PBIO-141
Sensory and Physiological Ecology of Plants

3: Signals, cues, information and evolution

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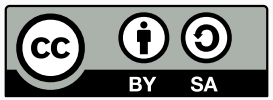

Outline

System and environment

The environment and fitness

Memory, communication, and intelligence

A new paradigm

General discussion

System and environment

Setting the “system boundary”

- *System* under study is the object whose response and behaviour we are interested in. It will depend on the objective of our research. In physiological plant ecology it is frequently the individual plant while in agronomy it is usually the farm plot.
- *Environment* is what is outside the system that we are studying, but affects it. The system (plant, crop field, etc.), in the time scale considered, is assumed not to affect significantly its own environment.

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What is the environment of a plant?

- Anything that affects a plant, but which is outside the plant is part of its environment.
- The soil, the atmosphere, animals, bacteria, fungi, other plants…
- Examples of environmental variables: air temperature, soil temperature, air water content, soil water content, soil fauna activity, density and species of herbivores, presence or absence of pathogens, soil nutrient availability, soil acidity, light (irradiance = quantity, and spectral quality = colour), daylength (= photoperiod)…
- These variables do not vary independently of each other, or through time (cross correlations and autocorrelations)…

The environment and fitness

Cues, Signals and information

I will use the following set of definitions, although different ones are used by some authors and in other related disciplines.

cue Stimuli and "carriers of information" originating from inanimate objects, or from organisms for which being a source of information provides *no* 'advantage' in fitness.

signal Stimuli and information emitted by organisms for which being a source of information provides an 'advantage' in fitness.

communication Transfer of information between organisms in situations where emission of information is plastic. The transfer of information can be uni- or bidirectional.

information Is that which informs, as well as that from which knowledge can be derived.

Acclimation: Definitions

Acclimation, acclimatization Adjustment by an organism to gradual change in its environment, always within its lifetime.

Concurrent acclimation The adjustment to tolerate/profit-from a change in a variable is triggered by the same change event in the same variable.

Preemptive acclimation The adjustment to tolerate/profit-from a change in a variable is triggered by the change in other variable(s) which provide an 'early warning' of a future environmental condition.

"Learning" The adjustment to tolerate/profit-from a change in a variable is triggered by an earlier exposure to a similar change in the same variable.

Cues, Signals and information

A plant in a maize field 10 + 5 min

- What cues and signals could a plant use to predict the future?
- What information could the plant extract from these cues and signals?
- What ‘decisions’ could a plant make based on this information?
- Would such decisions affect its success?
- Developmental decisions (timing) and acclimation (function and structure) are based on information (from environmental and metabolic signals).

