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# Resource Allocation in Plants

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**Abstract:** Plants can extract a limited amount of resources from their environment, which can be allocated to growth either above or below ground. A species' pattern of allocation is genetically determined, but is not completely fixed. In this lab, students compare allocation strategies between plant species, and within a single species under different abiotic conditions. The inquiry-based exercise was designed for freshman in introductory or non-majors courses, and includes an opportunity for students to design experiments of their own. The general methods can be adapted to more advanced courses as well.

**Keywords:** resource allocation; soil nitrogen; root to shoot ratio.

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## Introduction

This lab was developed for a freshman course in Ecology and Evolution, but the general methods can be adapted to a range of non–majors courses, as well as extended and used in a more advanced course. As written, the main exercise requires a 2- to 3–hour block to complete. The optional (but strongly recommended) student experiment requires about 1 hour to set up, and a 1- to 2–hour block scheduled for two weeks later when students collect data. Flats of seeds must be planted 2–3 weeks in advance of the lab meeting, but otherwise there is minimal advance prep work.

The major concepts we stress with this lab are:

- Organisms cannot obtain enough energy or resources to compete well in all possible conditions.
- Each species has a genetically pre–defined pattern of resource allocation, that causes them to emphasize one physical feature or another.
- Environmental factors can alter the pattern of resource allocation in specific ways. This is called phenotypic plasticity.
- In young herbaceous plants that are not yet flowering, nearly all resources are allocated either to roots or shoots.
- Allocation strategies that allow a plant species to survive and reproduce under one set of environmental conditions may make it less likely to survive in another set of conditions.

Practical skills students can learn as part of this exercise include how to use Excel to handle and graph large sets of data, and how ecological and physiological principles can be applied to horticultural practices.

## Student Outline: Resource Allocation in Plants

### Background

In an ecological community, plants and animals must interact with and adapt to each other, and the abiotic environment around them. Among animals, intra– and interspecific interactions often include some sort of movements. Plants interact with their neighbors in the community too, but unlike animals must do so where they are rooted. Plant interactions are less obvious than animal behaviors, but shape the entire community and in large part determine the number and types of animals that are present.

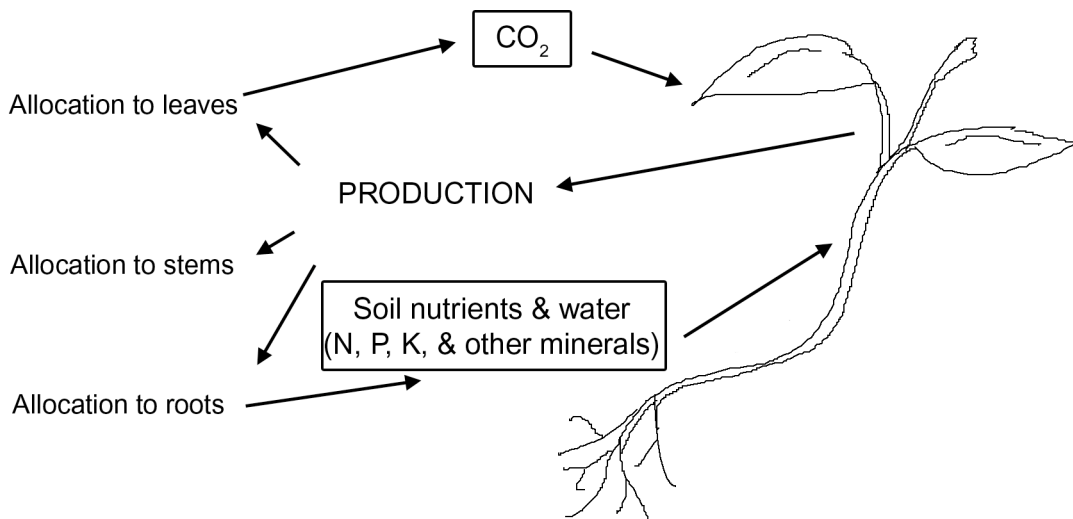
Many intra– and inter–specific plant interactions revolve around obtaining the essential resources of sunlight, nitrogen, and water. When these resources are limited, it affects what species are present in a community. For example, an abandoned field has abundant sunlight but fairly dry soil. Pine seedlings are drought–tolerant and grow well in full sun; they will colonize an open field fairly quickly. After pine trees become established, oak and other hardwood tree seedlings appear that eventually grow up and create a shady canopy. Most hardwood seedlings are shade tolerant but require moister soil than pines; they cannot easily colonize an open field, but thrive once pines or other hardwoods have appeared. In contrast, pines cannot tolerate the shade produced by maturing hardwoods, and are not replaced as they die out.

