Peduncle breaking resistance: a potential selection criterion to improve lodging tolerance in oat

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ARTICLE

Peduncle breaking resistance: a potential selection criterion to improve lodging tolerance in oat

A. Nakhforoosh, S. Kumar, T. Fetch, and J. Mitchell Fetch

Abstract: Breeding for tolerance to lodging is an objective, but also a challenge, in oat (*Avena sativa* L.) breeding programs. A widely adopted method to assess breeding lines for tolerance to lodging is based on visual scoring of plant standability (1 = standing upright; 9 = completely lodged). The lack of sufficient lodging pressure due to weather or growing conditions often renders the visual scoring method ineffective. We present an alternative approach that allows selection for tolerance to stem lodging by screening for peduncle strength in the absence of lodging pressure. This approach also provides objective selection of lodging tolerance using a quantitatively measurable plant trait rather than subjective scoring of the lodged plants. Stem structural and mechanical properties of six oat cultivars with varying levels of lodging tolerance were tested at field experiments over 3 site-years under three nitrogen rates. Results suggested peduncle breaking resistance (PBR), measured below the panicle, as a potential selection criterion for stem strength and therefore lodging tolerance. Significant genetic variation among oat cultivars ($p < 0.01$) was observed for PBR, which was significantly correlated with the strength of all lower internodes in all environments ($R^2 > 0.73$, $p \leq 0.05$). This suggests that PBR provides a good estimation of the whole culm strength. Phenotyping of PBR can be easily integrated into breeding programs because of the ease of sampling and rapid measurement.

Key words: Avena sativa L., lodging tolerance, stem strength, oat breeding.

Résumé : Améliorer la tolérance à la verse est à la fois un but et un véritable défi pour ceux qui hybrident l'avoine (*Avena sativa* L.). Une méthode largement adoptée pour évaluer la tolérance à la verse des souches généalogiques consiste à leur attribuer visuellement une note selon le degré d'érection du plant (1 = érigé; 9 = totalement abattu). Cette méthode perd toutefois son efficacité quand les conditions climatiques ou de croissance n'exercent pas de pression suffisante pour que la verse apparaisse. Les auteurs proposent une nouvelle approche en vertu de laquelle on sélectionne la tolérance de la variété à la verse d'après la robustesse du pédoncule en l'absence des pressions à l'origine du problème. Cette méthode permet aussi de sélectionner de façon objective la tolérance à la verse d'après un caractère quantifiable, plutôt que par l'évaluation subjective des plants qui ont versé. Les auteurs ont examiné les propriétés structurales et mécaniques de la tige de six cultivars d'avoine de tolérance variable à la verse dans le cadre d'expériences sur le terrain pendant 3 années-sites, sous trois régimes d'amendement azoté. Les résultats indiquent que la résistance du pédoncule à la rupture (PBR — « peduncle breaking resistance »), mesurée sous la panicule, pourrait être un critère de sélection pour la robustesse de la tige, donc la tolérance à la verse. Les auteurs ont observé une importante variation génétique ($p < 0{,}01$) de PBR chez les cultivars d'avoine, variation qui présente une corrélation significative avec la robustesse des entrenœuds inférieurs, peu importe les conditions ($R^2 > 0{,}73$, $p \leq 0.05$). On en déduit que ce paramètre procure une bonne estimation de la robustesse du chaume. Intégrer le phénotypage de PBR aux programmes d'hybridation serait aisé, car ce paramètre se mesure rapidement et est facile à échantillonner. [Traduit par la Rédaction]

Mots-clés : Avena sativa L., résistance à la verse, solidité du chaume, amélioration de l'avoine.

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Introduction

Oat (*Avena sativa* L.) is an important food and feed crop worldwide. Canada is the world's largest exporter of oats with up to 60% of total oat production being exported (FAO 2017). Despite a decline in total acreage over the past two decades (1998–2017), Canadian production has remained stable due to a 40% yield increase (Statistics Canada 2019). The genetic yield improvement of oat cultivars has been attributed to increased disease resistance (Rines et al. 2006) and improved agronomic traits such as lodging tolerance.

Lodging, which is defined as permanent displacement of the plant shoots from their vertical stance (Pinthus 1974), is an important factor that limits yield potential and reduces grower profits (Berry 2019). Breeding for lodging tolerance is a major objective in oat breeding programs. Several methods have been proposed to evaluate lodging tolerance in the field (Murphy et al. 1958; Fouéré et al. 1995; Berry et al. 2003*a*; Kelbert et al. 2004*a*; Singh et al. 2019). The "snap test" is one method practiced by some breeders for quick and nondestructive assessment of lodging tolerance in the field (Murphy et al. 1958; Hess and Shands 1966). This test involves rating straw strength based on the force required to pull a handful of culms to a reclining position and the rapidity of the snap back response of culms upon release. This is a subjective method and creates user bias during field rating and selection. Another widely adopted method to assess breeding lines for tolerance to lodging is based on visual scoring of plant standability [1 = standing upright and (or) resistant; 9 = completely lodged and (or) susceptible]; however, the efficiency of selection based on this approach can be limited by the erratic occurrence of weather conditions (rain and wind) that cause lodging (Berry et al. 2003*b*, 2004; Kelbert et al. 2004*a*). Recently, utilization of unmanned aerial vehicles (UAVs) for field-based high-throughput phenotyping (HTP) has been successful in the evaluation of breeding lines for lodging tolerance in large nurseries with thousands of plots (Singh et al. 2019). Although UAVs provide quicker assessment compared with visual scoring, without conditions to induce lodging, image-based assessment for tolerance to lodging will have the same limitation.

