Chapter 36

Transport in Vascular Plants

Key Concepts

36.1 Physical processes drive the transport of materials in plants over a range of distances

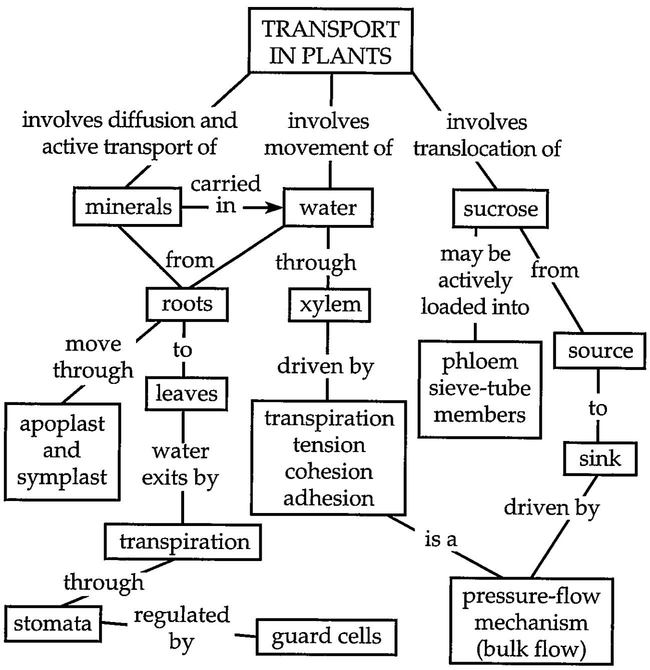
36.2 Roots absorb water and minerals from the soil

36.3 Water and minerals ascend from roots to shoots through the xylem

36.4 Stomata help regulate the rate of transpiration

36.5 Organic nutrients are translocated through the phloem

Framework



Chapter Review

Adaptations to life on land involved the specialization of roots to absorb water and minerals, shoots to absorb CO_2 and light, and vascular tissue for the transport of materials between roots and shoots.

36.1 Physical processes drive the transport of materials in plants over a range of distances

Transport in plants involves the transport of water and solutes by individual cells, the short-distance movement of substances from cell to cell within tissues, and the long-distance transport of sap in xylem and phloem.

Selective Permeability of Membranes: A Review Solutes may move across the selectively permeable plasma membrane by **passive transport** when they diffuse down their concentration gradients. **Active transport** requires the cell to expend energy to move a solute against its electrochemical gradient. **Transport proteins** speed passive transport and may be either proteins that selectively bind and transport a solute, or selective channels through a membrane. Some channels are gated: They open and close in response to certain stimuli.

The Central Role of Proton Pumps A plant **proton pump** uses ATP to pump hydrogen ions (H^+) out of the cell, generating an energy-storing proton gradient and a **membrane potential** resulting from the separation of charges. The membrane potential helps drive positively charged ions (such as K^+) down their electrochemical gradient and into the negatively charged cell. In **cotransport,** a solute can be pumped against its concentration gradient when a transport protein links its passage to the "downhill" movement of H^+. **Chemiosmosis** links energy-releasing and energy-consuming processes using a transmembrane proton gradient like that created by the proton pump.

Effects of Differences in Water Potential The passive transport of water across a membrane is called **osmosis. Water potential,** designated by Ψ *(psi),* is a useful measurement for predicting the direction that water will move when a plant cell is surrounded by a particular solution. It takes into account both solute concentration and the physical pressure exerted by the plant cell wall. Free water, which is not bound to solutes or surfaces, will flow from a region of higher water potential to one of lower water potential. Water potential is measured in **megapascals (MPa);** 1 MPa is equal to about 10 atmospheres of pressure. The water potential of pure water in an open container under standard conditions is assigned the value of 0 ($\Psi = 0$ MPa).

The combined effect of solute concentration and pressure is shown by the *water potential equation:* $\Psi = \Psi_S + \Psi_P$. **Solute potential (Ψ_S),** also called **osmotic potential,** is proportional to the number of solute molecules. Solutes bind water, reducing the number of free water molecules and the capacity of the water to do work. Solutes lower the water potential, and a solution's Ψ_S is always negative.