Why hasn't natural selection eventually resulted in a tree species that grows equally well everywhere? It has to do with **resource limitation**. Organisms can extract a finite amount of resources

from their environment for growth and reproduction. Any species with the ability to outgrow all others in every conceivable set of conditions would need more resources than are available. This physical limitation is a potent selection force; in response, most species have evolved to allocate their resources in a particular pattern.

Each species' pattern of **resource allocation** is genetically determined, but it is not completely fixed. Individuals can modify their typical allocation pattern somewhat to allow them to adapt to different abiotic conditions, and the presence of other species. The amount of **phenotypic plasticity** differs between species. Some have little, and do not tolerate any change from optimum conditions. Other species have significant plasticity, so can adapt to a variety of conditions. The way in which resource allocation changes may differ as well. For example, some plants respond to drought by shifting resources to rapid downward growth of existing roots, while others reallocate their resources to forming a waxy protective cuticle on leaves.

Plants can expend resources on growth either above or below ground (Figure 1). Above ground, plant shoots (leaves and stems) are the source of carbon compounds such as sugars derived from photosynthesis. These sugars get converted into storage, structural, and biochemical compounds (starch, cellulose and proteins, lipids and other carbohydrates required for metabolism). Below-ground structures take up water and essential nutrients like nitrogen, phosphorus, potassium and other minerals. Thus, allocation above or below ground is not just a matter of increasing body size; it affects the plant's ability to gather additional resources.



**Figure 1.** Locations where plants can allocate energy and nutrient resources

In terrestrial environments, nitrogen is often the limiting nutrient that determines growth rate for plants. In response, plants differ in how they allocate it among their roots, stems and leaves. The **leaves** are the principal photosynthetic organs of the plant. Many rapidly growing weeds like knotweed, burdock, and dandelions, favor placing more nitrogen in leaves, thereby increasing the photosynthetic ability of the plant and consequently the growth rate. However, these plants can only effectively grow in high light environments such as old fields with plenty of nitrogen around. They do not perform as well where light or nutrients are scarce. **Stems** are the primary supporting structure of the shoot. They are involved in light capture and competition by lifting the leaves above surrounding plants. In many plants there appears to be a trade-off between investment in stem and in leaves. For example, trees

invest heavily in woody stems that support the leaves for a long time. The cost of this expenditure is slower growth. In contrast, many vines rely on neighboring plants for support and have flexible, metabolically inexpensive material in their stems compared to self-supporting plants like trees. Vines now can partition more resources to leaves and fast growth. Good examples of species using this strategy are kudzu and honeysuckle. **Roots** not only serve as the primary absorptive organ, but they also anchor the plant to the soil. In many environments like the desert or the sand hills, soil water can be scarce and plants must allocate most resources to root growth and maintenance to survive. For example in the high desert of Utah, shrubs like the creosote bush have deep taproots that can access water 20 meters below the surface. These roots transport water to the shallow soil where it is utilized by roots in that region the next day. Yet the stems and leaves of the shrub may only be half a meter tall.

In this lab, you will be comparing allocation strategies between plant species, and within a species under different abiotic conditions. You will be measuring the root and shoot biomasses, then expressing them as a **root:shoot (R:S) ratio**. The R:S ratio is simply a measure of root size (weight, length, etc.) versus shoot size. The larger the ratio, the larger the roots relative to the shoots.

### Goals for this Exercise

Today you will quantify how seedlings of different crop plants allocate their carbon and energy resources. By the end of lab, you should be able to answer these questions.

- What is the normal resource allocation pattern for each species?
- Does this allocation pattern change when nitrogen is limited?
- If the allocation pattern changes for a species, in what ways does it change?

Based on this week's findings, you will design your own experiment relating to resource allocation. You will set up and start your experiment next week, and collect your data in 3 weeks.

### Procedure

In the lab, there are trays of seedling plants grown in vermiculite, a soil-less mixture that contains few minerals. When the seeds were planted, the vermiculite was supplemented with standard strength liquid fertilizer (1X) or fertilizer diluted to one-tenth normal concentration (0.1X). You and your classmates will measure the root and shoot lengths and weights for the same plants grown in both low and normal nitrogen levels. Once everyone has finished, you will compile and share these data.

