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## Soil-Weed Seed Communication Systems

Jack H. Dekker

*Iowa State University*, [newweedbiolab@gmail.com](mailto:newweedbiolab@gmail.com)

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# Soil-Weed Seed Communication Systems

## Abstract

The nature of weeds is a complex adaptive, soil-seed communication system. The nature of weedy *Setaria* life history is an adaptable, changeable system in which complex behaviors emerge when self-similar plant components self-organize into functional traits possessing biological information about spatial structure and temporal behavior. *Setaria* life history behavior is a Markov chain of irreversible and reversible processes regulated by morpho-physiological traits acting through environment-plant communication systems (environment-plant-seed, soil-seed). Heritable functional traits are the physical reservoirs of information guiding life history development, emergent behavior. The consequence of structural self-similarity and behavioral self-organization has been the evolution of a complex adaptive seed-soil communication system. Weedy *Setaria* life history is represented in algorithmic form as FoxPatch, a model to forecast seed behavior. Weedy *Setaria* seed life history behaviors are controlled by environmental information (signals) flowing from the soil to the seed embryo. The specific signal to which *Setaria* is tuned affecting seed behavior in the soil is the amount of oxygen and heat (T, thermal) in soil water over time, oxy-hydro-thermal time (O<sub>2</sub>-H<sub>2</sub>O-T-Time). The Shannon environmental-biological communication system between the soil and the *Setaria* seed contains the five elements (E) and components: E1, information source, soil; E2, transmitter, soil particle contact with seed surface water films; E3, channel, continuous soil particle-seed surface water films; E4, receiver, living seed interior from the transfer aleurone cell layer (TACL) membrane to aleurone layer to embryo; E5, destination, embryo. The signal is soil O<sub>2</sub>-H<sub>2</sub>O-T-Time; the message is O<sub>2</sub>-H<sub>2</sub>O-T stimulating embryo respiration. The *Setaria* soil-seed communication system seed behavior can be also expressed as operations (processes) computed by seed algorithms. Information is physical: memory resides in several locations in the *Setaria* seed. Memory is expressed in the long-term by responsiveness to O<sub>2</sub>-H<sub>2</sub>O-heat messages as determined by the morpho-physiological soil-seed communication system (hull, TACL membrane, scavenger protein). The message is remembered: plants pass on a range of heteromorphic seeds appropriate to continuing, successful local adaptation.

## Disciplines

Agricultural Science | Agriculture | Agronomy and Crop Sciences | Weed Science

## Comments

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# Soil-Weed Seed Communication Systems

Jack Dekker

Weed Biology Laboratory, Agronomy Department, Iowa State University, Ames, Iowa 50010, USA

\*Corresponding Author: [jdekker@iastate.edu](mailto:jdekker@iastate.edu)

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**Abstract** The nature of weeds is a complex adaptive, soil-seed communication system. The nature of weedy *Setaria* life history is an adaptable, changeable system in which complex behaviors emerge when self-similar plant components self-organize into functional traits possessing biological information about spatial structure and temporal behavior. *Setaria* life history behavior is a Markov chain of irreversible and reversible processes regulated by morpho-physiological traits acting through environment-plant communication systems (environment-plant-seed, soil-seed). Heritable functional traits are the physical reservoirs of information guiding life history development, emergent behavior. The consequence of structural self-similarity and behavioral self-organization has been the evolution of a complex adaptive seed-soil communication system. Weedy *Setaria* life history is represented in algorithmic form as FoxPatch, a model to forecast seed behavior. Weedy *Setaria* seed life history behaviors are controlled by environmental information (signals) flowing from the soil to the seed embryo. The specific signal to which *Setaria* is tuned affecting seed behavior in the soil is the amount of oxygen and heat (T, thermal) in soil water over time, oxy-hydro-thermal time (O<sub>2</sub>-H<sub>2</sub>O-T-Time). The Shannon environmental-biological communication system between the soil and the *Setaria* seed contains the five elements (E) and components: E1, information source, soil; E2, transmitter, soil particle contact with seed surface water films; E3, channel, continuous soil particle-seed surface water films; E4, receiver, living seed interior from the transfer aleurone cell layer (TACL) membrane to aleurone layer to embryo; E5, destination, embryo. The signal is soil O<sub>2</sub>-H<sub>2</sub>O-T-Time; the message is O<sub>2</sub>-H<sub>2</sub>O-T stimulating embryo respiration. The *Setaria* soil-seed communication system seed behavior can be also expressed as operations (processes) computed by seed algorithms. Information is physical: memory resides in several locations in the *Setaria* seed. Memory is expressed in the long-term by responsiveness to O<sub>2</sub>-H<sub>2</sub>O-heat messages as determined by the morpho-physiological soil-seed communication system (hull, TACL membrane, scavenger protein). The message is remembered: plants pass on a range of heteromorphic seeds appropriate to continuing, successful local adaptation.