Pressure potential (Ψ_P) measures the pressure on a solution and can be a positive or negative value. Negative pressure is tension. The positive pressure of a cell pushing against the cell wall is called **turgor pressure.**

A **flaccid** plant cell ($\Psi_P = 0$) bathed in a solution more concentrated than the cell will lose water by osmosis because the solution has a lower (more negative) Ψ. The cell's protoplast will shrink and **plasmolyze.** When bathed in pure water, the cell has the lower Ψ. Water will enter the cell until enough turgor pressure builds up so that Ψ_P and Ψ_S are equal and opposite in magnitude, and $\Psi = 0$ both inside and outside the cell. Net movement of water will then stop.

Plant cells are usually **turgid;** they have a greater solute concentration than their extracellular environment and turgor pressure keeps them firm. The loss of turgor can be seen when a plant's leaves and stems **wilt.**

Although small water molecules can move relatively freely across membranes, the rate at which they move is too rapid to be attributed entirely to diffusion through the lipid bilayer. Water-specific transport proteins called **aquaporins** increase the rate of water diffusion.

■ INTERACTIVE QUESTION 36.1

a. A flaccid plant cell has a water potential of −0.6 MPa. Fill in the water potential equation for this cell.

$\Psi_P =$

$+\Psi_S =$

$\Psi =$

b. The cell is then placed in a beaker of distilled water ($\Psi = 0$). Fill in the equation for the cell after it reaches equilibrium in pure water. Explain what happens to the water potential of this cell.

$\Psi_P =$

$+\Psi_S =$

$\Psi =$

c. Explain what would happen to the same cell if it is placed in a solution that has a water potential of −0.8 MPa. Fill in the equation for the cell after it is moved to this more concentrated solution and reaches equilibrium.

$\Psi_P =$

$+\Psi_S =$

$\Psi =$

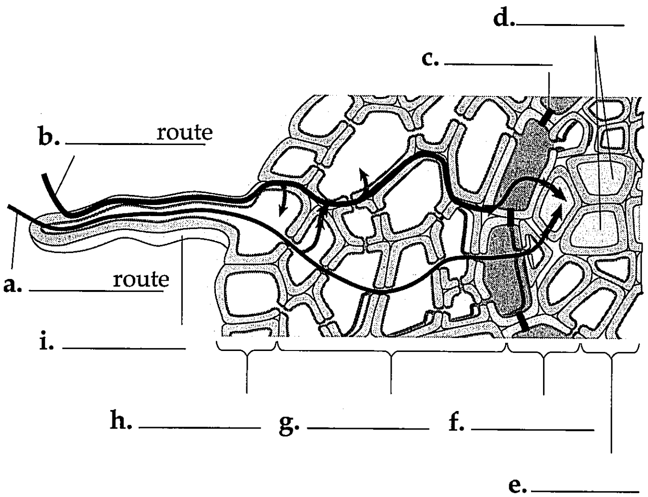
Three Major Compartments of Vacuolated Plant Cells The three compartments of most mature plant cells are the cell wall, cytosol, and the vacuole. The **vacuolar membrane,** or **tonoplast,** regulates solute movement between the cytosol and the cell sap of the vacuole. Its proton pumps move H^+ from the cytosol into the vacuole, creating a pH gradient that is used to move ions.

The cytosolic compartments of plant cells are connected by plasmodesmata, forming a cytosolic continuum called the **symplast.** The continuum of cell walls and intercellular spaces is called the **apoplast.**

Functions of the Symplast and Apoplast in Transport Short-distance or lateral transport of water and solutes within plant tissues can occur by three routes: transmembrane, by crossing plasma membranes and cell walls; symplastic, moving through plasmodesmata; and apoplastic, the extracellular pathway along cell walls and extracellular spaces. Solutes and water may change routes during transit.

■ INTERACTIVE QUESTION 36.2

Label the diagram of the cell layers and routes of transport of water and minerals from the soil through the root. (Letters a and b refer to routes of transport; letters c–i refer to cell layers or structures.)



Bulk Flow in Long-Distance Transport Long-distance transport throughout plants occurs by **bulk flow,** the movement of fluid driven by pressure. Water and minerals move through tracheids and vessels of xylem as the result of tension created by transpiration. Sap is forced through phloem sieve tubes by positive pressure.

Sieve-tube members lack most cellular organelles, and vessel elements and tracheids are dead (and empty) at maturity, both facilitating more efficient bulk flow.

