Modelling root and stem lodging in sunflower

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ABSTRACT

Stem and root lodging constitute significant adversities to sunflower (*Helianthus annuus* L.) cropping in Argentina. We have adapted previously developed models of the lodging process in cereals to the particularities of sunflower by using functions, developed using data obtained by mechanical lodging, for the [root failure moment/plant anchorage] and [stem failure moment/thickness of stem wall] relationships, and estimates of plant area loaded by wind gusts. The model uses this information to estimate wind failure speed (i.e., the wind speed at which lodging [stem or root, as appropriate] is expected to occur). The model was tested against information (plant and soil characteristics, measured wind gust velocity immediately preceding rainfall) obtained in 26 naturally lodged plots (6 stem-lodged, 20 root-lodged) which occurred across a network of trials (2 seasons, 4 sites, 3 hybrids, 4 crop population densities, all experiments fitted with automatic meteorological stations). Lodging events took place over a range of crop developmental stages between visible capitulum and harvest maturity. Lodging index (proportion of plants lodged) against the difference between observed and model-estimated wind failure speeds showed that the model had good predictive skill across the range of conditions explored in these experiments and was able to distinguish between hybrids of differential susceptibility to lodging within the same experiment. Sensitivity analyses showed that the principal determinants of lodging susceptibility were root plate diameter, stem wall thickness, and the area of the plant loaded by wind gusts. Within the observed ranges (almost twofold) of stem height and stem natural frequency, these two variables had little influence on lodging susceptibility. We conclude that the model, despite the simplifications incorporated into its structure, provides an effective and useful tool for the integration of the complex factors that determine lodging susceptibility in this species.

1. Introduction

Root and stem lodging (defined as the permanent displacement of the stem from its vertical position) cause important yield losses in sunflower (*Helianthus annuus* L.) production in Argentina. The prostrate capitulae of lodged plants are not retrieved during mechanical harvesting, and about 10% of sunflower crop lodges annually, for an estimated loss of US$40 million (Bragachini et al., 2001). In experimental trials and farmers plots (INTA, 2003) and in published studies (Ennos et al., 1993; Sposaro et al., 2008; Hall et al., 2010) sunflower lodging has been observed to result from failure of the root anchorage system or from tensile failure of the

stems. The susceptibility to lodging and its occurrence in stems or roots of crops exposed to high winds depends on complex interactions between the mechanical properties of the stems and the soil–root system that anchors the plants, the shape of the upper sections of the plant that capture wind gusts, and rain. The values of these variables vary throughout crop development, and can change with husbandry practices (e.g., sowing density), genotype, and soil properties. Stem lodging can occur in well-anchored crops when the force applied to the lower portion of the stem exceeds the stem failure moment. Root lodging is usually associated with rain that weakens the anchorage (i.e., the soil–root system) via a reduction in soil strength (Ennos et al., 1993; Sposaro et al., 2008).

The effects of crop development, crop population density and genotype on root lodging susceptibility in sunflower have been studied using artificial lodging (Sposaro et al., 2008). Ennos et al. (1993) observed that the most important anchorage component in sunflower was the resistance to breakage of the roots on the windward side of the plant. Sposaro et al. (2008) found that

anchorage strength, across genotypes, developmental stages and crop population densities was determined by the spread of the root plate, in agreement with studies on wheat and barley (Crook and Ennos, 1993; Baker et al., 1998; Berry et al., 2006). A study of stem lodging during grain filling using artificial lodging in crops of two sunflower genotypes growing at three crop population densities showed that stem lodging susceptibility increased as harvest maturity approached and at higher crop population densities (Hall et al., 2010). Stem failure yield stress (B_S) was positively related to the thickness of the epidermis plus cortex tissues ($Ep + Co$) close to the base of the stem (Hall et al., 2010). The lack of associations between B_S and the diameter of the friable stem medulla and of the stem diameter found in this study suggests that the sunflower stem functions, in mechanical terms and during the grain filling phase, somewhat like a hollow cylinder. In this, sunflower appears to be similar to species with true hollow stems (e.g., Crook and Ennos, 1994; Berry et al., 2003a,b, 2006).

Models of lodging have been developed for wheat (Baker et al., 1998; Berry et al., 2003a; Sterling et al., 2003) and more recently for barley (Berry et al., 2006). By considering the plants as damped harmonic oscillators subject to a stepped wind input (Baker, 1995) these models calculate the wind-induced base-bending moment (leverage) of a shoot from plant characteristics and meteorological data. The calculated base-bending moment is compared with the failure moments (strength at the point of failure) of the stem base and of the anchorage system to estimate the risks of stem and root lodging, respectively. The stem is considered as a hollow cylinder where the thickness of the stem wall and its material strength are the most important variables that determine stem failure moment (Baker et al., 1998; Berry et al., 2006). In the case of root lodging, the model considers the root plate spread and soil shear strength for the calculation of root failure moment. These models require, as inputs, other variables including the height of the centre of gravity and the natural frequency of the shoot and variables related to the aerodynamic properties of the plant: the area of the ear which captures wind-gust energy, the drag coefficient and damping ratio. These models can be used to estimate root or stem failure wind speeds (V_{gR} and V_{gS}, respectively).

Although recent studies have advanced our understanding of root (Sposaro et al., 2008) and stem lodging (Hall et al., 2010) in sunflower, the lack of an overall framework that can be used to integrate the various determinants of lodging is a serious obstacle to progress in the understanding of the nature of the process and to the formulation of crop management and breeding strategies aimed at minimizing the effects of this adversity on yield. The fact that the yield potential in the sunflower crop is constrained by the need to use crop population densities that are lower than those needed to maximise yield in order to reduce, among other things, susceptibility to lodging (López Pereira et al., 2004) is a further incentive to the formulation of a framework model of the process.

In developing a lodging model for sunflower, the wheat and barley models are helpful as many of the relevant principles also apply to sunflower. However, there are also important species differences which must be accounted for. The area of the sunflower plant that is loaded by the wind is very different to that of cereals because the capitulum is disc shaped and the leaves are much larger. The degree to which the wind loads the capitulum and leaves, which approximates the drag coefficient, is also unknown. Furthermore, there are significant changes in capitulum shape and position with crop development and between genotypes (Knowles, 1978).

The objectives of the work reported here were to develop and test a root/stem lodging model for sunflower, and to use the resulting model to explore the impact of the various determinants of crop lodging susceptibility on the overall process. Relationships between root and stem failure moments and root anchorage strength and stem structure, respectively, required for model development were taken from previous publications (Sposaro et al., 2008; Hall et al., 2010). Dynamics of plant area that is loaded by the wind and plant natural frequency and their responses to genotype, crop development, and crop population density were measured during three experimental seasons. The model was tested using an independent set of field experiments conducted at several sites, crop population densities and genotypes in which natural root or stem lodging occurred at different crop development stages. Rainfall prior to and wind speeds during these lodging events were recorded in the experimental plots.