Selection for traits associated with lodging tolerance provides a more efficient alternative to the popular visual scoring approach (Berry et al. 2000; Kelbert et al. 2004*b*). Trait-based breeding allows for the selection of tolerant lines regardless of weather or growing conditions and the absence of lodging, and it provides objective selection of lines using quantitatively measurable traits. Tolerance to lodging, however, is a complex trait (Keller et al. 1999; Berry et al. 2008; Singh et al. 2019) controlled by multiple plant characters such as plant height (Brown et al. 1980; Valentine et al. 1997; Kelbert et al. 2004*a*, 2004*b*; Piñera-Chavez et al. 2016*b*), basal internode strength, length and diameter (Berry et al. 2000, 2006; Tripathi et al. 2003; Kelbert et al. 2004*b*), stem wall width (Tripathi et al. 2003; Piñera-Chavez et al. 2016*b*; Mirabella et al. 2019), culm anatomy and chemical composition (Kong et al. 2013; Okuno et al. 2014), as well as mechanical properties and morphology of coronal roots (Mulder 1954; Crook and Ennos 1993; Easson et al. 1993, 1995; Berry et al. 2000). Reduced plant height has long been selected for in breeding programs, which has, through the development of semidwarf varieties, led to significant progress in reducing the risk of crop lodging (Cox et al. 1988; Berry et al. 2015; Hucl et al. 2015). Plant height can be assessed rapidly and effectively by direct measurement, molecular markers (Ellis et al. 2002), or HTP approaches (Hassan et al. 2019; Rebetzke et al. 2019); however, there is evidence demonstrating that yield potential in cereals is reduced by excessive shortening of plant height below an optimum, particularly under high temperature and drought stresses (Brown et al. 1980; Allan 1986; Richards 1992; Miralles and Slafer 1995; Flintham et al. 1997; Valentine et al. 1997). This limits the potential of using dwarfing genes to further increase tolerance to lodging (Berry 2019). Moreover, reduced plant height may not be a suitable character for dual purpose (forage and grain) cereals such as oat. Similarly, in organically managed systems, a relatively taller cultivar with increased competitive ability over weeds may be more desirable (Navabi et al. 2006). These all imply the necessity for consideration of other lodging-related traits as selection criteria. In contrast to plant height, integration of other lodging-related traits into breeding programs has been hindered by difficulties in ease of sampling and lack of tools capable of assessing thousands of plants or plots in a limited time (Kelbert et al. 2004*b*; Berry 2019).

Lodging in oat can either result from buckling of the lower internodes (stem lodging) or failure of the anchorage system (root lodging) (Mulder 1954). Susceptibility to stem lodging is determined by the morphological and mechanical characteristics of the basal internodes (Pinthus 1974). While new instrumentation has made rapid measurement of basal internode strength possible (Wu and Ma 2019), effective exploitation of this trait can be limited due to difficulties in sampling of basal internodes within the context of a breeding program. In contrast to basal internodes, sampling of peduncles is very convenient and is postulated to be a means to select for stem strength (strong basal internodes).

Strength of the peduncle below the oat panicle and its relation to basal internode strength have previously received no attention, although previous studies (e.g., Berry and Berry 2015) provided evidence of the strong correlation between strength characteristics of the first two basal internodes. Therefore, the present study tested the hypothesis that cultivars with a strong stem base, a key trait underlying tolerance to stem lodging, would have strong culms all along the stem length from base to peduncle. Due to the ease of sampling and measurement of peduncle breaking resistance (PBR) compared with that of the basal internode, this knowledge will allow breeders to enhance selection for tolerance to stem lodging in oat through screening for PBR, particularly in the absence of lodging pressure.

In the present study, six oat cultivars exhibiting varying lodging susceptibility (LS) were tested in different field conditions and with different nitrogen rates to (*i*) investigate the relationship between breaking resistance of oat peduncles and the strength of all culm internodes, (*ii*) evaluate genetic variation for PBR, and (*iii*) characterize the morphological and mechanical shoot and root traits related to lodging tolerance.

Materials and Methods

Plant materials

Six oat cultivars were chosen for their contrast in lodging tolerance. According to historical lodging data obtained from trials, known as Western Cooperative Oat Registration Trials (WCORT), or from provincial variety testing (e.g., Saskatchewan Seed Growers Association 2011, 2018), the selected cultivars were grouped as resistant (CS Camden, CDC Morrison, AC Morgan), intermediate (Leggett, HiFi), or moderately susceptible (CDC Sol-Fi).

Experimental design and field management

Field experiments were conducted at the Brandon Research and Development Centre (BRDC) in Brandon, MB, Canada (49°52′N, 99°58′W), in 2017 and 2018 and at the Canada-Manitoba Crop Diversification Centre (CMCDC) in Portage la Prairie, MB (49°57′N, 98°16′W), in 2018. The soil types were clay (sand:silt:clay of 13:42:45, organic matter 5.2%, and pH = 7.3) in Brandon and silty clay (sand:silt:clay of 7:53:40, organic matter 5.9%, and pH = 8.3) in Portage. The annual and long-term weather data for the tests in Brandon were sourced from a weather station at BRDC located approximately 4.3 km from the experimental farm. The weather data for the test in Portage were obtained from an Environment Canada weather station, located within 6.5 km of the experimental farm. The monthly accumulated precipitation and average temperature in relation to long-term averages for sites in Brandon (2017 and 2018) and Portage (2018) are shown in Figs. 1*a*–1*d*.

