3 Growth, Development, and Plant Movement

What is Growth?

Growth is an irreversible increase in the number and/or size of cells in a living organism. Depending on the tissue and stage of development, growth characteristics may change over time. For a while growth may rely on cell division, while later in development it may primarily rely on cell enlargement.

For example, consider the fruit of the peach (*Prunus persica*) tree. During the initial stages of fruit growth just after pollination and fertilization, much of the fruit growth is occurring inside the developing seed. Much of this early seed growth is due to an increase in the number of cells. If you observed the fruit on the tree during this time, you would not think that much growth was occurring, since the small green fruit does not enlarge very much. Later on when the flesh of the fruit begins to enlarge, growth is due to an increase in both cell number and cell size. Even later, during final fruit growth as the peach nears maturity, most of the growth is due to an increase in cell size.

A key part of the definition of growth is that of irreversibility. Once the number of cells in an organism increases, their number normally does not decrease. It is true that some cells may get sloughed off as they senesce. Even though certain plant tissues may appear to become smaller and shrink, making it appear as if growth has been reversed, this decrease in size is usually due to a reduction of water content or a depletion of stored food reserves. Consider a potato (*Solanum tuberosum*) that begins to shrivel and become smaller. This decrease in size is due to a depletion of starch in the tuber as it is metabolized during senescence.

Senescence can be envisioned as the opposite of growth; a decrease in size due to a decrease in cell size (due to water loss and utilization of cell reserves), number (due to cell death), or both. This is a great oversimplification of the senescence process. Many other things happen during senescence, and we'll address those in Chapter 16, this volume.

Growth curves

How do we measure growth? Most often growth is quantified by observing the increase over time of one or more selected variables. Growth is often measured at different levels. At the cellular level we might look at an increase in cell number, cell diameter, cell volume, etc. Or we might be interested on a whole plant or tissue level. We could measure shoot length, stem diameter, fruit volume, fruit weight, etc.

Once we have a series of measurements over time, we can create a picture of the growth over time of our organism. This graphical representation of growth over time is called a growth curve. We study growth curves so that we might better study the effects of various production practices or environmental factors on plant growth.

While entire textbooks have been devoted to the growth curves exhibited by plants, we will limit our discussion to several of the most common curves studied.

Exponential

Exponential growth is characterized by an increasing rate of growth over time. For example, supposed we were measuring the growth rate of a tomato (*Solanum lycopersicum*) seedling by measuring the length of the shoot (in millimeters) from the cotyledons to the shoot apex (the epicotyl). We begin measuring once the cotyledons are fully exposed during germination and continue for 14 days. We collect the data presented in Table 3.1.

Plotting the data, we produce the curve presented in Fig. 3.1.

Notice that the growth is not simply a straight line where the shoot length is increasing slowly over time. One of the major characteristics of the exponential growth curve is that growth increases at a faster and faster rate as time passes. Growth almost seems out of control, however, some of the factors

responsible for this incredible growth soon become limiting. Additionally, factors within the plant itself, such as age, change and soon become limiting.

We usually want to describe the growth we have measured with a mathematical equation. This is called modeling. We could determine the type of curve we are dealing with by looking in a textbook of plant growth curves and finding the one that most closely mirrors ours. We could also fit various models to our data using computer software and select the model which best fits our data. It is obvious just by looking at our plot that a straight line would not be the best fit for our data (Fig. 3.2).

Table 3.1. Epicotyl length of tomato seedlings from the day of complete cotyledon expansion until 14 days later.

Day	Epicotyl length (mm)	Day	Epicotyl length (mm)
1	2	8	54
2	3	9	87
3	5	10	140
4	8	11	224
5	13	12	359
6	21	13	575
7	34	14	920

The straight line implies that growth increases by a fixed amount for each unit increase in time. In our example, this would imply that shoot length increased by a constant amount each day. Our graph certainly shows that shoot length increases, on average, by a greater amount each day. You could verify this by calculating the increase in epicotyl length per day for the data in Table 3.1 to produce Table 3.2.

The growth rate itself is growing over time. By how much? The percentage increase in epicotyl length per day is presented in Table 3.3.

At first, the epicotyl length increases by relatively small amounts, 1 mm the first day, 2 mm the second, 3 mm the third, 5 mm the fourth, etc. Note that by the tenth or eleventh day, epicotyl length increases by 53 mm, then 84 mm and the increase continues to increase after that. This is exponential growth. If we calculate the increase as a percentage (as seen in the fourth column), we see that the epicotyl length is increasing by about 60% each day. This is classic exponential growth.

A property of exponential growth is that whenever the independent variable (time) increases by one unit, the dependent variable (epicotyl length) increases by a set percentage, in this case 60%.