36.2 Roots absorb water and minerals from the soil

The Roles of Root Hairs, Mycorrhizae, and Cortical Cells Much of the absorption of water and mineral salts occurs along young root tips where root hairs are located. The soil solution soaks into the hydrophilic walls of epidermal cells and moves along the apoplast into the root cortex, exposing a large surface area of plasma membrane for the uptake of water and minerals. Active transport of minerals allows cells to accumulate essential minerals. **Mycorrhizae,** symbiotic associations of plant roots and fungal hyphae, greatly increase the surface area for absorption of water and selected minerals.

The Endodermis: A Selective Sentry The **endodermis,** the innermost layer of cortex cells surrounding the vascular cylinder, selectively screens all minerals entering the vascular tissue. A ring of suberin around each endodermal cell, called the **Casparian strip,** prevents water from the apoplast from entering the vascular cylinder without passing through the selectively permeable plasma membrane of an endodermal cell. Water and minerals that had already entered the symplast through a cortex or epidermal cell pass through plasmodesmata of endodermal cells into the vascular cylinder.

By a combination of diffusion and active transport, minerals move from endodermal cells to the apoplast and enter the nonliving xylem tracheids and vessel elements along with water.

36.3 Water and minerals ascend from roots to shoot through the xylem

The branching of xylem veins provides water to the cells of each leaf. Through **transpiration,** the loss of water vapor from leaves, plants lose a tremendous amount of water that must be replaced by water transported up from the roots.

Factors Affecting the Ascent of Xylem Sap As minerals are actively pumped into the vascular cylinder and prevented from leaking out by the endodermis, water potential in the vascular cylinder is lowered. Water flows in from the cortex, resulting in **root pressure,** which pushes xylem sap upward. Root pressure may cause **guttation,** the exudation of water droplets from leaves when more water is forced up the xylem than is transpired by the plant.

By transpiration, water vapor from saturated air spaces within a leaf exits to drier air outside the leaf by way of stomata. The thin layer of water that coats the mesophyll cells lining the air spaces begins to evaporate. The adhesion of the remaining water to the hydrophilic walls and the cohesion between water molecules causes the water film to form a concave shape. This meniscus increases the tension of the water layer. This negative pressure pulls water from the xylem and through the apoplast and symplast of the mesophyll to the cells and surface film lining the air spaces. Water moves along a gradient toward the most negative water potential, from xylem to neighboring cells to air spaces to the drier air outside the leaf.

The transpirational pull on xylem sap is transmitted from the leaves to the root tips by the cohesiveness of water that results from hydrogen bonding between molecules. Adhesion of water molecules to the hydrophilic walls of the narrow xylem elements and tracheids also contributes to overcoming the downward pull of gravity.

The upward transpirational pull on the cohesive sap creates tension within the xylem, lowering the water potential so that water flows passively from the soil, across the cortex, and into the vascular cylinder.

A break in the chain of water molecules by the formation of a water vapor pocket in a xylem vessel, called cavitation, breaks the transpirational pull, and the vessel cannot function in transport.

Xylem Sap Ascent by Bulk Flow: A Review The transpiration-cohesion-tension mechanism results in the bulk flow of water and solutes from roots to leaves. Water potential differences caused by solute concentration and pressure contribute to the movement of water from cell to cell, but solar-powered tension caused by transpiration is responsible for long-distance transport of water and minerals.

■ INTERACTIVE QUESTION 36.3

Explain the contribution of each of the following to the long-distance transport of water.

a. Transpiration:

b. Cohesion:

c. Adhesion:

d. Tension:

36.4 Stomata help regulate the rate of transpiration

A plant's tremendous requirement for water is partly a consequence of making food by photosynthesis. To obtain sufficient CO_2 for photosynthesis, leaves must exchange gases through the stomata and provide a large internal surface area for CO_2 uptake, but also from which water may evaporate.

Effects of Transpiration on Wilting and Leaf Temperature When transpiration exceeds the water available, leaves wilt as cells lose turgor pressure. Transpiration also produces evaporative cooling, maintaining a cooler temperature in leaf cells for critical enzymes.