At the Brandon site, each experiment was a randomized complete block design in a split-plot arrangement with three replications. In 2017, the main plots consisted of three combinations of rate and timing of nitrogen (N, as urea) application: 40 kg N ha^{-1} (N_b) applied as base fertilizer at preplant and 40 kg N ha^{-1} at preplant plus 25 ($N_b + 25$) or 50 ($N_b + 50$) kg N ha^{-1} topdressed at the mid-tillering stage. For the experiment in 2018, nitrogen application treatments were 110 kg N ha^{-1} (N_b) applied in fall 2017 and 110 kg N ha^{-1} as base fertilizer plus 25 ($N_b + 25$) or 50 ($N_b + 50$) kg N ha^{-1} topdressed at the mid-tillering stage. In both years, six oat cultivars (CDC Morrison, CS Camden, AC Morgan, Leggett, HiFi, and CDC Sol-Fi) were the subplots.

The field experiment in Portage (2018) was carried out in a randomized complete block with the six above-mentioned oat cultivars and four replications. No excess nitrogen other than the base nitrogen fertilizer (60 kg N ha^{-1}) was used for this experiment because it was expected, due to historical experience, that lodging would naturally occur at this site.

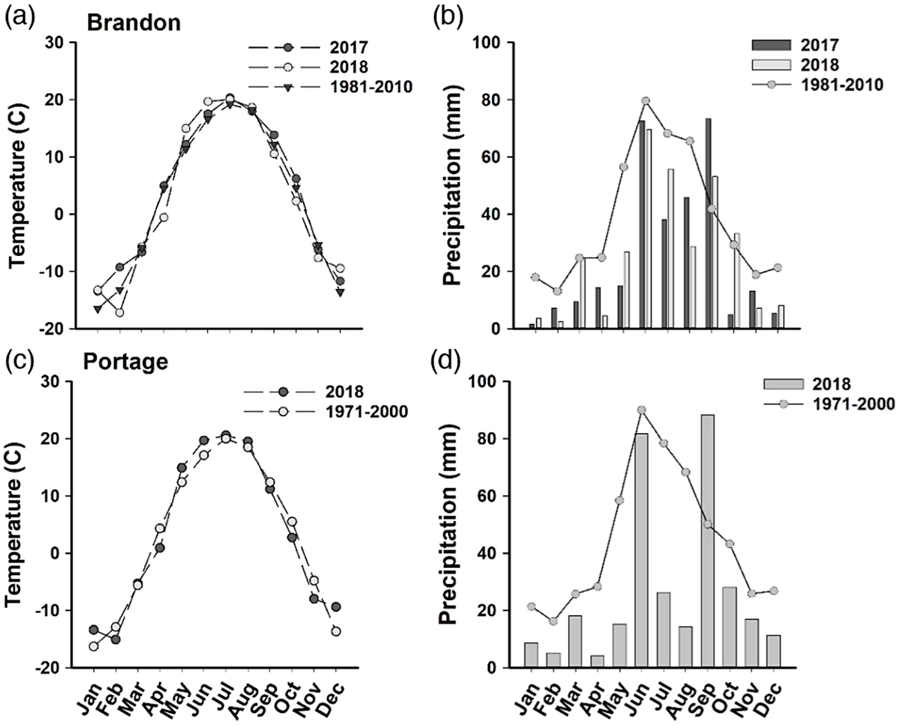
Field experiments were sown on 30 May 2017 and 17 May 2018 in Brandon and on 23 May 2018 in Portage. Seedbed preparation included disk plowing in the fall followed by 2–3 disk cultivations in the spring using a compact disk harrow. The base nitrogen, phosphorus, and potassium fertilizers were applied prior to seeding at levels recommended by soil tests. Plots were planted at a rate of 300 seeds m^{-2} with a plot size of 4.4 m^2 (five rows, 18 cm apart). Weeds and diseases were controlled with pesticides in accordance with the provincially recommended management practices. Following root and shoot sampling, experimental plots were irrigated with a linear irrigation system (2–3 events at 15–40 mm rates) between early grain filling and crop maturity (BBCH 71–89, Lancashire et al. 1991), to attempt to induce lodging stress.

Measurements

Stem structural and mechanical properties were measured on the largest shoot of eight randomly selected plants from each plot (Islam et al. 2007). Shoots were cut at the ground surface at late flowering to early grain filling (BBCH 69–71) when the crop is most susceptible to lodging (Fischer and Stapper 1987). Shoot fresh weight (FW), including leaves, stem, and panicle, was determined shortly after sampling. Plant height was measured as the distance from the plant base to the panicle tip. The height at the centre of gravity (HCG) of each main shoot was determined by balancing the shoot (leaves and panicle still attached) on a thin metal rod and recording the distance from the point of balance to the base of the shoot (van Delden et al. 2010). Shoot FW and HCG were not recorded for the test in 2017. Bending moment (BM) or self-weight moment was calculated as BM = FW × HCG (Islam et al. 2007).

After removing the leaves and leaf sheaths from the air-dried shoots, the shoots were cut into separate internodes, and the length and weight of all individual internodes of each shoot, from the basal internodes up to the peduncle, and the panicle were separately measured. The internode length was measured as the distance between the midpoint of its adjacent nodes. The internode diameter was measured using a digital caliper for all internodes in 2017, but only the second basal internode was measured in 2018. The internode diameter was the average of six measurements consisting of two measurements at right angles at three points along each

Fig. 1. The monthly mean temperature (*a*, *c*) and accumulated precipitation (*b*, *d*) in relation to long-term averages for Brandon (2017 and 2018) and Portage (2018), MB, Canada. The figure was prepared using the SigmaPlot version 13.0 (Systat Software, Inc., San Jose, CA, USA).



internode. Peduncle diameter was measured at 0.5 cm below the panicle neck node. Dry weight per unit area of internodes (mg cm^{-2}) was calculated as [weight/(length × diameter)]. As peduncle diameter noticeably tapers from the flag leaf node to the panicle node, peduncle dry weight per unit area was not measured.