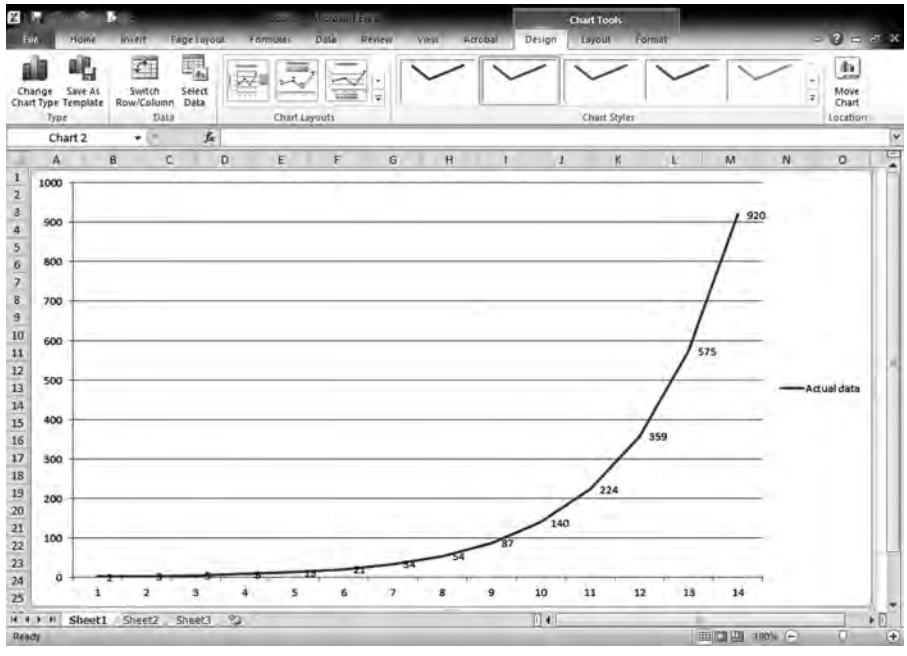

Fig. 3.1. Growth curve for data presented in Table 3.1.

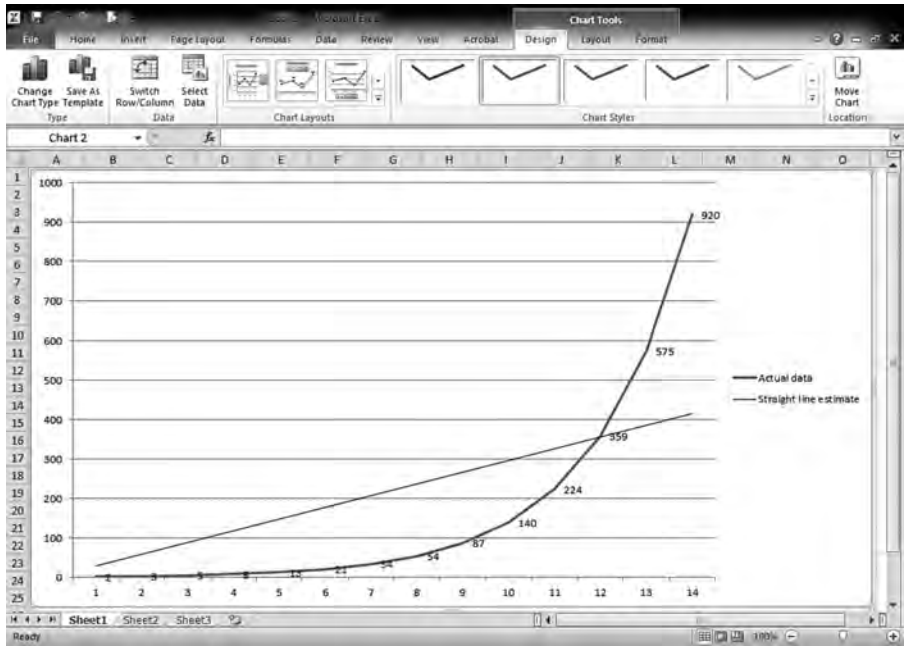

Fig. 3.2. A straight line 'fitting' the data presented in Table 3.1.

Table 3.2. Daily increase in epicotyl length for tomato seedlings measured for 14 days.

Day	Epicotyl length (mm)	Daily increase in length (mm)
1	2	0
2	3	1
3	5	2
4	8	3
5	13	5
6	21	8
7	34	13
8	54	20
9	87	33
10	140	53
11	224	84
12	359	135
13	575	216
14	920	345

Table 3.3. Daily increase in epicotyl length expressed as a percentage for the data presented in Table 3.1.

Day	Epicotyl length (mm)	Daily increase in length	
		(mm)	(%)
1	2	0	0
2	3	1	50
3	5	2	67
4	8	3	60
5	13	5	63
6	21	8	62
7	34	13	62
8	54	20	59
9	87	33	61
10	140	53	61
11	224	84	60
12	359	135	60
13	575	216	60
14	920	345	60

Growth is itself increasing over time. This type of curve often describes bacteria or yeast growth rates as well as the human population on earth.

The equation for an exponential growth curve is:

$y = ae^{bt}$

where t is time, and y is the growth variable, in our case, epicotyl length. The symbol 'e' is the base of natural logarithms and is equal to approximately 2.718.

The letters a and b are parameter symbols. Parameters are numbers that must be mathematically estimated. Since our equation is one of an

infinite number of exponential equations that may exist, the parameters *a* and *b* describe the one unique equation that fits our data.

These parameters can be estimated with many different software packages (or even by hand if you're so inclined). Microsoft Excel is a widely available program which is useful in plant growth modeling. Though there are other more sophisticated packages available, Excel is normally adequate for this purpose. In order to estimate the parameters *a* and *b* that uniquely describe the equation fitting our data, enter the data into a spreadsheet as shown in Fig. 3.3.

To estimate the parameters and fit the exponential curve to our data, first select 'Insert' and from the 'Charts' menu select 'Line', as shown in Fig. 3.4.