Stomata: Major Pathways for Water Loss A plant loses most of its water through stomata. Guard cells regulate the size of stomatal openings and control the rate of transpiration. Stomatal densities in many plant species are both genetically and environmentally influenced; densities have been shown to relate to CO_2 levels, providing a measure of such levels in past climates.

When the kidney-shaped guard cells of eudicots become turgid and swell, their radially oriented microfibrils cause them to increase in length and buckle outward, increasing the size of the gap between them. When the guard cells become flaccid, they sag and close the space.

Guard cells can actively accumulate potassium ions (K^+), which lowers water potential and leads to the osmotic inflow of water and an increase in turgor pressure. The exodus of K^+ (with water following) leads to a loss of turgor. The regulation of aquaporins may also vary the membrane's permeability to water. The movement of K^+ across the guard cell membrane is probably coupled with the generation of membrane potentials by proton pumps that transport H^+ out of the cell.

The opening of stomata at dawn is related to at least three factors. First, light stimulates guard cells to accumulate K^+, perhaps triggered by the illumination of blue-light receptors that activate the proton pumps. Second, stomata are stimulated to open when CO_2 within air spaces of the leaf is depleted as photosynthesis begins in the mesophyll. The third factor is a daily rhythm of opening and closing that is endogenous to guard cells. Cycles that have intervals of approximately 24 hours are called **circadian rhythms.**

Environmental stress can cause stomata to close during the day. Guard cells lose turgor when water is in short supply. Also, a hormone called abscisic acid, produced in the roots in response to a lack of water, signals guard cells to close stomata.

■ INTERACTIVE QUESTION 36.4

What is meant by the photosynthesis-transpiration compromise? How might a sunny, windy, dry day influence this compromise in a plant?

Xerophyte Adaptations That Reduce Transpiration Many **xerophytes,** plants adapted to arid climates, have leaves that are small and thick, limiting water loss by reducing their surface-to-volume ratio. Leaf cuticles may be thick, and the stomata may be sheltered in depressions. Some desert plants lose their leaves in the driest months.

Succulent plants of the family Crassulaceae and some other plant families assimilate CO_2 into organic acids during the night by a pathway known as CAM (crassulacean acid metabolism) and then release it for photosynthesis during the day. Thus, the stomata are open at night and can be closed during the day, reducing water loss.

36.5 Organic nutrients are translocated through the phloem

Movement from Sugar Sources to Sugar Sinks **Translocation,** the transport of photosynthetic products throughout the plant, occurs in the sieve-tube members of phloem. Phloem sap may have a sucrose concentration as high as 30% and may also contain minerals, amino acids, and hormones.

Phloem sap flows from a **sugar source,** where it is produced by photosynthesis or the breakdown of starch, to a **sugar sink,** an organ that consumes or stores sugar. The direction of transport in any one sieve tube depends on the location of the source and sink connected by that tube, and the direction may change with the season or needs of the plant.

■ **INTERACTIVE QUESTION 36.5**

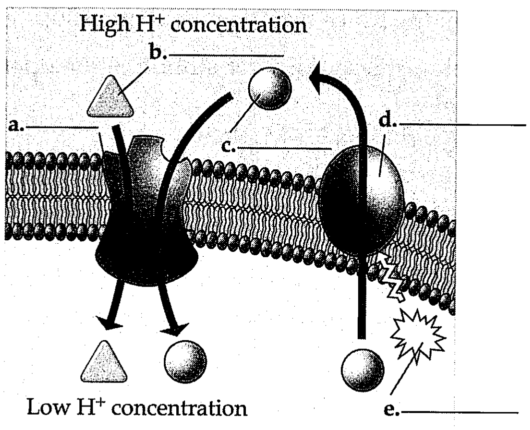
Explain how a root or tuber can serve as both a sugar source and a sugar sink.

In some species, sugar in the leaf moves through the symplast of the mesophyll cells to sieve-tube members. In other species, sugar first moves through the symplast and then into the apoplast in the vicinity of sieve-tube members and companion cells, which actively accumulate sugar. In some plants, companion cells are specialized as **transfer cells** with ingrowths of their wall that increase surface area for movement of solutes from apoplast to symplast.

Phloem loading requires active transport in plants that accumulate high sugar concentration in the sieve tubes. Proton pumps and the cotransport of sucrose through membrane proteins along with the returning protons is the mechanism used for active transport. Sugar is moved by various mechanisms out of sieve tubes at the sink end. The concentration gradient favors this movement because sugar is either being used or converted into starch within sink cells.

