $C_Y^{\max} > 1$. The
 183 precise value of C_Y where the base breaks depends on the initial truncation z_0 , but
 184 is always higher than a lower bound that can be computed from Eq. (12), which is
 185 shown in Fig. 8. We observe a significant increase of the ability of the system to
 186 sustain fluid-loading when $\beta > 1$.

187 [Figure 8 about here.]

188 In terms of base moment, the sequence of breaking events can be easily com-
189 puted, Fig. 9. For $\beta < 1$ the base moment increases linearly with C_Y until base
190 breakage occurs, $m_b = 1$ for $C_Y = 1$. For $\beta > 1$ the sequence of breaking events
191 results in sudden drops in base moment followed by linear increase up to the next
192 breaking, as illustrated in Fig. 9. Since the sequence of breaking events is a dis-
193 crete process that depends on the initial truncation z_0 , there exists, for a given
194 Cauchy number C_Y , a wide range of acceptable cone heights and thereby a wide
195 range of corresponding base moments. In practice, for all possible values of z_0 ,
196 the evolution of m_b remains bounded between its values for the shortest and high-
197 est cone that can exist at each Cauchy number. This is represented by the shaded
198 region in Fig. 9.

199 [Figure 9 about here.]

200 These results show that the simple cone model contains the key elements to
201 understand the effect of geometry on (i) the stress profile, (ii) the sequence of
202 breaking events and (iii) the consequences on the evolution of base load when
203 the fluid velocity is increased. Here again, the essential criterion concerns the
204 slenderness exponent β .

205 6. Discussion and conclusions

206 Starting from the case of a full walnut tree geometry, we have used models of
207 increasing simplicity. This allowed us to point out the role of various parameters
208 on the process of breakage under fluid-loading. The first issue that had to be
209 addressed was that of the flow-induced stress distribution. As noted by other

210 authors, the stress is not necessarily maximum at the base [11, 16]. In fact in
211 the walnut tree of Section 3, the stress has a local maximum at about mid height.
212 Using the ideal tree model in Section 4, we have shown that the existence of this
213 maximum is related to the value of the slenderness exponent, β , being larger than
214 one: in fact this allometry parameter is about 1.37 for this particular walnut tree
215 [25]. Following Bejan et al. [16], we recover the critical value of $\beta = 1$ in the
216 simplest model, that of a cone in Section 5.

217 Actually, some refinement is needed here to understand the precise location
218 of the maximum of stress. We have shown in Section 4 that the location of this
219 maximum was also dependent on the branching parameter λ , in the form of the
220 parameter n_c , which is the number of branching levels from the top to this maxi-
221 mum point. For our walnut tree, where $\lambda \approx 0.25$, we obtain $n_c = 6$ using Fig. 6.
222 This is smaller than the total number of branching levels in the walnut tree which
223 is about 8 [21]. A local maximum of stress is therefore expected in the branches,
224 and is actually observed in Fig. 3.

225 The second issue was that of the sequence of breaking events occurring when
226 the fluid-loading C_Y is increased. Using a brittle fracture model for the walnut tree
227 in Section 3, we have shown that most large branches broke in a short range of
228 flow velocity, and that breakage of the trunk occurred much later. The large size
229 of broken branches can be explained by the value of $n_c = 6$ found above. All large
230 branches do not break exactly at the same value of the Cauchy number. This is
231 due among other reasons to some variability in the allometry parameters λ and β
232 within the tree. Once all large branches are broken, the remaining tree shape, C in
233 Fig. 4a, does not have enough branching levels to have a local maximum, and the
234 next breaking event occurs at the base of the trunk. Note that the process of branch

235 breakage in the walnut tree allowed the tree to have a much larger acceptable
236 Cauchy number before breakage of the trunk. This can also be analyzed using the
237 cone model as in Section 5, where the critical Cauchy number for base breakage
238 is clearly dependent on β (Fig. 8).

239 The third issue was that of the evolution of the load at the base of the tree. For
240 the walnut tree, Fig. 4b, the sequence of successive breakage of the large branches
241 results in a significant decrease of the drag-induced moment at the base. This can
242 be understood using the cone model, where the sequence of breaking event and
243 corresponding drops of base moment can be tracked, Fig. 9. We may therefore
244 state that the essential characteristics of branch breakage and corresponding load
245 evolution in the walnut tree can be understood using our simple ideal tree model
246 and cone model.

