

Tree seedling establishment among C₄ grasses

Edmund C February, Joel R Lewis

The coexistence of leguminous trees and C₄ grasses in African savanna remains poorly understood. Trees are able to establish among grasses despite grasses being competitively superior for below ground resources. Here we test the hypothesis that trees are only able to establish when grass biomass has been reduced.

We do this at four locations in Limpopo Province South Africa where we locate young seedlings of *Senegalia nigrescens*. Where we found seedlings we determine grass species composition as well as grass percentage canopy cover, height above ground, and root length. We also make determinations of grass characteristics at two locations where we found no seedlings. For seedlings we determine rooting depth, plant height and stem diameter. To confirm that these are indeed young seedlings, less than a year old, we compare root length and plant height with that of seedlings germinated and grown for 77 days in a greenhouse.

Our results show that where seedlings are present grasses are dominated by short-lived species such as *Aristida congesta* and *Enneapogon cenchroides*. These species are often found in disturbed soils and would increase with overgrazing. On those sites with no seedlings grass species composition is dominated by perennial species such as *Panicum maximum*, *Panicum coloratum* and *Cenchrus ciliaris* that would decrease with overgrazing and/or repeated burning. The perennial species have a 90-100% canopy cover while the short-lived species have a much lower canopy cover of less than 50%. Within 77 days of germinating tree seedlings are able to develop a root system that is deeper than the short-lived grasses but not deeper than the perennial grasses.

These results demonstrate that tree seedlings are only able to establish among grasses if there are gaps in both grass canopy and root mass resulting from increased herbivory, frequent fire or extended drought.

1 **Tree seedling establishment among C₄ grasses**

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14

15 **Abstract**

16 The coexistence of leguminous trees and C₄ grasses in African savanna remains poorly
17 understood. Trees are able to establish among grasses despite grasses being competitively
18 superior for below ground resources. Here we test the hypothesis that trees are only able to
19 establish when grass biomass has been reduced.

20 We do this at four locations in Limpopo Province South Africa where we locate young seedlings
21 of *Senegalia nigrescens*. Where we found seedlings we determine grass species composition as
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24 seedlings we determine rooting depth, plant height and stem diameter. To confirm that these are
25 indeed young seedlings, less than a year old, we compare root length and plant height with that
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28 such as *Aristida congesta* and *Enneapogon cenchroides*. These species are often found in
29 disturbed soils and would increase with overgrazing. On those sites with no seedlings grass
30 species composition is dominated by perennial species such as *Panicum maximum*, *Panicum*
31 *coloratum* and *Cenchrus ciliaris* that would decrease with overgrazing and/or repeated burning.
32 The perennial species have a 90-100% canopy cover while the short lived species have a much
33 lower canopy cover of less than 50%. Within 77 days of germinating tree seedlings are able to
34 develop a root system that is deeper than the weakly perennial grasses but not deeper than the
35 perennial grasses.

36 These results demonstrate that tree seedlings are only able to establish among grasses if there are
37 gaps in both grass canopy and root mass resulting from increased herbivory, frequent fire or
38 extended drought.

39

40 **Key words**

41 Seedling establishment, savanna, below ground, above ground, resource competition.

42 Introduction

43 Savanna may be characterised as a discontinuous layer of trees set among a continuous layer of
44 grasses (Scholes & Archer 1997). While the structure of savanna may change from lightly
45 wooded grassland to dry woodland through changes in the relative proportions of these two life
46 forms there is no consensus as to the primary drivers that determine the proportions of each
47 (Sankaran et al. 2004). There is however general recognition that herbivory and fire may act as
48 top-down control agents with the availability of nutrients and water as bottom up controls (Frost
49 et al. 1986). Several hypotheses have been proposed explaining how these drivers may interact to
50 set limits on tree cover in savanna (Sankaran et al. 2004). These hypotheses may be grouped into
51 either resource based or disturbance based hypotheses both of which consider water availability
52 as a critical determinant for savanna vegetation structure (Higgins et al. 2000; Walter 1971).