The number of plants you must harvest is not the same for all species. Large plants like beans are heavy enough that you can measure height and weight of a single plant accurately. For small or light plants like rye, you must harvest and combine 5 or even 10 plants. If you must do the latter, each group of 5-10 plants represents one measurement.

When you make several measurements of the same trait or feature you always should report the **mean**, which is a more accurate estimate than a single measurement. Repeated measurements also allow you to calculate the **standard deviation**, which can be used to statistically test whether the mean for one group is significantly different from the mean of another group. So that you can perform statistical analyses of your data, you will harvest and measure 3 single plants, or 3 sets of 5 or 10 plants.

1. Your instructor will assign each work group one or two species/nutrient combinations to analyze. Record the species and nitrogen concentrations you were assigned in Table 1.

2. If your group is assigned small plants like alfalfa or ryegrass, plan to use 10 plants per replicate. If you are working with medium plants like oats or radish, plan to use 5 plants per replicate. If you are assigned very large plants like beans, use just 1 plant per replicate.
3. Carefully pull 1, 5, or 10 plants out of the tray of vermiculite. Be extremely careful not to break off any of the root mass. You may need to pull out some extra plants to ensure you do not damage the ones you intend to measure.
4. Gently rinse the plants in a container of water to remove the vermiculite and help separate the roots. Pat the plants dry with a paper towel.
5. Measure the maximum shoot length and root length to the nearest millimeter, and record the mean value for each group of 1, 5, or 10 plants in the table below.
6. Separate the roots from the shoots by cutting each plant apart at the “soil line” (the original level of the vermiculite.) Hint: usually there is a difference in stem color above versus below the soil line.
7. Weigh the shoots alone, then the roots alone. If you are measuring 5 or 10 plants per replicate, do not try to measure each plant; weigh all 5 or 10 roots together, and all 5 or 10 shoots together.
8. Record the weight data in Table 1.

### Results

If you measured 5 or 10 plants for each replicate, record the weight for all of the shoots or roots in the total wt. (T) column. Calculate the average weight of a single root or shoot by dividing total weight by the number of plants used for that replicate. Enter that result in the individual wt. (I) column.

**Table 1A: First Assigned Species**

Plant Species:					Nutrient Treatment:			
Replicate & # plants used	Roots (g)		Shoots (g)		R:S Weight Ratio (Use I)	Max. root length (cm)	Max. shoot length (cm)	R:S Length Ratio
	T	I	T	I				
1								
2								
3								
					Mean		Mean	
					St. dev.		St. dev.	

**Table 1B: Second Assigned Species**

Plant Species:				Nutrient Treatment:				
Replicate & # plants used	Roots (g)		Shoots (g)		R:S Weight Ratio (Use I)	Max. root length (cm)	Max. shoot length (cm)	R:S Length Ratio
	T	I	T	I				
1								
2								
3								
			Mean				Mean	
			St. dev.				St. dev.	

1. Use the maximum lengths of roots and shoots in each replicate to calculate individual root:shoot length ratios for each of the 3 replicates.
2. Calculate the root:shoot weight ratio for each of the 3 replicates, using the **individual (I)** root and shoot weights. Enter the values in the appropriate columns in Tables 1A and 1B.
3. Finally, calculate the mean and standard deviation for the R:S weight ratio, and R:S length ratios, in each nutrient condition. Enter the values in the heavily boxed cells at the bottom of the columns in Tables 1A and 1B.
4. Your instructor will put a table on the board similar to Table 2. When you finish your calculations for Tables 1A and 1B, add your mean and standard deviation values for the species and nitrogen concentrations you measured to the table on the board. Once the entire class has reported their results, copy the table from the board to Table 2 below.

**Table 2: Class Summary Data**

Species	R:S Weight Ratio Mean ± st. dev.		R:S Length Ratio Mean ± st. dev.	
	Low Nitrogen	High Nitrogen	Low Nitrogen	High Nitrogen

5. Using either Excel or graph paper, create two bar graphs that show the root:shoot length ratio for each treatment and each species. Put the R:S ratios for weight on one graph, and ratios for length on a separate graph. Include error bars to show the variation.

## Summary Questions

To answer these questions, refer back to your own and class summary data, and give specific evidence to support your statements and conclusions. Make your case based on what you *actually saw*, not what you would have expected.