247 The analytical results of Sections 4 and 5 were obtained considering that all
248 parameters have self-similar variations. However, this was not the case for the
249 walnut tree computations of Section 3, which suggests that the behaviors pointed
250 out in this study can be generalized to structures that do not necessarily have self-
251 similar variations of their parameters. Moreover, the ideal tree and cone models
252 can be easily extended to incorporate other features of the problem, such as a de-
253 pendence of all parameters with z : the flow velocity U , the material properties
254 through the critical parameter Σ_c , and even the drag coefficient C_D , which allows
255 one to take easily into account the additional drag of leaves. Preliminary results,
256 not shown here for the sake of brevity, showed that the criterion for branch break-
257 age takes the same form, but involves both β and the corresponding parameter
258 related to the additional z -dependence. Taking into account a significant elastic
259 deformation before load fracture, or incorporating dynamical effects, would be

260 much more complex.

261 [Table 1 about here.]

262 Considering the simplicity of the criterion that we have found for branch
263 breakage, we can test whether it is generally satisfied. MacMahon and Kronauer
264 [27] have noted that β is usually larger than 1 and typically around 1.5, while λ
265 is typically close to 0.25. This leads to a maximum stress located at a branching
266 level $n_c = 5$ counting from top down. This is clearly in the branches as trees gen-
267 erally have more than 5 orders of branching. We may therefore state that branch
268 breakage can be expected in most sympodial trees. This is illustrated in Table 1,
269 where the values of parameters are given for several trees.

270 Clearly the possibility of branch breakage is favorable in terms of survival of
271 an individual tree in the face of extreme fluid-loading. It may also be favorable in
272 terms of tree development by removing the less vigorous branches. The question
273 then arises as to whether this implies new constraints on the geometry of the tree.
274 It appears from our results that the constraint $\beta > 1$ is not incompatible with
275 other constraints such as the optimal resistance to buckling under gravity, which
276 requires $\beta = 3/2$ [8]. The same result was obtained considering the wind effect on
277 trees but for an overcrowded tree canopy [17]. Similarly $\beta > 1$ is compatible with
278 a constraint for optimal dissipation [25, 28], that modal frequencies have a ratio
279 of less than two, requiring that $\beta > 1$ for $\lambda = 0.25$.

280 The particular case of branched corals [9, 13, 14] is somewhat different. The
281 segments are similar in length and diameter, so that $\lambda \approx 1$ and $\beta \approx 1$ in our
282 variables, but with a number of branches emerging from one branching not equal
283 to $1/\lambda$. An analysis similar to that of Section 4 shows that breakage is expected at
284 the bottom. This is the case in most isolated corals.

285 More generally we may place these results in the overall context of reconfig-
 286 uration, as introduced by Vogel [4]. This originally referred to the reduction of
 287 loading made possible by elastic deformation. For a plant, it is a crucial mecha-
 288 nism to survive heavy fluid-loading. But plant tissues are not all very elastic, and
 289 plant parts are not all very flexible. Our results on the role of branch breakage in
 290 reducing loading show that, in parallel with elastic reconfiguration, there exists a
 291 mechanism of brittle reconfiguration. There are therefore two distinct strategies to
 292 overcome critical events. The first is evidently reversible in the short term by elas-
 293 ticity. The second is also reversible by re-growth, but only in the long term. Thus
 294 flow-induced pruning is possibly a widespread mechanism in plants or benthic
 295 organisms that support heavy loading by the surrounding fluid environment.

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302 **Appendix A. Stress derivation in finite branched tree model**

In order to compute the stress along the finite ideal tree, we introduce f_n the
 fluid force per unit length at level n , $f_n = \frac{1}{2}\rho C_D U^2 D_n$, with the same notations as
 Eq. (1). At each level n , we consider two force components: (i) the shear force τ_n
 in the flow direction and (ii) the bending moment M_n in the direction normal to

the flow. Due to the free condition at the top, $\tau_0 = 0$ and $M_0 = 0$, and for $n \geq 1$

$$\tau_n = f_n L_n + p \tau_{n-1}, \quad (\text{A.1})$$

$$M_n = \frac{1}{2} f_n L_n^2 + p (M_{n-1} + L_n \tau_{n-1}), \quad (\text{A.2})$$

where p is the number of branches emerging from one at a branching point ($p = 1/\lambda$).