2. Experimental methods

2.1. Estimation of plant area loaded by wind gusts (A)

Field observations of crop behaviour under gusty conditions at various stages of crop development indicated that substantial deformation of the stem and re-arrangement of leaf positions was limited to the upper third of the plant.

This is consistent with the work of Finnigan (2000), in various species, which assumes that the upper third of the plant could experiment significant wind loading. When exposed to a gust of wind, the leaves of the upper third tend to become organized into a somewhat vertical plane or sail, the shape of which could be approximated by a trapezium. In order to estimate the area involved in the capture of wind gust energy (A) at any given stage of crop development, we assumed that the leaves (laminae only) attached to the upper third of the plant formed a trapezium, this was then simply approximated as: $(B + b) \times h/2$, where B is the sum of the lengths of both leaves of the bottom, b is the sum of the lengths of the apical leaves and h is the sum of the widths of each leaf in the upper third of the plant (Fig. 1a). The capitulum could be represented by a disc of finite thickness which could assume a range of positions (from horizontal, through vertical, to hidden among the upper leaves) as the crop passed through different stages of development (Fig. 1). Fig. 1 summarizes the relationship between estimates of A and crop development as noted in the Schneiter and Miller (1981) development scale. Many sunflower hybrids grown in Argentina have capitulae that "hide" within the upper stratum of the canopy after flowering, but the scheme shown in Fig. 1 can be accommodated to hybrids that remain with erect capitulae (Knowles, 1978) after flowering. It should also be noted that the lower limit of the trapezium, present at flowering, moves upwards after basal leaf senescence progresses beyond that limit, resulting in a decrease in A as development proceeds towards harvest maturity.

Measurements of A were made at the R2, R5.9, R7, and R8 Schneiter and Miller (1981) developmental stages, and at harvest maturity (HM), in a set of six experiments described in Sposaro et al. (2008) (Experiments: E1, E2 and E3) and Hall et al. (2010) (Experiments: E1, E2 and E3). Each experiment involved plots of Zenit (Sursem Argentina) and another hybrid (either CF29 or V70597 (experimental stay green), both from Advanta Semillas Argentina) sown at either three or four crop population densities in the 3–16 plants m^{-2} range. It is not unreasonable to assume that as the wind speed increases, the area of A will decrease as the leaves bend with the wind. However, within the scope of the current study it was difficult to quantify this reduction and the range of wind speeds over which it may occur. Also, it must have taken into account that the lower limit of the trapezium, that represent a portion of this A, moves upwards after basal leaf senescence reaches that limit. Hence, it is acknowledged that our estimates of A must be regarded as approximate. In spite of these uncertainties, we believe our approach to estimating A is consistent with the spirit of the lodging models developed for cereals referred above.
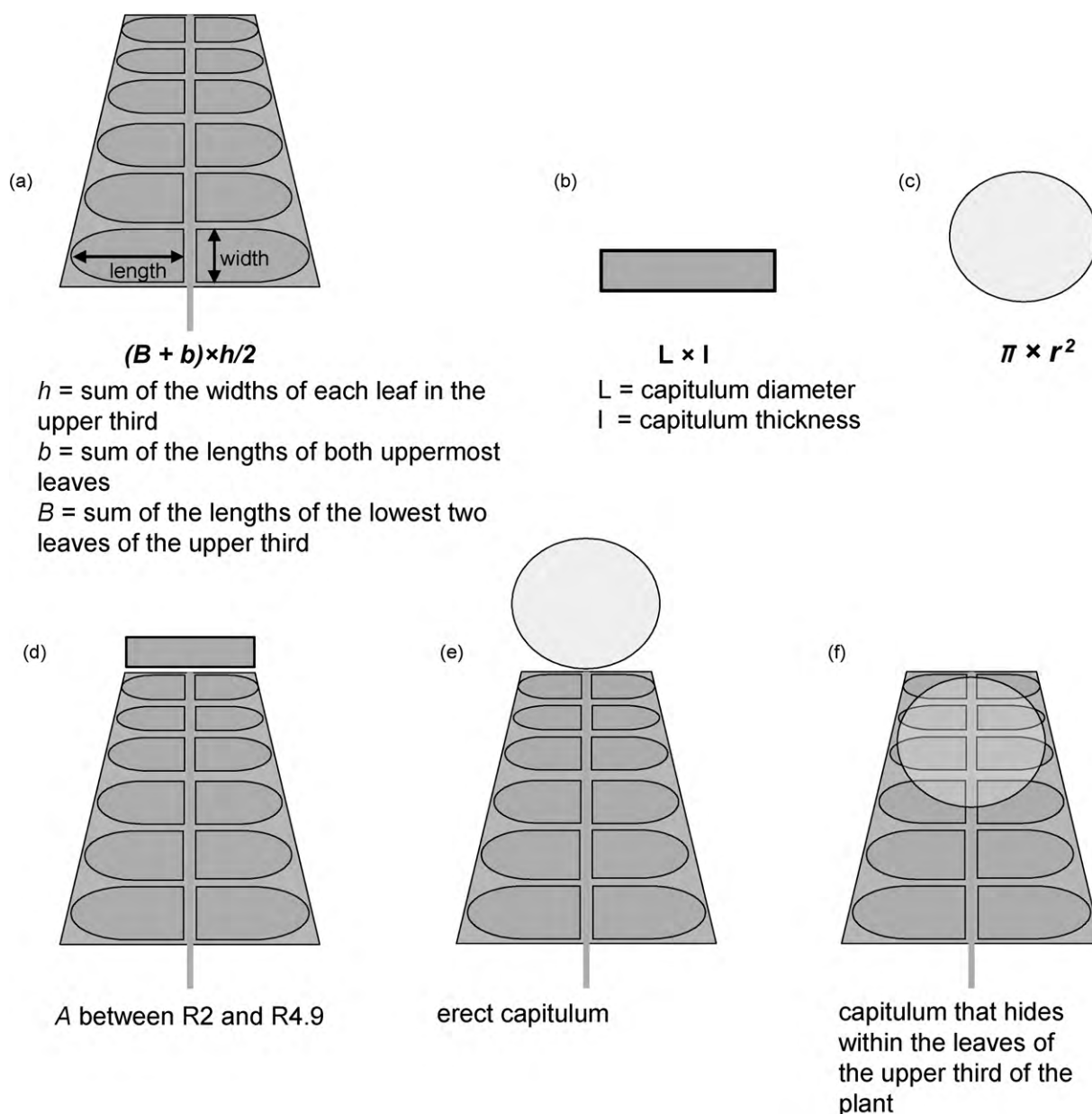
Fig. 1. Plant area expected to be loaded by wind gusts (A). (a) Area formed by the leaves (laminae only) in the upper third of the plant under loading by wind; (b) capitulum shape between R2 and R4.9; (c) capitulum shape between R5 and harvest maturity; (d) A between R2 and R4.9; (e) A between R5 and harvest maturity for capitulum with an erect capitulum; (f) A between R5 and harvest maturity for a hybrid with a capitulum that hides within the leaves of the upper third (note that the area of the capitulum is not considered).