53 More recently it has been shown that the fine roots of both trees and grasses are primarily located
54 in the upper layers of the soil where nitrogen concentrations are highest (February et al. 2013a;
55 February & Higgins 2010). Several studies have also shown that grasses may outcompete
56 juvenile trees for both nutrients and water (Bond 2008; February et al. 2013a). This superior
57 ability for nutrient acquisition combined with high water and nitrogen use efficiency and a lack
58 of woody tissue allow grasses to respond very rapidly at the beginning of the growing season
59 when nitrogen and water become available (Bond 2008).

60 Here we make the distinction between seeds germinating and establishing as seedlings and
61 juvenile trees establishing into adult size classes. We do this because once seedlings establish as
62 juvenile trees these established trees may persist as juveniles for several decades caught in the
63 grass layer through herbivory and fire (Bond & van Wilgen 1996). Even after their above ground
64 structure has been killed by fire juvenile trees may re-sprout from the base by utilising stored
65 reserves for growth (Schutz et al. 2011). These juvenile trees may be caught in a continuous
66 negative feedback loop not reaching reproductive maturity even after several decades (Higgins et
67 al. 2007). In this study we refer to seedlings that have recently germinated and established within
68 the previous growing season.

69 Despite an apparent competitive advantage grasses do not prevent tree seedlings from
70 germinating and establishing. Rather, over the past century there has been a global increase in

71 woody vegetation cover with several studies suggesting that grasses have relatively little
72 influence on woody seedling germination and establishment (Brown & Archer 1999; Ward
73 2005). More recently, however, it has been suggested that tree seedling establishment is not
74 possible in dense grass swards and that it is only when grass biomass has been reduced through
75 herbivory, drought or increased fire frequency and intensity that seedlings are able to establish
76 (D’Odorico et al. 2006; February et al. 2013b; Wakeling et al. 2015).

77 We test this prediction in the field at four locations in Limpopo Province, South Africa,
78 representing differing geologies, herbivory and disturbance by fire. We concentrate our study on
79 the critical germination to establishment phase represented by young seedlings. To confirm that
80 these were individuals around one year old that we have sampled we compare diameter, height
81 and rooting depth to that of seedlings grown from seed for six months in the laboratory. We
82 specifically ask: Under what circumstances are tree seedlings able to establish among grasses?
83 We hypothesised that even at intermediate levels of grass biomass tree seedlings would not be
84 able to establish because grasses are able to outcompete seedlings for both above and below
85 ground resources (February et al. 2013b; Riginos 2009).

86

87 **Methods**

88 The study was comprised of two parts, the first was conducted in the field. The second was a
89 seedling-growth experiment in the University of Cape Town’s greenhouse. Field data were
90 collected from 12 study sites in the Limpopo Province, South Africa between 12 May and 1
91 June, 2014 (middle of the dry season). The green house experiment was conducted between 21
92 July and 9 October, 2014.

93 **Study site**

94 Our study site is centred around and south of the town of Phalaborwa (23°56’36.07”S
95 31°8’27.50”E) in Limpopo Province, South Africa. The climate of the region is typified by a hot,
96 wet, season and a cool, dry, season. Mean annual rainfall is 486 mm at Phalaborwa and 502 mm
97 at Satara (24°23’38.00”S 31°46’37.45”E) 80 kms to the south east (Venter et al. 2003). Monthly
98 maximum and minimum temperatures are 24°C and 18.5°C at Phalaborwa and 29.8°C and 16°C

99 at Satara (February & Higgins 2010; Stevens et al. 2014). Rainfall is distinctly seasonal resulting
100 in a growing season that starts at the end of October and ends in April (February et al. 2013b).

101 Our study was conducted at four locations, two Associated Private Nature Reserves (APNR)
102 Grietjie Private Nature Reserve (24° 7'2.68"S, 31° 1'19.69"E), and Balule West Private Nature
103 reserve (24°09'S, 30°59'E), the outskirts of the town of Phalaborwa (23°55'39.37"S, 31°
104 7'37.27"E) and in a section of the Buffalo enclosure near Satara rest camp in the Kruger
105 National Park (24°24'22.41"S, 31°44'51.63"E). The APNR's are a group of privately owned
106 reserves all bordering on the Kruger Park. There are no fences between the APNR's and the
107 Kruger National Park allowing access for large herbivores such as elephant, rhino, buffalo and
108 zebra.