**Keywords** Communication Theory, Information Theory, *Setaria* Species-Group, Shannon Communication System

## 1. The Nature of Weeds: Environment-Biology Communication

"What lies at the heart of every living thing is not a fire, not a warm breath, not a 'spark of life'. It is information, words, instructions ... If you want to understand life, don't think about vibrant, throbbing gels and oozes, think about information technology." (Dawkins, 1986; 2).

The nature of weeds is an environment-biology communication system. Biology is information. Evolution itself embodies an ongoing exchange of information between organism and environment. For biology, information comes via evolution; what evolves is information in all its forms and transforms. Information is physical. Biology is physical information with quantifiable (Kolmogorov) complexity. The gene is not the information-carrying molecule, the gene is the information.

Information in biological systems can be studied. An important problem in science is to discover another language of biology, the language of information in biological systems. "The information circle becomes the unit of life. It connotes a cosmic principle of organization and order, and it provides an exact measure of that." (28). This information circle for weedy plants is the predictable developmental events of the annual life history.

### 1.1. Shannon Communication Systems

Information theory was developed by Claude E. Shannon (42) to find fundamental limits on signal processing operations such as compressing data and on reliably storing and communicating data. Since its inception it has broadened to find applications in statistical inference, networks (e.g. evolution and function of molecular codes, model selection in ecology) and other forms of data analysis. A communication system of any type (e.g. language, music, arts, human behavior, machine) must contain the following five elements (E) (figure 1):

A Shannon communication system includes these elements, as well as the concepts of message and signal. A message is the object of communication; a vessel which provides information, it can also be this information; its meaning is dependent upon the context in which it is used. A signal is a function that conveys information about the

behavior or attributes of some phenomenon in communication systems; any physical quantity exhibiting variation in time or variation in space is potentially a signal if it provides information from the source to the destination on the status of a physical system, or conveys a message between observers, among other possibilities.

**1.2. The Nature of Weeds**

The nature of weeds is a complex adaptive system. Weed life history is an adaptable, changeable system in which complex behaviors emerge as a consequence of structural self-similarity and behavioral self-organization.

The nature of weeds is an environment-biology communication system. Biology is information. Information comes via evolution, an ongoing exchange between organism and environment. Information is physical. Biology is physical information with quantifiable complexity.

The nature of communities is revealed with a complete phenotype life history description of each plant species in a local community. Local plant community structure and behavior is an emergent property of its component species. Community dynamics emerges from the interacting life histories of these self-similar, self-organizing, specific components. Understanding an individual weed species in detail can provide the basis of comparison among and within weed species of a local plant community. The challenge is to discover the qualities of each member of the weed-crop community, the nature and variation of species traits used to exploit local opportunity. These insights provide a deeper, specific, understanding of biodiversity responsible for community assembly, structure and (in) stability.