The breaking resistance (Newton, N) of internodes was determined using a three-point bending tester, with the distance between the two fulcra of the tester set at 3 cm (van Delden et al. 2010). A pushing pressure was applied at an even rate at the midpoint of each internode using a digital force meter (AFG 100N, Mecmesin Ltd., Horsham, UK). The breaking resistance was considered as the maximum force leading to the internode buckling, which was identified by cracking noises. PBR was measured at 5 cm below the panicle neck node. Breaking resistance of all internodes of each culm was measured individually for two experiments in 2018, but only PBR was measured in 2017.

Assessment of LS for each plot was carried out by recording the lodging scores (*S*) visually detectable in each plot and the respective area of each plot affected for each score (*A*). The lodging score used the scale of 1 = no lodging (100% upright) to 9 = completely lodged (100% flat). Readings were expressed as scores between 1 and 9 based on the angle of lodging from the vertical axis. The LS for each plot was calculated following Caldicott and Nuttall (1979), with a minor modification, as LS = Σ (*S* × *A*). Lodging was observed and recorded shortly after initial lodging occurrences, but only final ratings taken at maturity were analyzed.

Tolerance to root lodging was determined only in 2017 through characterizing morphological properties of coronal roots of cultivars at the topsoil level. At full flowering (BBCH 65), two root samples were taken from the middle rows of each plot using a garden spade to a depth of 15 cm, with a soil surface area of about 144 cm^2 (12 cm × 12 cm). Root samples were placed in plastic bags to prevent desiccation and stored in a cold chamber at 4 °C before the roots were washed. The removal of soil from roots was facilitated by first immersing the root samples in tap water for about 1 h followed by careful washing through two stacked sieves (1.6 mm on top and 0.6 mm at bottom). After cleaning, roots were stored in 30% ethanol at 4 °C for subsequent root morphological analysis (total root length and diameter) by WinRhizo, an image-based root analyzer (Regent Instruments Inc., Québec, QC, Canada).

Statistical analysis

Analysis of variance (ANOVA) for individual experiments was performed on each trait to test the main (nitrogen and cultivar) and interaction effects using the PROC MIXED procedure in SAS version 9.2 (SAS Institute, Inc., Cary, NC, USA). Nitrogen level, cultivar, and their interaction were considered as fixed effects, whereas block effect was considered as random. The statistical significance of differences between means was determined using the least significant difference (LSD) at the critical level of significance of $p = 0.05$. The PROC REG and PROC CORR were used to assess the linear regressions and Pearson's correlations and Spearman's rank correlations, respectively, among the traits or among the environments for the same trait. All figures were prepared using the SigmaPlot version 13.0 (Systat Software, Inc., San Jose, CA, USA).

Results

Weather conditions

Figures 1*a*–1*d* illustrate the monthly accumulated precipitation and average temperature in relation to long-term averages for sites in Brandon (2017 and 2018) and Portage (2018). Although the mean air temperature during the two growing seasons was similar to the long-term normal temperature, the annual precipitation and its in-season distribution revealed that the 2017 and 2018 seasons were relatively dry at both sites. The annual precipitation was 20% (Brandon 2017), 31% (Brandon 2018), and 37% (Portage 2018) less than normal annual precipitation in Brandon (461.7 mm) and Portage (532.5 mm). Comparison of total rainfall during June and July (the time span from stem elongation to full heading) with long-term normal rainfall showed less reduction in June; however, there were notable declines in July precipitation (44% Brandon 2017, 18% Brandon 2018, and 49% Portage 2018).

Basal internode characteristics

The ANOVA results for the basal internode characteristics at 3 site-years are presented in Tables 1–3. The first basal internodes had variable lengths, sometimes not long enough to enable breaking resistance to be measured (Berry et al. 2000); therefore, the results from the second basal internode are discussed and hereafter referred to as basal internode. Averaged across cultivars, the basal internodes were longer, heavier, and wider but had lower dry weight per unit area at the Portage location (Tables 1–3). Significant varietal differences were observed for all characteristics of the basal internode in each trial. Averaged over 3 site-years, CDC Sol-Fi and Leggett had the longest (10.3 cm) basal internode lengths, while CS Camden (7.7 cm) and CDC Morrison (8 cm) had the shortest basal internodes. AC Morgan had the thickest basal internode, contrasted with Leggett, which had the thinnest basal internode in all three trials (Tables 1–3). Averaged across the three tests, AC Morgan and CDC Sol-Fi contrasted with CS Camden and CDC Morrison in accumulating more biomass in the basal internode. AC Morgan had the highest dry weight per unit area of basal internode in each of the three experiments (Tables 1–3). The basal internode characteristics, i.e., length, weight, diameter, and dry weight per unit area, were not significantly intercorrelated.

Breaking resistance: peduncle vs. culm internodes

There was a significant genotypic variation for the breaking resistance of all internodes measured at all locations (Tables 1–3). Averaged across genotypes, all culm internodes appeared to be stiffer in Brandon compared with Portage. AC Morgan clearly had the strongest internodes all along the culm from basal internodes up to peduncle. CDC Morrison, with the second strongest internodes and peduncle, significantly contrasted with the rest of the cultivars, which had relatively weaker culms (Tables 2 and 3).

In 2018, breaking resistance decreased from basal to upper internodes such that PBR was respectively 61% and 53% less than that of the basal internodes in Brandon and Portage (Tables 2 and 3). Breaking resistance of the basal internode was significantly correlated with its dry weight per unit area (Fig. 2), which is composed of length, weight, and diameter, but not with any of these internode characteristics individually. For the experiment in Brandon in 2017, PBR was significantly correlated with dry weight per unit area of all lower internodes (Fig. 3*a*). In 2018, PBR was highly correlated with breaking resistance of all lower internodes in Brandon (Fig. 3*b*) and Portage (Fig. 3*c*) in 2018. Individual internodes from stem base up to the peduncle were significantly and positively intercorrelated in terms of breaking resistance (2018) and (or) internode dry weight per unit area (2017) ($R^2 > 0.72$, $p < 0.05$). Breaking resistances of peduncles were highly correlated among tests over 3 site-years, suggesting a nonsignificant genotype × environment interaction ($R^2 > 0.66$, $p < 0.05$); however, analysis of Spearman's rank correlation revealed crossover interactions or changes in the ranking of cultivars for PBR in different tests ($0.83 < r_s < 0.49$, $0.36 < p < 0.06$). The most variability in ranking of PBR within the three tests was found for CS Camden and CDC Sol-Fi.

