Complementary patterns of stiffness in stem and leaf sheaths of *Triticale*

Measurements of ultrasound velocity

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Abstract. The variation in the stiffness of stem and leaf sheaths along the shoot axis of *Triticale* (*Triticosecale W.*, cv. Jago) was examined, using an ultrasonic method, at two stages of development, (i) at the stage of high stem mechanical instability when upper internodes are forming (heading), and (ii) at milk maturity when development of strengthening tissues is completed (three weeks after anthesis). The squared velocity of low-frequency longitudinal pulse waves was used as a measure of the specific modulus of elasticity, averaged over the whole cross section of the structures and related to the unit density of the material. Structural material of varying effective stiffness was found to be utilized along leaf sheaths with a pattern complementary to that in growing stems. The stiffness increased basipetally along leaf sheaths in the direction of increasing flexibility of internodes. Maximum values of the specific modulus of elasticity in particular leaf sheaths were enhanced acropetally, ensuring the stronger mechanical protection of those meristematic zones which were actively elongating and were located at the upper internodes. The stiffest material present in leaf sheaths covered only those stem sections which could be the most critical for plant safety during stem elongation. This characteristic and very regular pattern of stiffness alteration along the shoot axis was structurally determined as it remained similar after air drying the specimens. It is concluded that adaptation of cereals to withstand environmental loads is realized not only on morphological and anatomical levels but is also reflected in a specific heterogeneity in the material properties of the cell walls which support the plant.

Key words: Cell wall – Leaf sheath – Modulus of elasticity – Stem – *Triticosecale* – Ultrasound velocity

Introduction

Shoots of grasses exhibit a telescoped structure (Eames 1961), segments of which emerge successively as the plants grow. In earlier developmental stages the internodal design of the plant stem is characterized by the alternate occurrence of meristematic and mature sections (Esau 1977). Because of the pronounced gradient of stiffness in growing internodes (Żebrowski 1991), the stems exhibit a high structural instability. Growing stems themselves are not capable of withstanding their own weight and easily fail through Euler buckling (Timoshenko and Gere 1961) or bending. The mechanical stability of the shoots in the earlier growth stages is essentially ensured by the presence of the stem-clasping leaf sheaths, the formation of which apparently precedes elongation of the corresponding internodes.

The strengthening contribution of leaf sheaths in grasses has been examined in only a few studies (Prat 1935; Hozyo and Oda 1965; Bashford et al. 1976; Matsuda et al. 1983; Niklas 1990). Most of the authors reported measurements which averaged the mechanical properties over the whole length of the internodes. Only Prat (1935) studied the stiffness of structural material as it varies within particular internodes and leaf sheaths. However, these data cannot be related directly to the elastic stability of the plants as they refer rather to behaviour in shear.

The objective of the work reported in this paper was to examine the axial alteration of longitudinal composite stiffness in stems and the clasping leaf sheaths. The studies were carried out in *Triticale* at two stages: that of apparent stem instability and when the development of strengthening tissues was completed. An ultrasonic method was employed instead of a static one as it was much simpler and was much less affected by random experimental errors. Owing to the latter advantage, the method allowed fairly small axial alterations in composite stiffness to be followed, demonstrating details of support design in these plants in terms of material quality.

Material and methods

Plant material. *Triticale* (*Triticosecale W.*, cv. Jago) plants were grown in the field in Radzikow in 1989. The plants were harvested
at heading when ear emergence was completed \( \text{(stage ZGS 59; Zadoks et al. 1974)} \) and also at the milk stage of the kernels three weeks after anthesis \( \text{(stage ZGS 76)} \). Six shoots with the same number of internodes, and where possible, equal internode lengths and leaf-sheath lengths, were chosen for the measurements. The plants harvested at the second developmental stage were selected to be morphologically similar to those sampled earlier and to exhibit nearly the same linear dimensions of those internodes and leaf sheaths which completed their growth at heading. After discarding the pulvinus zones, the internodes and corresponding leaf sheaths were divided into an equal number of sections, so that the specimen length ranged from 3.5 to 4.8 cm. Care was taken to ensure that the specimen ends, cut with a new sharp razor blade, were smooth and, to the extent possible, perpendicular to their longitudinal axis. Prior to the measurements, specimens of fresh material were immersed in distilled water for a few hours to fully hydrate tissues. After measuring, they were air-dried \( \text{(initially in an oven at 80 °C for 24 h and then at room temperature for a few hours to a constant weight)} \) to about 10% water content, and all the ultrasonic tests were repeated to distinguish between structural and moisture effects in the measurements.

