

Analysing lodging of the panicle bearing cereal teff (*Eragrostis tef*)

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Summary

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- Lodging, the permanent displacement of crop plants from their vertical because of root or shoot failure, is a major yield constraint of the gluten free, panicle bearing cereal teff. The objective of this paper was to analyse the causes of lodging of teff by using, modifying and validating conventional biomechanical models.
- The model parameters were obtained from a field trial with two contrasting teff cultivars, using novel *in situ* and laboratory measurements under wet and dry conditions. Cross-species model validation was done with rice (*Oryza sativa*).
- Teff is more susceptible to root lodging than to shoot lodging, although the data indicated that shoot strength is also insufficient. Hence, simultaneously breeding for both improved root anchorage and shoot strength is advocated.
- The study showed that the lodging model, derived for the spike-bearing cereal wheat, needed modifications in order to be able to deal with panicle-bearing plants such as teff and rice. Water adhering to plants owing to rain or dew increased calculated lodging susceptibility. To prevent underestimation of lodging susceptibility, future lodging research should be done under completely wet conditions (water saturated soil and wetted shoots)

Introduction

Teff (*Eragrostis tef* (Zuccagni) Trotter) is a panicle bearing C_4 cereal crop (Kebede *et al.*, 1989) originating from Ethiopia. Teff grains and flour do not contain gluten (Spaenij-Dekking *et al.*, 2005) and are rich in minerals, especially iron (Mengesha, 1966; Abebe *et al.*, 2007; Verdonshot *et al.*, 2008). These two characteristics make teff a desirable ingredient in health products, particularly for celiac disease patients. Teff can replace gluten-containing cereals in products such as pasta, bread, beer, cookies and pancakes. Ethiopia, where teff is the main cereal crop and food shortage a recurring phenomenon, exerts an export ban on teff. Therefore, interest in growing teff outside Ethiopia increased. It was recently introduced in north-western Europe (Hopman *et al.*, 2008). As in other regions where teff is cultivated, teff yields in the Netherlands are modest (1000–1500 kg ha⁻¹) and quality is often low. A major factor limiting yield and quality is lodging. Lodging can be defined as the permanent displacement of a plant from the vertical (Berry *et al.*, 2004). In teff, lodging frequently occurs before the grain-filling period starts. Lodging prevents the crop from

ripening properly and often results in mouldy panicles, inferior seed quality and sprouting seeds on the panicle.

In Ethiopia, lodging of teff is also a common phenomenon and one of the causes for the current low grain yields: the Ethiopian national average grain yield of teff is in the order of 800 kg ha⁻¹ (Tulema *et al.*, 2005). This low national average is partly associated with constraints such as waterlogging, drought and nutrient limitation (Tulema *et al.*, 2005). The yield of well-fertilized unsupported plants in 'on station' field experiments is, on average, in the order of 2500 kg ha⁻¹ (Tulema *et al.*, 2005). However, Teklu & Tefera (2005) reported yields up to 4600 kg ha⁻¹ for teff supported with nets to prevent lodging. Yizengaw & Verheye (1994) consider 4600 kg ha⁻¹ as a good approximation of the yield potential of teff under rainfed conditions in Ethiopia. The difference in yield between naturally growing teff and supported teff implies that solving teff's lodging problems would dramatically increase actual yield. Lodging resistance, therefore, is the main focus in several breeding programmes (Berhe, 1973; Ketema, 1991; Hundera *et al.*, 2000; Zhang *et al.*, 2001; Tefera *et al.*, 2003; Yu *et al.*, 2006).

Crook *et al.* (1994) developed simple equations to investigate lodging phenomena in cereals. These static equations predict a relative degree of susceptibility to anchorage failure and shoot failure, known as root and shoot lodging, respectively. According to Crook & Ennos (1994), lodging susceptibility in cereals depends on three factors: first, the size and dynamics of the forces to which the plant is subjected (Pinthus & Brady, 1974); second, the bending strength of the shoot and its resistance to buckling; and third, the anchorage strength of the root system. Although the static equations developed by Ennos and coworkers only take the second and third factors into account, while neglecting influences by wind, the results corresponded well with field observations (Crook & Ennos 1994). Yet, these equations do not aim to predict the actual onset of lodging in the field as a result of weather conditions (Baker *et al.*, 1998).

In this study, three main issues are addressed. The first and main objective of the study is to measure the biomechanical properties of teff in order to distinguish whether the plant is more susceptible to shoot or root lodging. To analyse the lodging susceptibility of teff during a Dutch growing season we designed an apparatus to assess *in situ* biomechanical properties of teff. Two morphologically contrasting cultivars were studied.

The second objective is to examine the applicability of the models of Crook *et al.* (1994) to the problem of assessing the effects of plant structure on lodging risk of teff and rice. These authors worked with wheat (i.e. shoots with erect spikes), whereas teff has a drooping panicle. Hence, for teff, the self-weight moment of an erect shoot is not zero as is assumed in these model equations. Moreover, a second model assumption is that the shoots as a whole behave as uniform rigid beams. This assumption is incorrect for most rice and teff cultivars, given that their tapering shoots are known to bend under their own weight.

The third aspect addressed is the modifying effects on lodging of water adhering to the shoots owing to dew or rain. Lodging of cereals often occurs as a consequence of rainstorms (Berry *et al.*, 2004). The common perception is that the effect of rain water on lodging is primarily brought about via the lubricating effect on the soil, reducing root anchorage strength (Crook & Ennos, 1993; Baker *et al.*, 1998; Sposaro *et al.*, 2008). Wind gusts exercise forces on the shoot system which can lead to root lodging or shoot lodging in firmly anchored plants. We observed that root lodging of teff also occurred in the absence of wind when plants became wet because of dew or drizzle while the soil surface was practically dry (see the Supporting Information, Video S1). This points to a direct physical effect of the weight of water adhering to the shoot on lodging. Although papers presenting more elaborate models, such as those of Baker *et al.* (1998), Berry *et al.* (2003) and Berry *et al.* (2007), mention a possible influence of water adhering to

stem, leaves and panicle on lodging susceptibility, no data to verify this hypothesis have been published; neither is adhering plant surface water accounted for in any of the current models for cereal lodging.

This paper elaborates first on the theoretical background of equations which were used and modified during the current work. The experimental procedures and applied statistical methods are provided followed by the results of these experiments. The major findings of this work are summarized and the morphology and lodging characteristics of teff are compared with other cereals. The conclusions of this work are placed in context and recommendations are made for breeding and further research.

