Plants sense and respond to other plants

Often, but not always, plants compete with each other for limiting resources, such as light and nutrients. How do they perceive competition? Are all of the interactions competitive? How do interactions between plants affect higher organizational levels (e.g., communities)?

Key definitions and concepts

Phenotypic plasticity: The capacity of an individual (or a genotype) to exhibit a range of phenotypes in response to variation in the environment.

Phenotypic plasticity in animals

Prenatal rearing can affect formation in Daphnia cucullatae

Phenotypic plasticity in plants

Root plasticity in response to localized nutrient availability

Not all plants display the same range of phenotypic plasticities

The extent of phenotypic plasticity is variable, and may depend on the species, genotype, or environmental conditions.
Some traits are more plastic than others

- Length of vegetative parts
- Flowers
- Architecture
- Number of shoots
- Leaves and flowers
- Root hairlessness

Fruits and flowers are not highly plastic - plasticity between these parts is very limited. These bonsai show the fast-growing roots, which look bogus on real trees.

Allometry and externally versus internally

Sizing up the shape of life

The study of the relative size, scale, or growth rate of parts, and the consequences of allometric scaling

The hormone ABA is synthesized in response to environmental factors, and can cause a deviation from standard allometry. Allometry can be plastic. Environmental conditions or genetic change can cause a deviation from standard allometry.

Signals and cues

Signals and cues convey information

SIGNS

- Sensations are cues
- Odors and light can be cues

Cues inform decisions about when and how to allocate finite resources

- Signals and cues indicate the "best bet"
- Sensations indicate future conditions and circumstances are particularly important.
- Plants grow slowly, and can't run away, so they have to live with the consequences of their decisions.

Plant behavior

What a plant does in the course of its lifetime, in response to an event or change in the environment

- Example: Phototropic curvature towards light source

Plant behavior affects morphological and biochemical phenotypes


Phenotypic outcomes:
- Number and length of leaves and shoots
- Number, size and architecture of leaves, branches, and root systems:
  - Production of metabolites
  - Production of radiation
  - Etc.

Plant behavior is mediated through phenotypic plasticity

Case study: Plasticity of leaf morphology in aquatic plants

Many species prone to periodic submergence show phenotypic plasticity of their leaf forms. Submerged leaves are often thinner and without domatia or ocelli.

Some allelic factors:
- Light, moisture, nutrients, etc.
- Biotic factors: competitors, pathogens, herbivores, etc.

Plant behavior is affected by many environmental parameters

The plant behavior affects morphological and biochemical phenotypes

- The induction of different responses is hereditary or pathogenic in another way, or phenotypic plasticity. For example, response factors can induce the synthesis of an oligopeptide, such as a protein inhibitor.
Summary: Behavior is the variable response to the environment

Plants are affected by each other positively and negatively

With similar needs, competition between plants can be intense

Light can be a limiting resource in many environments

Responses to shading: confrontation, avoidance, tolerance

Plants perceive light levels and color (or: light quantity and quality)

Detection of light levels and quality

Phytochrome detects the boundary of photosynthetically active radiance

We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature..." - Charles Darwin, 1859, On the Origin of Species, Ch. 3, Struggle for Existence
A low ratio of red to far-red light is indicative of vegetative shading

Phytochrome's conformation and absorption spectra “switch”

Transduction of light information downstream of photoreceptors

Shade avoidance is a collection of responses to vegetative shading

Plants can also anticipate and respond to probable future shade

Case study: Portulaca oleracea, light responses in recumbent plant

Future shade can be more important than present shade

Some plants have evolved to tolerate shade – life in the dim lane

Shade tolerance takes many forms
Energetics of shade tolerance: max. assimilation, min. expenditure

- Typically, shade-tolerant plants have a lower rate of respiration in the dark, lower light compensation point, and lower light saturation point.

Light information: Angle, gradients, quality, and time of day

- Light information is MORE than just quantity and spectrum. It is likely plants respond to a richer gamut of light cues.
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Fire (heat and smoke) can promote seed germination

- Fire stimulates seed release or germination in some plants.
- Germination plasticity: light and other cues for seed germination

Karrikins are germination-promoting compounds found in smoke

- Karrikins are compounds found in smoke that promote seed germination.
- Fire-induced germination lets smaller plants become established with less competition from taller plants.

Somatic competition: When plants compete with themselves

- Plants produce many redundant organs that compete with each other.
- Somatic competition increases plant performance by putting resources into more successful organs.

Branch autonomy may vary according to circumstances

- There is experimental evidence to support the idea of light responses between elements independent, competitive and cooperative.