Shoot and root lodging-related characters

The ANOVA showed significant differences among the cultivars for all structural and morphological characteristics of shoot and root in each trial. All cultivars grew taller in Portage compared with Brandon (Tables 1–3). Across 3 site-years, CDC Sol-Fi (110 cm) and CDC Morrison (95 cm) were the tallest and shortest varieties, respectively. In 2018, the results for HCG were similar to that observed for plant height (Tables 2 and 3), and significant correlations were found between plant height and HCG at both sites (Brandon 2018: $R^2 = 0.86$, $p < 0.01$; Portage: $R^2 = 0.70$, $p < 0.05$). In 2018, the total shoot FW (leaves, stem, and panicle) and BM of all cultivars in Portage were higher than those in Brandon (Tables 2 and 3). In each experiment, AC Morgan had the significantly heaviest shoots and largest BM.

There was significant variation in topsoil root properties of the cultivars as assessed in the field experiment in Brandon in 2017 (Table 1). The largest root system in

Table 1. Analysis of variance and mean values of fixed effects for stem and root characters associated to lodging tolerance of six oat cultivars at the Brandon, (MB, Canada) site in 2017.

		2nd internode				Dry weight per unit area (mg cm^{-2})				Root		
Variables	Shoot height (cm)	Length (cm)	Diameter (mm)	Dry weight (g)	PBR (N)	IN4	IN3	IN2	IN1	Length (cm)	Diameter (mm)	LS (1–9)
Nitrogen (N)												
N_b	101.5	7.0	4.2	0.15	4.8	40.2	43.6	52.7	54.8	2041.9	0.333	1.8
$N_b + 25$	99.0	6.9	4.2	0.15	5.2	40.1	43.7	51.4	54.6	2779.5	0.331	1.3
$N_b + 50$	98.5	6.9	4.1	0.14	5.0	39.6	42.9	51.5	51.8	2653.1	0.324	1.3
LSD (0.05)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.24
Genotype												
CS Camden	98.3	6.3	4.3	0.13	4.3	35.9	39.7	47.4	52.5	2207.5	0.323	1.2
HiFi	107.3	7.8	4.3	0.16	5.1	38.8	41.4	48.9	47.6	2027.4	0.313	1.5
Leggett	93.3	7.0	3.8	0.14	4.6	41.0	42.2	51.5	50.8	2421.1	0.344	1.5
AC Morgan	98.8	6.1	4.5	0.17	6.5	46.3	50.6	61.7	71.8	2853.5	0.348	1.3
CDC Morrison	94.5	6.2	4.0	0.13	5.3	41.8	45.7	52.6	45.8	2578.6	0.326	1.2
CDC Sol-Fi	105.9	8.2	4.0	0.16	4.2	36.0	40.9	49.2	57.2	2860.7	0.322	2.1
Mean	99.7	6.9	4.1	0.15	5.0	40.0	43.4	51.8	53.8	2491.5	0.329	1.5
LSD (0.05)	3.30	0.99	0.22	0.024	0.46	2.7	3.27	4.64	NS	625.45	0.023	0.34
p												
Genotype (G)	<0.001	<0.001	<0.001	0.001	<0.001	<0.001	<0.001	<0.001	0.523	0.056	0.033	<0.001
N	0.201	0.940	0.312	0.850	0.068	0.800	0.792	0.801	0.136	0.110	0.656	<0.001
G × N	0.277	0.169	0.798	0.807	0.805	0.699	0.434	0.199	0.431	0.849	0.029	0.059

Note: PBR, peduncle breaking resistance; IN1, 2, 3, 4 refer to the position of the internodes from stem base to top; LS, lodging scale; NS, nonsignificant; LSD, least significant difference.

Table 2. Analysis of variance and mean values of fixed effects for structural and mechanical plant characters associated to lodging tolerance of six oat cultivars at the Brandon (MB, Canada) site in 2018.

	Shoot				2nd internode				Breaking resistance (N)					
Variables	Height (cm)	FW (g)	CG (cm)	BM (g cm)	Length (cm)	Diameter (mm)	Dry weight (g)	Dry weight per unit area (mg cm^{-2})	PBR	IN5	IN4	IN3	IN2	IN1
Nitrogen (N)														
N_b	101.4	12.4	67.7	844.8	7.5	3.7	0.14	50.1	4.0	6.9	7.3	8.3	10.7	12.6
$N_b + 25$	100.2	12.1	66.1	800.6	7.7	3.6	0.13	48.8	3.9	6.5	7.0	8.0	9.8	12.1
$N_b + 50$	98.3	12.5	65.2	823.0	7.4	3.7	0.13	48.0	4.0	6.8	7.3	8.2	10.1	12
LSD (0.05)	1.98	NS	1.53	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Genotype														
CS Camden	96.4	12.5	66.2	828.0	7.0	3.8	0.12	46.5	3.8	6.0	6.6	7.4	8.7	10.1
HiFi	103.9	11.2	69.0	767.2	7.2	3.7	0.13	49.2	3.8	5.7	6.0	7.1	9.6	10.5
Leggett	94.9	10.9	63.2	688.2	8.0	3.4	0.13	47.7	3.4	6.2	6.4	7.2	9.3	11.8
AC Morgan	101.7	16.7	68.1	1141.6	7.3	4.1	0.17	57.6	5.2	10.1	10.8	11.9	13.9	17.7
CDC Morrison	93.4	11.4	61.4	701.7	6.2	3.5	0.11	48.2	4.3	7.3	7.8	9.2	11.8	13.9
CDC Sol-Fi	109.5	11.5	70.1	810.2	9.4	3.5	0.15	44.7	3.3	5.1	5.5	6.3	7.9	9.49
Mean	100.0	12.4	66.3	822.8	7.5	3.7	0.13	49.0	4.0	6.7	7.2	8.2	10.2	12.25
LSD (0.05)	2.79	1.13	2.16	97.49	0.57	0.14	0.016	2.18	0.31	0.66	0.63	0.75	0.89	2.62
p														
Genotype (G)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
N	0.010	0.495	0.009	0.441	0.567	0.350	0.532	0.438	0.199	0.349	0.266	0.448	0.209	0.754
G × N	0.178	0.929	0.178	0.818	0.322	0.855	0.561	0.068	0.332	0.304	0.302	0.703	0.518	0.734