Materials and Methods

Theory

Crook *et al.* (1994) were the first to apply the concept of 'factor of safety' to a phenomenon in plant science, namely lodging. The safety factor (SF; see Table 1 for the full list of Abbreviations) indicates the number of times a support organ can bear the self-weight moment (M) of the organ it

Table 1 Abbreviations

SF	Safety factor
a_1 and a_2	Major outer and inner diameter of the ellipse, respectively (m)
b_1 and b_2	Minor outer and inner diameter of the ellipse, respectively (m)
D	Root cone diameter (m)
E	Young's Modulus (N m^{-2})
EI	Flexural rigidity (Nm^2)
F_{\max}	Maximum force (N) a stem can withstand before it fails
g	The acceleration owing to gravity ($\text{N}\cdot\text{kg}^{-1}$)
h_p	The height (m) of the centre of gravity of the plant
h_s	The height (m) of the centre of gravity of the shoot
I	Second moment of area (m^4)
k	Dimensionless proportionality constant linking S_A to τ and D
L	Distance (m) between the supports of the three-point bending test
M_p	Self weight moment (Nm) of the whole plant
m_p	Fresh plant mass (kg)
M_s	Self weight moment (Nm) of the shoot
m_s	Fresh shoot mass (kg)
S_A	Root anchorage strength (Nm)
S_{FA}	Safety factor against anchorage failure
S_{FS}	Safety factor against stem failure
S_s	Maximum self weight moment (Nm) before shoot failure
α	Constant derived by regression
β	Constant derived by regression
τ	Soil shear strength (Nm^{-2})
θ°	Angle of inclination from the vertical for shoots or plants

is supporting. Crook *et al.* (1994) defined a safety factor against anchorage failure (root lodging) and a safety factor against shoot failure (shoot lodging). The safety factor against anchorage failure (SF_A) is given by:

$$SF_A = S_A/M_P \quad \text{Eqn 1}$$

(S_A , root anchorage strength (Nm; i.e. the maximum moment at θ° from the vertical that a root system can withstand before rotating further in the soil); M_P , self weight moment (Nm) of the whole plant at θ° from the vertical; see Eqn 4).

Analogous to this, the safety factor against shoot failure (SF_S) is given by:

$$SF_S = S_S/M_S \quad \text{Eqn 2}$$

(S_S , maximum self-weight moment (Nm) which the shoot can support before it fails and M_S is the self weight moment (Nm) at θ° from the vertical; see Eqn 3).

The parameters M_S , M_P , S_A and S_S can be directly measured with a dedicated device (lodging meter) or calculated with the following equations.

Under the assumption that the whole shoot behaves as a rigid beam, M_S (Nm) is given by:

$$M_S = \sin \theta \times h_S \times m_s \times g \quad \text{Eqn 3}$$

(θ , angle of inclination from the vertical; h_S , height (m) of the centre of gravity of the shoot; m_s , mass (kg) of the shoot; g (N kg^{-1}), acceleration owing to gravity). Similarly M_P (Nm) is given by:

$$M_P = \sin \theta \times h_P \times m_P \times g \quad \text{Eqn 4}$$

(h_P , height of the centre of gravity (m) of the plant; m_P , mass of the plant (kg)). As plants often have a whimsical, three-dimensional structure, h_P can be hard to obtain; alternatively, M_P is given by:

$$M_P = \sum_{i=1}^n M_{Si} \quad \text{Eqn 5}$$

(n , number of tillers per plant; M_{Si} , moment of an individual shoot (Nm) at θ° from the plant's vertical).

Root system anchorage strength is influenced by four main factors: root strength and rigidity, the number of roots, the angle of inclination of roots and the soil shear strength (Ennos, 1991). Crook & Ennos (1993) developed an equation that theoretically integrates these parameters. Baker *et al.* (1998) replaced the theoretical proportionality constant k with an empirical constant derived by regression. Assuming the roots will not snap, S_A can now be estimated by:

$$S_A = \tau \times D^3 \times k \quad \text{Eqn 6}$$

(τ is the soil shear strength (Nm^{-2}); D , root cone diameter (m); k , a dimensionless constant).

The bending strength of the base shoot section represents the maximum self-weight moment (S_S , Nm) that the stem base can support before it fails. S_S can be measured in a three-point bending test (for measuring procedure see the 'Bending tests and microscopic observations' section in this paper). Considering the base stem section as a uniform beam, S_S is given by:

$$S_S = F_{\max} \times L/4 \quad \text{Eqn 7}$$

(F_{\max} is the maximum force (N) a stem will withstand before it fails; L , distance (m) between the supports in the three-point bending test).

According to Crook *et al.* (1994) the measure for stiffness of the stem section (i.e. flexural rigidity, EI in Nm^2), is given by:

$$EI = L^3(dF/dY)/48 \quad \text{Eqn 8}$$

(dF/dY is the initial slope of the force/deflection curve (N m^{-1}), obtained from the bending tests). Estimation of the slope (dF/dY) was restricted to the linear elastic part of the force/deflection curve. Young's Modulus (E) (N m^{-2}), the measure for material elasticity for the stem as a composite (the higher value E , the stiffer the material), is given by:

$$E = EI/I \quad \text{Eqn 9}$$

where I is the second moment of area (m^4) of a hollow, ellipse-shaped beam given by:

$$I = \frac{\pi}{4(a_1^3 \times b_1 - a_2^3 \times b_2)} \quad \text{Eqn 10}$$

(a_1 and a_2 , large diameters of, respectively, the outer and inner ellipse (m)); b_1 and b_2 , short diameters of, respectively, the outer and inner ellipse (m).

Field conditions and plant material

Two contrasting cultivars, coded cv 04T19 and cv Ayana were obtained from Foundation Share (the Netherlands). Cultivar 04T19 is thicker-stemmed, more robust, taller and later flowering cultivar than cv Ayana; at similar plant population density (200 m^{-2}) cv Ayana tillered more profusely than cv 04T19. Both genotypes have been developed by mass selection from landraces.

Seeds were hand sown in a 7×7 cm grid in *c.* 8 mm deep holes, in a smooth sowing bed in a sandy soil near Wageningen (the Netherlands, $51^\circ 59' 22''$ N, $5^\circ 39' 38''$ E) on 23 May 2008. Both cultivars were grown under two conditions: without and with support of plants through

nets. Cultivars and netting treatments were set up in a completely randomized block design containing six blocks and four treatments (two cultivars \times two levels of support).

At the two-leaf stage, plots were thinned and plants were occasionally transplanted to obtain one plant per grid hole. Transplanted plants were labelled and discarded from the actual observations. Plot dimensions were 0.98 m (15 plants) by 5.32 m (76 plants) resulting in a plant population density of *c.* 219 plants per m².

Shortly after sowing, a vertically moveable construction with two layers of 10 \times 10 cm meshed gauze was installed in the netting treatments. Nets were raised according to the crop height, to keep the plants as stable as possible. The outer four rows of the plots were not sampled in consideration of atypical border effects (Scott *et al.*, 2005). With these restrictions, each week, plants were randomly chosen from a randomly selected spot at the top or bottom end of the plot (in order to keep the crop structure in the middle of the plot intact during the whole experiment). Plots were bordered with at least 2 m of land planted to maize, starting at 0.5 m from the edge of the plot. These maize plants were trimmed to the crop height of teff.