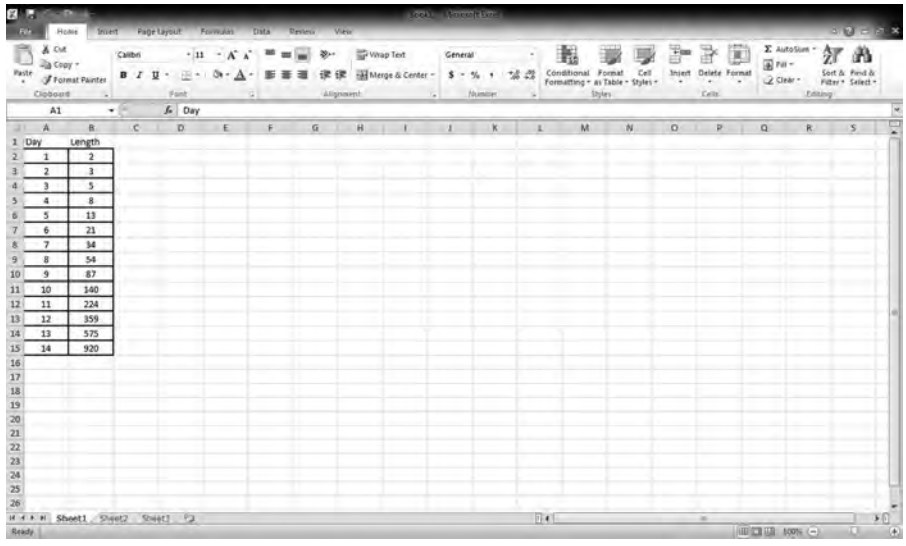

Fig. 3.3. The data for Table 3.1 entered into a simple Excel spreadsheet for estimating the parameters *a* and *b* of an exponential equation.

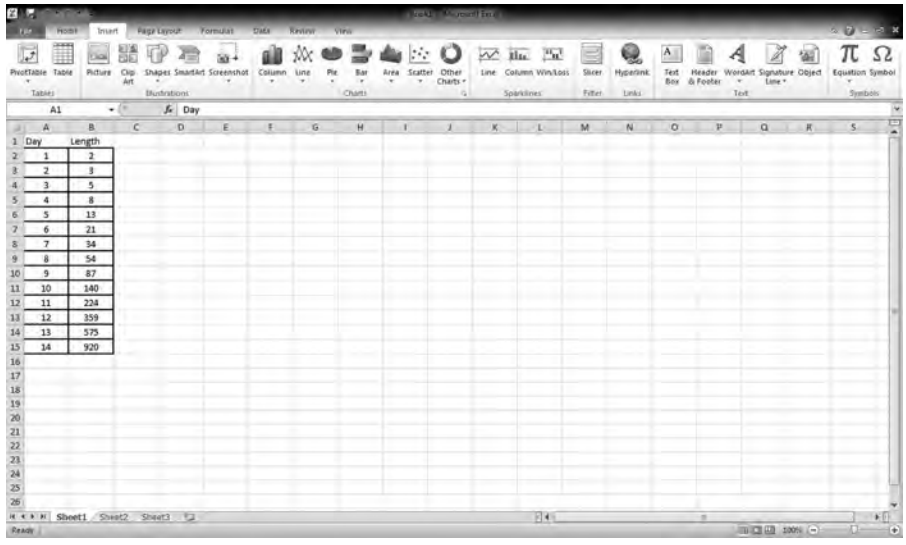

Fig. 3.4. Selecting 'Insert' and then 'Line' from the 'Charts' menu in Excel.

The chart should resemble Fig. 3.5.

The appropriate data must be selected (i.e. highlighted using the cursor) to produce the correct plot as shown in Fig. 3.6.

By right-clicking on the chart a menu appears from which click on 'Select Data' and this brings up a 'Select Data Source' pop-up window as shown in Fig. 3.7.

Change the chart data range to B2:B13. This will now produce a chart with only epicotyl length plotted against time as shown in Fig. 3.8. (We won't get into formatting the chart to look nice, we'll just see how to use Excel to get some quick information about our data.)

To fit an exponential curve to this data, right-click on the plotted line and select 'Add Trendline'.

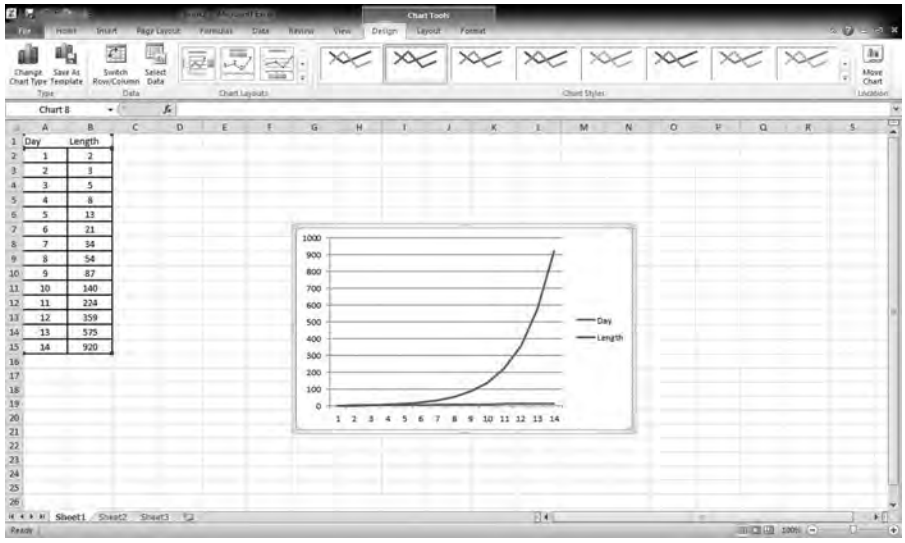

Fig. 3.5. A simple line chart for the Excel tomato epicotyl data.