2.2. Plant natural frequency (n)

There is no published information on natural frequency (n) values for sunflower. To determine the effects upon this variable of genotype, crop population density, and crop developmental stage, n was routinely measured during a set of four experiments conducted during the first two seasons reported in each of Sposaro et al. (2008) and Hall et al. (2010). Each of these experiments involved two out of a set of 3 hybrids, and one to three crop population densities in the 5.6–16 plants m^{-2} range. In each experiment, measurements were performed at either three or four developmental stages between R2 and R8 on the Schneiter and Miller (1981) scale, and at harvest maturity. To determine n, individual plants, with all their leaves and capitulum attached, were pulled 10° from its vertical position and allowed to oscillate freely without any inter-ference of neighbouring plants in the same row. The time taken for the plant to stop oscillating and the number of oscillations were recorded and used to estimate natural frequency (Hz) (Baker et al., 1998).

2.3. Statistical analyses for A and n

The data bases for A and n across experiments were unbalanced in terms of the treatments (combinations of genotypes, crop population densities, and developmental stages at which measurements were performed). A Linear Mixed Model Analysis using REML (residual maximum likelihood) (Multi-environment/Meta-analysis) was implemented on GenStat® (2007) for Windows™ to establish the significance and relative importance of the various factors and their interactions. Fixed effects were taken to be

G (genotype), D (density), S (developmental stage) and the double and triple interactions between these factors, while random effects were E (experiments) (Sposaro et al., 2008; Hall et al., 2010) and the E × replicate interaction. The REML analysis for the fixed effects generates the Wald Statistic which, divided by the appropriate degrees of freedom, has an F distribution. Resulting F-values and their probabilities (p) are similar to those generated by ANOVA, and can be interpreted in the same way.

3. Results

3.1. Plant area loaded by wind gusts (A) and plant natural frequency (n)

Between R2 and R4.9 the position of the capitulum was similar across all genotypes used, corresponding to that shown in Fig. 1d (data not shown). By contrast, between R5 and HM (harvest maturity) CF29 and V70597 had erect capitulae (Fig. 1e), while those of Zenit hung down and were covered by the uppermost leaves of the canopy (Fig. 1f) (data not shown). In decreasing order of importance, developmental stage, crop population density and genotype had significant effects on A (Table 1). Two-way and three-way interactions, although significant, were of relatively little importance (in terms of their relative contribution to total non-error variance). Measurements of A were not performed at all stages of crop development in every experiment, but the composite pattern emerging from Fig. 2a–c, is for a crop sown at low density, is one of an increase in A between R2 and R5.9 and a fall between R8 and harvest maturity. Increased crop population density tended to flatten the initial increase, but the terminal fall, although attenuated, was still evident.

There were significant differences in n between developmental stages (S) and genotypes (G) (Table 1). Developmental stage was the fixed effect which contributed most to the total variance, with genotype having a much smaller (albeit significant) influence. There were no significant effects of crop population density, but the stage by density interaction was significant.

Although the records of the dynamics of n covering all five developmental stages between R2 and HM was restricted to Zenit at 5.6 pl m^{-2}, the composite picture emerging from Fig. 2d–f is a decrease in n between R2 and R5.9, relative stability between R5.9 and R8, followed by a final increase to values similar to those of R2. Given the dominant contribution of "S" effects to the total non-error variance for n (Table 1), together with only small (albeit significant) contributions to non-error variance of G and the $D \times S$ interactions to non-error variance, we judged it reasonable to suppose that the dynamics of n found for Zenit at 5.6 pl m^{-2} will approximate crop behaviour across a broad range of conditions. The unbalanced nature of the data sets exhibited in Fig. 2d–f also indicated that a deeper exploration of the small contributions of G and $D \times S$ effects would not be appropriate.

4. Model development

4.1. Modelling the stem base-bending moment

Field observations of crop behaviour under gusty conditions during three seasons of experiments showed that the sunflower shoot behaves, like wheat and barley, as a damped harmonic oscillator. Consequently, the function used for calculating the wind-induced base-bending moment of the sunflower shoot (B) was based on that developed by Baker (1995) for wheat:

$$B = \frac{1}{2}\rho A C_d h_T V_g^2 \left(1 + \frac{g}{(2\pi n)^2 h_T}\right)\left(1 + e^{-\pi\xi}\frac{\sin(\pi/4)}{\pi/4}\right) \quad (1)$$

where ρ is the density of air (1.2 kg m^{-3}), A the area that captures the energy of wind gusts, C_d the drag coefficient of A, h_T the height of the shoot at which the wind acts (point of application of the wind), V_g the gust speed (m s^{-1}), n the shoot natural frequency (Hz), g the acceleration due to gravity (9.81 m s^{-2}) and ξ the shoot damping ratio.

In keeping with the work of Finnigan (2000) it is assumed that the top one-third of the plant experiences significant wind loading. Hence the point of application of wind loading is assumed to be $5h/6$, where h is the height of the plant. This differs from the wheat model which assumes the point of application is at the height of the centre of gravity of the stem.

Unfortunately little information is available concerning the appropriate value for the drag coefficient (C_d) of sunflower. A value of 0.5 was chosen from engineering literature (Massey, 1990) based on values of idealised objects of equivalent shape subjected to wind velocities similar to those observed in this study.

The value of the damping ratio (ξ) chosen (0.08) is similar to that obtained from a detailed investigation of the dynamics of wheat (Sterling et al., 2003).

It is acknowledged that the values of both the drag coefficient and the damping ratio are estimates and as such are somewhat uncertain and should be treated with care. Notwithstanding the assumptions involved, the values adopted are considered sufficiently accurate for the purposes of the current work.