1. Did you see a general pattern in how allocation changes with the amount of nitrogen available? If so, what was the pattern, and what is your evidence?
2. Large differences in R:S ratio between the two nutrient treatments indicates a high rate of phenotypic plasticity. What other types of environmental conditions would likely favor plants with high phenotypic plasticity? With low plasticity?
3. What factors other than nutrient or light conditions might affect plants' R:S ratio?
4. When nitrogen was limited, did you see any species in which R:S weight ratio changed, but the R:S length ratio did not? Any species in which the R:S length ratio changed, but the weight ratio did not? How would you interpret any such differences between length ratio and weight ratio?
5. Think about the relative contributions of roots, stems, and leaves to the survival of a plant. Which type of plant would be better suited for living in the diffuse light of a forest understory: one with high root:shoot ratio or one with a low ratio? Why?
6. What would be the best allocation strategy for a plant living on a windy summit near treeline? Why?
7. What would be the best allocation strategy for a plant living in a seasonally dry climate like that found in southern California where they typically have a rainy winter followed by a dry summer?

## Performing Your Own Experiment

In the preceding exercise, you saw how plant resource allocation changes in response to different nitrogen levels. However, many other abiotic and biotic factors can affect resource allocation. The following lists summarize available materials, and independent and dependent variables that can be manipulated easily. These lists are not all-inclusive; if you want to examine different independent or dependent variables, ask your instructor. Most likely, the necessary arrangements can be made. Just remember, your experiment should explore how plants allocate resources in some way.

### Materials Available

- Seed of various crop species  
(e.g., oats, ryegrass, wheat, field peas, beans, alfalfa, radish, buckwheat)
- Vermiculite or similar nutrient-free planting mix
- Greenhouse flats and inserts
- Support stakes
- Shade cloth
- Colored acetate
- Growth chambers with light timers
- Balanced liquid fertilizer solution
- Nutrient supplementation solutions

**Independent Variables You Might Test**

- Light intensity and wavelength. Shade cloth tents can be used to reduce the above ground contribution to production. Colored acetate can be used to change the spectrum of light reaching the plants.
- Temperature. Plants can be grown in warm versus cold conditions.
- Soil composition
- Macronutrient levels (nitrogen, phosphorus, potassium, calcium, sulfate)
- Micronutrient levels (copper, zinc, molybdenum, etc.)
- Water availability (excessive vs. normal vs. restricted)
- Particle size (clay versus sand vs. loam)
- Presence of symbionts. Alfalfa can be grown with vs. without *Rhizobium* sp.
- Biotic factors
  - Seed size: small (alfalfa) vs. large (peas or beans)
  - Planting density (ample room versus crowded)
  - Herbivory (mimic this with occasional LIGHT clipping)
  - Normal growth season (cool weather field peas vs. warm weather buckwheat)
  - Monocots vs. dicots

**Dependent Variables You Might Measure**

- Total, root, leaf and stem mass, or root:shoot ratio
- Growth rate or plant height
- Shape or architecture of plant
- Mortality

## Notes for Instructors

### Materials and Preparation

#### *On a Side Bench*

- Prepared, labeled flats of plants grown in vermiculite. Typically we use these 6 species:
 

Mung beans	High nutrients
	Low nutrients
Radish	High nutrients
	Low nutrients
Alfalfa	High nutrients
	Low nutrients
Ryegrass	High nutrients
	Low nutrients
Oats	High nutrients
	Low nutrients
Wheat	High nutrients
	Low nutrients
- Mop, bucket, broom, and dustpan (for cleaning up spilled solutions and vermiculite)
- Large bin for collecting vermiculite and plant waste

#### *At Each Work Station*

- Top-loading balance (able to read 0.01g)
- 15cm or 30cm ruler
- Scissors (dissection scissors are a convenient size)
- Plastic boxes or beakers for rinsing soil from plants
- Paper towels
- Large weigh boats

#### *Supplemental Materials (only required if doing student experiments)*

- Seed for wheat, annual rye, oats, mung beans, radishes, & alfalfa
- Seed for “unknown” plants: field peas, triticale, & buckwheat
- *Rhizobium* inoculant for alfalfa  
(Caution: pea and bean inoculants are available; be sure to purchase correct type)
- Large bin or container of vermiculite
- Empty nursery flats, 1 per working group
- (4) 6-inch square inserts for nursery flats
- Pre-mixed 1x, and 0.1x liquid plant fertilizer
- Large bowls or dishes that can hold 6-inch square inserts (for soaking vermiculite)
- Small bowls or weigh boats (for soaking seeds)
- Labeling tape
- Specific nutrient solutions (only prepared if requested)
- Shade cloth (10%, 25%, 50%)
- Colored acetate film (available in craft stores)
- 24-inch bamboo or other small plant stakes
- Light chambers, or a bank of fluorescent lights with broad spectrum or daylight tubes