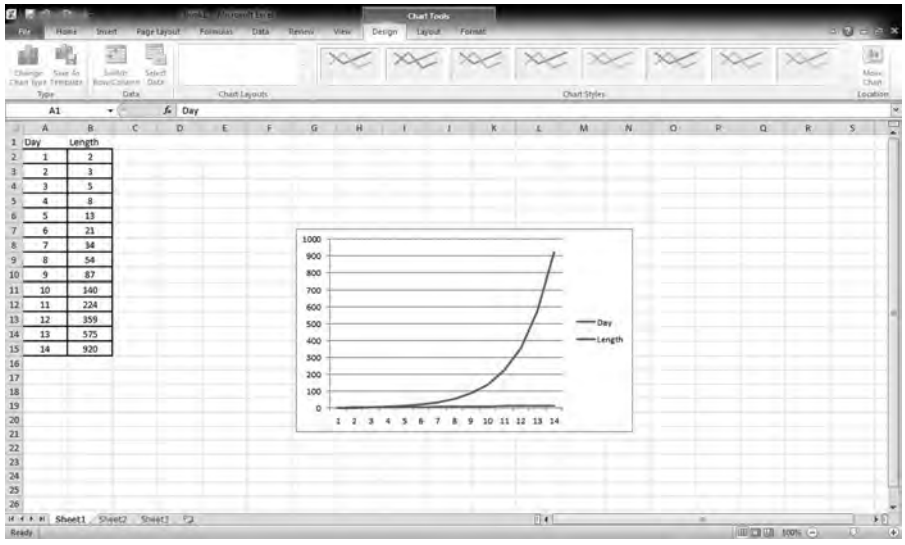

Fig. 3.6. Selecting the appropriate data to plot for the Excel tomato data.

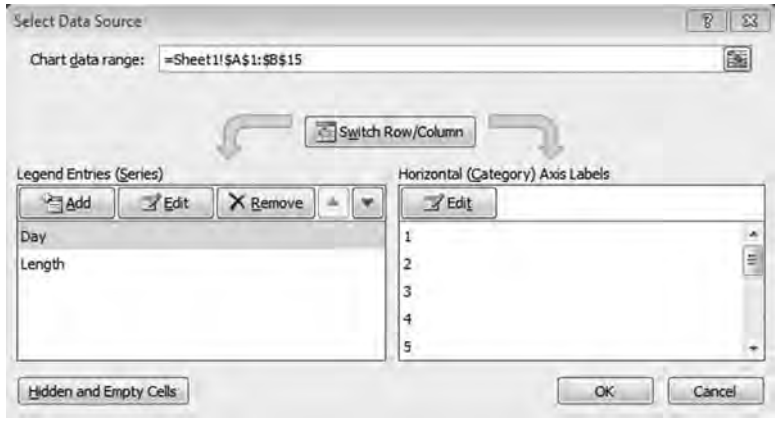

Fig. 3.7. 'Select Data Source' pop-up window for the tomato epicotyl data of Table 3.1.

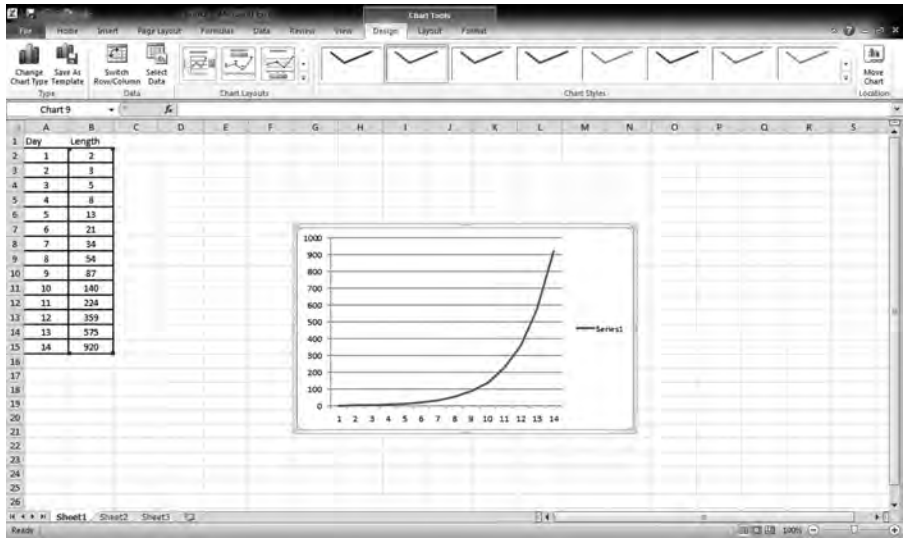

Fig. 3.8. Epicotyl length plotted against time for the tomato data of Table 3.1.

Select 'Exponential', 'Display Equation on chart' and 'Display *R*-squared value on chart' in the pop-up window as shown in Fig. 3.9.

This will cause Excel to provide the equation of the line and the *R*-squared (R^2) value for the equation on the chart (Fig. 3.10).

The equation describes the mathematical relationship between day and epicotyl length while the *R*-squared value gives an indication of how well the data fit the model chosen. *R*-squared values are between 0 and 1.00 with values closer to 1.00 considered a better fit.

From Fig. 3.10, we get the equation of our line as $y = 1.2092e^{0.4745x}$ with an *R*-squared value of 0.99 (a particularly good fit).

We can predict what the epicotyl length would be at any time between days 0 and 14 by plugging our x value of time into the equation. Don't go out farther than 14 days, since we did not make any measurements past day 14. This is called extrapolation and is not acceptable.

Normally to get a better estimate of the line we would measure more than one seedling and repeat the experiment several times. We would then alter

some factor during seedling growth, take measurements and determine if our alteration had any effect on the growth curve. We would use sophisticated statistical methods for comparing line equations to determine the effect of our alteration. Just for fun, ask Excel to fit a straight line and see what you get.