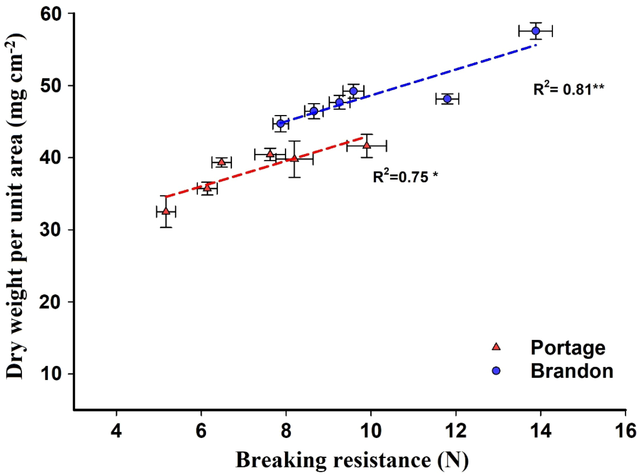
Note: PBR, peduncle breaking resistance; IN1, 2, 3, 4, 5 refer to the position of the internodes from stem base to top; FW, fresh weight; CG, centre of gravity; BM, bending moment; NS, nonsignificant; LSD, least significant difference.

Table 3. Analysis of variance and mean values of fixed effects for structural and mechanical shoot characters associated to stem lodging tolerance of six oat cultivars at the Portage la Prairie (MB, Canada) site in 2018.

	Shoot				2nd internode				Breaking resistance (N)					
Variables	Height (cm)	FW (g)	CG (cm)	BM (g cm)	Length (cm)	Diameter (mm)	Dry weight (g)	Dry weight per unit area (mg cm^{-2})	PBR	IN4	IN3	IN2	IN1	LS (1–9)
Genotype														
CS Camden	103.6	14.3	71.1	1020.2	9.7	4.3	0.15	36	2.7	3.6	4.1	6.1	8.3	1.0
HiFi	109.1	12.0	70.0	844.3	12.4	4.1	0.20	39	3.2	4.5	4.5	6.5	11.7	1.4
Leggett	110.0	11.9	70.8	845.3	15.9	3.7	0.20	33	3.2	4.5	4.2	5.2	8.1	1.5
AC Morgan	107.1	18.3	71.3	1306.7	11.4	4.8	0.23	42	4.3	7.0	8.2	9.9	14.2	1.0
CDC Morrison	98.3	11.8	63.3	746.8	11.5	3.9	0.18	40	3.7	5.7	6.3	8.2	10.3	1.2
CDC Sol-Fi	114.2	14.0	73.1	1024.1	13.2	4.2	0.23	40	3.3	4.8	5.1	7.6	11.2	3.2
Mean	107.0	13.7	69.9	964.5	12.4	4.2	0.20	38	3.4	5.0	5.4	7.3	10.6	1.5
LSD (0.05)	3.95	1.05	2.34	92.06	1.47	0.20	0.027	4.1	0.44	0.81	0.92	1.45	2.29	1.26
p	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.002	<0.001	<0.001	<0.001	<0.001	<0.001	0.018

Note: PBR, peduncle breaking resistance; IN1, 2, 3, 4, 5 refer to the position of the internodes from stem base to top; FW, fresh weight; CG, centre of gravity; BM, bending moment; LS, lodging scale; NS, nonsignificant; LSD, least significant difference.

Fig. 2. Relationship between breaking resistance and dry weight per unit area of the second internode of six oat cultivars at sites in Brandon and Portage (2018), MB, Canada. Dry weight per unit area of internode (mg cm^{-2}) was calculated as [weight/(length × diameter)]. The figure was prepared using the SigmaPlot version 13.0 (Systat Software, Inc., San Jose, CA, USA). $^*p \le 0.05$, $^{**}p \le 0.01$.



terms of root length was observed for CDC Sol-Fi and AC Morgan, whereas CS Camden and HiFi showed the smallest root systems. AC Morgan and Leggett, with the thickest root systems, differed significantly from other cultivars.

Visual lodging score and nitrogen effect

The severity of lodging was either very low (Brandon 2017 and Portage 2018, Tables 1 and 3) or did not occur (Brandon 2018). CDC Sol-Fi was the only cultivar that lodged at varying degrees in different field plots in Brandon (2017) and Portage (2018). There were no significant differences among the other cultivars (Tables 1 and 3).

