TRANSPIRATION

G.V. Menzhulin

State Hydrological Institute, St.Petersburg, Russia

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Summary

Practically all water taken out of soil goes to the atmosphere and only a small portion of the absorbed water is used by plants during their metabolism. Though all above-ground parts of the plants lose water, these losses differ greatly in different plant tissues. The major water quantity lost by the plants as water vapor is the result of transpiration of leaves. Other plant parts e.g. buds, branches and fruits also lose water as vapor, but sometimes this quantity is significant. Sometimes a small portion of water can be lost during guttation or as a solution of secretion of glands and tissue juice when the plant is damaged, but the major water loss occurs through stomata as transpiration.

1. Introduction: water loss by plants

The major portion of water from plants evaporates through stomata, cuticula or lenticels; but the most significant water loss is through stomata. Some water evaporates from buds because bud scales do not completely protect buds against water loss. It has been established that the intensity of bud transpiration per unit of bud surface is similar to the intensity of cuticular transpiration of leaves. The amount of bud transpiration greatly differs between different plant species and varies within a day and season. For example, bud transpiration in pines is much more intensive than elms. Bud transpiration depends on bud size, water content in the bud and water deficit in the surrounding air. Sometimes buds absorb water out of the air but this process is of not ecological importance. It has been discovered that bud transpiration in the regulated conditions of

the medium was three times more intensive than water absorption. In general, buds seldom absorb water, and only in small quantities.

Reproductive plant organs also lose water, and in some cases this loss may be quite significant. For example, calathides of sunflowers, poppy capsules and pepper fruits can transpire more intensively under certain conditions than the leaves of these plants. A definite amount of water evaporates from the surfaces of the branches and stems of trees. In these cases the major quantity of water is lost through lenticels. Though the total amount of water evaporated through lenticels is much less than that lost through the leaves the actual intensity of transpiration per unit of the evaporating surface differs little. Transpiration of branches in winter time often causes water deficit and plants die because of dehydration.

It is assumed that transpiration consists of two processes: the first one is water migration from the ends of the xylem (leaf veins) to the cellular walls of the outer layer of cells. The second process is evaporation of water from the outer layers of plants into the air through cuticula or from the cellular walls of the mesophyll into the intercellular space, with subsequent diffusion of vapor to the atmosphere through stomata.

The water migration from the tips of xylem to the evaporating surface can occur either through protoplasts or in microscopic strims in the cellular walls. The intensity of water migration, however, within the system of cellular walls is quantitatively more significant than its motion through protoplasts. Water moving within the system of cellular walls reaches the evaporating surface avoiding the live protoplasm of the cells.

2. Cuticular Transpiration

Water vapor loss through the leaf epidermis is usually small if compared with the total transpiration through open stomata. But if stomata are closed, as happens during droughts, the cuticular component of transpiration becomes very important in the water regimes of many plant species. The cuticular transpiration rate varies greatly in different species from small losses to 50% of the total water loss. In most plant species it is on average less than 10% of the total water loss. For example, in tree species such as Grecian laurel (*Laurus nobilis*), Grecian strawberry tree (*Arbutus andrachne)*, Aleppo pine (*Pinus halepensis*) and Italian cypress (*Cupressus sempervirens*), typical of the east Mediterranean region, the cuticular transpiration was very weak or there was no transpiration at all at the end of the dry season. In conditions of extreme soil and air aridity the cuticular transpiration from holly oaks (*Quercus ilicifolia*) was almost not observed, too. Conversely, in semi-arid regions of northeast Brazil, the cuticular transpiration from some plant species varies from 6% to 30% of the total water loss.

Variability of cuticular transpiration from different plant species is much greater than variability of stomatal transpiration. The transpiration rate of plants with widely open stomata can vary from 2 to 6 milligrams of water per 1 gram of leaf tissue per minute. Variations in the cuticular transpiration rate of plants with closed stomata were more intensive, usually from 0.10 to 1.5 milligrams of water per 1 gram per minute.