Fig. 3.9. The 'Format Trendline' pop-up window for selecting equation options in Excel.

Sigmoid

The sigmoidal growth curve consists of three (some scientists say five, but three will suffice for our purposes) main stages: (i) the lag phase; (ii) the log phase; and (iii) the stationary phase. The first stage, the lag phase, is characterized by an initial gradual increase in the growth parameter. This is followed by the second stage, the log phase, in which there is a rapid increase in the parameter. In the final phase, the stationary phase, there is a gradual decline in the rate of increase of the parameter. Usually the increase ceases and the curve levels out. If the organism is observed long enough, evidence of senescence might be observed by a gradual decrease in the growth parameter.

Fruit growth often follows the sigmoid growth curve. Remember the type of growth you might observe depends on the parameter you measure. For example, the number of cells in an organism may be increasing steadily while the organism's weight may not be changing much at all. In the first case you might say you are in a log stage of growth while in the second case, you may say you are in a lag stage of growth.

If we measure the weight of an apple as it grows on a tree, we can make some interesting observations which will help us understand the sigmoid growth curve. Consider the observations recorded in Table 3.4.

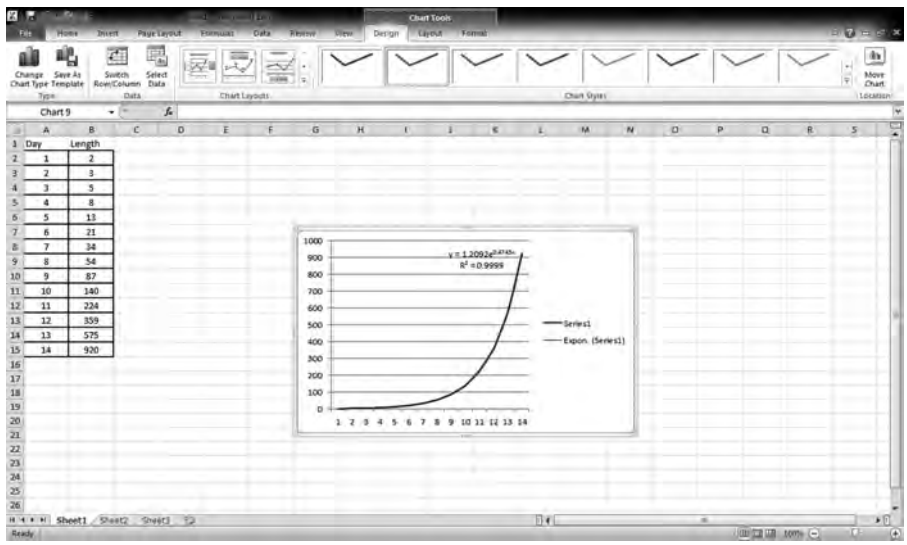

Fig. 3.10. The final Excel graph with equation and *R*-squared displayed.

Table 3.4. Fruit weight of an individual apple fruit at fertilization and for 24 weeks thereafter.

Weeks after fertilization	Fruit weight (g)	Weeks after fertilization	Fruit weight (g)	Weeks after fertilization	Fruit weight (g)
0	0	9	41	18	130
1	5	10	48	19	140
2	9	11	56	20	147
3	14	12	64	21	154
4	18	13	74	22	160
5	23	14	85	23	165
6	27	15	96	24	170
7	31	16	105		
8	36	17	118		

A plot of this data is presented in Fig. 3.11. Notice that fruit weight increases steadily up to around 9 weeks or so and then increased more rapidly until about 19 weeks where the increase in fruit weight gradually tapers off.

Mathematical modeling of a sigmoid, also called a logistic growth curve, is difficult. The Richards' growth function is often used when modeling a sigmoid relationship. For more information regarding mathematical modeling of plant growth, consult any good mathematical modeling text.

Double sigmoid

While an apple fruit follows a sigmoid growth curve, a peach fruit follows a double sigmoid growth curve. A double sigmoid curve can be thought of as two sigmoid growth curves joined together as what is called the d point. The first sigmoid curve represents growth of the fruit mesocarp (flesh), primarily by cell division and is often called phase I. The second sigmoid curve represents the period called final swell which is due to mesocarp cell enlargement, often called phase III. The d point is the period of endocarp or pit hardening, often called phase II.

What is Development?

Development versus differentiation

Differentiation and development describe a forward movement in plant growth. Differentiation usually refers to the specialization of cells followed by tissues for their ultimate function within the plant. Development usually refers to the forward growth of organs and the whole plant, all towards achieving the plant's ultimate horticultural functionality.

Although differentiation and development refer to forward growth and neither is reversible in the horticultural sense, de-differentiation can occur at the cellular level. Cells that once held a differentiated function may de-differentiate to form a mass of non-differentiated tissue called callus.

Development is part of differentiation. At the cellular level, differentiation is the process wherein a cell becomes the specific type of cell it was destined to become due to genetics and environment. All cells begin similarly. As their differentiation occurs, each takes on specific anatomical and physiological characteristics which fit their purpose. A collenchyma cell develops a thick, flexible cell wall while a root epidermal cell develops a root hair. Since all cells of a given organism have the same genetics, differentiation within an organism is largely directed by environment.

Development follows differentiation. Where you make the cut-off between the two is often subjective. In academic discussions, it is wise to explicitly convey your own definition of differentiation and development with respect to the plant material you are working with.

Growth of undifferentiated tissue into differentiated tissue

What makes a cell or tissue grow in one direction and not another? In other words, why does cell 'A' become a spongy mesophyll cell rather than a companion cell in a leaf? This is one of the mysteries of plant growth.