Case study: Two-shoot peas and correlative inhibition

- Two shoots compete for resources, but the best shoot is the one that produces the most seedlings. A shoot in the dark can survive 10 days when deprived of resources, but in competition with another shoot, the last shoot dies. The plant selectively allocates resources to the stronger shoot.
- Case study: Two-shoot peas and correlative inhibition

Germination plasticity: light and other cues for seed germination

- Many seeds germinate in response to white or red light, but low light is inhibitory.
- Fire can stimulate seed release in some plants.

Many seeds germinate in response to white or red light, but low light is inhibitory.

Germination plasticity: light and other cues for seed germination

- Many seeds germinate in response to white or red light, but low light is inhibitory.
- Fire can stimulate seed release in some plants.
Within and between trees, branches in the best conditions prevail

Summary: Perception of and response to vegetative shading

Competition belowground: Root growth is extremely plastic

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Belowground competition: Cues, signals and responses

Plants compete for nutrients, which are frequently limiting for growth

Most plants enhance nutrient uptake through associations with mycorrhizal fungi or nitrogen-fixing bacteria

In some cases, roots avoid contact or proximity to other roots

Plants integrate information about nutrients and neighbors

- Light is a resource and also a source of information that affects plant growth
- Adaptive responses to competition for light can be architectural (shoot position, size and number), morphological (stem elongation), increased leaf area, physiological (amount of chlorophyll or Rubisco), etc.

- Some plants avoid contact with other roots

- Roots respond to the presence of other roots

- Many studies have found that roots have a tendency to grow away from each other

- In some cases, roots avoid contact or proximity to other roots

- Most plants enhance nutrient uptake through associations with mycorrhizal fungi or nitrogen-fixing bacteria

- Bacteria in nodules associations with mycorrhizal fungi or nitrogen-fixing bacteria

- Competition belowground: Root growth is extremely plastic

- Plants compete for nutrients, which are frequently limiting for growth

- Some plants fix atmospheric nitrogen

- Nutrient rich patches

- Plants cannot overproliferate or underproliferate

- Confront, avoid, tolerate

- Resource limitation

- Resource distribution

- Resource status

- Photoinhibition

- Light can be architectural (shoot position), physiological (stem elongation, increased leaf area), morphological (amount of chlorophyll or Rubisco), etc.

- Light is a resource and also a source of information that affects plant growth

- Adaptive responses to competition for light can be architectural (shoot position, size and number), morphological (stem elongation), increased leaf area, physiological (amount of chlorophyll or Rubisco), etc.
Many plants make allelochemicals that deter competitors.

Allelochemicals are produced by plants and can interfere with the growth of nearby plants. These compounds are often produced in response to stress or as a defense mechanism against herbivores.

Allelochemicals can suppress plant growth directly or indirectly.

Allelochemicals suppress plant growth by inhibiting the growth of other plants. This can be done directly, by toxic effects, or indirectly, by altering the availability of resources such as nutrients.

Summary: Plants compete belowground.

Plants compete with each other for resources such as light, water, and nutrients. This competition can be facilitated by allelochemicals, which can suppress the growth of competing plants.

Plants can respond differently to self, kin and alien.

Plants can differentiate between self and non-self, and respond differently to kin and alien. This helps them to avoid self-inhibition and to compete effectively with related and non-related plants.

Do plants respond differently to relatives and unrelated plants?

Yes, this study showed that roots tend to avoid roots of plants that are not related. The closer the genetic relatedness, the less overlap and competition.

Do roots discriminate self from non-self?

Yes, plants discriminate self from non-self. Roots competing with non-self, makes ~50% more root mass than self. Competing only with self, plants become progressively alienated from each other and related to each other as genetically alien plants.

Case study: Parasitic plants are extreme competitors.

Parasitic plants, such as Striga hermonthica, develop specialized organs to overcome host defenses. These plants can cause significant losses in crop yields and are a major agricultural problem.

Parasitic plants perceive their hosts through chemical cues.

Parasitic plants, such as Striga, use chemical cues to locate and attach to their hosts. These cues, such as terpenoids, are produced by the host and help the parasitic plant to locate and attach to its host.

S/NS may rely on self recognition, rather than on NS discrimination.

Self/non-self discrimination is an important mechanism for plants to avoid self-inhibition and to compete effectively with related and non-related plants. This discrimination can be based on chemical or physiological cues.