### Seed Sources

Bulk seeds and *Rhizobium* inoculant can be purchased from farming supply or hardware stores. Annual ryegrass also is available as lawn seed from home improvement stores. Mung beans, alfalfa, and radish seed are sold by organic groceries for growing edible sprouts; check the bulk foods section. A reliable commercial vendor is Seeds of Change ([www.seedsofchange.com](http://www.seedsofchange.com)). Their seed is more expensive but consistently has higher germination rates than seed from educational supply houses.

Two nursery flats (enough for ~150 students) requires the following amounts of seed:

Beans, peas	1 cup (8 ounces) of each
Oats, wheat, buckwheat	1/2 cup (4 ounces) of each
Alfalfa, radish, rye	1/4 cup (2 ounces) of each

If your students will perform their own experiments, purchase twice the amount of seed listed. Unused, dry seed can be stored in a refrigerator in closed plastic bags for up to 1 year. Do not try to store seed that has gotten wet; it will sprout or rot instead.

### Preparing Flats of Plants for the Exercise

We start flats 2 weeks in advance of the lab week for summer or fall courses, and 3 weeks ahead for spring courses. Twelve flats (6 species X 2 nitrogen levels) are sufficient for ~150 students to complete this lab; scale up as needed for your course. It is not necessary to prepare separate flats of each species for each section; the same flats can be used for several sections. Plan to use one large bag (~18 lb or 4 cu.ft. size) of agricultural grade vermiculite for every 12 nursery flats. If students conduct their own experiments, plan to use twice as much vermiculite.

1. To speed germination, soak seed before planting. Soak mung beans and field peas overnight in 2 changes of warm water. Soak all other types for 30 minutes in lukewarm tap water, then drain.
2. Label 12 nursery flats (12 x 24 x 2 inches deep) with the species to be planted and either “High Nitrogen” or “Low Nitrogen.” **Completely** fill the flats with dry vermiculite, then pre-wet it thoroughly. The easiest way to pre-wet vermiculite is by soaking filled flats from the bottom in a tray of water. A hose fitted with a fine misting nozzle also works well.
3. Seeds are planted about 3 “seed lengths” deep, and 3 “seed lengths” apart. For example, to plant mung beans scrape off 3/4 inch (the length of 3 beans end to end) of vermiculite from the tops of the 2 flats for beans. Spread the soaked bean seeds on the exposed surface, about 3/4 inch apart; it is not necessary to measure the distance accurately. Press the seed gently onto the surface, then re-cover them with the vermiculite that was just removed.
4. Plant the remaining seeds, adjusting depth and spacing for seed size.
5. Place all 12 flats in a sunny room, greenhouse, or a growth chamber set for a 12h:12h light/dark cycle. Keep all flats evenly moist until the seeds germinate.
6. When ~75% of the seeds have germinated in a flat, water that flat thoroughly with liquid fertilizer. For the flats labeled “High Nitrogen,” use a 1x solution of liquid 10:10:10 plant food. For flats labeled “Low Nitrogen,” use plant food diluted 1:10.
7. When the plants are well above the soil, and the first true leaves appear, reduce watering frequency. Normally we water when the top 1/2 inch of the vermiculite becomes dry. Watering more frequently encourages damping off and overgrown plants.
8. About one week before the lab, apply 1x or 0.1x liquid fertilizer one more time to each flat.

### **Preparing Materials for Students' Experiments**

We provide students with dry seed, dry vermiculite, 6-inch square inserts for nursery flats, and an empty nursery flat to hold them. We assume each work group of 3–4 students will need 2–4 inserts for their experiment. Students must pre-soak their own seed and vermiculite, and sow the seed as described above. Unless their experimental design specifically prohibits it, students add 1x balanced fertilizer to the vermiculite at planting. If students intend to manipulate specific macro- or micronutrients, they still **must** water their flats at least once with 0.1x balanced fertilizer. If they do not add any fertilizer at all, the seedlings will die before the end of the experiment.

To ensure sufficient light, we keep our students' experiments in the departmental greenhouse. We also have used portable growth chambers that we constructed of plywood and 1x6 lumber, then fitted with 24-inch fluorescent fixtures.