Soil tests indicated more than sufficient availability of phosphorus (P) and potassium (K). Nitrogen (N) fertilizer was applied at a rate of 35 kg ha⁻¹ resulting in free available mineral N of *c.* 60 kg ha⁻¹ including dry and wet N deposition. As a precaution, to prevent manganese deficiency, sulphur-manganese (0.35 kg ha⁻¹ MnSO₄²⁻) was sprayed on the foliage on 18 June and 2 July 2008.

Rice (*Oryza sativa*) cultivar Quinai was used for a cross-species equation validation (Eqn 13). Seeds were obtained from Qingdao Agricultural University in China. Plants were cultivated in containers with *c.* 220 plants per m² on a half strength Hoagland nutrient solution in a climate chamber at 26 \pm 23°C night : day temperatures and 12 h day length under a mixture of SON-T and HPI (500 μ mol m⁻² s⁻¹).

Measurements on whole plants, shoots and panicles

The percentage of plants lodged by $> 45^\circ$ was estimated twice per week. Crop height, defined as the distance between the soil and average plant height on a plot, was measured in the field before each sampling. Directly after each sampling the plants were individually placed in a cooled container, in moist plastic bags that were loosely wrapped around the plants. Within 20 min after harvest the plants were ready for examination in the laboratory. When measurements required plants to be dry, plants were dried with strongly absorbing soft paper towels.

Following the measurements on the whole intact plants, the three biggest individual shoots were cautiously removed from the plant. The centres of gravity of the whole plant and of separate shoots were determined by balancing them on a thin, smooth metal tube and measuring the distance

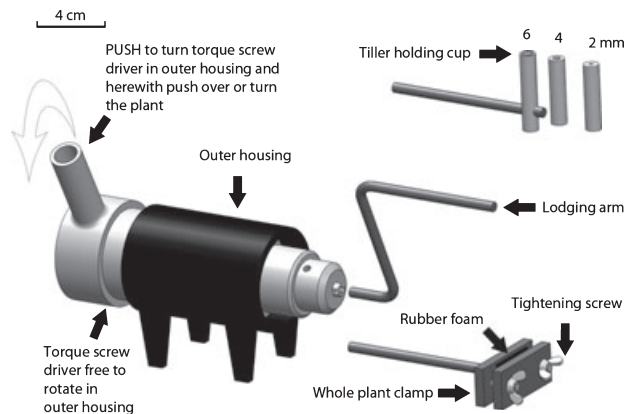


Fig. 1 Plan of the lodging meter (parts are exchangeable). By pushing the turning arm the torque screwdriver rotates in its outer housing. Rotating the screwdriver also rotates attached lodging arm or tiller holding cup or whole plant clamp. Security spikes fix the meter in the soil. Concept based on Crook & Ennos (2000).

between the balance point and their base end. The gravitational moment of plants, shoots and panicles under 0°, 30°, 45° and 60° was established with a custom constructed lodging meter (Fig. 1), built from a sensitive digital 'torque screwdriver' (reading up to 1.5 Nm in 0.001 Nm intervals; Mecmesin Ltd, Broadbridge Heath, UK). Plant or separate shoot fresh weight and the lengths of stem, peduncle and panicle were recorded.

To study the effect of adhering water, plants and separated shoots were sprayed with a plant spray until they showed water runoff. Under these standardized wet conditions, FW, the centre of gravity and gravitational moment were measured again for intact plants and individual shoots. Wetting and drying the same stem repeatedly demonstrated that the weight increase by wetting had a maximum deviation of $\pm 7\%$. All measurements made on both teff cultivars were also made on rice stems.

The number of heading plants (i.e. cereal plants that show the tip of their inflorescence) was scored each subsequent day when heading was expected. Flowering is, however, a more generally used term. As teff plants are cleistogamic (i.e. in general do not open their flowers) (Mengesha & Guard, 1966) and heading and pollination almost coincide in teff (Mengesha & Guard, 1966) we used the term flowering instead of heading and defined the moment of flowering for a cultivar when 50% of all the plants showed the tip of their panicle.

Bending tests and microscopic observations

After the measurements on the whole shoot the plants were kept overnight in a plastic bag with *c.* 10 cm water at 4°C to bring the plants to a standardized turgor level. For shoots larger than 10 cm, 10-cm sections were taken at the base,

the geometrical middle, 80% of the stem length and from the peduncle just above the leaf sheath collar. These four sections were subjected to a standard three-point bending test, analogous to Oladokun & Ennos (2006), using a Zwick Universal Testing Machine (model BZ2.5/TS1S, Ulm, Germany with positioning, repetition accuracy $\pm 2 \mu\text{m}$ and at most 0.02% deviation of the set speed). Stem sections were placed on two supports set 60 mm apart, while a blunt rubber probe with a diameter of 20 mm, attached to the crosshead of the Zwick, was moved down at a speed of 50 mm min^{-1} , touching the stem midway between the supports and bending it. A force/displacement graph was simultaneously recorded by a connected computer and was used to calculate the mechanical properties of the stem section.

After the bending test, cross-sections were made from all stem parts near the location of impact by the probe. Stem cross-sections were coloured with phloroglucinol (Jensen, 1962); high-resolution digital images were made under a stereo-microscope. The stem tissue layers were distinguishable and their dimensions were measured using IMAGEJ, version 1.42 (Rasband, 2009).

Measurements on the root system

The evening before measuring the root system, only the relevant plot locations were watered to soil saturation. Next morning, before the actual measurements began, these plot locations were watered again and allowed to drain to field capacity under gravity for at least 1 h. This gave simulated soil conditions typical of conditions after rain and comparable to other studies (Crook *et al.*, 1994; Baker *et al.*, 1998; Oladokun & Ennos, 2006; Sposaro *et al.*, 2008). Soil shear strengths (i.e. the maximum resistance of a soil to shearing stresses) were measured with a shear-vane; the average was 13.1 kPa (SE 1.7). Plants were cut at 11 cm height. To make the remaining shoot parts (stubble) behave like a rigid beam, a pointed lightweight hollow metal pin was placed in the middle of the bundle of stem bases joining at the bottom of the plant. Next, all stem bases and the metal pin were bundled together with a fastener. Lastly, the stubble-pin combination was slowly pushed to an angle of 30° , 45° and 60° , respectively, from the vertical while the lodging meter (Fig. 1) recorded the maximum resistance of the rooting system. Measurements were corrected for the self-weight moment of the pushing device and stubble-pin combination.

