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Biomechanics of plant anchorage at early development stage

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HIGHLIGHTS

- We develop a model for the response of seedlings to pullout constraints.
- The model accounts for the stochastic component of the uprooting process.
- We validate our model with stress–strain curves from uprooting experiments.
- We identify a crossover in the response of young vegetation to pullout constraints.

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ABSTRACT

We propose a minimal model for the response of seedlings to pullout constraints. Central to our approach is the idea of capturing not only average mechanical properties but also the stochastic component of the uprooting process. Our model accounts on one hand for the tensile elastic response of root fibres and on the other hand for the friction between root fibres and the soil matrix. We present for validation a dataset of 98 uprooting experiments using *Avena sativa* L. seedlings (common oat), growing in non-cohesive sediment under controlled conditions. We show that even if the architecture of the roots used in the experiments and, as a consequence, the components of our model are very basic, the uprooting curve (stress vs. strain) presents a complex response, with sudden jumps followed by partial elastic recovery. Depending on the maturity of the root system, we identify a crossover in the response of the seedling to the constraint. While for younger seedlings the anchorage rapidly fails after the peak force has been reached, more mature root systems recover from partial failures. Finally, we discuss the importance of the characteristics of the uprooting curve (maximal uprooting force and total uprooting work) regarding the ability of seedlings to withstand environmental constraints in terms of duration or intensity.

1. Introduction

Much of the theoretical studies on the mechanics of roots focus on the anchorage of mature trees and/or on complex root architectures, for a review see for example Ennos (2000), Smit et al. (2000) and Waisel et al. (2002). In particular, recent theoretical studies on uprooting modelled the anchoring force as the result of a fibre-bundle dynamics. In this direction, one may cite as examples Michlmayr et al. (2012), Schwarz et al. (2010) and references therein, together with the associated case study by Schwarz et al. (2012) and the pullout experiments by Schwarz et al. (2011). In those works, load redistribution within the fibre bundle is modelled and a progressive mechanical failure of stochastic nature (breaking or slipping) of single fibres is introduced. Pollen and Simon (2005) also used a fibre-bundle approach to model river bank stabilisation by riparian vegetation. Their model was subsequently refined and tested in Pollen (2007).

On uprooting of smaller or younger vegetation one may cite first the work by Ennos (1991) on the mechanics of anchorage in wheat, together with a study on the anchorage of leek seedlings (Ennos, 1990) and a systematic theoretical study on the scaling of root anchorage (Ennos, 1993). In Ennos (1991), however, the roots already present a quite complex structure (more mature stage than in our work) with 7 to 15 roots, some pointing outwards and some downwards (vs. only three roots for the seedlings considered in this work).

In the present study, we focus on the mechanics of uprooting of young vegetation in non-cohesive soil where root slipping without fibre breaking tends to occur most of the time (Ennos, 1990). Hence, the recorded stress–strain signal shows all the characteristics of a tensile elastic system associated to sudden jumps leading to partial elastic recovery (see Fig. 1). The succession of jumps and recoveries continues until complete uprooting has occurred. This type of uprooting process is representative for the first stage of vegetation anchorage: the sequence of an initial tap root followed by secondary roots is almost universal when considering seedlings (see for example the review article by Reubens et al., 2007). The primitive root system plays an important role at the field scale: the processes of seedling

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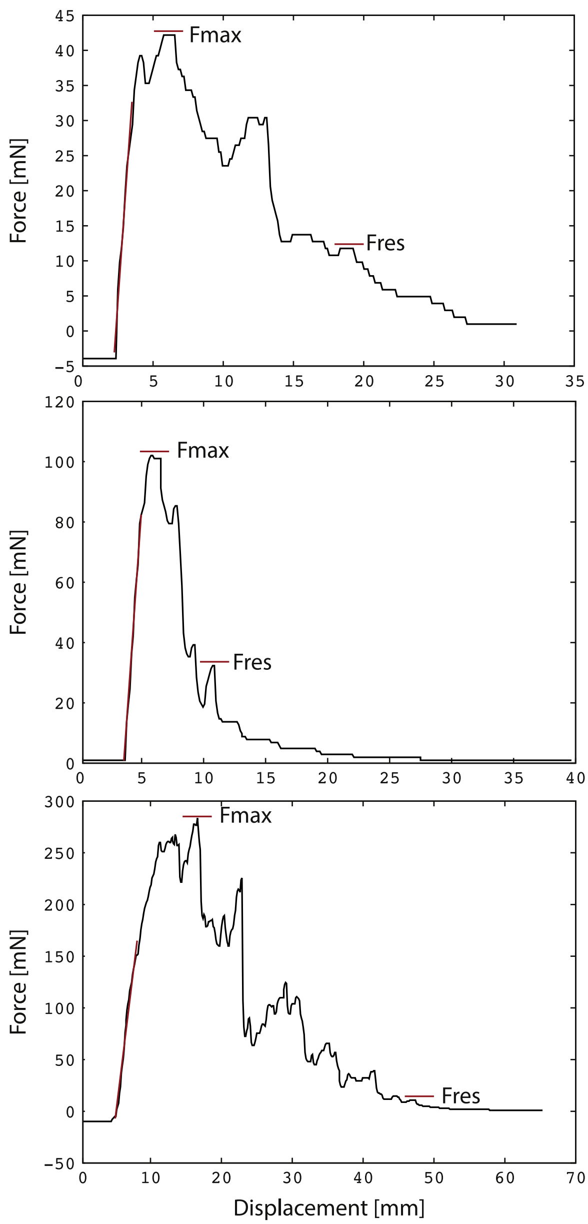