■ **INTERACTIVE QUESTION 36.6**

Label the components of this diagram of the chemiosmotic mechanism used to actively transport sucrose into companion cells or sieve-tube members.



Pressure Flow: The Mechanism of Translocation in Angiosperms The rapid movement of phloem sap from source to sink is due to a pressure flow mechanism. High solute concentration at the source lowers the water potential, and the resulting movement of water into the sieve tube produces positive pressure. At the sink end, the osmotic loss of water following the exodus of sucrose into the surrounding tissue results in a lower pressure. The difference in these pressures causes sap to move by bulk flow from source to sink. Innovative tests of this hypothesis support it as the explanation for the flow of sap in the phloem of angiosperms.

Word Roots

apo- = off, away; **-plast** = formed, molded (*apoplast:* in plants, the nonliving continuum formed by the extracellular pathway provided by the continuous matrix of cell walls)

aqua- = water; **-pori** = a pore, small opening (*aquaporin:* a transport protein in the plasma membranes of a plant or animal cell that specifically facilitates the diffusion of water across the membrane)

chemo- = chemical (*chemiosmosis:* the production of ATP using the energy of hydrogen-ion gradients across membranes to phosphorylate ADP)

circa- = a circle (*circadian rhythm:* a physiological cycle of about 24 hours, present in all eukaryotic organisms, that persists even in the absence of external cues)

co- = together; **trans-** = across; **-port** = a gate, door (*cotransport:* the coupling of the "downhill" diffusion of one substance to the "uphill" transport of another against its own concentration gradient)

endo- = within, inner; **-derm** = skin (*endodermis:* the innermost layer of the cortex in plant roots)

gutt- = a drop (*guttation:* the exudation of water droplets caused by root pressure in certain plants)

mega- = large, great (*megapascal:* a unit of pressure equivalent to 10 atmospheres of pressure)

myco- = a fungus; **-rhizo** = a root (*mycorrhizae:* mutualistic associations of plant roots and fungi)

osmo- = pushing (*osmosis:* the diffusion of water across a selectively permeable membrane)

sym- = with, together (*symplast:* in plants, the continuum of cytoplasm connected by plasmodesmata between cells)

turg- = swollen (*turgor pressure:* the force directed against a cell wall after the influx of water and the swelling of a walled cell due to osmosis)

xero- = dry; **-phyto** = a plant (*xerophytes:* plants adapted to arid climates)

Structure Your Knowledge

1. Describe the ways in which solutes may move across the plasma membrane in plants.
2. Both xylem sap and phloem sap move by bulk flow in an angiosperm. Compare and contrast the mechanisms for their movement.

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Which of the following is *not* a component of the symplast?
   a. sieve-tube members
   b. xylem tracheids
   c. endodermal cells
   d. cortex cells
   e. companion cells
2. Proton pumps in the plasma membranes of plant cells may
   a. generate a membrane potential that helps drive cations into the cell through their specific carriers.
   b. be coupled to the movement of K^+ into guard cells.
   c. drive the accumulation of sucrose in sieve-tube members.
   d. contribute to the movement of anions through a cotransport mechanism.
   e. be involved in all of the above.
3. The Casparian strip prevents water and minerals from entering the vascular cylinder through the
   a. plasmodesmata.
   b. endodermal cells.
   c. symplast.
   d. apoplast.
   e. xylem vessels.
4. The water potential of a plant cell
   a. is equal to 0 MPa when the cell is in pure water and is turgid.
   b. is equal to that of air.
   c. is equal to -0.23 MPa.
   d. becomes greater when K^+ ions are actively moved into the cell.
   e. becomes 0 MPa due to loss of turgor pressure in a concentrated sugar solution.
5. Guttation results from
   a. the pressure flow of sap through phloem.
   b. a water vapor break in the column of xylem sap.
   c. root pressure causing water to flow up through xylem faster than it can be lost by transpiration.
   d. a higher water potential of the leaves than of the roots.
   e. specialized structures in transport cells that accumulate sucrose.
6. Which of these is *not* a major factor in the movement of xylem sap up a tall tree?
   a. transpiration
   b. plasmodesmata
   c. adhesion
   d. cohesion
   e. tension
7. Adhesion is a result of
   a. hydrogen bonding between water molecules.
   b. the pull on the water column as water evaporates from the surfaces of mesophyll cells.
   c. tension within the xylem caused by a negative pressure.
   d. attraction of water molecules to hydrophilic walls of narrow xylem tubes.
   e. the high surface tension of water.
8. What is a function of the tonoplast?
   a. regulate movement of solutes between cells joined by plasmodesmata
   b. help move water and minerals past the Casparian strip into the vascular cylinder
   c. help maintain low cytosolic H^+ concentration by pumping H^+ into the vacuole
   d. increase the surface area for pumping H^+ out of transfer cells
   e. control the expansion of turgid guard cells so that the space between them opens up
9. Which of these does *not* stimulate the opening of stomata?
   a. daylight in a CAM plant
   b. depletion of CO_2 in the air spaces of the leaf
   c. stimulation of proton pumps that results in the movement of K^+ into the guard cells
   d. circadian rhythm of guard cell opening
   e. an increase in the turgor of guard cells