4.2. Calculation of root (B_R) and stem (B_S) failure moments

Root failure moment (B_R) is estimated from the relationship between B_R (N m) and plant anchorage (sd^3) strength (N m), where s is the shear strength (N m^{-2}), measured at successively deeper planes at 5 cm increments over the 0–20 cm soil depth, using an E-285 Pocket Vane Shear Tester (Humboldt Mfg Co., IL, USA). Samples needed to determine soil water content (g/g) were also taken at 5 cm intervals to a depth of 20 cm, and d (m) is the root plate diameter of a root-lodged plant found by Sposaro et al. (2008) (their Fig. 4). This relationship ($B_R = 0.2382$ sd^3; $R^2 = 0.812$, $P < 0.025$) is based on measurements made at three developmental stages, in

Table 1
Components of the variance table for REML for fixed effects: genotypes (G), plant densities (D, 3–5.6–10 y 16 plants m^{-2}), developmental stages (S) and the respective interactions for the area loaded by wind gusts (A) and plant natural frequency (n). Values in brackets under each F-value indicate the proportion of non-error variances in each response variable explained by the fixed effects and their interactions.

Fixed effects							
F	G	D	S	G × D	G × S	D × S	G × D × S
A	23.32**	51.75**	99.21**	2.49*	6.69**	3.9**	2.46**
	(6.6)	(22.2)	(56.5)	(1.8)	(3.8)	(5.6)	(3.5)
n	12.35**	2.4 NS	166.88**	0.45 NS	2.26 NS	6.05**	0.52 NS
	(3.3)	(0.6)	(91)	(0.12)	(1.23)	(3.3)	(0.28)

NS: non-significant.
* P values indicated as <0.05.
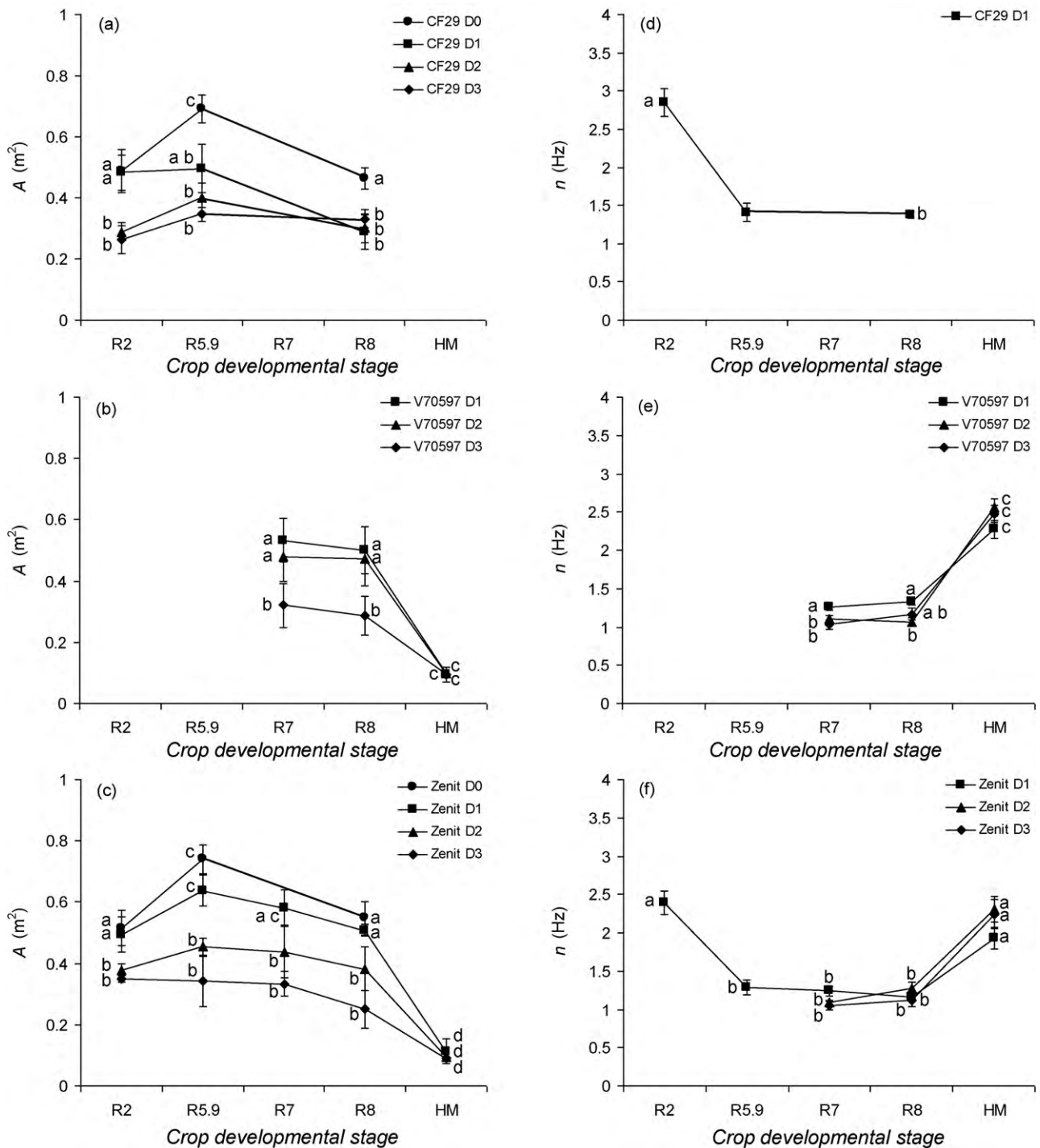** P values indicated as <0.001.

Fig. 2. Area loaded by wind gusts (A, m^2) (a–c) and plant natural frequency (n, Hz) (d–f) for CF29, V70597 and Zenit, between R2 and harvest maturity (HM) for plants growing at four plant densities, D0: 3 plants m^{-2}; D1: 5.6 plants m^{-2}; D2: 10 plants m^{-2}; D3: 16 plants m^{-2}. Three experiments were used for panels a (E1, E2 and E3 from Sposaro et al., 2008) and b (E1, E2 and E3 from Hall et al., 2010); six experiments were used for panel c (from Sposaro et al., 2008 and Hall et al., 2010); Two experiments were used for panels a (E1 and E2 from Sposaro et al., 2008) and b (E1 and E2 from Hall et al., 2010); four experiments were used for panel c (first two seasons from Sposaro et al., 2008 and Hall et al., 2010). Error bars indicate +/− one standard error (with 3 replicates) Different letters next to symbols indicate significant ($p < 0.05$) differences across crop population densities and developmental stages for each hybrid.

experiments conducted at two sites, over three years and involving two genotypes (CF 29 and Zenit) sown at four crop population densities. In the model B_R is calculated using Eq. (2):

$$B_R = k_1 \mathrm{sd}_3 \tag{2}$$

where k_1 is 0.24, and s assumes values which are dependent on soil texture (0.12991 kg cm^{-2}: clay soil, i.e., FAUBA; 0.12081 kg m^{-2}: coarse soil, VT).