Spatially, intact peas produced more roots toward their neighbors, indicating that they can respond to spatial cues.
Facilitative behaviors: Plants benefitting from their neighbors

- Tempering of harsh abiotic environments
- Improved physical characteristics of soil
- Wind breaking
- Enhanced nutrient uptake

Benefit from others is commonly higher in harsher environments

Plants can protect others from harsh abiotic and biotic environments

Plants can benefit from amelioration of abiotic stresses by their neighbors

- Increased soil moisture
- Decreased evaporation and soil salinity
- Increased nutrient availability
- Stressed plants may emit volatile emission

Intercropping and crop rotation confer many benefits

- Diverse crops can lead to higher yields
- Ground-hugging crops can suppress weeds
- Root competition for nutrients

A common mycorrhizal network can facilitate resource sharing

Case study: Community-level effects of phenotypic plasticity

- Variation in root architecture affects the plant community
- Resistance to stress

Cues from other plants can prime plants for defense or tolerance

- Stressed plants may emit alarm signals
- Alarm signals are well described in social animals

Perception of and responses to stress and stress cues

- Mechanical damage
- Herbivore-derived chemicals
- Genomic instability
- Volatile emission
- Inhibition and priming of defense responses
- Induction and priming of defense responses
- Stomatal closure
- Photodamage

Plant Architecture
- Variation in root architecture affects the plant community

**Volatile compounds from damaged plants can initiate defenses in others**

- When nearby sagebrush was drought-stressed, it emitted volatile compounds that induced changes in other plants.
- Wild tobacco increased production of defensive compounds (PPO) upon mechanical damage and suffered less herbivore damage when within a mixed species community.

**What are the active compounds and how far do they spread?**

- Volatile signals may have evolved for intra-plant communication.
- Indirect defenses may benefit the emitter's kin.
- Some volatile signals are also inhibitory allelochemicals that reduce competition.
- Volatile signals may signal to predators and enhance the emitter's defenses.

**Case study: Plants may also communicate drought stress**

- Can other stressors be communicated between plants?
- Can unstressed plants respond to stress cues emitted from their stressed neighbors?

**Testing for root-to-root and relay communication**

- Roots share soil with the induced (IND) plant without a soil connection and plants whose roots were not connected to the induced plant.
- After treatment, stomatal aperture was not reduced in plants whose roots shared soil with the induced plant.

**Why do plants emit volatile signals?**

- Volatile signals can prime for stress cues to attract predators and enhance emitter defenses.
- Volatile signals may have evolved for intra-plant communication.
- Some volatiles promote indirect defenses by acting as signals to attract predatory arthropods.

**Summary: Cooperative and facilitative behaviors**

- Plants can benefit from other plants, which can
  - Modulate the abiotic environment,
  - Facilitate nutrient uptake, and
  - Emit cues that prime for stress.

**Putting knowledge to work**

- Some invasive plants show greater than average phenotypic plasticity, but many do not.
- Some invasive plants have shared phenotypes in similar environments.

**Do invasive plants have shared phenotypes?**

- Some invasive plants show greater than average phenotypic plasticity, but many do not.
- Some invasive plants succeed by making lots of small seeds, growing very quickly, producing allelochemicals, or storing water or nutrients.
Case study: Knotweed, “from prize-winners to pariahs”

Fallopia japonica


In 1847, the plant of the year “medal to

This involves intercropping maize with a legume. Donkeytail is a field dominated by Napier grass (Pennisetum purpureum)

Case study: Push-pull planting systems to enhance productivity

Pests are a particular problem in tropical agriculture. An intercropping system called push-pull was developed to protect crops from stem borer caterpillars

Case study: Push-pull planting systems to enhance productivity

Maze

Observation

Napier grass

Case study: Allelopathic rice plants

Efforts are underway to increase momilactone production in cultivated rice varieties, to reduce the need for herbicide use and mechanical weed removal

Archeological records show that Native Americans have grown corn, beans and squash together for millennia

Case study: Maize, bean, squash – the three sisters

Maize

Bean

Squash

Case study: Exploiting light-response plasticity for increased productivity

Greenhouse covers, including a fluorescent segment that absorb some of the blue and green sunlight and emit additional red light, increased the ratio between RED and FAR-RED light

In response to such spectral cues, some plants reduce their allocation to competitive organs and increase allocation to agriculturally important organs such as flowers and fruits. LDR can produce similar effects

Summary of plant-plant interactions

A plant phenotype depends on its genotype and environment, and relies on its plasticity. The environment includes cues from and interactions with other plants, many of which we are just beginning to understand, and which continue to be very active research areas

Summary of plant-plant interactions

Their responses depend on their age, genotype and other endogenous and environmental factors, and may include competition, facilitation, resistance or tolerance

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Future directions (1)
Can fragile ecosystems and biological diversity be protected by better understanding plant–plant interactions?

Aggressive aliens, moved by human actions, damage ecosystems

Japanese knotweed (Fallopia japonica)

Future directions (2)
Can food yields be increased by suppressing competition and competitive responses, enhancing facilitation and increasing production of desired organs?

• Human population growth demands more food production, and higher crop yields
• Plant-plant interactions can decrease yields, but these effects can be ameliorated

Future directions (3)
Can crop yields be increased, especially in marginal agricultural land, by inducing and priming plants to better fit their particular expected growth conditions, forthcoming opportunities and stresses?