It is in the nature of weedy *Setaria* to process ambient environmental information as a communication system in

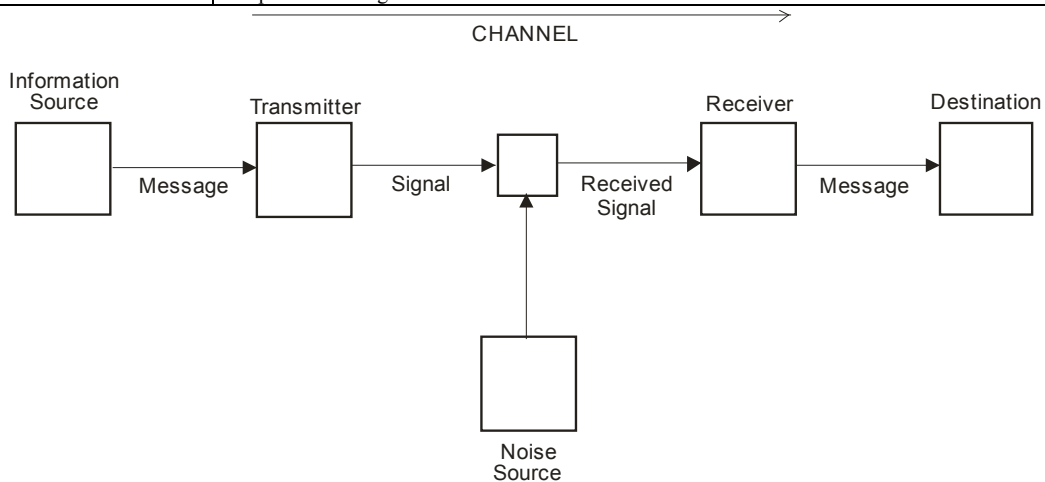
the process of life history seizure and exploitation of local opportunity. The setting of weed evolution, the stage upon which diversifying evolution takes place, is a local population of variable phenotypes of a weed species in a particular locality. The nature of a particular locality is defined by the opportunity spacetime available to the weed population to seize and exploit, to survive and reproduce. Opportunity spacetime for a population is the locally habitable space for an organism at a particular time. It is defined by its available resources (e.g. light, water, nutrients, gases), pervasive conditions (e.g. heat, terroir), disturbance history (e.g. tillage, herbicides, frozen winter soil), and neighboring organisms (e.g. crops, other weed species) with which it interacts (9). It is the local niche, the niche hyper volume (22).

**1.3. The Nature of the Weedy *Setaria* Species-Group**

The weedy *Setaria* species-group (green foxtail, *S. viridis*; bristly foxtail, *S. verticillata*; giant foxtail, *S. faberi*; yellow foxtail, *S. pumila*; knotroot foxtail, *S. geniculata*) (32) is presented herein as a weed exemplar of a complex adaptive, soil-seed communication, system. The nature of the weedy *Setaria* species-group as a complex communication system is an exemplar in the sense of Kuhn (1962; 27), "...concrete problem-solutions ...".

The weedy *Setaria* species-group provides an exemplar of widely distributed species whose complex life history behavior arises from multiple interacting traits. The specific nature of *Setaria* seed-seedling biology provides strong inferences of the nature of all weeds, elucidating the range of adaptations used by individual species to seize and exploit opportunity in agro-communities.

| Communication Element | Description        |
|-----------------------|--------------------|
| 1                     | Information source |
| 2                     | Transmitter        |
| 3                     | Channel            |
| 4                     | Receiver           |
| 5                     | Destination        |



**Figure 1.** Schematic diagram of Shannon information communication system (Shannon and Weaver, 1949; 42)

It is in the nature of weedy *Setaria* to process ambient environmental information as a communication system in the process of life history seizure and exploitation of local opportunity. The setting of weed evolution, the stage upon which diversifying evolution takes place, is a local population of variable phenotypes of a weed species in a particular locality.

## 2. The Nature of Weedy *Setaria* Seed-Seedling Life History

The nature of weedy *Setaria* seed-seedling life history can be described as a complex adaptive, soil-seed communication, system arising from its component functional traits. Complex seed structures and behaviors emerge as a consequence of self-organization of self-similar parts forming this adaptive soil-seed communication system.

Functional traits controlling seed-seedling behavior are physical information that has evolved in ongoing communication between organism and environment leading to local adaption.