**Ultrasound-velocity measurements.** A through-transmission method was used to determine the velocity of ultrasound along stems and leaf sheaths. The specimen to be tested was held coaxially between transmitting and receiving transducers \( \text{(01T40 and 01R40, respectively; UNIPAN, Warszawa, Poland)} \) through which short pulses of longitudinal waves of 100 kHz were propagated. Pulse travel time, \( t \), through the specimen was measured by means of an ultrasonic-material tester \( \text{(type 543; UNIPAN)} \) with an accuracy of 0.1 \( \mu \text{s} \). The velocity was calculated according to the formula \( v = l/t \) where \( l \) was the specimen length measured with slide caliper to the nearest 0.1 mm. Care was taken to ensure that the face of each of the transducers was properly coupled to the specimen ends by applying distilled water \( \text{(for fresh material)} \) or technical vaseline \( \text{(for air-dried samples)} \) at the interface. During the measurements the specimens were slightly compressed between the two transducers to ensure effective introduction of the waves into the sample and to minimize pulse delay at interfaces. For calculations, the lowest observed transit time was taken to indicate the best coupling. A steel reference bar \( \text{(2.00 gs)} \) was used for calibration of the instrument.

The velocity of ultrasound is known to be related to the elastic properties of the material through which the wave propagates \( \text{(Krautkramer and Krautkramer 1977)} \). When longitudinal waves exhibit wavelengths \( \lambda \) much higher than the dimensions of the structural elements in cross-section, as well as of the perpendicular dimensions of the specimen, then the so-called bar velocity \( (v) \) is related to elastic modulus \( (E) \) through the formula

\[
v^2 = \frac{E}{d}
\]

where \( d \) is the density of the material \( \text{(Lynnworth 1973)} \). In the case of a homogeneous medium, \( E \) is simply Young’s modulus. However, for composites, like cereal stems, which exhibit a heterogeneity where \( d \) is the density of the material \( \text{(Lynnworth 1973)} \). In the case of composites, like cereal stems, which exhibit a heterogeneity

<table>
<thead>
<tr>
<th>Internode Length (cm)</th>
<th>Table 1. Lengths of internodes and leaf sheaths of Triticale cv. Jago plants at heading and milk maturity. SDs are shown in ( )</th>
</tr>
</thead>
<tbody>
<tr>
<td>No.</td>
<td>Heading</td>
</tr>
<tr>
<td></td>
<td>Internode Leaf sheaths</td>
</tr>
<tr>
<td>1</td>
<td>25.3 (1.3)</td>
</tr>
<tr>
<td>2</td>
<td>22.2 (0.7)</td>
</tr>
<tr>
<td>3</td>
<td>19.0 (0.8)</td>
</tr>
<tr>
<td>4</td>
<td>12.4 (0.4)</td>
</tr>
<tr>
<td>5</td>
<td>7.9 (0.8)</td>
</tr>
<tr>
<td>6</td>
<td>1.9 (0.5)</td>
</tr>
</tbody>
</table>

Ultrasound propagated in shoot sections was found to have a wavelength from about 10 to 50 mm, depending on the location in the shoots. Since the stem diameter did not exceed 5 mm, the ratio \( d/\lambda \) was low enough for the majority of the tested specimens to show a bar velocity \( (v) \). This confirmed the validity of using Eq. 1, according to which \( v^2 \) may be considered as a measure of the specific modulus of elasticity \( (E') \) averaged over the whole cross-section. In additional measurements, not presented here, it was shown that neither differences in weight per unit length nor diameter of tested specimens significantly affected the ultrasonic measurements.

Variations of the modulus along stem and leaf sheaths in relation to the distance from the shoot base for plants harvested at heading and three weeks after anthesis are shown in Figs. 1 and 2, respectively. Absolute lengths of internodes and leaf sheaths in plants harvested at heading and at milk maturity, three weeks after anthesis, are given in Table 1. At heading, the specific modulus of elasticity ranged, over the entire shoot length, from below 0.15 MPa \( \cdot \text{m}^{-2} \cdot \text{kg}^{-1} \) to 6.00 MPa \( \cdot \text{m}^{-2} \cdot \text{kg}^{-1} \) and from 0.39 MPa \( \cdot \text{m}^{-3} \cdot \text{kg}^{-1} \) to 6.74 MPa \( \cdot \text{m}^{-3} \cdot \text{kg}^{-1} \) in stems and leaf sheaths, respectively. Modulus values increased in stems, particularly in upper internodes, during the course of differentiation of strengthening tissues and did not change in leaf sheaths during the period between heading and milk maturity. At milk maturity, the stiffness of tissue material, as measured ultrasonically, ranged from 1.71 MPa \( \cdot \text{m}^{-3} \cdot \text{kg}^{-1} \) to 7.26 MPa \( \cdot \text{m}^{-3} \cdot \text{kg}^{-1} \) in stems and from 0.41 MPa \( \cdot \text{m}^{-3} \cdot \text{kg}^{-1} \) to 6.35 MPa \( \cdot \text{m}^{-3} \cdot \text{kg}^{-1} \) in leaf sheaths. At heading, there was a characteristic pattern of

\[
E v^2 = \frac{d}{\lambda}
\]