The non-dimensional stress σ_n at level n reads

$$\sigma_n = \frac{32 M_n}{\pi \Sigma_c D_n^3} \quad (\text{A.3})$$

By integration of Eqs. (A.1) and (A.2), the stress at each level can be obtained,

$$\sigma_n = C_Y \lambda^{\frac{1-\beta}{\beta} N} \left(A \lambda^{\frac{\beta-1}{\beta} n} + B \lambda^{\frac{n}{2}} + C \lambda^{\frac{\beta-1}{2\beta} n} \right), \quad (\text{A.4})$$

with

$$C_Y = \left[\frac{8}{\pi} \left(\frac{L_N}{D_N} \right)^2 \right] \frac{\rho C_D U^2}{\Sigma_c}, \quad (\text{A.5})$$

and

$$A = \frac{\lambda^{\frac{1-\beta}{2\beta}} + 1}{\left(\lambda^{\frac{1-\beta}{2\beta}} - 1 \right) \left(\lambda^{\frac{2-\beta}{2\beta}} - 1 \right)}, \quad (\text{A.6})$$

$$B = \frac{\lambda^{\frac{1}{2\beta}} + 1}{\left(\lambda^{\frac{2-\beta}{2\beta}} - 1 \right) \left(\lambda^{\frac{1}{2\beta}} - 1 \right)}, \quad (\text{A.7})$$

$$C = \frac{-2}{\left(\lambda^{\frac{1-\beta}{2\beta}} - 1 \right) \left(\lambda^{\frac{1}{2\beta}} - 1 \right)}. \quad (\text{A.8})$$

303 Appendix B. Stress derivation in the slender cone model

The stress state for the slender cone model is obtained by direct integration of the fluid force defined in Eq. (1), using Eq. (9) for the diameter. The shear force

and resulting bending moment read

$$\tau(z) = \int_{z_0}^{\infty} f(z')dz', \quad M(z) = \int_{z_0}^z \tau(z')dz', \quad (\text{B.1})$$

with $z_0 \geq 0$. The local non-dimensional skin stress reads

$$\sigma(z) = \frac{32M(z)}{\pi\Sigma_c d(z)^3}. \quad (\text{B.2})$$

304 The integration of these equations give Eq. (10) and Eq. (12) depending on z_0 .

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373 **List of Figures**

374	1	Schematic view of breakage process in a branched brittle system	
375		under flow. (a) Base breakage, (b) Trunk breakage, (c) Branch	
376		breakage.	25
377	2	Geometries of the models used in the paper: (a) Section 3: Walnut	
378		tree, as in [21]; (b) Section 4: Idealized branched system, as in	
379		[25]; (c) Section 5: Tapered beam, as in [8, 16].	25
380	3	Non-dimensional stress profile σ in a tree under cross-flow. (a)	
381		Schematic view of the stress profiles given by Niklas and Spatz	
382		[11] for cherry trees, showing a local maximum near the top.	
383		(b) Computed stress profiles along four branching paths, A (\times),	
384		B (\square), C (\triangle) and D (\circ) in the digitized tree geometry shown in (c).	26
385	4	Computed sequence of branch breakage in the walnut tree: (a) A:	
386		initial tree for $C_Y \leq 0.67$; B: after breakage in large branches,	
387		$C_Y = 1.7$; C: just before trunk breakage, $C_Y = 10.7$. (b) Corre-	
388		sponding evolution of the bending moment at the base of the tree	
389		m_b , in three distinct ranges. The dashed line shows the moment	
390		that would exist without breakage. The dotted line shows the crit-	
391		ical value m_b that causes trunk breakage.	26
392	5	Idealized branched system. (a) Infinite iterated tree. The sub-	
393		tree II is equivalent to the whole tree I but for a change of scales.	
394		(b) Finite iterated tree and corresponding notations.	27

395	6	Location of the maximum of stress under cross-flow in an ideal-	
396		ized tree model, as a function of the slenderness exponent β and	
397		the branching parameter λ . The location is given in the form of	
398		the number of branching levels counted from the top of the tree,	
399		Fig. 5b. For $\beta \leq 1$, the breakage is directly at the base of trunk. . .	27
400	7	The slender cone model: geometry and stress profile under uni-	
401		form cross flow. (a) cone with $\beta < 1$ (here 0.75), showing a max-	
402		imum of stress at the base; (b) cone with $\beta > 1$ (here 2), showing	
403		a maximum at the top; (c) cone truncated arbitrarily at $z_0 = 0.3$	
404		showing a local maximum.	28
405	8	Maximum fluid load that the cone can support as a function of the	
406		slenderness exponent. Note that for $\beta > 1$ the curve is the lower	
407		bound of all possible evolutions.	28
408	9	Moment at the base of the cone as the fluid-loading is increased. (-	
409		- -) direct base breakage occurring when $\beta < 1$; (—) progressive	
410		breaking for $\beta > 1$ (here $\beta = 2$). The shaded region shows all	
411		possible values depending on the initial truncation z_0 . The cone	
412		state is shown for three values of C_Y	29
413	List of Tables		
414	1	Predicted breakage type using the results of Section 4. Branch	
415		breakage is predicted when $n_c \leq N$	30