The cuticular transpiration is controlled mainly by the thickness of the cutin layer. Magnolia species and conifers with thick cutin lose little water through the leaf epidermis. Conversely, plant species with thin cutin layers lose water even after the closure of stomata and can consequently suffer greatly during droughts. Stomatal transpiration is regulated to a less extent by tarry substances covering the leaves, and by volatile oils secreted by the glands. The cuticular transpiration of old leaves is more intensive than the cuticular transpiration of young leaves, probably due to stronger solution and destruction of their cuticles, and splitting and formation of cracks caused by periodic water deficits.

3. Stoma Opening and Transpiration

Stoma opening is a biological process caused by various interrelated factors. The complexity of this process provides the possibility of extremely intricate control of the process.

Difference in the turgor of the cells closing and adjacent to the stoma crack is the moving force causing changes in the aperture of the stoma. As the closing cell absorbs water in the osmotic way, a thinner and elastic part of the envelope remote from the crack tends to a stretch. As a thicker and less elastic part of the envelope around the crack stretches less intensively, the shape of the closing cells becomes semicircular, resulting in the stoma opening. Different factors of the environment affect the stoma both directly and indirectly and cause inner changes which, in turn, lead to changes in the turgor. These environmental factors affecting the stomata opening and closing include water deficit, carbon dioxide concentration, intensity of light and air temperature.

When transpiration exceeds water absorption by roots in such a way that the turgor decrease attains a critical level, the stomata can close. It is usually assumed that the regulating capacity of the stomata motions explained by the water deficit can be subdivided into hydropassive and hydroactive reactions. In case of a passive reaction observed in the condition of weak water deficit, stomata can be open as a result of the weaker pressure of the surrounding cells. The hydroactive closing of the stomata occurs with heavier water deficit at crest values depending on plant species, leaf age and rate of plant adaptation to the environment. For example, stomata in *Vicia faba* begin closing at water deficit of 3%, but in different herbs stomata closing is observed at water deficit of 10 to 15%. The threshold value of water deficit causing stomata closing in the needles of *Pinus excelsa* in the shade is 5 to 6%, and in the sunshine, 8 to 9%. With higher light intensity higher water deficits are required for stomata closing; this emphasizes the effect of different factors on the mechanism of stomata motions.

As to the effect of carbon dioxide concentration on stomatal control, it is possible to note that in *Vicia faba* and *Ranunculus ficaria* the stomata motions are sensitive to variations in carbon dioxide concentration over several hours with weak water deficit of 2 to 5%. But if water deficit exceeds the threshold values, the stomata opening is accompanied by a hydroactive closing. The hydroactive reaction of stomata closing becomes more intensive as the water deficit becomes longer and more intensive. Some authors believe that water deficit is the most important factor determining stomatal

motions, not light or carbon dioxide concentration. During long droughts the stomata close earlier every day because turgor decreases every day to a level lower than the threshold value, as a result of transpiration.

Low carbon dioxide concentration in the stomata causes their opening but the mechanism of operation of this factor is not yet completely clear. Light affects the stomata indirectly, reducing carbon dioxide concentration in the intercellular space through the more intensive photosynthesis, and there is also some evidence of a direct effect of light on stomata motions. It depends on the light intensity and it happens in air without carbon dioxide. The temperature of the air probably has an effect in two ways, causing stomata closing with rise of minimum CO_2 concentration in the intercellular space, and stomata opening when extreme accumulation of carbon dioxide is not observed in the intercellular space. These experimental results emphasize once again that opening and closing of the stomata depend on a very complicated interaction of various factors.

Photosynthesis and enzymatic reactions in the closing cells probably also contribute to control of stomatal motions. More intensive synthesis of carbohydrates in the closing cells increases a deficit of pressure of moisture diffusion and causes water seepage thus stimulating the stomata opening. Experiments are known which demonstrate that high photosynthetic activity in the closing cells of stomata is not sufficient to explain the maximum rate of osmotic pressure change observed during the stomata opening. This proves that in any case the major effect of photosynthesis in the closing cells in some plant species on the control of stomata motions is produced by the removal of carbon dioxide rather than by the synthesis of carbohydrates.