It is impossible to provide a comprehensive list of items that might be used for experiments, but the most common ones become obvious after 2–3 semesters. For us, the most common student experiments are variations on two-species competition. Students measure the rate of germination, growth, and root:shoot ratios of two plant species grown alone versus together in the same insert. We keep seed on hand for 4 monocot and 4 dicot species, which provides considerable variety. If students want to use another species, they must provide the seed.

The next most common experiments our students design look for effects of light intensity or wavelength on allocation. Individual 6-inch inserts can be fitted with tents of shade cloth or acetate film supported by bamboo stakes. The colored acetate craft film is available at most craft stores or from educational suppliers. We recycle scraps of shade cloth from the departmental greenhouse.

Some students have examined the effects of acid rain, salt deposition, or other environmental contaminants on allocation. We ask them to search the web and provide us with a "typical" contaminant concentration (both EPA and USDA are good resources). We prepare a solution that matches it, and students apply the solution directly to the vermiculite in the same way as regular fertilizer.

### **Nutrient Solutions**

It is best to use a balanced 10–10–10 or 20–20–20 liquid fertilizer (Peter's Professional or local generic equivalent). Read the package carefully; some liquid plant foods have a 10–20–10, or other unbalanced formulation that can adversely affect the allocation pattern. Follow package directions (usually 1 tablespoon per gallon of water) to prepare a 1x solution of fertilizer. For the 0.1x solution, dilute the 1x solution 1:10 with tap water. For convenience, we make up 20 liters of the 1x and 0.1x fertilizer solutions at a time in carboys, and use them for several weeks.

To test for effects of specific single nutrients on allocation or plasticity, students can water plants 2–3 times with the appropriate solution listed below. Unless it is convenient for you to make them all in advance, do not prepare these solutions unless students request them.

Ion or Condition of Interest	Acceptable Range in Cropland Soils	To Match Acceptable Range, Water Vermiculite With This Solution
Soil pH	6.0 to 7.0 (Fertile acid soils may reach 5.0, but are rarely any lower)	Prepare 20mM sodium citrate; adjust pH between 5.0 and 7.0 with 0.1M HCl or NaOH. Dilute to a final concentration of 10mM citrate.
Ammonium	2–10 ppm (Excess burns roots)	10mg/L ammonium chloride (NH <sub>4</sub> Cl) in water
Nitrate	10–30 ppm (Excess burns roots)	25mg/L sodium nitrate (NaNO <sub>3</sub> ) in water.
Phosphate	20–100 ppm	50mg/L phosphorus pentoxide (P <sub>2</sub> O <sub>5</sub> ) in water
Potassium	150–800 ppm	400mg/L potash (potassium superoxide, KO <sub>2</sub> ), OR 900mg/L KCl in water
Calcium	1000–2000 ppm	2 g/L calcium carbonate (CaCO <sub>3</sub> ) in water
Magnesium	60–180 ppm	45mg/L anhydrous magnesium chloride (MgCl <sub>2</sub> ) in water
Sulfate	2–10 ppm	6mg/L sodium sulfate (Na <sub>2</sub> SO <sub>4</sub> ) in water
Zinc	>1 ppm	2mg/L zinc chloride (ZnCl <sub>2</sub> ) in water
Boron	0.5–2 ppm	2mg/L boric acid (H <sub>3</sub> BO <sub>3</sub> ) in water
Copper	>0.6 ppm	1.5mg/L cupric chloride monohydrate (CuCl <sub>2</sub> ·H <sub>2</sub> O) in water
Manganese	>1.5 ppm	5mg/L manganese chloride tetrahydrate (MnCl <sub>2</sub> ·4H <sub>2</sub> O) in water
Molybdenum	>0.1 ppm	0.2 mg/L ammonium molybdate tetrahydrate (NH <sub>4</sub> ) <sub>6</sub> Mo <sub>7</sub> O <sub>24</sub> ·4H <sub>2</sub> O)
Sodium & related salts	640–1280ppm	1.3 g/L sodium chloride (NaCl) in water. Note: salinization is a major cause of soil decline in California's Central Valley and other areas that rely on intensive agricultural irrigation.

### General Comments

The main exercise is a structured inquiry by which students can discover for themselves that the resource allocation pattern for a plant species is directly related to the environmental conditions in which it evolved, and to which it is best adapted. For further reading, see Hegazy (2005), Johnston (2004), Tolvanen (2005), and Yang (2005) and references therein.