Stem failure moment (B_S) was estimated using a function fitted to the pooled data obtained by Hall et al. (2010). The relationship between B_S and the thickness of the stem epidermis + cortex ($Ep + Co$) (m) for the pooled data could be described by a single linear function that integrated two different environments, two genotypes (V70597 and Zenit: resistant and susceptible to stem lodging respectively), four crop population densities, and three development stages during grain filling measurements (Fig. 3). Because the
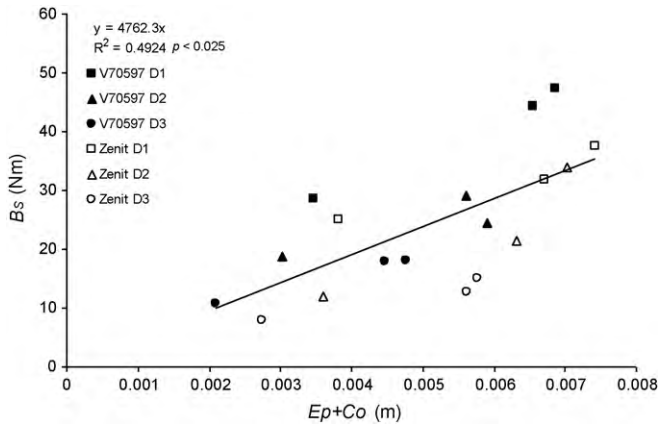
Fig. 3. Relationship between B_S (stem failure moment) and the thickness of the epidermis plus cortex tissues ($Ep + Co$) close to the base of the stem (data from Hall et al., 2010). Measurements performed on stay green (V70597, solid symbols) and Zenit (open symbols) grown at 5.6 (D1), 10 (D2) and 16 (D3) pl. m^{-2} at three different development stages between mid-grain fill and harvest maturity. The fitted function is significant ($p < 0.025$) and is forced through the origin.

sunflower stem functions, in mechanical terms and during the grain filling phase, somewhat like a hollow cylinder (Hall et al., 2010) similar to species with true hollow stems such as wheat and barley (Berry et al., 2003a,b, 2006), B_S was estimated from $Ep + Co$ using:

$$B_S = k_2[Ep + Co] \qquad (3)$$

where k_2 is 4762.3 Nm m^{-1} and $[Ep + Co]$ is the thickness of the epidermis plus cortex tissues at 15 cm from the base of the stem. It should be noted that Hall et al. (2010) found (small but significant) genotype differences for this relationship between V70597 and Zenit. In the model, for reasons of simplicity, we have preferred to use a single relationship.

4.3. Estimation of root (V_{gR}) and stem (V_{gS}) failure wind speeds

Lodging risk is calculated in terms of the minimum wind speed required to cause stem or root lodging. These are referred to as the stem failure wind speed (V_{gS}) and root failure wind speed (V_{gR}). These are calculated by combining and rearranging Eqs. (1)–(3), resulting in:

$$V_{gR} = \sqrt{\frac{2B_R}{(\rho A C_d h_T)\left(1 + \frac{g}{(2\pi n)^2 h_T}\right)\left(1 + e - \pi\xi \frac{\sin(\pi/4)}{\pi/4}\right)}} \qquad (4)$$

and

$$V_{gS} = \sqrt{\frac{2B_S}{(\rho A C_d h_T)\left(1 + \frac{g}{(2\pi n)^2 h_T}\right)\left(1 + e - \pi\xi \frac{\sin(\pi/4)}{\pi/4}\right)}} \qquad (5)$$

A flow chart of the stem or root lodging risk assessment procedure used in the model is given in Fig. 4. The aim is to calculate the root or stem failure wind speed using as variables stem and soil–root system characteristics. These variables can be measured and provided by the user or can be derived from information contained in Sposaro et al. (2008) and Hall et al. (2010) or presented in this paper.

5. Model validation

5.1. Experimental validation trials

During 2006–2007 season, four meteorological stations (Vantage Pro2^{TM}, Davis Instruments Corp. 3465 Diablo Ave. Hayward,
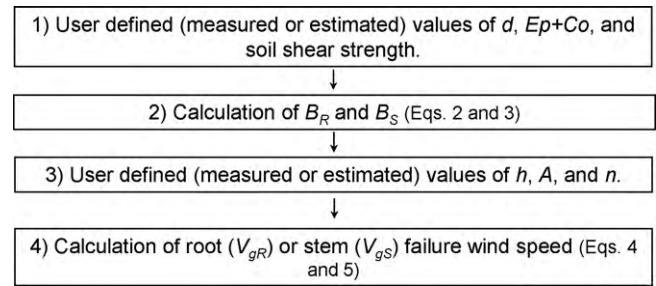

Fig. 4. Flow chart of the method used to estimate root or stem failure wind speed.

CA 94545, USA) were installed at four different locations, chosen to maximise the probability of root or stem lodging and ensure daily surveillance: Faculty of Agronomy, University of Buenos Aires (FAUBA) (34°35′ S, 58°29′W); Advanta Semillas Research Centre, Venado Tuerto (VT), Argentina (33°41′S, 61°57′W); Daireaux, Buenos Aires (36°36′S, 61°45′W); General Pico, La Pampa (35°40′S, 63°45′W). At FAUBA a meteorological station was also installed during 2005–2006 season and data generated in this season also contributed to the validation exercise. The stations were sited approximately 1 m above the sunflower canopy in the middle of the experimental plot avoiding any interference of trees or buildings, and registered rainfall, and wind speed and direction.

At each site, a randomized complete block trial with 3 replicates was established using 3 hybrids (CF29, root lodging resistant; V70597, stem lodging resistant; Zenit, root and stem lodging susceptible) sown at each of four crop population densities (3, 5.6, 10 and 16 plants m^{-2}). Plots were six rows (spaced at 0.7 m) by 6 m long. After each storm that produced lodging, the proportion of root or stem-lodged plants was determined, giving rise to a lodging index that ranged between 0 (no lodging) and 1 (the entire plot lodged).