The soil core containing the bristles and rooting system was dug up and preserved in a cooling box. In the laboratory, cores were pushed on a 2 cm grid pinboard and soil was gently washed away exposing the rooting structure. Photographs were made from the root system and root dimensions were measured with IMAGEJ version 1.42 (Rasband, 2009). Root plate diameter was measured at the

theoretical rotation point of the root-soil cone. Like Crook & Ennos (1993) we estimated this rotation point to be half the plant base diameter, the diameter of merging tillers at the soil surface, below the shoot to root transition.

Statistical analysis

SAS version 9.1.3 SP4 (SAS Institute Inc., Cary, NC, USA) was used when data were statistically analysed. To test whether the safety factor (SF) of wetted plants deviated from that of the dry plants, the data were modelled with the PROC MIXED procedure of SAS taking wetting and time as main effects and regarding blocks and differences between shoots from the same plant as random effects:

$$\text{SF} = \text{time} + \text{wet} + \text{time} \times \text{wet} \quad \text{Eqn 11}$$

Assessment for significant differences was done with the least square means (LSMEANS) statement ($P \leq 0.001$).

The increase in height of the centre of gravity (h_p) (cm) of wet and dry plants with time (t , d) was described by Richards sigmoids (Berry *et al.*, 1988):

$$h_p(t) = h_{p\text{MAX}}[1 - b \times \exp(Rt)]^{1/(1-c)} \quad \text{Eqn 12}$$

($h_{p\text{MAX}}$ (cm), asymptotic maximum of h_p ; b , scale-dependent parameter; R , rate at which the function of h_p changes (cm d^{-1}); c is the shape parameter). Richards sigmoids and power regression lines (Eqns 13, 14) were estimated using PROC NLIN procedure. Whether the data of wet plants could be described by a Richards sigmoid fitted for dry plants or whether other parameter values were necessary for wet plants was tested with an F -test on the residual sum of squares of both models. Means in the text are followed by their standard error in parenthesis.

Results

Crop and plant morphology

After a precipitation event on 17 July 2008, the plants of cultivar cv Ayana started to deviate from the vertical but did not exceed a displacement of 30° . On 30 July 2008 we observed severe lodging in the unsupported plots of cv Ayana (Fig. 2). Then, some of the unsupported plots of cv 04T19 also started to deviate from the vertical. Within 2 wk after the start of lodging the plants in the unsupported plots of both cv Ayana and cv 04T19 were totally root lodged, whereas plants in the supported stands were undamaged and upright.

Crop height (Fig. 2) and the plant's centre of gravity (Fig. 3) displayed a similar pattern of change over the season. After both crop height (Fig. 2) and plant FW (Fig. 4a)

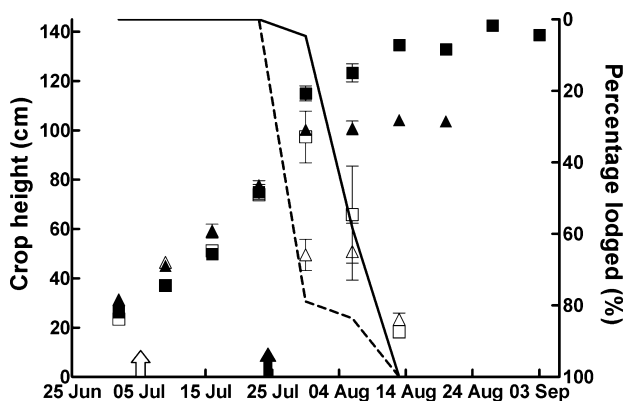


Fig. 2 Development of crop height (cm) over time of teff cv Ayana, either supported (closed triangles) or unsupported (open triangles) and cv 04T19 either supported (closed squares) or unsupported (open squares). Flowering time, defined as 50% flowering plants: open arrow, cv Ayana; closed arrow, cv 04T19. Percentage of lodged plants: broken line, cv Ayana; solid line, cv 04T19. Error bars indicate standard error ($n = 6$) and when not visible fall within the symbol.

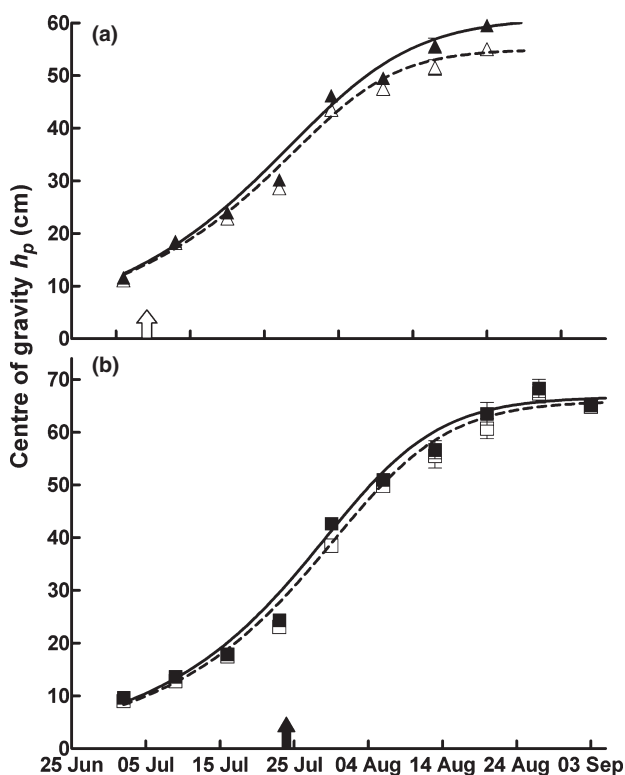


Fig. 3 Height of the centre of gravity (h_p , cm) and fitted Richards sigmoids of wet (closed symbols, solid line) and dry (open symbols, broken line) plants of (a) teff cv Ayana and (b) cv 04T19. Flowering time, defined as 50% flowering plants, is shown for cv Ayana (open arrow) and cv 04T19 (closed arrow). Error bars indicate standard error ($n = 6$) and when not visible fall within the symbol.