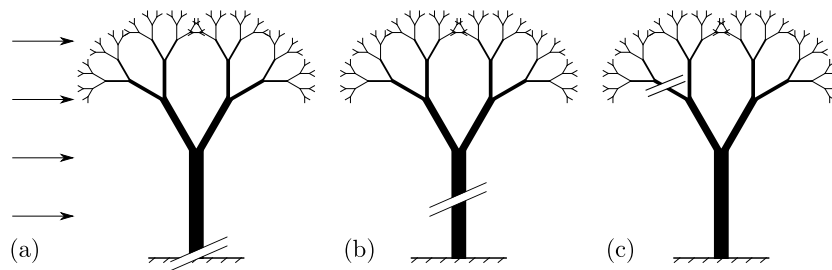


Figure 1: Schematic view of breakage process in a branched brittle system under flow. (a) Base breakage, (b) Trunk breakage, (c) Branch breakage.

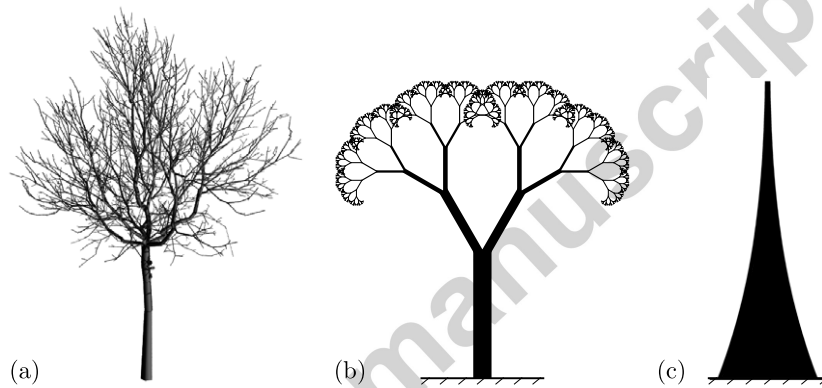


Figure 2: Geometries of the models used in the paper: (a) Section 3: Walnut tree, as in [21]; (b) Section 4: Idealized branched system, as in [25]; (c) Section 5: Tapered beam, as in [8, 16].

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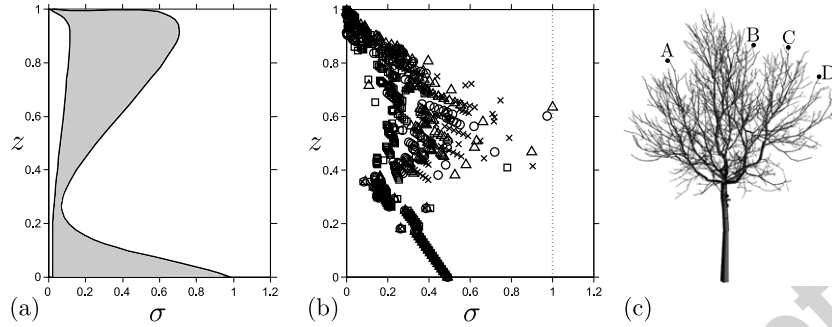


Figure 3: Non-dimensional stress profile σ in a tree under cross-flow. (a) Schematic view of the stress profiles given by Niklas and Spatz [11] for cherry trees, showing a local maximum near the top. (b) Computed stress profiles along four branching paths, A (\times), B (\square), C (\triangle) and D (\circ) in the digitized tree geometry shown in (c).

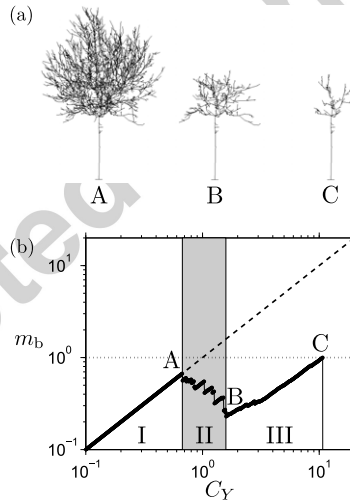


Figure 4: Computed sequence of branch breakage in the walnut tree: (a) A: initial tree for $C_Y \leq 0.67$; B: after breakage in large branches, $C_Y = 1.7$; C: just before trunk breakage, $C_Y = 10.7$. (b) Corresponding evolution of the bending moment at the base of the tree m_b , in three distinct ranges. The dashed line shows the moment that would exist without breakage. The dotted line shows the critical value m_b that causes trunk breakage.