The time course of acclimation

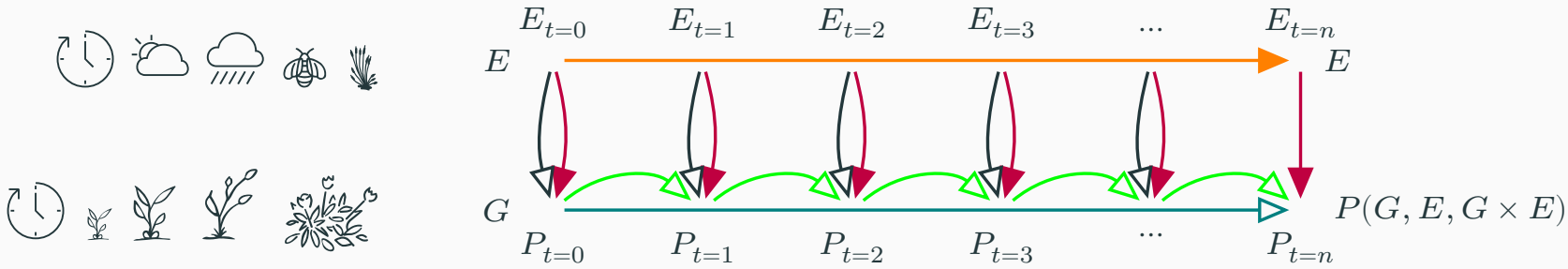
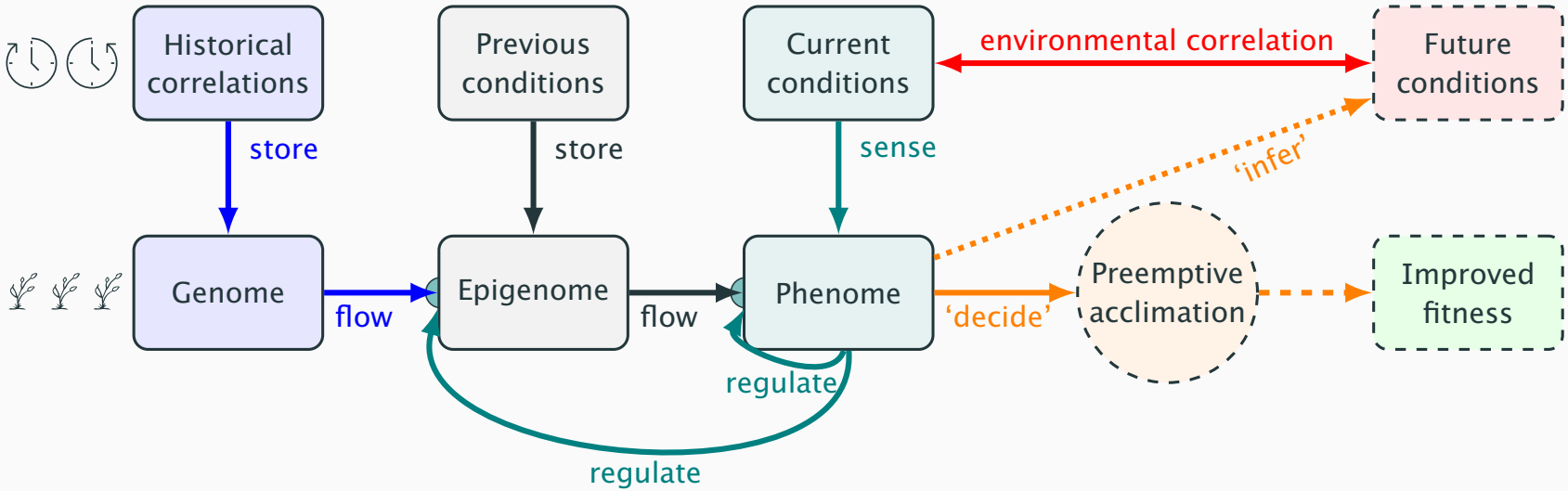


Figure: Time course of one realization of the environment (E) during the lifetime of an individual of a genotype (G) resulting in a phenotype (P).

Preemptive acclimation: A simple model



Flow of information in preemptive acclimation. Arrows represent flows of information: **blue** = retrieved from genome (stored during evolution), **black** = acquired during an individual's or its progenitor's lifetime, **teal** = regulation of gene expression by phenome or downward causation, **red** = lagged correlation between two or more environmental variables, **orange** = outcome of information processing, which is a developmental 'decision' based on an implicit environmental forecast and with implications for fitness. **green** = future phenotype with 'improved fitness' relative, in probabilistic terms, to no acclimation. Dashed boxes and arrows represent the likely or forecasted future. Conditions refer to cues and signals both in the environment and plant's internal status, corresponding to phenotypic plasticity, and developmental plasticity respectively.

Acclimation and developmental plasticity

Problem-solving or decision-making perspective

- What problems does a plant need to solve through its lifetime?
- Discussion
- Some examples:
  - Timing and place of germination.
  - How to reach the soil surface.
  - When to start producing chlorophyll.
  - How tall to grow.
  - In which direction to grow (both above- and belowground).
  - Where to position the leaves and roots.
  - How to protect from enemies.
  - When to emit signals and which ones.
  - When to flower.

Environmental correlations and forecasting

- Correlations in the environment of a plant
- What information do they carry?
- Can you think examples of their use by plants?
- Can organisms ‘generate’ environmental correlations to their benefit?
- Do organisms cheat? Provide false information to deceive other organisms?

Memory, communication, and intelligence

What is memory?

- Memory is storage of information in a way that can be recalled
- Long-term ‘memory’ in organisms is the genome
- Medium-term ‘memory’ is mostly in the epigenome
- Shortest-term ‘memory’ is in cell signalling and metabolic regulation
- This is a useful oversimplification, so be careful!
- The world cannot be described in three shades of grey...

Plants store information

- It has been shown that plants can ‘remember’ past experiences.
- For example the experience of cold is remembered (this is called vernalization).
- There is also evidence that seeds of equal genotype, but that have formed under different environmental conditions, can produce plants with different phenology.
- There is also some recent evidence of trans-generational memory, by which the environment under which parents have grown affects the behaviour of siblings.