The differentiation of cells and tissues is highly regulated and not well understood. While we know how the many different factors influence the differentiation of plants on a macroscopic level, we have limited understanding of what is happening at a more basic level. For example, we may know that

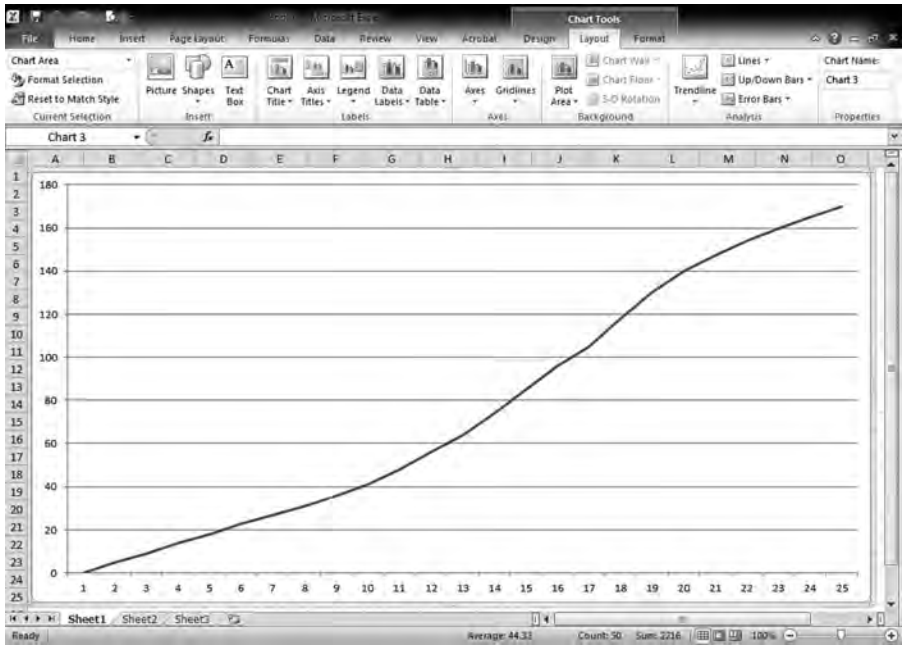

Fig. 3.11. A sigmoid growth curve of apple fruit growth from the data in Table 3.4.

short days may cause flowers to be initiated in certain species, but we don't really understand much of why the shorter days cause flowers instead of leaves to be formed by a meristem.

Development of differentiated tissue

Development is that part of the growth process where cells or tissues that are already differentiated continue to enlarge and attain their final form and function within the plant. The distinction between differentiation and development is that development can only proceed once all parts necessary for development exist. If all parts are not available for growth to progress, the cell or tissue is still in the differentiation process.

There may even be a lag between when differentiation ceases and development commences. We will see this clearly when we study flower formation. All parts might exist, but movement towards final form and function may not occur for some time.

Growth of plant from an embryo through maturity

A new plant that is formed via sexual reproduction (as opposed to asexual reproduction) starts out as a single-celled zygote formed from the union of an egg cell and a sperm cell. This single cell reproduces via mitosis to form a multi-cellular embryo. The embryo continues to increase in size via cell division and enlargement. Root tissues begin to become distinguishable from shoot tissues. Leaves begin to be distinguished from stems, and the development of the new plant proceeds. There may be a lull in growth as a seed lays dormant, waiting for conditions to be acceptable for further movement towards final form and function. Conversely, the embryo may not stall in its movement, and may quickly develop via germination into a young seedling. The seedling then proceeds towards its final destination.

Factors Affecting Both Growth and Development

The two main factors responsible for growth and development in plants are: (i) genetics; and (ii) the environment. Genetics hold the potential for what might happen in the course of plant growth while environmental factors control how the genetic potential is expressed.

Genetics is a simply elegant code for one of the most sophisticated processes on earth: life.

Essentially, four nucleotides (adenine, guanine, cytosine, and thymine) pair up (adenine with thymine and guanine with cytosine) to form sequences of base pairs which ultimately code for the 20 amino acids commonly found in proteins. The proteins formed from combinations of these amino acids form enzymes which run the whole show.

How do these sequences of base pairs run the show? In addition, how does the environment affect the expression of this life code? The first question is studied by geneticists while the second is studied by physiologists. Working together, lifetimes of research have been devoted to answering these questions.

In order for the expression of a plant's genetics to be influenced by the environment, a mechanism for the detection of environmental signals must exist. There are specific proteins in plants that change in response to environmental stimuli. One of the most highly studied signal-catching proteins in plants is phytochrome, and the signal it catches is light. This molecule changes shape when exposed to light of differing wavelengths, particularly red (660 nm) and far-red light (730 nm). The phytochrome molecule's shape or form, most often called P_r or P_{fr}, then influences what sort of physiological response occurs. But how?

The idea is that the original light signal perceived by the plant (or other signals in other situations) is passed along within the plant itself via secondary messages in a process called transduction. This secondary message may directly affect some process or it may induce a change in or synthesis of another protein (remember enzymes run the show) which may lead to the actual response. Remember, all life processes are run by enzymes and all enzymes are proteins.

Generally the result of signal transduction is in the activity of an enzyme. The enzyme activity can be regulated in either of two ways. The first is called 'transcriptional regulation'. Here factors such as modified proteins or chemical messengers, resulting from the modification of a protein, directly bind to specific regions of DNA and control the transcription (the conversion of the code contained in DNA to RNA) of specific genes which code for the specific enzymes important in some physiological process. In other words, the synthesis of an enzyme is controlled by the signal. The second way is when the activity of an already-existing enzyme is regulated by the signal. This is called 'post-translational modification of proteins'.