The wind gust that produced stem lodging was assumed to be the maximum occurring in the 24 h prior to the observation of the event, the wind speed that produced root lodging was assumed to be the maximum occurring in the 24 h prior to the observation of the event after an amount of rain sufficient to saturate the upper 20 cm of soil that had fallen in the 48 h prior to the event (i.e., a strong gust of wind that preceded the accumulation of sufficient rainfall would not be considered). After a root or stem lodging event the plant variables required as inputs to the model (except n) were measured in the lodged plots only on the lodged plants (10 per plot in the 4 central rows) and in the un-lodged plots the variables were measured on 10 un-lodged plants in the 4 central rows. When the plot was partially lodged the variables were measured on lodged (10 plants) and un-lodged plants (10) in the four central rows. Soil shear strength values were estimated from soil texture and natural frequency values were interpolated as a function of crop development stage (Fig. 2). Measurements and estimates of the variables were used to calculate root (V_{gR}) and stem (V_{gS}) failure wind speeds, and these contrasted with observed wind speeds.

5.2. Results of validation trial

Four storms that caused root lodging were registered: 30/01/05, 17/12/06 (this lodging occurred at a neighbouring experimental plot [Hybrid 1] at FAUBA and was recorded), 03/03/2007 at FAUBA and 01/12/06 at VT. Stem lodging was registered on 02/03/2007 at FAUBA.

The model proved to have good predictive ability: for 14 of the 15 treatments in which lodging took place the observed maximum gust wind speed was always greater than the predicted failure wind speed; while for 8 out of the 10 treatments in which lodging did not occur, the observed wind speed was less than the predicted

Table 2
Lodging index, observed and predicted (mean ± 1 standard error, with 3 replicates, 10 plants per plot were used to measure model variables) root or stem failure wind speed, and type of lodging (R, root; S, stem) for the lodged plots at different locations (FAUBA and Venado Tuerto [VT]), crop population densities, dates of lodging and developmental stages (Schneiter and Miller (1981) scale; HM: harvest maturity). Horizontal dotted lines separate between lodging events.

Hybrid	Crop population density (pl. m^{-2})	Date and development stage	Location	Type of lodging exhibited in event[a]	Lodging index	Observed failure wind speed (m s^{-1})	Predicted failure wind speed (m s^{-1})
V70597	5.6	30/01/05:R2	FAUBA	R	0.5	14.7	6.6 ± 0.7
Zenit	5.6	30/01/05:R2	FAUBA	R	0.8	14.7	5.7 ± 0.56
CF29	5.6	30/01/05:R2	FAUBA	R	0	14.7	14.4 ± 0.06
Zenit	3	01/12/06:R3	VT	R	0.3	13	7.4 ± 0.77
Zenit	5.6	01/12/06:R3	VT	R	0.37	13	6.1 ± 0.65
Zenit	10	01/12/06:R3	VT	R	0.6	13	5.6 ± 0.48
Zenit	16	01/12/06:R3	VT	R	0.85	13	4.3 ± 0.22
CF29	3	01/12/06:R3	VT	R	0	13	25.2 ± 1.22
CF29	5.6	01/12/06:R3	VT	R	0	13	16.7 ± 0.85
CF29	10	01/12/06:R3	VT	R	0.05	13	12.1 ± 0.27
CF29	16	01/12/06:R3	VT	R	0.05	13	11.5 ± 0.69
Hybrid 1	4.8	17/12/06:R6	FAUBA	R	1	14.8	6.1 ± 0.52
Zenit	3	03/03/07:HM	FAUBA	R	0	8.3	8.8 ± 0.78
Zenit	5.6	03/03/07:HM	FAUBA	R	0.3	8.3	7 ± 0.46
Zenit	10	03/03/07:HM	FAUBA	R	0.5	8.3	2.6 ± 0.25
Zenit	16	03/03/07:HM	FAUBA	R	0.95	8.3	2.5 ± 0.24
CF29	3	03/03/07:HM	FAUBA	R	0	8.3	12.7 ± 0.9
CF29	5.6	03/03/07:HM	FAUBA	R	0	8.3	10.9 ± 0.57
CF29	10	03/03/07:HM	FAUBA	R	0.05	8.3	8.6 ± 0.21
CF29	16	03/03/07:HM	FAUBA	R	0.1	8.3	7.5 ± 1.2
Zenit	5.6	03/03/07:HM	FAUBA	S	0	8.9	9.9 ± 0.39
Zenit	10	03/03/07:HM	FAUBA	S	0.95	8.9	5.3 ± 0.61
Zenit	16	03/03/07:HM	FAUBA	S	0.5	8.9	5.9 ± 0.65
V70597	5.6	03/03/07:HM	FAUBA	S	0	8.9	8.7 ± 0.3
V70597	10	03/03/07:HM	FAUBA	S	0	8.9	8.9 ± 0.48
V70597	16	03/03/07:HM	FAUBA	S	0	8.9	8.9 ± 0.66

[a] Type of lodging observed in each event is indicated, independently of whether lodging occurred for a given treatment (hybrid × density combination).

failure wind speed (Table 2). Importantly, the predictions of the model recreated the differences in lodging susceptibility between hybrids and crop population densities reported in Sposaro et al. (2008) and Hall et al. (2010). In the case of root lodging root failure wind speed diminished when crop population density increased and CF29 needed higher failure wind speeds than Zenit.

The relationship between lodging index and the difference between predicted failure wind speed and observed wind speed (Fig. 5a and b) shows that the model could accurately and quantitatively assess the risk of root/stem lodging events in the field.

6. Sensitivity analysis of model variables

A sensitivity analysis was performed in order to explore the response of predicted failure wind speed to changes of each separate variable of the model and to establish their relative importance in determining lodging susceptibility. To do this the values of each variable were varied independently across its entire observed range in Sposaro et al. (2008), for stem lodging, and Hall et al. (2010) for root lodging (across hybrids, crop population densities, and developmental stages). Failure wind speeds were calculated for each decile interval across the range of each variable, using values for the remaining variables fixed at the mid-point (5th decile) of their ranges.

Root failure wind speed was most affected by changes in root plate diameter (d), and varied in a roughly symmetrical fashion around the mid-point value (Fig. 6a). The area loaded by wind gusts was an important variable for both root (Fig. 6a) and stem (Fig. 6b) lodging, but its influence was asymmetrical across its range, such that its effects were only predicted to be important for values of A below the mid-point of its range. Stem failure wind speed (Fig. 6b) was fairly sensitive to changes in the thickness of epidermis plus cortex tissues ($Ep + Co$), and this effect tended to be greatest in the lower half of the range of this variable. Although variations in height (h) and natural frequency (n) produced changes in root and stem

failure wind speeds these were not important. The mean value for root failure wind speed (V_{gR}) (7.8 m s^{-1}) was lower than stem failure wind speed (V_{gS}) (8.5 m s^{-1}).