Fig. 1. Typical response (force) measured while uprooting seedlings of *Avena sativa* L. at constant velocity. The different panels correspond to seedlings with three roots and a length of the main root of 25 mm (upper panel), 29 mm (middle panel) and 49 mm (lower panel). Red lines are used to highlight the initial elastic regime, the maximal force F_{max}, and the residual force F_{res} indicating failure of the last fibre. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

uprooting by floods and root reinforcement (i.e., root strengthening due to plant growth) controls the colonisation and stabilisation of alluvial bare sediment, see Gurnell et al. (2012) for a review. The statistical distributions of surviving riverbed vegetation characteristics (e.g. root length and number) are the result of the selective uprooting of weaker vegetation (Perona et al., 2012; Crouzy and Perona, 2012).

In addition, specific information on the anchorage of seedlings (average *and* fluctuations) can be useful since seedlings of *Avena sativa* L. (common oat) and *Medicago sativa* L. have been extensively used in flume experiments as an alternative to artificial surrogates for vegetation. As an example for the use of artificial vegetation in a flume experiment, see McBride et al. (2007). Flume experiments involving real vegetation aimed for example at reproducing channel narrowing and widening (Gran and Paola, 2001; Tal and Paola, 2007) and more recently at studying the dynamics of pioneer biomass selection by floods both in uniform (Crouzy et al., 2013; Perona et al., 2012) and in convectively accelerated streams (Crouzy et al., 2013; Perona et al., 2014). In the experiments, the interplay between the vegetation and the river morphodynamics was studied and geomorphological patterns were reproduced in the lab, even if a rigorous upscaling from the lab scale to the field scale could not been achieved (Paola and Leeder, 2011).

We propose a minimal model for the response of simple plant root architectures to pullout constraints. In order to quantify the process, we compute the maximal uprooting force, the total uprooting work and the statistics of the jumps associated with the slipping of single root fibres. As proposed by Edmaier et al. (2011) the maximal force expresses the ability of the root system to withstand an instantaneous constraint, while the total uprooting work relates better to the resilience of the plant subject to continuous or repeated constraints – for example the case when considering the uprooting of vegetation by flooding events (Perona et al., 2012; Crouzy and Perona, 2012). Finally, the analysis of the statistics of the jumps allows us to quantify the resilience of the root system. Central to our study is that we do not restrict ourselves to averaged mechanical properties but also try to capture the important stochastic component of the uprooting process (significant *fluctuations* over averaged properties).

We formulate a minimal mechanistic model of friction (with stochasticity in the friction properties) that is able to reproduce experimental observations from previous works (Edmaier et al., 2012, 2014). Uprooting experiments on *Avena sativa* L. (common oat) seedlings growing in non-cohesive sediment were conducted and allow to test our model on a simple root architecture. The maximal uprooting force, the total uprooting work and the statistics of the jumps in the stress–strain curve are obtained experimentally. In addition to the choice of the simple root architecture of *Avena sativa* L., the use of non-cohesive sediment allows to limit the number of relevant physical variables and increase the reproducibility of the results: all the relevant root (length and diameter of the root fibres) and sediment (saturation, sediment size) physical parameters could easily be determined. The friction between the sediment matrix and the root fibres is obtained by matching the predictions of the model to the experimental statistics of the maximal force and uprooting work. The ability for the seedlings to recover from partial failure increases with the maturity of the plant. In order to quantify this recovery potential, we perform an analysis of the jumps in the force displacement signal. Younger seedlings present a monotonous decrease in the force signal after the peak force has been reached, while for older seedlings root failures are followed by recoveries until the root has completely been taken out of the sediment.

The paper is organised as follows: we first present observations from uprooting experiments conducted on seedlings (Section 2.1) and our modelling framework (Section 2.2); the validation of the model (Section 3) allows us to determine the friction between roots and the soil matrix; in Section 4 we discuss the relevance of our findings for seedlings subject to environmental uprooting constraints (uprooting by flooding events) and comment on the ability of seedlings to recover from partial failure (analysis of the jumps in the stress–strain signal); finally, Section 5 summarises our findings and concludes the work.

2. Seedling anchorage: experimental observations and modelling

2.1. Uprooting experiments

Our modelling efforts are guided by our observations in the experiments by Edmaier et al. (2012, 2014). We aim at explaining and reproducing the main features of the stress–strain curves obtained experimentally (see Fig. 1 for typical realisations of the