

ANALYSIS OF STRESS DISTRIBUTION AND LEAF BLADE BENDING DURING BOUNDED GROWTH

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INTRODUCTION

Mechanical factors play an important role in plant tissues growth and development. Plant growth is tightly connected with cell divisions, new cell walls appearing and cell volumes increasing caused by turgor pressure and cell walls loosening and yielding. In biomechanics the plant tissue is considered as integral porous deformable skeleton of cell walls filled with viscous incompressible liquid (intracellular liquid and contents of plant vessels) [1]. Xylem sap moves through the xylem vessels, delivers mineral and regulatory components into cells and provides increasing of mass of the solid skeleton. The rate of cell growth is controlled by wall loosening caused by biochemical factors and wall yielding under the influence of the turgor pressure. The tissues consist of elements with different geometry and mechanical properties which are arranged in regular patterns. For instance, plant leaves possess vascular bundle embedded into the main tissue (mesophyll). During the growth the vascular elements elongate along their axes while the mesophyll cells divide and remain isometric. Local mechanical stress appearing at the borders between the tissues with different growth properties supplies the driving force for coordinated growth of inhomogeneous plant material [1,2]. During the natural growth the stress field plays a regulatory role promoting the fibers and new cell walls orientation accordingly the principal directions of the stress tensor σ_{ik} [3-5]. In the whole tissue a zero-stress state can be achieved as a result of stress relaxation at time $t > t^*$, where $t^* = 1-2$ days – characteristic time of growth deformations.

Leaf growth kinematics observations let determine one set of the rheological parameters of the plant material – the own growth rates [6]. The other parameters can be determined at the non-zero stress conditions only [2,5]. Investigation of constrained growth makes it possible to determine the role of mechanical stress in plant growth regulation at tissue level [5]. In the present paper some results of experimental and theoretical investigation of plant leaf growth are presented.

EXPERIMENTATION

Plants of nasturtium (*Tropaeolum major*) were cultured in a phytotron. The nasturtium leaf has peltate shape with a palmed venation. Seven main veins originate in the center of the blade and stretch in radial directions toward the blade edge. At unbounded conditions the nasturtium leaf exhibit quasiisotropic growth with $e_{ii} = const$ [1,2]. In the experiment a thin layer of special polymeric material was glued on the contour of the unfolded new leaf blade. After drying a thin flexible nonstretchable string was formed at the leaf perimeter. Leaf growth deformations were followed by daily digital photographs (three projections) of the leaf right up to the end of the leaf growth. The gradually bulging of leaf blade was observed and blade shapes were digitized by the image analysis of 59 leaves. The secondary bulgings bounded by the second-order veins appeared in the areas with maximal curvature (Fig.1). The curves of the deflection in the center of the blade (Fig.2) confirm the influence of the stage of leaf

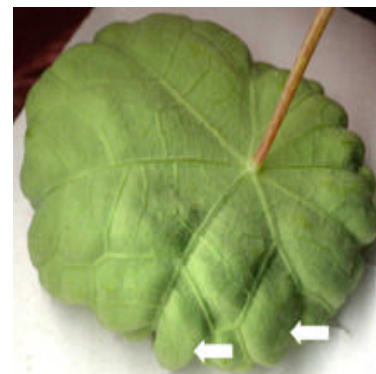


Figure 1. Growth bulging of perimeter-bounded Nasturtium leaf.

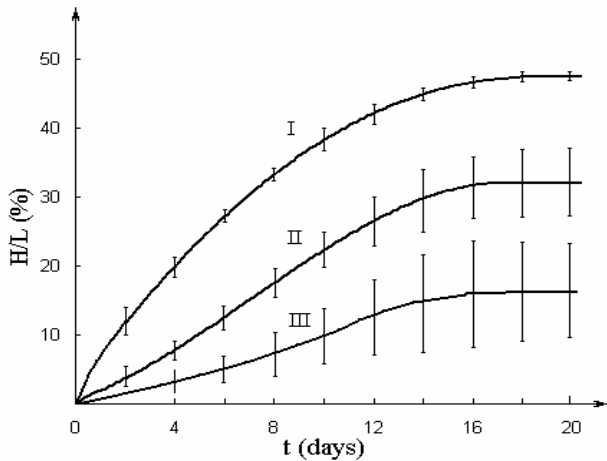


Figure 2. The deflection H in the center of the blade as a function of time. L – the constant initial diameter of the leaf blade. I,II,III – the groups of leaves, bounded immediately, a day and two days after the blade unfolding.