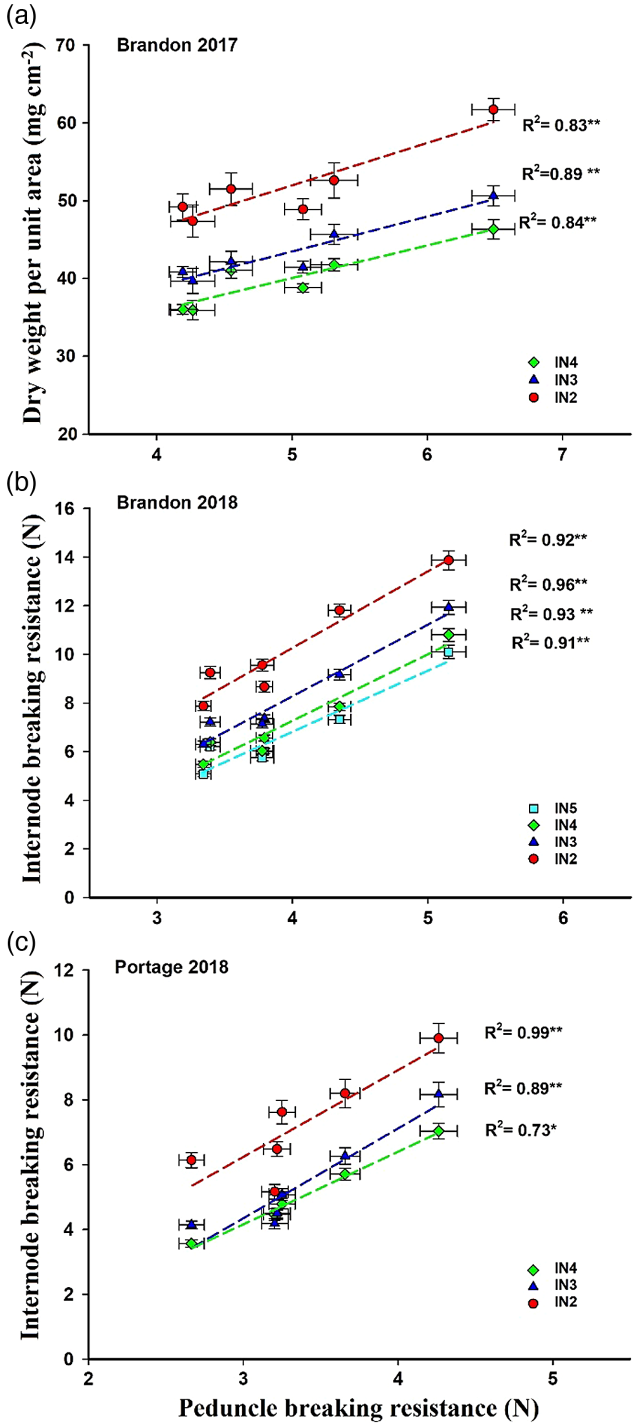
For experiments at Brandon, super-optimal supply of nitrogen ($N_b + 25$ or $N_b + 50$) at mid-tillering had no significant effect on most of the traits ($p > 0.05$). Topdressing nitrogen slightly, though significantly, reduced the visual lodging score in 2017 and plant height and HCG in 2018. With exception of root diameter, the genotype × nitrogen interactions were not significant for all other traits.

Discussion

Lack of lodging stress limits differential selection by visual rating

In this study, due to the relatively dry growing seasons (Fig. 1) and its resultant effect on shortening plant stature, the differential LS among cultivars was not seen (Tables 1 and 3, no detectable lodging in Brandon 2018), even under super-optimal supply of nitrogen ($N_b + 25$ or $N_b + 50$). CDC Sol-Fi, the lodging-prone tall cultivar, was the only cultivar that lodged slightly,

Fig. 3. Relationships between breaking resistance of peduncle and that of individual culm internodes from second internodes up to peduncle for six oat cultivars [Brandon 2017 (*a*), Brandon 2018 (*b*), Portage 2018 (*c*)]. For the experiment in Brandon (2017), the strength of all internodes other than peduncle was calculated based on the dry weight per unit area of internodes (mg cm^{-2}) as [weight/(length × diameter)]. IN1, 2, 3, 4, and 5 refer to the position of the internodes from stem base to top. The figure was prepared using the SigmaPlot version 13.0 (Systat Software, Inc., San Jose, CA, USA). $^*p \le 0.05$, $^{**}p \le 0.01$.



though significantly; however, according to the multi-environment long-term lodging data obtained from registration trials (WCORT dataset; Supplementary Fig. S1[1]) or provincial variety testing (e.g., Saskatchewan Seed Growers Association 2011, 2018), CDC Morrison, CS Camden, and AC Morgan are tolerant to lodging while Leggett and HiFi are intermediate and CDC Sol-Fi is somewhat prone to lodging.

In the past, progress in breeding for increased lodging tolerance in cereals including oat has been largely achieved through selection for short-statured breeding lines standing strong in the field (Berry 2019). While phenotypic and genotypic selection for reduced plant height is straightforward (Kelbert et al. 2004*b*), the effective selection for improved plant standability using the common method based on visual rating of lodged plants can be hindered due to lack of weather (rain and wind) or growing conditions that induce lodging pressure (Berry et al. 2003*b*; Kelbert et al. 2004*a*). According to our historical WCORT lodging data (Supplementary Fig. S1[1]), over the course of 13 yr the average severity of lodging scores was <3 at about 60% of the test sites (61 site-year trials). Similar to the results of this study, the WCORT historical lodging data has shown that effective visual assessment is contingent on a reasonable degree of lodging pressure, which is not reliable.