Communication within the plant

- There is communication within plants.
- The responses of different parts of an individual plant are coordinated.
- This is not just a question of resource partition.
- In plants there are hormones, small proteins, miRNAs, likely even electrical signals, moving from one place to another and transferring information.
- For example a short time after irradiation of the shoot of a maize plant with ultraviolet radiation, gene expression changes both in the shoots and roots of the plant, and regulated genes are not all the same ones in both parts.
- Soil drying is sensed by roots and plant hormones transfer this information to leaves (and leads to adjustment of stomatal opening).

Communication outwith the plant I

- There is communication between plants.
- The responses of different plants are to some extent coordinated.
- This is not just a question of resource depletion.
- Plants change the light environment (most likely a cue) allowing the detection of neighbours before competition for light starts.
- Plants can recognize their own roots as different from those of neighbours and use this information to adjust behaviour.

Communication outwith the plant II

- Plants emit volatile metabolites that work as ‘alarm signals’, informing other plants and other parts of the same plant, of for example impending attack by herbivore insects.
- Plants emit volatile metabolites that work as ‘alarm signals’, informing the predators of the herbivores that there are insects to be eaten.
- It has been proposed that plants being eaten by herbivore insects can produce UV-absorbing pigments that ‘tag’ the attacked leaves making them easier for predator birds to find.

Communication outwith the plant III

- There is current research on signaling between roots through the soil: for example closure of stomata in unstressed plants when they partially share the rooting space with salt stressed plants. The phenomenon has been demonstrated, but the mechanism is still under investigation, but release of the plant hormone ABA seems to be involved.
- Research on the synchronization of other responses like flowering has shown that communication through roots is used.
- I am not yet aware of research on the fitness advantages of synchronization, but one can imagine advantages at the population level…
- …on the other hand there are analyses explaining how altruism could have evolved, for example in birds and even in bacteria.

Are plants intelligent? 5 min

- This is very controversial.
- As proposed by *Plant Behaviour and Intelligence* (Trewavas 2014), plants could be considered intelligent with a similar definition of intelligence as used for ‘artificial intelligence’ in computer science.
- If they are intelligent, they have a very different implementation of the problem solving capacity.
- If one stretches the definition far enough, I think one could consider every living organism as intelligent.
- But is it necessary to use the word ‘intelligent’ for plants and bacteria? Does it help understanding or makes it more difficult?

What do you think? (5 min)

A new paradigm

A new paradigm is emerging

An exciting time to study plants‼

- Currently it is a very exciting time to study plants…
- …especially how their molecular biology, evolution and ecology are linked.
- We are in the middle of a paradigm shift…
- …for a long time we have disregarded the sensory and problem-solving abilities of plants.
- However, we should be open minded and use our imagination to understand plant life as it is…
- …rather than to project ‘human’ features and qualities onto plants.

Preemptive acclimation: What is the evidence?

- Several plant responses can be only explained from the evolutive/fitness point of view as being a ‘preparation’ to tolerate or escape future stress events or take advantage of future favourable conditions.
- Preemptive shade avoidance as a response to reflected far-red light from neighbouring plants.
- Possibly (a hypothesis we are studying) preemptive acclimation to future soil drying in response to high ultraviolet-B irradiance.
- Eavesdropping-on/communicating-with neighbours to preemptively acclimate/prepare for drought, herbivore attacks, even to synchronize flowering among individuals.

Self vs. alien recognition: What is the evidence?

- Roots in the soil grow differently when near another root of the same plant than when near roots of a different plant (even if the two plants have the same genotype).
- There is keen recognition by shoots dependent on light perception (plants respond differently depending on the species of the neighbours).

General discussion

Environmental correlations and forecasting

Can plants 'predict' the arrival of the cold season?
What sources of information do they use?

Environmental correlations and forecasting

Can plants ‘predict’ the arrival of the spring?
What sources of information do they use?

Environmental correlations and forecasting

Can plants emit ‘signals’ for their benefit?
What are the signals used to attract pollinators?

Environmental correlations and forecasting

Can plants emit 'signals' for their benefit?
What are the signals used to enlist "helpers" for seed dispersal?

Environmental correlations and forecasting

Can plants emit signals to deceive other organisms?
How does mimicry work?

Environmental correlations and forecasting

Can plants ‘generate’ environmental correlations for their benefit?

How does release of organic volatile compounds create a correlation?

Symbioses: ectomycorrhizas

Do symbioses involve communication?

References

References

 Trewavas, A. (2014). *Plant Behaviour and Intelligence*. Oxford University Press. ISBN: 9780199539543.