There are many ways to measure allocation, but the simplest is a R:S ratio. When R:S  $\approx$  1.0, allocation to roots and shoots is equal. This pattern of allocation is common in generalists like ryegrass, which are moderately successful under a variety of conditions. When the R:S ratio is >1.0, roots predominate. Often these species excel at pulling nutrients and water from dry or poor quality soils.

Alfalfa is a good example of this allocation strategy. Legumes that have nodules of symbiotic nitrogen-fixing bacteria also tend to have high R:S ratios. Plants also may have a high R:S ratio if their roots act as storage organs; good examples are radishes, potatoes, carrots, and other root crops. These species often thrive where growing conditions vary seasonally, because the plant can go dormant while conditions are unfavorable. When plants have a R:S ratio  $<1$ , the shoots predominate. These species have a relatively high rate of solar energy capture. They usually grow quickly to reproductive maturity, and often are annual plants like oats.

Differences in allocation strategy are not limited to herbaceous plants or crops. We link this exercise to another lab on pine/hardwood succession by pointing out that even large trees like pines and oaks can have different allocation strategies and R:S ratios. These differences mean they colonize and come to dominate new sites at different rates, resulting in the classical pattern of forest succession.

Students also learn for themselves that each plant species has a different amount of phenotypic plasticity. Species that have a great deal of phenotypic plasticity tend to be more adaptable and will grow in a wider range of conditions than will species with very little phenotypic plasticity. For example, out of the six crop plants listed in Table 3 (Sample Summary Data), radishes are the only species that does not have a significant change in R:S weight ratio between low and high nitrogen conditions. From this, students could rightly predict that radishes are less adaptable than the other species. Horticulture references confirm this prediction, stating that garden radishes require supplemental nitrogen to thrive and form usable roots. The opposite is true for alfalfa, which has a large change in R:S weight ratio, and can grow in a variety of conditions.

### **Practical Suggestions and Common Problems**

The first time your students perform this exercise, make detailed notes of exactly how you grew your plants and where you obtained seed. Attach a copy of the class summary dataset. Every 3–4 semesters, repeat the process. Longitudinal datasets let you see if your seed suppliers' stocks perform consistently. Backup datasets can be used to fill in gaps in datasets collected by small groups.

This lab exercise is hard to complete when there are fewer than 12 students in a lab section. When this happens, we simply divide the species between smaller sections. For example, one lab section may measure just the monocots grown in low and high nutrients, and another lab section just the dicots. After the smaller sections have collected the data for all 6 species, we collate it and distribute the pooled class summary via e-mail. If necessary, we can provide supplemental data from another section for the balance of the species and treatments, or use archived data from past years.

Our students complete the exercise and design and set up their own experiment in a single 3-hour lab period, then collect their data during a second lab period two weeks later. While this schedule works, it would be better if students had more time to read background material and think about their experimental design. If possible, have students take their measurements, calculate the root:shoot weight and height ratios, and complete Table 2 during the first lab period. Wait until the next lab period to have students design and set up their experiments. Remember to schedule time two weeks later for students to collect data from their experiments.

This lab should work well for institutions that have 2-hour rather than 3-hour lab periods. If time runs short, simply assign the graphs and summary questions as homework.

## Sample Data

Table 3: Sample Set of Class Summary Data

Species	R:S Weight Ratio				R:S Length Ratio			
	Low N		High N		Low N		High N	
	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
<b>Beans</b>	2.64	0.150	2.06	0.060	1.478	0.17	1.920	0.180
<b>Alfalfa</b>	5.00	0.100	1.00	0.120	0.641	0.048	0.600	0.034
<b>Radish</b>	3.06	0.040	3.37	0.180	0.494	0.37	0.661	0.050
<b>Rye</b>	1.39	0.135	0.43	0.086	1.488	0.055	0.841	0.015
<b>Oats</b>	0.63	0.041	2.00	0.091	0.900	0.08	0.606	0.088
<b>Wheat</b>	1.03	0.062	0.41	0.007	1.04	0.09	0.72	0.016
<b>Field peas</b>	0.60	0.053	0.43	0.034	0.54	0.09	0.43	0.074
<b>Triticale</b>	0.73	0.004	0.35	0.011	1.17	0.061	0.71	0.013

## Key to the Summary Questions

Most of these questions require students to make inferences from the class summary dataset. There are no specific “correct” answers; we grade on logic and proper interpretation. Supplemental information has been included for the instructors’ reference; we also do not expect students to provide answers as complete as the ones given here.