Tolerance to lodging: a complex trait

Dry seasons prevented the differential susceptibility to lodging for the tested cultivars in this study to be realized, as previously observed in the multi-environment registration trials or provincial variety testing. Nevertheless, results from this study revealed the complex nature of lodging. For instance, CDC Sol-Fi had the largest coronal root system, suggesting increased anchorage strength; however, due to its tall stature and long, relatively weak basal internodes, CDC Sol-Fi was the most lodging-prone cultivar in this study (Tables 1–3). Also, according to the registration and provincial trials, CS Camden and Leggett, with similar plant height, differ from each other in terms of tolerance to lodging (WCORT dataset; Saskatchewan Seed Growers Association 2018). Even though no lodging occurred in this study, our results showed that CS Camden, historically known as a lodging-tolerant cultivar, had shorter and thicker basal internodes compared with Leggett, an intermediate lodging-tolerant cultivar, which might explain the differential lodging tolerance of these cultivars despite their similarity in plant height.

Trait-based breeding using traits related to lodging has been suggested as an alternative to a visual scoring approach, particularly in the absence of lodging stress (Berry et al. 2000); however, tolerance to lodging is a complex trait influenced by multiple plant characteristics and this makes differential selection based on the individual lodging-related traits ineffective. It has been previously shown that tolerance to lodging can be better estimated using a combination of plant characteristics determining the three major lodging components: stem strength, anchorage strength, and self-weight moment or BM (Berry et al. 2000). The "safety factor", a lodging index, was used to estimate tolerance to stem and root lodging based on the ratio of strength of stem and anchorage system to the self-weight moment of the shoot (Crook et al. 1994; Wu and Ma 2019). These lodging models were further developed to predict the risk of lodging by incorporating multiple plant characteristics along with soil and meteorological data (Berry et al. 2000). To facilitate the use of these models for screening purposes, Mirabella et al. (2019) attempted to overcome the challenges related to measuring model traits by replacing them with several agronomic traits (e.g., plant height, spike dry weight, and basal stem diameter), which can be measured at crop maturity. Although these models and lodging indices are useful to evaluate the tolerance of commercial cultivars in the absence of natural lodging, they involve time-consuming measurements of stem base and root parameters that limit their applicability for screening large groups of breeding materials.

PBR as a proxy of whole stem strength and a potential selection criterion to improve straw strength

In this study, the correlations between the morphological and mechanical characteristics of culm internodes with lodging scores in the field were nonsignificant because of no, or low, lodging pressure (data not shown). Among lodging-associated traits, plant height and length of the basal internode were most correlated with visual lodging scores (Berry et al. 2004, 2015; Kelbert et al. 2004*a*, 2004*b*; Piñera-Chavez et al. 2016*b*; Mirabella et al. 2019). Despite the lack of significant lodging stress, our results revealed a strong association between PBR and whole culm strength in two field experiments in 2018. This suggests the possibility to enhance selection for stem-lodging tolerance by selecting for straw strength through screening for PBR (Figs. 3*b* and 3*c*). A significant genetic variation was found for PBR at field experiments over 3 site-years, which is a fundamental requirement if PBR is to be chosen as a criterion of selection (Jackson et al. 1996). Moreover, in contrast to basal internodes, the ease of peduncle sampling would facilitate the integration of stem strength into breeding programs.

Among traits related to lodging tolerance, plant height, as the most selectable trait, has long been

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjps-2019-0286.

selected for in breeding programs to improve lodging tolerance (Kelbert et al. 2004*b*); however, there is evidence indicating variation in tolerance to lodging among genotypes with the same plant heights (Navabi et al. 2006). This suggests that due to the complex nature of lodging tolerance, the further enhancement in selection for this trait requires other lodging-related traits to select for while breeding for optimized plant height.

Morphological and mechanical characteristics of the basal internodes, particularly stem base strength, are the key determinants of tolerance to stem lodging (Berry et al. 2003*b*; Tripathi et al. 2003; Islam et al. 2007). Phenotyping of basal internode strength has been facilitated by the application of new instrumentation capable of measuring breaking resistance of internodes within seconds; however, difficulty in sampling of basal internodes within the context of a breeding program is still a challenge. Our results provided a proof-of-concept for application of PBR as a potential selection criterion to improve tolerance to stem lodging.

It should be noted that strengthening the stem base involves significant investment of biomass in structural stem tissues, which can compromise yield potential (Berry et al. 2007; Piñera-Chavez et al. 2016*a*). In our study, no significant correlations were found between breaking resistance and dry biomass accumulated in basal internodes. This implies the possibility for selection of stiff-stemmed genotypes with low accumulation of biomass in stems, i.e., a strong but light stem. For example, CDC Morrison was the second stiffest stemmed oat variety following AC Morgan and had the lightest basal internode compared with the other cultivars (Tables 1–3). We speculate that integration of PBR assessment into multi-environment preliminary yield trials might have two advantages: (*i*) selection of breeding lines can be performed using data collected for both yield and PBR and this will prevent advancing stiff-stemmed but low-yielding lines, and (*ii*) the challenge related to the effect of genotype × environment interaction on PBR will be overcome by evaluation of breeding lines for PBR through multi-environment trials (Yan 2016).

Conclusions

This study found, as have many others, that effective visual selection is contingent on a reasonable degree of lodging pressure, which is not reliable. Thus, the use of traits related to lodging tolerance in lieu of visual scoring is desirable. Our study provided a proof-of-concept for application of PBR as a potential selection criterion to improve tolerance to stem lodging. This study revealed a strong association between PBR and whole culm strength, suggesting that stem stiffness can be selected for through screening for PBR. The results verified the availability of genetic variation for PBR that can be exploited by breeders in breeding for increased straw strength. Moreover, the ease of peduncle sampling and rapid measurements of PBR makes this suitable for integration into breeding programs. Overall, we speculate that screening for straw strength (based on PBR), particularly at advanced generations (e.g., preliminary yield trials) in which yield data are also available, would enhance the selection gain for lodging tolerance while retaining high yield potential.

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