109 The soils for Phalaborwa and the two sites immediately south of the town are derived from the
110 underlying Phalaborwa igneous complex comprised of syanite and can be described as nutrient
111 poor coarse sands (Barton et al. 1986). The soils at Satara are derived from the Letaba Formation
112 basalts of the Karoo supergroup resulting in clay soils that are more nutrient rich (February &
113 Higgins 2010; Scholes 1990).

114 Grietjie Private Nature Reserve is a 2, 800 hectare reserve bordering on the Kruger National Park
115 at the Olifants River. Grietjie borders on Balule Private Reserve and as with all the APNR's has
116 very high grazing pressure and a managed fire regime with a return interval of less than 3 years
117 (Palmer et al. 2006; van der Waal et al. 2011). The vegetation for the area is classified as
118 Lowveld Rugged Mopane veld by Mucina and Rutherford (2006) with *Senegalia nigrescens* and
119 *Sclerocarya birea* subs. *caffra*, the dominant trees and *Aristida congesta*, *Enneapogon*
120 *cenchroides* and *Sporobolus panicoides* the dominant grasses.

121 The town of Phalaborwa borders onto the Kruger National Park to the north of Grietjie near the
122 confluence of the Selati and Olifants Rivers. We sampled on the edge of town where fire is
123 suppressed and all grazing and herbivory has been excluded for several years. The vegetation for
124 the area is also classified by Mucina and Rutherford (2006) as Lowveld Rugged Mopane veld.

125 Balule West Private Nature Reserve is a 40 000 hectare APNR bordering onto the Kruger
126 National Park at the Olifants River to the south of Grietjie. The vegetation for the area is
127 classified as Granite Lowveld by Mucina and Rutherford (2006) with *Senegalia nigrescens* and

128 *Sclerocarya birea* subs. *caffra*, the dominant trees and *Brachiaria nigropedata*, *Digitaria*
129 *eriantha* subsp. *eriantha* and *Eragrostis rigidior* the dominant grasses.

130 The Buffalo enclosure is located close to Satara Rest Camp in the Kruger National Park. We
131 sampled in a 7.7 hectare section of the enclosure that had been protected from fire and herbivory
132 for 13 years (February et al. 2013b). The vegetation for the area is classified as Tshokwane-
133 Hlane Basalt Lowveld by Mucina and Rutherford (2006) with *Senegalia nigrescens* and
134 *Sclerocarya birea* subs. *caffra*, the dominant trees and *Bothriochloa radicans*, *Digitaria eriantha*
135 subsp. *eriantha* and *Panicum coloratum* the dominant grasses.

136 **Field sampling**

137 Seedlings that are around one or two year old are extremely rare at our study site. To locate these
138 we searched large areas of each location on foot. Where seedlings were located we set up a series
139 of plots for measurements on both seedlings and grasses. We also set up a series of random plots
140 for measures of grasses at two locations where we found no seedlings. This sampling technique
141 resulted in 12 plots at our four locations, 5 at Grietjie, 4 at Phalaborwa, 2 at Balule and 1 in the
142 Satara Buffalo enclosure.

143 On each plot we identified and visually estimated the percentage canopy cover of the dominant
144 grass species in ten randomly located 1 m² quadrats (Mueller-Dombois & Ellenberg 1974). We
145 then determined for a maximum of ten individuals of the dominant species on each plot height
146 above ground, root length and stem diameter for tree seedlings and for grasses height above
147 ground and root length. Stem diameter for seedlings was obtained, at ground level, using a steel
148 rule. Height for both trees and grasses was determined by measuring the height of the plant from
149 the soil surface to the highest point of the plant using a steel rule. Individual specimens of both
150 tree seedlings and tufts of the dominant grass species were carefully excavated by hand to
151 determine rooting depth. The length of the longest root was then measured from the base of the
152 plant using a steel rule.