1. Did you see a general pattern in how allocation changes with the amount of nitrogen available? If so, what was the pattern, and what is your evidence?

First, students need to understand that a R:S ratio of 1.0 means a plant is allocating carbon and nitrogen equally to roots and shoots. R:S values  $> 1$  means relatively more allocation to roots, and  $< 1$  means relatively more resource allocation to shoots. According to the sample dataset, alfalfa, beans, and rye all allocate relatively more resources (by weight) to shoots as nitrogen increases. This increases the denominator and makes the R:S ratio smaller. So the trend is for additional nitrogen to decrease R:S weight ratios. Oats are an exception to this trend; they put more resources into roots as nitrogen increases. Radishes do not appear to change their allocation as nitrogen increases. In contrast, there is not a clear trend in R:S length ratio as nitrogen increases.

2. Large differences in R:S ratio between the two nutrient treatments indicates a high rate of phenotypic plasticity. What other types of environmental conditions would likely favor plants with high phenotypic plasticity? Low plasticity?

Plants with high plasticity tend to grow better in habitats where conditions change frequently. On a global scale, high plasticity is common in temperate zone plants. Stable climates are better suited to species with low plasticity. Many subtropical and tropical plants will exhibit low plasticity, but there are many exceptions to that generalization.

3. What factors other than nutrient or light conditions might affect plants' R:S ratio?

Other common factors include temperature, water availability, soil pH, wind velocity, and the presence of competitors, mutualists and herbivores. The point of this question is not to come up with an exhaustive list, but to stimulate students' thinking as they design their own experiments.

4. When nitrogen was limited, did you see any species in which R:S weight ratio changed, but the R:S length ratio did not? Any species in which the R:S length ratio changed, but the weight ratio did not? How would you interpret any such differences between length ratio and weight ratio?

This question helps students connect allocation to other ecological phenomena discussed in lecture. For example, our students would have already learned that highly branched roots have a larger absorptive surface. Plants with highly branched roots can extract water and nutrients more effectively from soil, and may even kill competing species. If your students have already learned about root fungi, they should be able to explain how and why mycorrhizal structures improve a plant's competitive abilities below ground. If you have discussed allelopathic compounds, students should be able to predict that toxic chemicals secreted by roots (such as juglone from walnuts) will reduce competition below ground. Above ground, the size and orientation of individual leaves can have significant effects on competition. A plant with just a few large, thin leaves can successfully shade out and kill a second plant that has more total above-ground mass, but the second plant has smaller leaves or a shorter stem.

5. Think about the relative contributions of roots, stems, and leaves to the survival of a plant. Which type of plant would be better suited for living in the diffuse light of a forest understory: one with high root:shoot ratio or one with a low ratio? Why?

Conditions of low light but relatively high moisture favor plants with large or numerous leaves. So a lower root:shoot weight ratio would be favored. A more favorable length ratio is harder to predict, because some plants compete against shallow tree roots by sending down a single taproot. Others capture light by spreading as ground covers. It is possible to see plants in the understory that have larger root:shoot length ratios.

6. What would be the best allocation strategy for plants on a windy summit near treeline? Why?

Plants with large root systems and fewer shoots fare better in these sites, so the best strategy is a root:shoot weight ratio that is relatively large. We would expect the length ratio to favor roots as well, since the wind will tend to force plants to remain short.

7. What would be the best allocation strategy for a plant living in a seasonally dry climate like that found in southern California where they typically have a rainy winter followed by a dry summer?

In these conditions, plants may undergo considerable growth below ground during the rainy season, followed by growth above ground in drier seasons. These plants tend to switch back and forth depending on season. When averaged over the course of a year though, the root:shoot ratio will be intermediate to the two extremes described above.

### Comments and Suggestions from the ABLE Conference Workshop

We want to increase the number and variety of plant species that are available for this exercise. So during the major workshop, participants tested two new species: field peas (aka, Austrian winter peas, *Pisum sativum*, ssp. *arvense*), and triticale (*Triticum* x *Secale*). Both are cold-adapted cover crops that are planted to prevent soil erosion in winter and to serve as green manure. Field peas are legumes, but unlike beans have a low R:S ratio. Triticale is a fertile hybrid of wheat and rye, but has growth habits that resemble oats. Both performed as well as the six species listed previously in the **Materials** section. Attendees also suggested buckwheat (*Fagopyrum esculentum*), because it is heat-adapted and matures quickly. Another suggestion was to assess hybrid vigor by comparing rye, wheat, and triticale.

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### About the Author

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