In summary, whatever the environmental signal is (light, temperature, gravity, carbon dioxide concentration, etc.), a plant generally perceives the signal via a protein molecule. The protein molecule then sends the signal along a chain of events which ultimately results in some sort of physiological response by the plant.

Plant Movements

One of the areas where plant signal perception is highly noticed is in plant movements (Fig. 3.12).

Autonomous

Some plant movements are autonomous and are not caused directly by some external stimulus. The most commonly observed autonomous movement is circumnutation. This is a slow, circular movement of shoot or root tips or tendrils as they grow. The movement is most easily observed using time-lapse photography as each complete circle takes from 1 to 3 h to complete. This movement is caused by differential growth of cells in the growing tissue. Another example of autonomous movement is when a stem wilts and bends due to desiccation. The stem wilts due to a physical change in the turgidity of the cell, not due to some external stimulus.

Induced

Induced movements are those plant movements directly caused by some external stimulus. There are two types of induced movements: (i) nastic; and (ii) tactic.

Nastic movements

Nastic movements are plant movements that are independent of the direction of the stimulus. The most widely cited example is seismonasty which is a special case of thigmonasty which is characterized by an especially fast reaction to a stimulus by a plant. Thigmonasty is a response due to touch. When a *Mimosa* leaf is touched the leaflets fold upwards and that folding is not oriented in any direction related to the direction of the touch. You can touch the top, bottom or sides of the leaf and the leaflets will always fold up.

In addition you can stimulate the leaflets to fold (again always upwards) by heating or cooling the leaf.

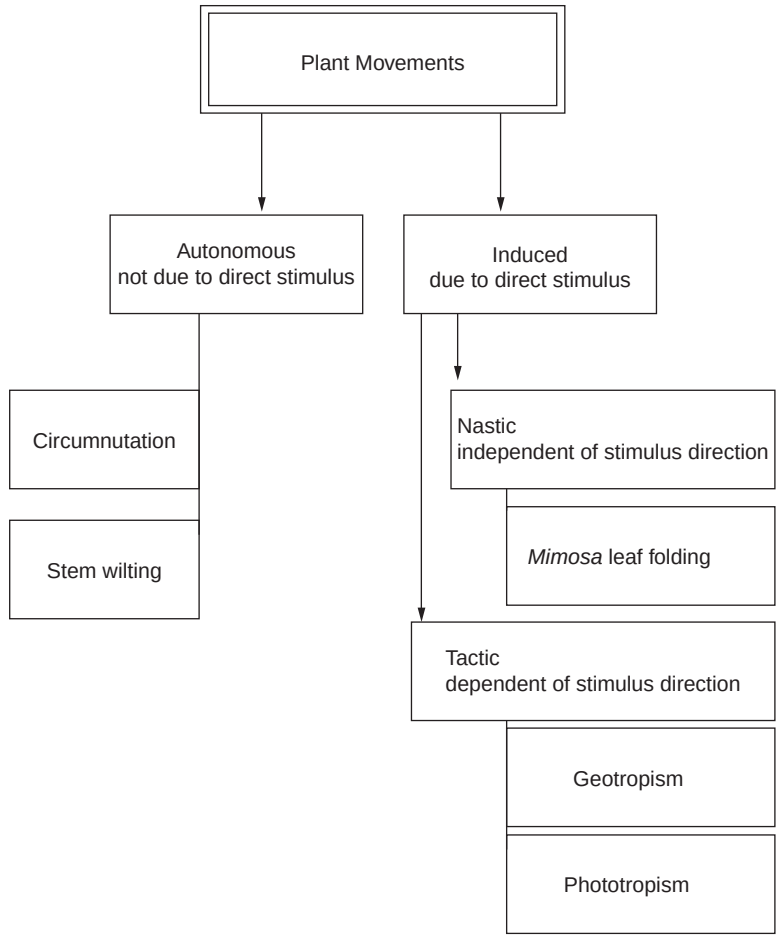

Fig. 3.12. The different types of plant movements.

But how do the leaflets fold up from a physiological standpoint? The stimulus (mechanical, heat, cold) causes an electrical signal to move from cell to cell down the leaf very rapidly. When the signal reaches specialized cells called 'motor cells' in a structure called the pulvinis at the base of the leaflet, a rapid efflux of potassium ions out of the motor cells occurs. Water molecules quickly follow, the motor cells loose turgor and the leaflets fold upwards. Once the stimulus is gone, potassium slowly re-enters the motor cells, water follows and turgidity is restored causing the leaflets to re-open. The potassium ion movement and hence leaflet folding can also be controlled photoperiodically.

Another example of thigmotropism is tendril curling around a support.

Nastic movements are typical in dorsiventral organs such as leaves. Dorsiventral describes an organ that has two sides, each differing in structure and appearance. Tissues within a dorsiventral organ have different growth capacities on the upper versus the lower surface. Uneven growth of the upper and lower surfaces results in a predetermined direction of movement. Regardless of the direction of the stimulus, the resultant movement is always in the same direction.

Other nastic movements include the opening and closing of flowers due to some external stimulus. Flowers of members of the family *Cucurbitaceae* open during the day and close at night. This regulation by light is called photonasty. Tulips (*Tulipa* spp.) and crocus (*Crocus* spp.) flowers open when warm

and close when cool (thermonasty). Epinasty is the downward curving of leaves induced by some external stimulus such as ethylene gas. Chemotropism is movement induced by a chemical substance. For example, digestive glands of the insectivorous plant *Drosera* curl inwards as a response to the nitrogen in their insect prey.