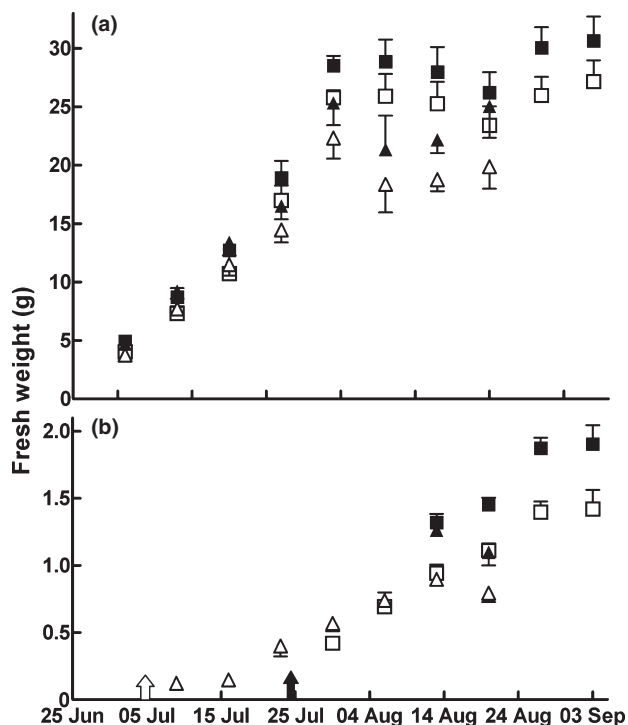


Fig. 4 (a) Average total shoot fresh weight for teff cv Ayana (wet, closed triangles; dry, open triangles) and for cv 04T19 (wet, closed squares; dry, open squares). (b) Fresh weight of the wet and dry panicles separately. Flowering, defined as 50% flowering plants, is shown for cv Ayana (open arrow) and for cv 04T19 (closed arrow). Error bars indicate standard error ($n = 6$) and when not visible fall within the symbol.

had reached their plateau, the height of the plant's centre of gravity still kept increasing (Fig. 3) because of the continued accumulation of dry matter in the top of the plant.

The relative weight increase over time, owing to wetting, was not constant but followed a quadratic polynomial. The relative weight increase caused by wetting was 25% at the beginning of the season, 15% in the middle and 25% at the end of the season. The seasonal average of the relative weight increase by wetting of cv Ayana and cv 04T19 was 18% and 15%, respectively. Wetting also significantly increased the plant's centre of gravity ($P > 0.001$) (Fig. 3), although the magnitude of the effect was, on average, 5%.

Shortly after flowering tillering ceased, tiller number reaching values of 9–10 tillers per plant for cv Ayana and 5–6 tillers per plant for cv 04T19. From this moment onwards the number of viable tillers started to decrease resulting in around seven mature basal shoots per plant for cv Ayana and 3–4 for cv 04T19.

Until the lodging started in unsupported plants there were no significant differences in the trends between the supported and unsupported plant stands for any of the characteristics measured.

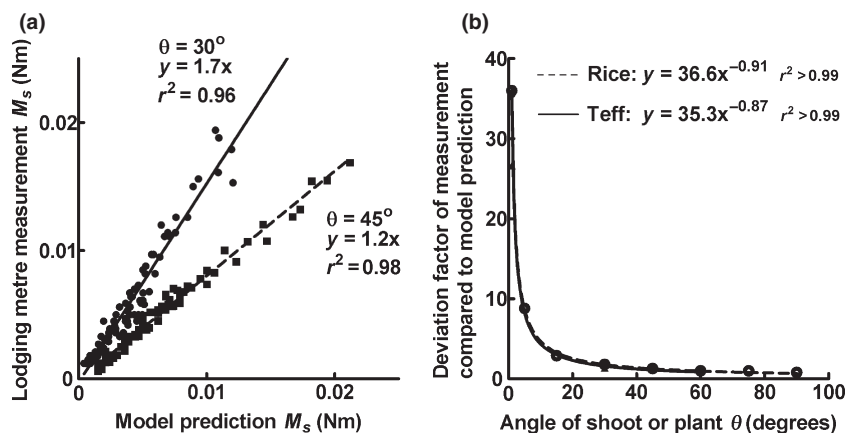


Fig. 5 (a) Scatter plots and regression lines of measured shoot self-weight moment (M_s) vs predicted moment of M_s (Eqn 3) at angles (θ) of 30° (circles, solid line) and 45° (squares, broken line). (b) Deviation factor of measured M_s compared with equation prediction of M_s over a range of angles (θ); that is, data points are slopes like those presented in (a) for teff plants. Teff shoots, closed circles; rice shoots, open circles. ($x = \sin \theta \times h_s \times m \times g$ (Eqn 3 or 4) and (ab (Eqn 13 or 14)).

Morphological and mechanical properties of the shoot

Teff shoots are known to bend easily under their own weight; and in combination with the drooping panicles this will generate a gravitational moment even if the shoot base is standing up straight. This complicates the usage of Eqns 3 and 4, because these equations assume M_s and M_p to be

zero in a perfectly upright position. Nevertheless, measuring the actual moment of plants or separated shoots and plotting them against the calculated moment (Eqns 3, 4) at a particular θ° did reveal a systematic deviation (Fig. 5a). Plotting the deviation from the equation as a function of θ° provided a correction for the estimated M_s and M_p given by:

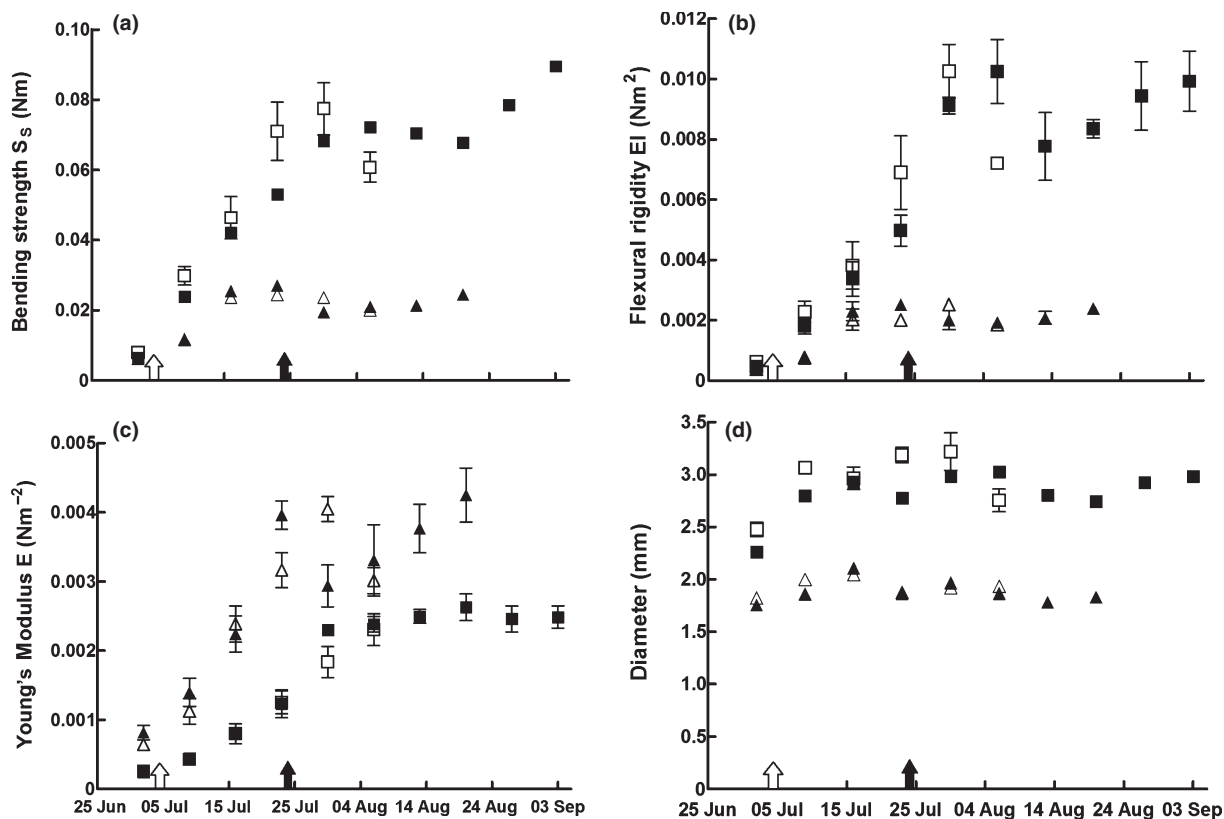


Fig. 6 Mechanical properties of the basal region of the teff shoots during the growing season. (a) Bending strength S_s (Eqn 7), (b) flexural rigidity EI (Eqn 8), (c) Young's Modulus E (Eqn 9), (d) smallest shoot diameter at 5 cm height. Cultivar Ayana: closed triangles, supported; open triangles, unsupported. Cultivar O4T19: closed squares, supported; open squares, unsupported. Flowering time, defined as 50% flowering plants, is shown for cv Ayana (open arrows) and cv O4T19 (closed arrows). Error bars indicate standard error ($n = 6$) and when not visible fall within the symbol.

$$M_S = \alpha(\sin \theta \times b_S \times m \times g)^\beta \quad \text{Eqn 13}$$

$$M_P = \alpha(\sin \theta \times b_P \times m \times g)^\beta \quad \text{Eqn 14}$$

(α and β , constants derived by regression analysis). Rice and teff showed strikingly similar values for α and β (Fig. 5b).

Between the two cultivars, there were marked differences in measured parameter values for: bending strength (S_S) (Eqns 2, 7), flexural rigidity (EI) (Eqns 8, 9), Young's Modulus (E) (Eqn 8) and stem dimensions (Eqn 10) (Fig 6). Bending strength (S_S) and flexural rigidity (EI) increased rapidly with time but levelled off *c.* 8 d after flowering in both cultivars (Fig 6a,b). Shoots often failed instead of breaking and therefore bending strength and flexural rigidity were strongly correlated ($r^2 = 0.92$).

Cultivar cv 04T19 showed values for both bending parameters S_S and EI that were four times higher than values measured in cv Ayana. By contrast, cv Ayana showed higher tissue stiffness (Young's Modulus; Fig. 6c) than cv 04T19. Therefore, predictably (Eqns 9, 10), the second moment of area was higher for cv 04T19 than for cv Ayana as was the independently measured stem diameter (Fig. 6d). Dry weight per volume of tissue (i.e. 'tissue density') was on average higher for cv Ayana 0.060 (0.017) g cm⁻³ than for cv 04T19 0.046 (0.020) g cm⁻³. In both cultivars the increase in Young's Modulus over time coincided with an increase in 'tissue density' ($r^2 = 0.76$ for cv Ayana and $r^2 = 0.83$ for cv 04T19) (data not shown).

Stem cross-sections showed an elliptic shape. The smallest width of the ellipse (Fig. 6d) showed a seasonal pattern of increase comparable to that of the largest stem width (not shown); the largest width of the ellipse was, on average, $\times 1.07$ (0.08) (cv Ayana) and $\times 1.22$ (0.14) (cv 04T19) greater than the smallest width.

Microscopic analysis of stem cross-sections stained with phloroglucinol, showed the lignified surface of epidermal, sclerenchymatic and parenchymatic tissue. The total lignified tissue surface was not correlated to the Young's Modulus ($r^2 < 0.05$, data not shown) for both cultivars. Neither was the Young's Modulus correlated with the cross-sectional surface area of any of the three individual tissues. Results did not improve if cross-sectional areas were expressed as fractions of the total stem tissue surface area ($r^2 < 0.05$, data not shown). There was also no significant correlation between the number of vascular bundles per unit surface area and the Young's Modulus ($r^2 < 0.05$, data not shown).

The absolute weight increase by wetting individual shoots showed a linear increase with time ($r^2 > 0.96$ for both cultivars; data not shown). The panicle of cv 04T19 contained *c.* 56% of the plant's total adhering water and for cv Ayana this was 64%. The fraction of adhering water present in the panicle was larger than would be expected on basis of its

length or fresh weight. Panicle length was *c.* 30% of the total stem length in both cultivars; the fraction of shoot fresh weight present in panicles was 0.3 for cv Ayana and 0.2 for cv 04T19.

For both cultivars the safety factor against shoot lodging (SF_S) (Eqn 2) dropped to values close to one half-way the growth cycle (Fig. 7a). The M_S of cultivar cv 04T19 kept increasing whereas the S_S did not increase. Therefore, SF_S declined to low values during the season; moreover, the SF_S was systematically reduced by wetting the plants. However, the absolute critical SF_S value of 1 was not reached (Fig. 7a). This implies it is unlikely that gravitational forces alone could break the basal region of the shoots.

The safety factor against breaking of the peduncle by its own weight was two to three times higher than the SF_S (data not shown).

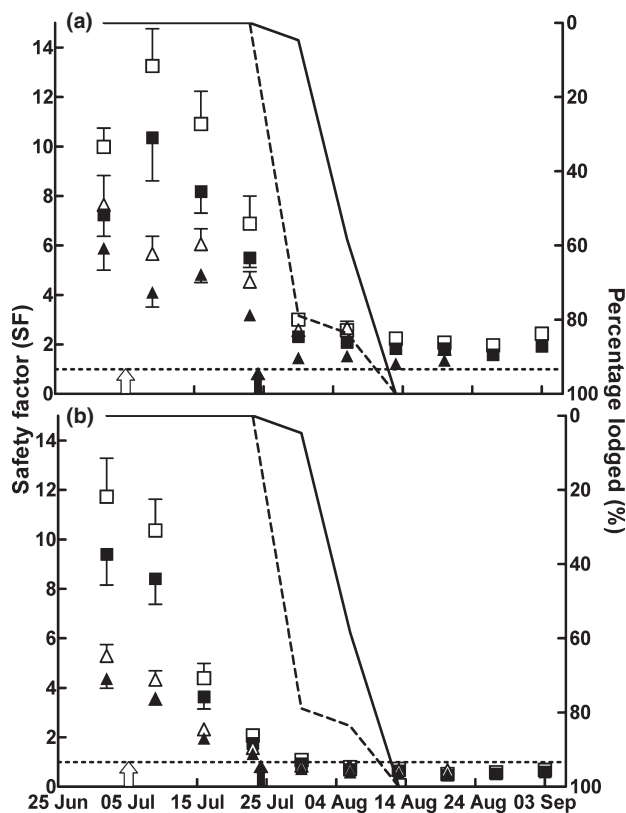


Fig. 7 Factor of safety for (a) shoot (SF_S) and (b) root anchorage (SF_A), of teff during the season. Cultivar Ayana: closed triangles, wet; open triangles, dry. Cultivar 04T19: closed squares, wet; open squares, dry. Observed lodging percentage in unsupported fields for cv Ayana (broken line) and cv 04T19 (solid line). Horizontal dotted line is critical safety factor ($y = 1$). Flowering time, defined as 50% flowering plants, is shown for cv Ayana (open arrows) and for cv 04T19 (closed arrows). Error bars indicate standard error ($n = 6$) and when not visible fall within the symbol.