The reversible transformation of starch into sugar also affects changes in the deficit of the diffusion pressure and turgor in the closing cells. It is shown that the rate of stomata closure depends on the starch content in the closing cells. Though it is not yet proved completely, it is assumed that control of the stomatal mechanism greatly affects the hydration of colloids and changes in the permeability of the plasmalemma of the closing cells. For example, during experiments with *Zebrina* species, stomata opening caused by light, higher temperatures or the effect of buffer solutions was accompanied by reduced starch content in the closing cells. Correlation between the colloid content in the closing cells and stomata closing is usually not discovered. Malnutrition of plants decreased the starch content but it did not affect the content of colloidal substances in the closing cells and greatly decreased the rate of stomata opening and stomata apertures. This made it possible to conclude that the enzymatic mechanism related to starch phosphorolysis played an important role in the control of stomatal motions, especially as phosphorylase was discovered in the closing cells.

With complete turgescence of leaves, light is probably the main factor regulating stomata openings. As transpiration proceeds, however, increase of water deficit in the plant is inevitable. A subsequent turgor decrease causes stomata closing—an effect which is stronger than the effect of light stimulating stomata opening. Thus, the state of the stomata often depends on two opposing forces. Hydropassive reaction of stomata at weak water deficits probably does not greatly affect the control of stomata opening. The rate of the inner pressure development in the water regime in plants and a trend towards

this change probably more greatly affect the stomatal motions than the actual rate of water deficit. Hydropassive and hydroactive mechanisms can operate jointly but turgor change, however, if it does occur, is the main factor in the mechanism of stomatal motions.

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Biographical Sketch

Gennady Menzhulin was born in 1942 in Batumi, Georgia. He attended the Physics Faculty of St. Petersburg State University, and obtained a PhD, in 1970, from the Main Geophysical Observatory, St. Petersburg. In 1986 he gained a ScD, State Hydrological Institute, St.Petersburg and in 1993 he became Professor in the National Supreme Classifying Committee, Moscow.

He has been Deputy Director of Science, since 1998, of the Research Center for Interdisciplinary Environmental Cooperation of Russian Academy of Sciences. Since 2001 he has been Professor and Chair of Climatology and Environmental Monitoring at St. Petersburg State University.

International experience:

He has been the organizer and secretary of 5 Symposiums (1976-1990) for the US-USSR (Russian) Agreement on Protection of the Environment. Project 02.08-11: Climate Change (1976-1994), and Co-Chair of Joint US-Russian Project on Climate Changes and their Consequences. (1990-1994).

Intergovernmental Panel on Climate Change (UNESCO, WMO, ICSU):

- Co-Head of Agriculture and Forestry Subgroup, Working Group II. (1991).
- Expert Contributor to the Second Report of Working Group II (1996).

Russian-German Agreement on Protection of Environment.

- Project IV.1. Scientific Basis of Global Ecosystem Monitoring Including Monitoring in Biosphere Reserves. Co-Leader of Subproject (1989-1994).

International Country Studies Program: US Support for Climate Change Studies, Communications and Technology Assessments.

- Expert Contributor for the Study of the Russian Agriculture Sector. (1994-1996).

INTAS (European Union) International Projects.

- Expert Contributor in the Project on the Dynamics of the Terrestrial Biota (1994-1996).
- Principal Investigator in the Project on Evaluation (1994-1996).

INCO-Copernicus (European Union) International Project.

- Russian team leader in the project "Adaptation of Efficient…" (1999-2002).

Lecturing activities:

Courses in St. Petersburg State University, on climatology, paleoclimatology, climate changes, and modern problems of climatological research.

Research activities:

Global warming, ecological and economic consequences of modern climate changes, eological modeling, energy and matter transport in the "soil-vegetation-atmosphere" system.

Books:

Budyko M.I., Menzhulin G.V. et al. 1987. Anthropogenic Climate Changes. Leningrad, Gidrometeoizdat. 404p. (in Russian).

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Publications:

More than 120 publications (USSR, Russia, USA, etc.) in journals and proceedings of international, bilateral and national conferences.