153 **Seedling growth**

154 We grew *Senegalia nigrescens* from seed in a greenhouse on the campus of the University of
155 Cape Town. We did this as a calibration to ensure that our field sampled seedlings were indeed
156 around one or two years old. For this we soaked 50 seeds overnight in warm water before placing
157 these between layers of moist absorbent-paper. After three days all the seeds (13) that

158 germinated were planted in pots (9 cm X 8 cm) filled with washed river sand (Consol filter sand,
159 Cape Silica Suppliers, Cape Town) containing no organic matter. Seedlings were then left to
160 grow for five weeks (36 days) before being transferred to larger (50 cm X 10 cm) pots filled with
161 the same sand. At the time of this transfer, seedling height above ground, root length and stem
162 diameter at the widest point were determined as described above. The seedlings were then left to
163 grow for a further seven weeks (41 days) before harvesting and height above ground, root length
164 and stem diameter determined again. During this time the seedlings were watered three times a
165 week and received a twice weekly dose of 300 ml of fertilizer.

166 **Statistics**

167 We analysed the data from each site using simple regression. As our root-length data were not
168 normally distributed a non-parametric Wilcoxon rank sum test was employed to test the means
169 for significant difference. For age calibration the stem diameter and root length for field
170 seedlings was used to estimate age by substituting the value into a linear model (with y-intercept
171 = 0) created from glasshouse seedling data and solving for time (x-axis). Linear models were
172 forced through zero to reflect germination from seed. The estimated ages of all seedlings were
173 then used to calculate the average age of the seedlings based on stem diameter or root length
174 found in the field. All statistical analysis were performed using R statistical software
175 (R_Development_Core_Team 2011).

176 **Results**

177 The dominant tree species on all of our plots was *S. nigrescens* while the dominant grasses
178 differed considerably between locations. At Grietjie these were *Aristida congesta subsp.*
179 *Congesta*, *Enneapogon cenchroides* and *Tricholaena monachne*. At Phalaborwa *Panicum*
180 *maximum*, *Cenchrus ciliaris*, and *Eriochloa meyeriana*. At Balule *Aristida congesta subsp.*
181 *congesta*, *Sporobolous panicoides*, *Enneapogon cenchroides* and *Tricholaena monachne*. In the
182 Buffalo enclosure at Satara *Panicum coloratum*, *Themeda triandra* and *Setaria sphacelata*
183 (Table 1). All grass identifications follow the nomenclature of van Oudtshoorn (2002).

184 An increase in grass canopy cover from 36 % at Grietjie to 99 % at Phalaborwa is strongly
185 correlated with an increase in grass sward average height from 52.9 cm at Grietjie to 92.6 cm at
186 Satara (Fig. 1, Table 2, $R^2 = 0.66$). Our results also show that grass root length increased from
187 10.6 cm at Balule to 22 cm at Satara (Fig.1, Table 2, $R^2 < 0.001$).

188 There is a strong positive correlation between grass canopy cover and tree seedling density with
189 the highest density of seedlings at Grietjie (50) and none at Phalaborwa and Satara (0, $R^2 = 0.92$,
190 Fig. 1, Table 2). Where tree seedlings are able to establish these consistently root deeper than
191 coexisting grasses ($P < 0.001$, Table 2, Fig. 1). At Grietjie and Balule grasses root with a mean
192 depth of 13.2 cm, while tree seedlings root with a mean depth of 27.6 cm (Fig. 1, Table 2).

193 The results of our greenhouse study show that stem diameters of seedlings are indistinguishable
194 from field samples and after 60 days our greenhouse seedlings had root lengths and canopy
195 height slightly lower than but similar to those found in the field demonstrating that our field
196 samples are indeed less than a year old (Table 2).

197 Discussion

198 Our four sites represent different levels of fire and herbivory. The two APNR sites Grietjie and
199 Balule have fire return intervals of less than 3 years with relatively high stocking rates (4 880
200 kg/km^2) when compared with our study site at Satara in the Kruger National Park and the
201 outskirts of the town of Phalaborwa where there are no large herbivores (Palmer et al. 2006). Our
202 results show that these differences in fire return intervals and herbivory have resulted in large
203 differences in the dominant grass species on each of our plots. At Grietjie and Balule the
204 dominant grasses *Aristida congesta* and *Enneapogon cenchroides* are species that increase with
205 disturbance such as overgrazing (van Oudtshoorn 2002). At Satara and Phalaborwa where
206 grazing is absent, the grass sward is dominated by *Panicum maximum*, *Panicum coloratum*,
207 *Themeda triandra* and *Setaria sphacelata* which are all highly-palatable perennial grasses that
208 grow for more than five seasons. These species also decrease with disturbance and overgrazing
209 (Fish L. 2015; van Oudtshoorn 2002).