Table 2 Overview of estimated plant characteristics during late development of two genotypes of teff (this study), winter wheat (Crook & Ennos, 1993; Crook *et al.*, 1994)^a and rice (Chuanren *et al.*, 2004; Oladokun & Ennos, 2006)^b

	Teff cv Ayana	Teff cv 04T19	Winter wheat	Rice
Flexural rigidity (EI) in (Nm ²)	0.002	0.01	0.04	1.8
Young's Modulus (E) in (N m ⁻²)	3.8–4.2 × 10 ⁻³	2.4–2.7 × 10 ⁻³	1.8–2.6 × 10 ⁻³	1.2–3.0 × 10 ^{-3b}
Shoot diameter (mm)	1.8	3.2	4.5	6.6
Bending strength (S _S) in (Nm)	0.02	0.07	0.16	2.5
Shoot length (m)	1.3	1.7	0.8	1.0
Factor of safety shoot (SF _S)	1.3	2.2	6	–
Plant base diameter	10.7	13.9	–	–
Angle of root inclination (°)	37	45	93–103 ^a	–
Lignified crown roots	23	23	6–9	100
Root plate diameter (mm)	11.3	14.9	26.3–29.5 ^a	–
Factor of safety root (SF _A)	> 1	> 1	3	5

Morphology and mechanical properties of the roots

Because of its small seeds teff has to be sown at a maximum depth of 10 mm, resulting in crown roots that emerge at or above the soil surface. These crown roots form a bundle of *c.* 23 initially vertically growing lignified roots (Table 2). Approximately 1 cm below the soil surface these root bundles started to spread out at an angle of 35° (cv Ayana) and 45° (cv 04T19) from the vertical. During a short period early in the season the crown roots became thicker (Fig. 8); these changes coincided with a measured increase in anchorage strength (Fig. 8). In cv 04T19 we observed thick, rigid roots compared with the thinner, flexible roots of cv Ayana. The anchorage strength of cv Ayana showed a low correlation ($r^2 = 0.14$) with the product of the cube of root plate diameter and shear strength (Eqn 6), whereas in cv 04T19 the correlation was higher ($r^2 = 0.55$) (Fig. 9). This sug-

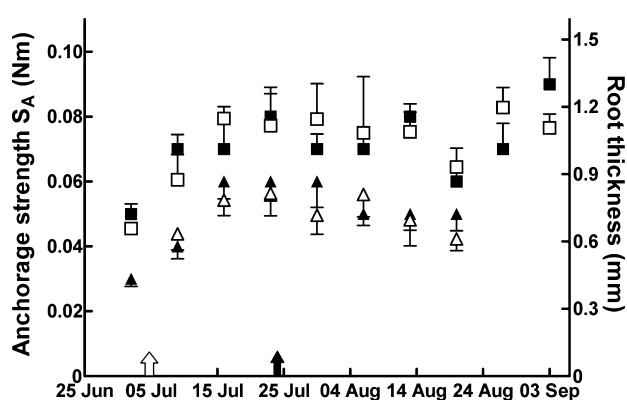


Fig. 8 Anchorage strength (SA) (closed symbols, left vertical axis) and root thickness of six thickest roots (open symbols, right vertical axis), during the growing season. Triangles, teff cv Ayana; squares, cv 04T19. Flowering time, defined as 50% flowering plants, is shown for cv Ayana (open arrow) and cv 04T19 (closed arrow). Error bars indicate standard error ($n = 6$) and when not visible fall within the symbol.

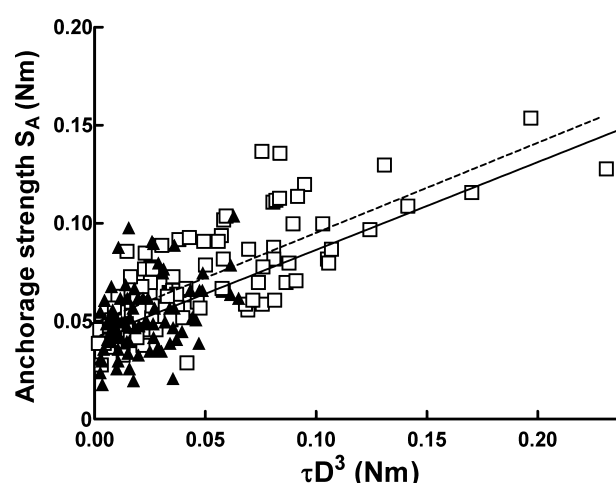


Fig. 9 Measured anchorage strength at 45° vs calculated anchorage strength (shear strength (τ) × root plate diameter³ (Eqn 6)); for teff cv 04T19 (open squares, broken line: $y = 0.46 + 0.049x$, $r^2 = 0.55$, $n = 89$) and cv Ayana (closed triangles, solid line: $y = 0.45 + 0.042x$, $r^2 = 0.14$, $n = 70$).

gests that, unlike cv Ayana, (thin roots), cv 04T19 (thick roots) was able to form a root–soil cone to some extent.

Until flowering, the SF_A was sufficiently high for both cultivars to support the plants. Shortly after flowering, however, the safety factor dropped below the threshold value of 1 (Fig. 7b), implying that root anchorage was too weak to prevent lodging even while only gravitational forces are taken into account, so, for instance, disregarding wind events. This calculated point in time when the average SF_A dropped below 1 coincided with the independently observed onset of lodging in the field (Fig. 7b).

Discussion

The results of this study show that like wheat (Crook *et al.* 1994) and rice (Oladokun & Ennos, 2006), teff is also most susceptible to root lodging. This study explains why lodging

was observed to occur during all years of practice since the introduction of teff in the Netherlands (2002). Teff root anchorage strength (S_A) reached its maximum early during development (Fig. 8). About 2 wk later plant fresh weight reached its plateau level (Fig. 4). The plant's centre of gravity, however, kept increasing in height because of panicle emergence, and later on grain filling (Fig. 3). This caused an increase in whole-plant moment (M_p) until 2 wk before harvest. The absolute critical safety factor against anchorage failure of 1 (i.e. the moment when lodging of unsupported plants is inevitable) was reached shortly after root anchorage strength, S_A , reached its maximum but long before the maximum value of the whole plant moment, M_p , was reached. Therefore, the current *in situ* measurements of the biomechanical properties of the teff cultivars cv Ayana and cv 04T19 indicate that, regardless of wind force, lodging of unsupported teff plants is inevitable on sandy soils.