10. Your favorite spider plant is wilting. What is the most likely cause and remedy for its declining condition?
  a. Water potential is too low; apply sugar water.
  b. The stomata won't open; no remedy available.
  c. Plasmolysis of its cells; water the plant.
  d. Cavitation; perform a xylem vessel bypass.
  e. Circadian rhythm has stomata closed; place it in bright light.

11. A turgid plant cell placed in a solution in an open beaker becomes flaccid.
  a. The water potential of the cell was initially higher than that of the solution.
  b. The water potential of the cell was initially equal to that of the solution.
  c. The pressure (Ψ_P) of the cell was initially lower than that of the solution.
  d. The Ψ_S of the cell was initially more negative than that of the solution.
  e. Turgor pressure disappeared because the cell no longer needed support.

12. What facilitates the movement of K^+ into epidermal cells of the root?
  a. cotransport through a membrane protein
  b. bulk flow of water into the root
  c. passage through selective channels, aided by the membrane potential created by proton pumps
  d. active transport through a potassium pump
  e. simple diffusion across the cell membrane down its concentration gradient

13. What are aquaporins?
  a. cytoplasmic connections between cortical cells
  b. pores through the ends of sieve-tube members through which phloem sap flows
  c. openings in the lower epidermis of leaves through which water vapor escapes
  d. openings into root hairs through which water enters
  e. water-specific channels in membranes that may speed the rate of osmosis

14. The formation of a meniscus along the cell walls surrounding the air space of a leaf contributes to water transport by
  a. creating a more positive water potential than in the surrounding mesophyll cells.
  b. creating tension, thus lowering pressure and the water potential of the leaf.
  c. raising the water potential of the surrounding saturated air.
  d. increasing the adhesion of water molecules to the cell walls.
  e. increasing the rate of transpiration from the leaf.

15. Considering an animal cell (first group) and a plant cell (second group) placed in test solutions, which of the following choices gives the *correct* direction for water flow by osmosis?
  a. hypertonic → hypotonic; higher Ψ → lower Ψ
  b. hypertonic → hypotonic; lower Ψ → higher Ψ
  c. hypotonic → hypertonic; higher Ψ → lower Ψ
  d. hypotonic → hypertonic; lower Ψ → higher Ψ
  e. One cannot tell unless told the Ψ_p for the plant cell.

16. All of the following increase the surface area available for absorption of water and minerals by a root *except*
  a. mycorrhizae.
  b. numerous branch roots.
  c. root hairs.
  d. cytoplasmic extensions of the endodermis.
  e. the large surface area of cortical cells.

17. By what method do most mineral anions (negatively charged ions) enter root cells?
  a. apoplastic route
  b. symplastic route
  c. diffusion
  d. cotransport using a proton gradient
  e. bulk flow

18. What mechanism explains the movement of sucrose from source to sink?
  a. evaporation of water and active transport of sucrose from the sink
  b. osmotic movement of water into the sucrose-loaded sieve-tube members creating a higher pressure in the source than in the sink
  c. tension created by the differences in pressure in the source and sink
  d. active transport of sucrose through the sieve-tube cells driven by proton pumps
  e. the hydrolysis of starch to sucrose in the mesophyll cells that raises their water potential and drives the bulk flow of sap to the sink