7. Discussion

This study documents, for the first time in sunflower, the development and validation of a mathematical model for calculating root and stem failure wind speeds. The model draws strongly on predecessor models for wheat and barley (Baker et al., 1998; Berry et al., 2003a, 2006), but incorporates sunflower specific values for relationships such as root failure moment/plant anchorage (Sposaro et al., 2008) and $B_S/(Ep + Co)$ (Hall et al., 2010 and Fig. 3). Model formulation also required the development of procedures for the estimation of the area of the plant loaded by wind gusts and the documentation of the dynamics of this variable and its responses to crop development and management factors such as crop population density (Fig. 2). The sunflower model also covers a broader developmental window (R2 to harvest maturity) than the cereal models, which are restricted to the post-anthesis phase. This allows the sunflower model to incorporate the R2 to anthesis phase, during which the species is known to be susceptible to root lodging (A. de la Vega, pers. comm.).

Formulation of the model required adopting some estimates and/or simplifications. Important among these were the portion of the plant area loaded by wind gusts (Fig. 1), the assumption that the point of application of this wind load is 5h/6, and the use of a genotype-insensitive $B_S/(Ep + Co)$ relationship (Fig. 3). Although all these simplifications merit further investigation, the skill of the model in predicting root and stem lodging (Table 2 and Fig. 5) is certainly encouraging, especially for root lodging. In particular, the model proved effective in reproducing the effects of crop population density, developmental stages and hybrid on root and stem lodging susceptibility found by Sposaro et al. (2008) and Hall et al. (2010). It is also worth noting that this model is probably the one
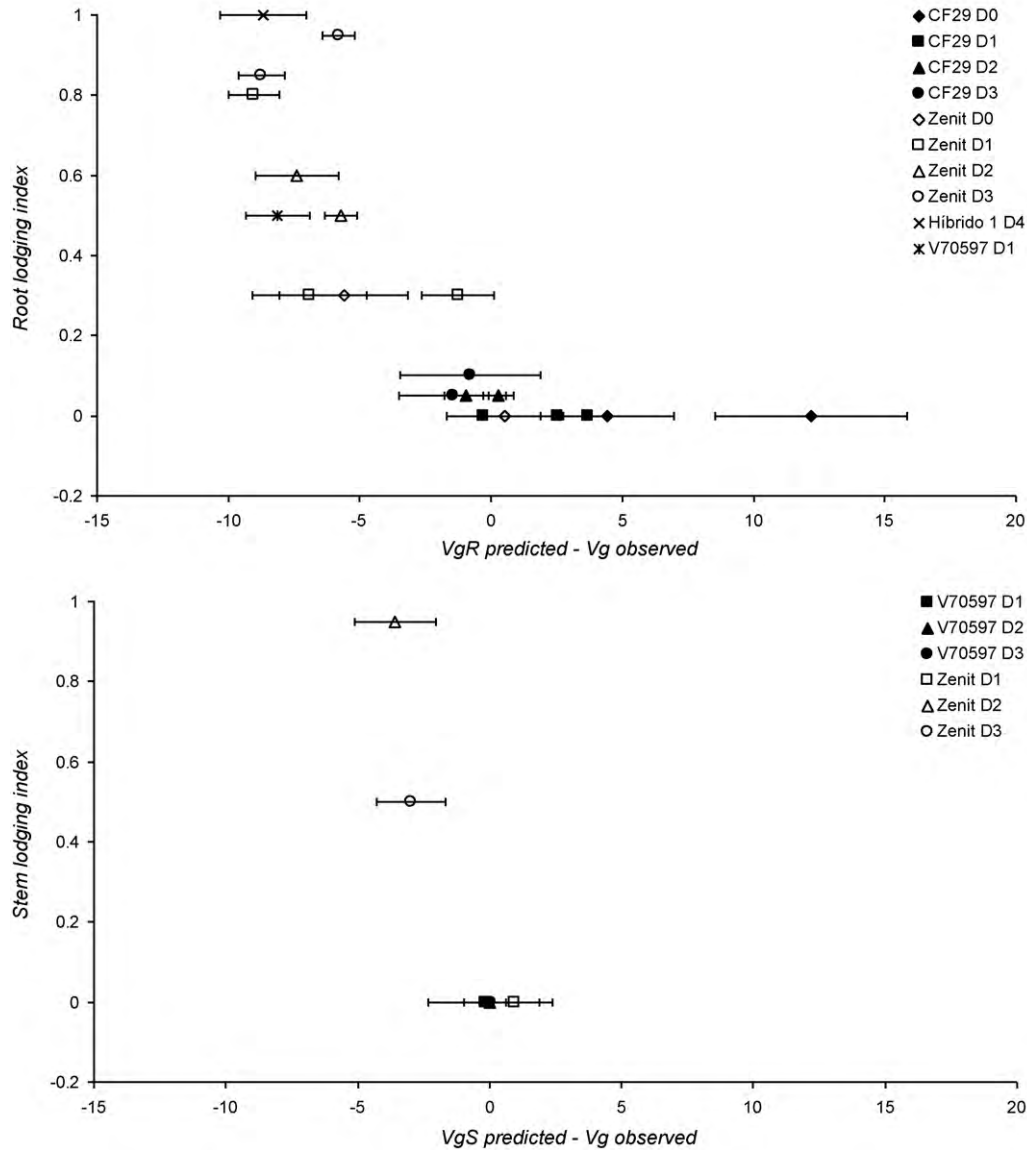
Fig. 5. Relationship between root (a) or stem (b) lodging index and the difference between predicted and observed root (V_{gR}) or stem (V_{gS}) failure wind speed for each lodging event. D0: 3 plants m^{-2}; D1: 5.6 plants m^{-2}; D2: 10 plants m^{-2}; D3: 16 plants m^{-2}. Horizontal bars indicate ± 1 standard deviation ($n = 10$).

that has been subjected to the most intensive validation under field conditions. Using the data of Hall et al. (2010), who found genotype differences in the $B_S/(Ep + Co)$ relationship for the V70597 and Zenit hybrids, we performed a sensitivity analysis using their values of the slope of this relationship (5635 N for V70597 and 4086 N for Zenit). Use of these values produced estimates of V_{gS} (m s^{-1}) which represented +8.77% (for V70597 slope) and −7.37% (for Zenit slope) of the values reported in Fig. 6b for all variables at the lower end of the observed range (i.e., the portion showing the greatest change in response to the slope of the $B_S/(Ep + Co)$ relationship) with no change in the response patterns and relative weight of these variables. These, relatively modest, changes suggest that the model is not excessively sensitive to changes in the $B_S/(Ep + Co)$ relationship, although further inter-genotype comparisons are required to establish whether the differences between V70597 and Zenit are fully representative of the intraspecific variation for this relationship (Hall et al., 2010). Further research may, in fact, support the use of different functions for different densities and different hybrids. Other model variables that require further investigation include the drag coefficient and the damping ratio. The model, with

appropriate inputs from historical meteorological records and soil properties, could be used as a tool for predicting risks for root or stem lodging in sunflower across regions. However, it is important to note that more work is needed to quantify the effects of husbandry practices (tillage type, seed rate, sowing date, fertilization, etc.) and their interactions with environmental factors (soil type, rainfall and wind speed) on the critical plant variables.