Plant base diameter, the diameter of joining tillers at the soil surface, and the average root plate diameter were small compared with other cereals (Table 2). The plant base diameter was, furthermore, frequently larger than the root plate diameter in both cultivars. The root bundles did not spread out from their onset but did so after *c.* 1 cm below the soil. As the plant base was, in general, larger than the root onset there was a narrowing in plant shape at the shoot–root transition. Therefore, we hypothesize that plants were not well anchored: first because they were standing on bundles of flexible vertical roots and second, the stem did not penetrate the soil and therefore crown depth was shallow, which most likely reduces anchorage strength as Berry *et al.* (2000) have argued similarly for wheat.

The value of 0.46 in teff for the dimensionless constant k (Eqn 6) (Fig. 9), a scalar serving to link shear strength and root plate diameter with anchorage strength, is similar to values found in other cereal species: 0.43 (Baker *et al.*, 1998) and 0.39 (Berry *et al.*, 2006) for wheat and 0.58 for barley (Berry *et al.*, 2006). Each of these authors forces the line relating anchorage strength to τD^3 through the origin (Fig. 9). However, an intercept of zero would theoretically imply no anchorage strength without a root plate. This is inconsistent with reality, as the joined shoots of cereals at the bottom of the plant can form a small plateau (plant base) in or on the soil which provides a certain degree of anchorage strength. Reanalysing the published data of Baker *et al.* (1998) and Berry *et al.* (2006) revealed intercepts of 0.058 Nm (with new $k = 0.36$) and 0.039 Nm (with new $k = 0.36$) for wheat and 0.045 Nm (with new $k = 0.54$) for barley. These values are comparable to the intercepts of 0.042 Nm (cv Ayana) and 0.049 Nm (cv 04T19) that we found for the teff cultivars. In this line of thinking, a higher intercept would need to be found for the thicker stems of sunflower compared with the smaller cereal stems. Reanalysis of data of Sposaro *et al.* (2008) confirmed this: an intercept value of *c.* 3.9 (Nm) was found. There-

fore, we argue that not only the root plate but also the plant base diameter can have a significant contribution to the plant's anchorage strength. This suggests that an additional component must be added which accounts for both: the resistance of the plant's stem base to being pushed through the soil and the possible simultaneous influence of the stem on the root soil cone's shape. This component seems to be similar in all the cereal species tested (*c.* 0.05 Nm). Consequently, an intercept should be included in Eqn 6. As a practical consequence breeding for thicker stems will most likely also contribute to an increase of root anchorage strength.

Although teff is clearly susceptible to root lodging, the safety factor against shoot failure for both cultivars is also low. When during a previously conducted pilot field experiment the shoot bases were supported, the moment of lodging was postponed (unpublished data). Such supported plants did not break but were severely bent before harvest. This observation is in line with the current results and provides a further indication that both the root system and the shoots should be improved in order to enhance lodging resistance.

As in wheat, teff's bending strength and flexural rigidity rapidly increased during initial crop development, although the values of bending strength and flexural rigidity are very low compared with wheat and rice (Table 2). However, the Young's Modulus is higher in teff than in wheat, while the stem diameter is smaller in teff than in wheat. Therefore, stem rigidity (EI) could be enhanced by increasing the stem diameter and thus the second moment of area (I) of teff, while preserving the current tissue density (i.e. Young's Modulus). Furthermore teff flexural rigidity and bending strength were strongly correlated; teff shoots fail instead of breaking, suggesting that an increase in stem rigidity will also increase stem bending strength.

Adhering water on stem, leaves and especially the panicle significantly reduced both the shoot safety factor (on average 31% in cv Ayana and 23% in cv 04T19) and the anchorage safety factor (on average 16% in cv Ayana and 18% in cv 04T19). The calculated self-weight moment (Eqns 3, 4) for plant angles (θ) smaller than 50° underestimated the actually measured self-weight moment of both the whole plant and separated shoots (Fig. 5b). As teff does not grow a straight spike but has a panicle type of inflorescence the simple classical lodging equations developed for wheat (Crook *et al.* 1994) and rice (Oladokun & Ennos, 2006) are not entirely valid for the panicle-bearing crops and need adjustment (Eqn 13) or to be replaced by more sophisticated models such as a modified version of Berry *et al.* (2006). In our opinion, a future model should be able to calculate the safety factor for wet plants at any given point along the shoot. Considering the safety factors of different sections of the whole shoot is important as the plant's base is not necessarily the weakest point of the

stem. According to Żebrowski (1999) the mechanical behaviour of the stems is a result of rather complex shoot–wind interactions, where dynamic loads and thus oscillations are involved. Therefore, to be able to accurately predict the lodging moment in the field any future model should include the effect of the forces encountered during strong winds, so integrating the effects of wind drag that cause large deflections in any cereal. This approach can be used to calculate the appropriate shoot dimensions for panicle-bearing cereals in general. The model calculations of self-weight moment at any point along the stem can be verified with measurements of our lodging meter.

Based on field observations in teff we presupposed that the shoot base is the most vulnerable shoot part in terms of lodging susceptibility. Our measurements confirmed that the safety factor against peduncle failure was significantly higher than the safety factor for the shoot base in both cultivars. In general the strength of the plant's base, however, is not necessarily the critical point for lodging. In barley (Berry *et al.*, 2006) the peduncle is viewed as being the weakest point along the shoot. Breaking peduncles has also been reported in a few teff cultivars that are commonly not cultivated (Ketema, 1991).

In conclusion, the *in situ* field measurements were able to point out the main lodging causes of teff. To the best of our knowledge all published work on lodging in teff has focused on the shoots; here we show that enhancing the anchorage strength of the roots has priority over stem enhancement. Nevertheless, breeding efforts should not only focus on a wider root plate diameter and more rigid horizontally growing roots but also on shorter and thicker stems. This study also infers that the high safety factor against shoot lodging reported for rice (Oladokun & Ennos, 2006) is probably too optimistic. This is concluded from both the data on rice reported in this study and from a study by Ishimaru *et al.* (2008) showing shoots rather than the roots failed during severe rain and winds.

We argue that further biomechanical lodging research should be done under totally wet conditions a wetted root-system as well as wetted stems, leaves and inflorescences. We surmise that the lack of incorporation of plant surface water partially explains the mismatch between lodging model predictions and reality (Berry *et al.*, 2003).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Video S1 Root lodging of teff.

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