Tactic movements

Tactic movements are often observed in organs of radial symmetry like a shoot or root and are oriented in either the same or opposite direction of the stimulus causing the movement. Two widely observed examples are phototropism and gravitropism (also called geotropism). In phototropism, movement is towards the stimulus (i.e. a plant bending towards a light source). In gravitropism, the direction of the movement depends on the organ. Movement is away from gravity when discussing the shoot, while it is towards gravity when discussing the root. A clear example of gravitropism can be observed by placing a potted plant on its side and watching it curve to grow upright again. The response can be observed within 15 min!

Turgor versus growth movements

Many plant movements are due to either local growth responses to a stimulus or changes in turgor of selected cells within tissues responsible for the movement. These responses rely on the elasticity and plasticity of cell walls.

Plasticity of the cell wall is the result of the deposition of new cell wall material into a stretched or stretching cell wall in order to stabilize it and results in an irreversible increase in cell volume. An example would be a cell on the non-illuminated side of a stem which stretches with the resultant bending of the shoot towards a light source.

Elasticity is the ability of the cell wall to stretch without the deposition of new wall material which results in a reversible change in cell size. An example of is the motor cell responsible for *Mimosa* leaflet folding. As water moves into the cell in response to the influx of potassium ions, the cell walls stretch and the cell enlarges. When potassium ions leave the cell in response to a stimulus, water also leaves resulting in a decrease in cell size.

The movements of *Mimosa* leaflets are based on reversible turgor changes and are often called turgor movements to distinguish them from growth movements. Bending of a shoot towards the light or away from gravity is a growth movement and is not reversible.

In turgor movements, changes in pressure in one cell may exert pressure on neighboring cells which may lead to tissue deformations and plant movement. If the cells are different sizes, the pressure is transmitted in very specific directions causing very specific movements. Other examples of turgor movements include the opening and closing of stomata and the circadian lifting and falling of leaves, such as that seen in *Phaseolus* sp.

In growth movements turgor pressure increases as a result of a stimulus and does not decline afterwards. This results in an irreversible growth movement. Sometimes the pressure continues to build causing tissue rupture. Seed pod rupture in *Impatiens* is a good example of this type of irreversible movement.

Stimulus perception, forwarding, and conversion into movement

A series of metabolic processes which are coded for by the genetics of the organism are responsible for autonomous movements. There is no identifiable stimulus responsible for the movement.

Induced movements, however, require a signal, its perception, forwarding to the appropriate tissue, and conversion into the actual movement.

A model of signal perception is fairly straightforward using light perception as an example. The light signal is perceived by the plant via specialized molecules called pigments. When light of a specific wavelength hits the molecule, the energy in the light is used to change the structure of the molecule. The pigments responsible for light signal perception in plants include blue light receptors called phototropins and cryptochromes, and the red light receptor phytochrome.

Let's look at phytochrome. Only specific wavelengths of light will convert one form of the molecule to another. Red light will convert phytochrome red (P_r) to phytochrome far red (P_{fr}) and only far-red light will convert P_{fr} back to P_r. P_{fr} stimulates shoot elongation, which for this discussion we will consider a plant movement (even though some would argue that shoot elongation really isn't movement per se, but rather simply irreversible growth). Once enough red light has caused enough accumulation of P_{fr}, how is the light signal forwarded to cells to cause them to elongate?

The forwarding of the perceived signal and its ultimate conversion into movement is not understood as well as signal perception.

The coleoptile, a tubular protective sheath surrounding the young shoot of a germinating grass seedling, is quite responsive to phototropic bending. There is work which suggests that the actual site of light signal perception in oat (*Avena*) coleoptiles is the chloroplast. Coleoptiles grown in the dark are etiolated and accumulate violaxanthin and antheraxanthin but no zeaxanthin. All three compounds are yellow xanthophyll pigments in the carotenoid group of plant pigments.

If dark-grown coleoptiles are irradiated with red light, zeaxanthin accumulates in proportion to the length of time they are irradiated. Thus phytochrome is important in regulating zeaxanthin synthesis, since irradiating with red light would cause a conversion of P_r to P_{fr}, the active form of phytochrome.

If coleoptiles with differing levels of zeaxanthin are exposed to brief bursts of blue light, their phototropic bending is proportional to the amount of zeaxanthin present. If there is no zeaxanthin present, there is no phototropic response. Thus the coleoptile bending is regulated by both blue and red light. The red light regulates the production of zeaxanthin and the blue light regulates the bending by acting on the zeaxanthin. (Guard cell movement (stomatal opening and closing) is also sensitive to blue light and depends on the presence of zeaxanthin in the guard cell chloroplasts.)

But how does the light regulate the levels of the pigments controlling the tropic response? Different colors of light affect different pigments (phytochrome, phototropins, and cryptochromes) which probably promote the formation or activity of enzymes responsible for the synthesis of other pigments (zeaxanthin) which pass the signals message onto other enzymes.

What other enzymes? Well we know that one of the plant hormones, auxin, is synthesized in coleoptile tips when irradiated with light. We also know that auxin diffuses basipetally down the coleoptile where, when it reaches the sub-apical cells of the coleoptile, it accumulates on the dark side of the shoot. Even though light stimulates auxin production, it also causes auxin degradation. We also know that auxin makes cell walls more elastic, thus allowing turgor pressure to enlarge the cells on the dark side of the shoot. The cells on the light side of the shoot do not elongate (no auxin to loosen the cell wall), thus there is an uneven growth of the stem with the dark side longer than the light side. The shoot bends toward the light!