210 The perennial grasses at Satara and Phalaborwa root significantly deeper than the more
211 ephemeral grasses at Grietjie and Balule. Our greenhouse data show that trees are able to develop
212 a tap root averaging 15 cm long within 30 to 60 days after germination. This rooting depth is
213 deeper than that of the annual or weakly perennial grasses at Grietjie (14.1 cm) and Balule (10.6
214 cm) but not deeper than the perennial grasses at Phalaborwa (16.3 cm) and Satara (21.7 cm). Not
215 only are grasses deeper rooted at our Phalaborwa and Satara sites but the canopy cover at these
216 sites is also close to 100% whereas, it is much lower at Grietjie (36%) and Balule (51%).

217 Our results demonstrate that tree seedlings are only able to establish when there has been a
218 change in grass species composition and biomass resulting in a reduction in both above and
219 below ground competition for resources. We demonstrate that this establishment is not possible
220 in dense swards of perennial grasses where establishment opportunities may only be created
221 through increased fire and herbivory or extended drought. Such disturbances may allow for a
222 change in grass species composition resulting in gaps in both canopy and root mass (O'Connor et
223 al. 2001; Wakeling et al. 2015).

224 The tree seedlings at our study site are rooting down to 28 cm which is even deeper than that of
225 our perennial grasses. These results suggest that tree seedlings avoid competition for water by
226 rapidly deploying roots below that of grasses. Several recent studies have demonstrated that trees
227 do indeed use moisture from deeper soil layers than grasses and our results for rooting depth
228 merely confirm this (Kambatuku et al. 2013; Kulmatiski & Beard 2012). A number of studies
229 have however also shown that nitrogen is highest in the upper layers of the soil and that the
230 competition between trees and grasses is in these upper layers of the soil for nutrients and not
231 water (Cramer et al. 2010; February & Higgins 2010; February et al. 2013b). Tree seedlings have
232 to establish fine roots in these upper soil layers primarily for nutrient acquisition. In African
233 savannas, tree seedlings are able to form symbiotic relationships with bacteria to fix atmospheric
234 nitrogen (Cramer et al. 2010). Once established however these trees no longer form this
235 relationship (Cramer et al. 2007). Future research should focus on the role of nitrogen fixation in
236 allowing for trees to establish roots in the upper layers of the soil where grasses are
237 competitively superior.

238 **Conclusion**

239 Our results demonstrate that grass species composition is critical in allowing for seedling
240 establishment in savanna where competitively superior C₄ grasses dominate the shallow nutrient-
241 rich soil horizons. Tree seedling are only able to establish with a change in grass species
242 composition allowing for gaps in grass biomass both above and below ground. They do this by
243 very rapidly establishing a deep tap root that is able to access water below the grass root layer.
244 Despite this seedlings have to access the upper layers of the soil for nutrients as this is where
245 nutrients are highest (February & Higgins 2010). Future research should concentrate on
246 understanding how this is possible with grasses dominating the upper layers of the soil (Bond

247 2008; February et al. 2013b). We hypothesis that many African tree seedlings are able to form
248 symbiotic relationships with bacteria to allow for the uptake of atmospheric nitrogen (Cramer et
249 al. 2007; Cramer et al. 2010). We speculate that once established with a deep root system for
250 water these seedlings are able to use nitrogen fixation to avoid direct competition with grasses
251 and establish more shallow roots primarily for nutrient acquisition.