The sensitivity analysis (Fig. 6) showed that the most important variables determining susceptibility to lodging were root plate diameter (d), thickness of epidermis plus cortex (Ep + Co), and the area expected to be loaded by wind gusts (A). The aims for breeders to improve root/stem lodging seem to be these three variables. López Pereira et al. (2004) showed that grain yield of experimental sunflower crops, protected from lodging and disease, increased with crop population density up to populations almost three times denser than those usual in current commercial practice (4–6 plants m^{-2}) but in denser crops plants are more likely to lodge. By the other hand, Sposaro et al. (2008) and Hall et al. (2010) showed that at higher crop population densities root and stem lodging susceptibility increased due to a reduction of root
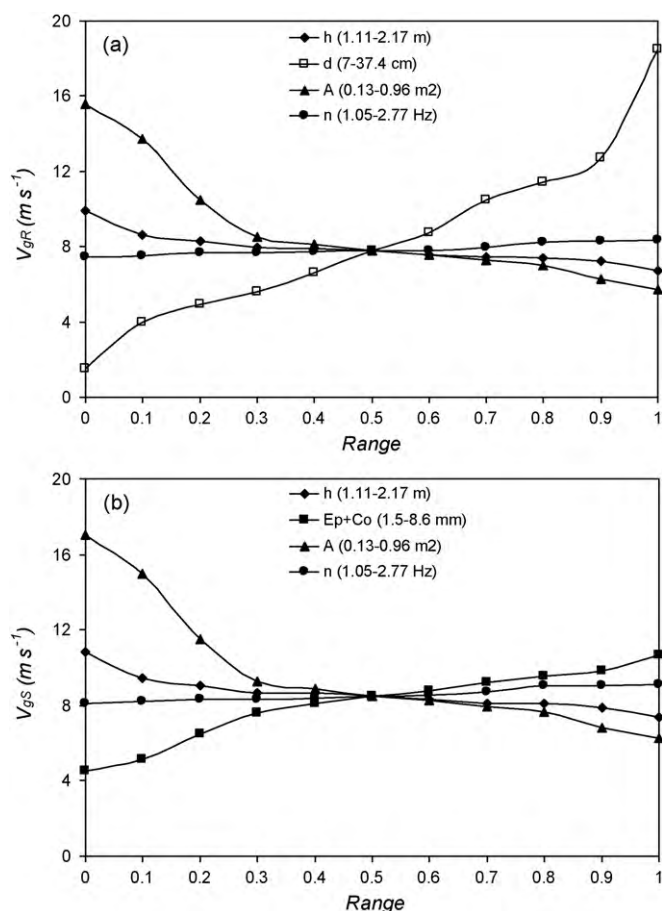
Fig. 6. Sensitivity analysis for model variables. Variations in root (V_{gR}) (a) or stem (V_{gS}) (b) failure wind speed (m s^{-1}) in response to changes in the values of model variables between 0 (minimum) and 1 (maximum). h: plant height; d: root plate diameter; $Ep + Co$: thickness of epidermis plus cortex; A: area expected to be loaded by wind gusts; n: natural frequency. Calculations were performed at decile intervals across the full observed range (indicated in brackets next to symbol codes) for each variable and are centred on the observed mean value (i.e., 0.5) for each variable.

plate diameter and thinner stem walls. This indicates that plant breeders should select for wider root plates and thicker stem walls, in normal or denser crop densities, in order to improve sunflower for lodging resistance and tolerance to high crop population densities. Selection for reduced A would likely result in yield penalties due to reduced interception of radiation, and is therefore unlikely to be an option worth pursuing. Analyses using the wheat and barley models (Berry et al., 2003a, 2006) showed that the most important variables for lodging tolerance were those related to root and stem structure, but A in these species had little relative importance in determining lodging susceptibility. It is notable that changes in plant height (h) did not generate great variations in failure wind speeds for sunflower (Fig. 6). Our analyses suggest that, other factors being equal, a tall hybrid is not necessarily more prone to lodging. This may arise because of the over-riding importance of other characteristics such as root plate diameter and thickness of epidermis plus cortex in determining susceptibility to lodging.

Berry et al. (2003a) calculated a stem failure wind speed of 16.5 m s^{-1} and root failure wind speed of 8 m s^{-1}, for high crop population density wheat. In another study (Berry et al., 2006) calculated root failure wind speeds of 24.6 and 41.1 m s^{-1} for wheat and barley respectively at a low crop population density, diminishing to 15.8 and 23 m s^{-1} at high crop population density. Observed and predicted sunflower wind failure speed values (Table 2) were lower than those for wheat and barley, suggesting that this crop is

more susceptible to lodging. There are several potential contributing factors underlying this difference. A in sunflower (0.13–0.96 m^2, Fig. 3) is much larger than wheat (0.006–0.0012 m^2, Baker et al., 1998); and the slope of the root failure moment/root anchorage relationship is much smaller in sunflower (0.24, Sposaro et al., 2008) than wheat (0.39, Crook and Ennos, 1993; 0.43, Baker et al., 1998) and barley (0.58, Berry et al., 2006). The observed range of natural frequency (n) for sunflower was higher (1.05–2.77 Hz, Fig. 3) than that reported for wheat (0.4–1.8 Hz, Berry et al., 2003a). While this indicates that sunflower shoots are more springy than those of wheat, something which will reduce leverage for a given wind gust and area of plant loaded by wind, the sensitivity analysis showed that n, across its observed range in our experiments, had almost no effect on wind failure speeds (Fig. 6). Median shoot and root failure speeds for sunflower were very similar, and the ranges of these two variables across the observed ranges of their most important determining variables were also fairly similar (Fig. 6). This similarity of wind failure speeds contrast with that of cereals, in which stem failure wind speed can be of the order of twice the root failure wind speed (Berry et al., 2003a).

To summarize, we have successfully adapted previous models for lodging in cereals to the sunflower crop, and the sunflower model has been shown to perform well under field conditions. Analyses using the model, which provides a systemic framework that can handle the multiple determinants of lodging, have served to establish the relative importance of the various plant variables critical to the determination of root and stem lodging susceptibility, providing useful guidelines for breeders and agronomists. In addition, the exercise has served to pinpoint a number of issues that require further investigation.

Acknowledgements

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