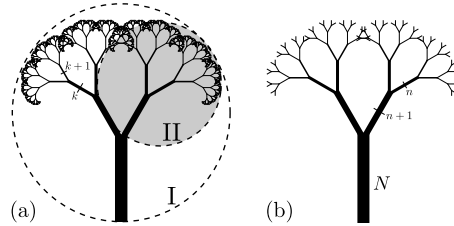


Figure 5: Idealized branched system. (a) Infinite iterated tree. The sub-tree II is equivalent to the whole tree I but for a change of scales. (b) Finite iterated tree and corresponding notations.

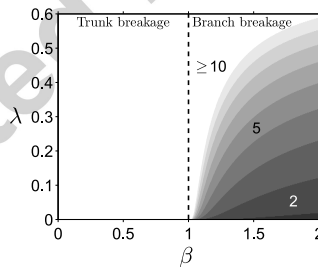


Figure 6: Location of the maximum of stress under cross-flow in an idealized tree model, as a function of the slenderness exponent β and the branching parameter λ . The location is given in the form of the number of branching levels counted from the top of the tree, Fig. 5b. For $\beta \leq 1$, the breakage is directly at the base of trunk.

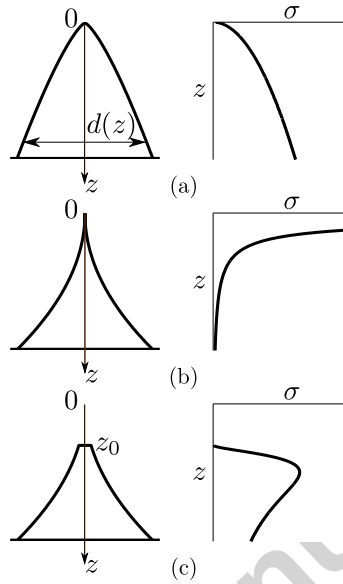


Figure 7: The slender cone model: geometry and stress profile under uniform cross flow. (a) cone with $\beta < 1$ (here 0.75), showing a maximum of stress at the base; (b) cone with $\beta > 1$ (here 2), showing a maximum at the top; (c) cone truncated arbitrarily at $z_0 = 0.3$ showing a local maximum.

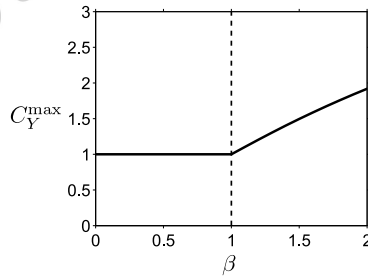


Figure 8: Maximum fluid load that the cone can support as a function of the slenderness exponent. Note that for $\beta > 1$ the curve is the lower bound of all possible evolutions.

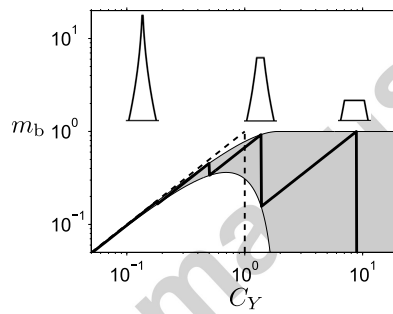


Figure 9: Moment at the base of the cone as the fluid-loading is increased. (---) direct base breakage occurring when $\beta < 1$; (—) progressive breaking for $\beta > 1$ (here $\beta = 2$). The shaded region shows all possible values depending on the initial truncation z_0 . The cone state is shown for three values of C_Y .

Ref.	Tree	Slenderness exponent β	Branching parameter λ	Total orders of branching N	Predicted branch breakage level n_c	Predicted breakage type
[21, 25]	Walnut Tree <i>Juglans Regia L.</i>	1.37	0.25	> 8	6	Branch
[27]	Red Oak <i>Quercus Rubra</i>	1.51	0.41	> 6	7	Branch or Trunk
--	White Oak 1 <i>Quercus Alba</i>	1.41	0.28	> 6	6	Branch
--	White Oak 2 <i>Quercus Alba</i>	1.66	0.29	> 6	5	Branch
--	Poplar Tree <i>Populus Tremoloides</i>	1.5 (estimated)	0.29	> 6	5	Branch
--	Pin Cherry <i>Prunus Pennsylvanica</i>	1.5	0.24	> 4	5	Branch or Trunk
--	White Pine <i>Pinus Strobus</i>	1.37	0.24	> 5	5	Branch

Table 1: Predicted breakage type using the results of Section 4. Branch breakage is predicted when $n_c \leq N$.

425

- Flow-induced pruning of branched systems may be predicted from usual allometry parameters
- Flow-induced pruning is strongly beneficial to a living branched system
- The condition for flow-induced pruning is compatible with other constraints on growth.

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