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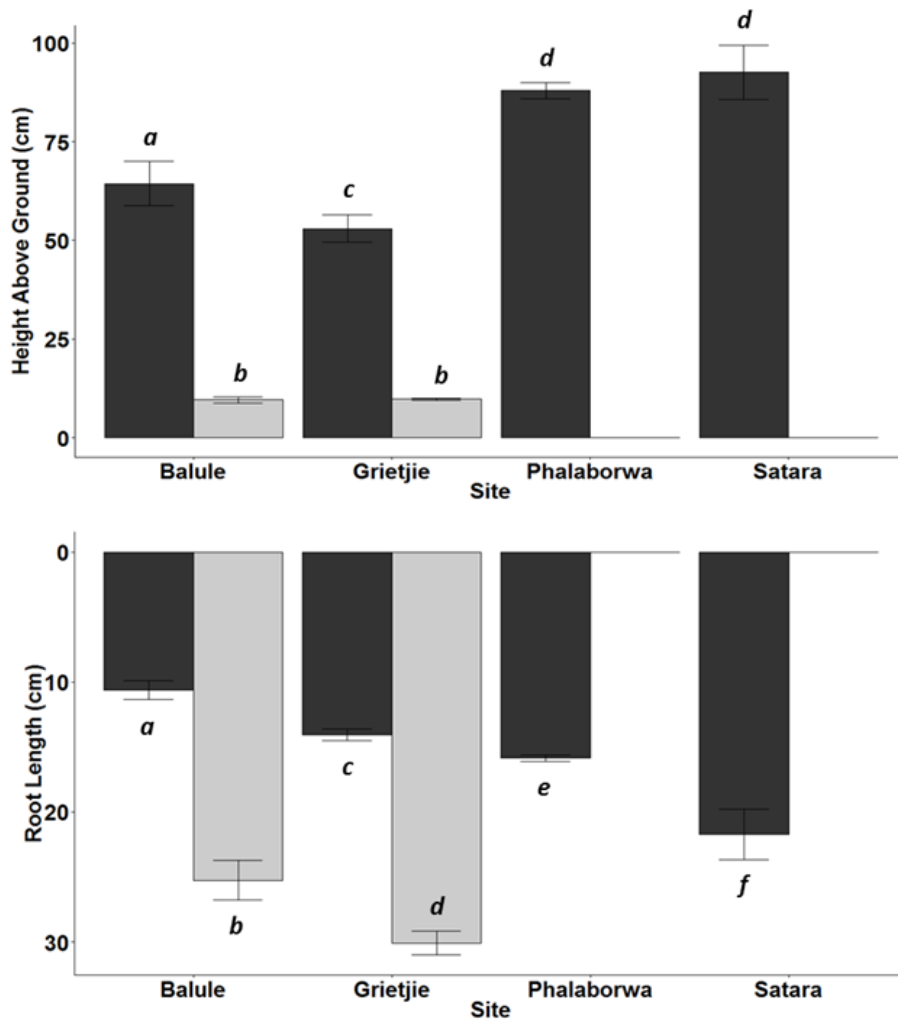
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340 Figure 1. Plant height (top) and root length (bottom) for both trees (grey) and grasses (black) at
341 the four locations at our study site (means \pm S.E.). Values not sharing the same letters indicate
342 significant differences ($P < 0.01$) between means.

344 **Table 1.** Grass species composition at the four locations at our study site.

	Grietjie	Balule	Phalaborwa	Satara
<i>Aristida congesta</i>	X	X		
<i>Enneapogon cenchroides</i>	X	X		
<i>Tricholaena monachne</i>	X	X		
<i>Sporobolous panicoides</i>		X		
<i>Panicum maximum</i>			X	
<i>Cenchrus ciliarus</i>			X	
<i>Eriochloa meyeriana</i>			X	
<i>Panicum coloratum</i>				X
<i>Themeda triandra</i>				X
<i>Setaria Sphacelata</i>				X

346 **Table 2.** Averages and standard error for measured traits as determined on the four locations at our study
 347 site and in the green house after 60 days.

	Grietjie	Balule	Phalaborwa	Satara	Greenhouse
Number of seedlings	50	16	0	0	26
Number of grasses	50	20	40	10	0
Grass canopy cover (%)	36 ± 2.6	51 ± 6.0	99 ± 0.2	98 ± 1.0	N/A
Grass height (cm)	52.9 ± 3.5	64.4 ± 5.5	85.5 ± 2.1	92.6 ± 6.8	N/A
Grass root length (cm)	14.1 ± 0.4	10.6 ± 0.7	16.3 ± 0.2	21.7 ± 6.1	N/A
Seedling height (cm)	9.7 ± 0.3	9.6 ± 0.7	N/A	N/A	6.5 ± 0.2
Seedling root length (cm)	30.2 ± 0.9	25.3 ± 1.5	N/A	N/A	15 ± 1.2
348 Seedling stem diameter (mm)	2.4 ± 0.1	2.2 ± 0.1	N/A	N/A	2.5 ± 0.1