growth and mechanical stress on the growth rate. The leaves in the groups had different initial diameters ($L_I < L_{II} < L_{III}$) and final deflections ($H_I > H_{II} > H_{III}$). The total surfaces of the curved blades were practically equal. Existence of mechanical stress (compression in radial directions) in growing bounded leaf was revealed by incision of the blade in different directions and edges motion observation.

MODEL OF GROWING CONTINUUM

In mechanics of biological continuous media the growing plant tissues are considered as viscoelastic heterogeneous anisotropic materials. The mechanical model of the growing plant tissue is based on the static equation (at $t > t^*$ and at the absence of external forces) [1,7]:

$$\sigma_{ik,k} = 0 \quad (1)$$

The strain velocity tensor $e_{ik} = (v_{i,k} + v_{k,i})/2$ is introduced as

$$e_{ik} = A_{ik} + B_{iklm}\sigma_{lm} \quad (2)$$

where \hat{A} , \hat{B} – tensorial rheological coefficients, \hat{A} – the own growth rate at the absence of stress, \vec{v} – velocity.

At unloaded borders the problem (1)-(2) has the trivial solution $\hat{\sigma} \equiv 0$ and zero-stress growth is achieved. At loaded borders the boundary conditions are given in common form:

$$\sigma_n|_{\Gamma_1} = \hat{\sigma}^*, \quad \vec{v}|_{\Gamma_2} = \vec{v}^* \quad (3)$$

where $\Gamma = \Gamma_1 \cup \Gamma_2$ – the surface of the growing body. The system (1)-(3) in one- and two-dimensional forms was used for plant root, leaf and stem natural (unbounded) growth modeling [1,2,6,7].

Numerical Investigation

The problem (1)-(3) as applied to a round thin plate of growing orthotropic material is solved by finite element method. The thin non-

stretched flexible string was attached at the plate perimeter. The stress distribution in the plate during the plane stress state is investigated. The initial deflection $H_0 = 0.02L$ was established for the bending of the plate. The stress field in the bent plate (Fig.3) led to growth acceleration and the bulging enhancement. The maximal stresses are comparable with the value $\hat{\sigma}^* \sim 0.03-0.05$ MPa, that influenced the growth rate at the cellular level [8].

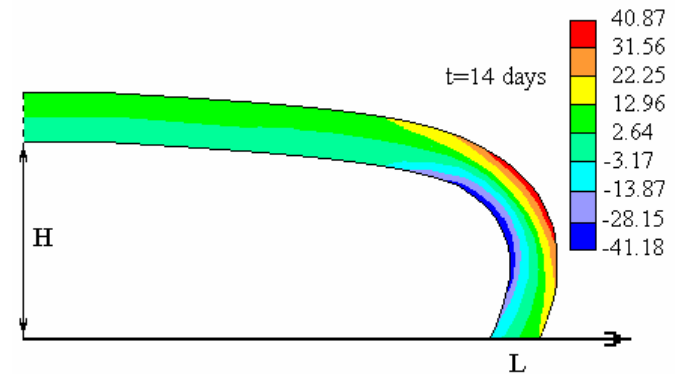


Figure 3. Stress distribution in the cross-section of leaf blade, σ (kPa).

The compressing mechanical forces reduce the main veins growth to a greater extent than the mesophyll growth. As a result the bounded leaf has the smaller diameter and almost the same total photosynthesized surface then the unbounded one. The fields of principal directions of stress tensors in bounded and unbounded growing plates are quite different. The appropriate experimental data of cell walls alignment in bounded growing leaf would clarify the role of mechanical stress in whole leaf blade growth.

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