The nature of weedy *Setaria* life history emerges when self-similar plant components self-organize into functional traits possessing biological information about spatial structure and temporal behavior. The interaction of self-similar plant components leads to functionally adapted traits, self-organization. These heritable functional traits are the physical reservoirs of information guiding life history development, emergent behavior. Information contained in structural and behavioral traits is communicated directly between seed and soil environment during development. The specific nature of *Setaria* is elucidated in table 1 (1, 4-7, 10-20, 23-26, 29-39, 41, 43-45, 47-8).

**Table 1.** Plant structure (spatial, temporal) and emergent behavior examples of self-similar components, self-organization functional traits, and communication-information in the life history of weedy *Setaria*

|                           |                                     | Self-Similar Components                                     | Self-Organization: Functional Traits   | Biological Information                      | Emergent Behavior                           |  |
|---------------------------|-------------------------------------|---|--|---|---|--|
| <b>SPATIAL STRUCTURE</b>  |                                     |   |  |   |   |  |
| Plant Structure           | Morphological                       | embryo  |  | somatic polymorphism                        | environment-plant-seed communication system | induction of differential dormancy-germinability capacity in individual seeds of inflorescence |
|                           |                                     | seed envelopes  | aleurone layer   |   |   |  |
|                           |                                     |   | caryopsis coat   |   |   |  |
|                           |                                     |   | hull   |   |   |  |
|                           |                                     |   | glumes   |   |   |  |
|                           |                                     | seed  |  | •somatic polymorphism                       | gene flow communication system              | light capture architecture   |
|                           |                                     | inflorescence   | spikelet   |   |   |  |
|                           | fascicle                            |   |  |   |   |  |
|                           | panicle                             |   |  |   |   |  |
|                           | tiller                              | primary   | •phenotypic plasticity   |   |   |  |
| 2°                        |                                     |   |  |   |   |  |
| 3°                        |                                     |   |  |   |   |  |
| Genetic                   | individual plant                    |   |  |   |   |  |
|                           | local population (deme)             |   | self-pollination mating system   | gene flow communication system              | control of genetic novelty                  |  |
|                           | intra-specific variants             |   |  |   |   |  |
|                           | species associations                |   | polyploidization speciation  |   | trait dispersal for local adaptation        |  |
|                           | meta-populations                    |   | trait reservoir  |   |   |  |
| <b>TEMPORAL STRUCTURE</b> |                                     |   |  |   |   |  |
| Life History Behavior     | Seed formation                      | time of embryogenesis of individual seeds on inflorescence  | seed germination heteroblasty: differential development: hull, placental pore, TACL membrane; oxygen scavenger protein | environment-plant-seed communication system | heterogeneous seed germinability capacity   |  |
|                           |                                     | time of tillering inflorescence branching                   |  |   |   |  |
|                           | Seed dispersal                      | time of abscission of individual seeds                      | invasion and colonization  |   | seed dispersal in space                     |  |
|                           | Seed pool behavior in soil          | individual seeds from several inflorescences, plants, years | •hull topography: water film oxygenation   | soil-seed oxygen communication system       | •seed dispersal in time                     |  |
| Seedling emergence        | •placental pore: water film channel |   | •annual dormancy-germination cycling in soil   |   |   |  |
|                           |                                     | •TACL membrane: O <sub>2</sub> transport                    |  | locally adapted emergence patterns          |   |  |
|                           |                                     | •oxygen scavenger: embryo O <sub>2</sub> regulation         |  |   |   |  |
|                           |                                     | <b>Self-Similar Components</b>                              | <b>Self-Organization: Functional Traits</b>  | <b>Biological Information</b>               | <b>Emergent Behavior</b>                    |  |

One of the most important events in a plant's life history is the time of seed germination and seedling emergence, the resumption of embryo growth and plant development. Emergence timing is crucial, it is when the individual plant assembles in the local community and begins its struggle for existence with neighbors. Resumption of growth at the right time in the community allows the plant to seize and exploit local opportunity at the expense of neighbors, allowing development to reproduction and replenishment of the local soil seed pool at abscission. Soil seed pools are the source of all future local annual weed infestations, and the source of enduring occupation of a locality.

Any complete description of an organism includes the concept of phenotypic function, which consists of two universes: the physical (the quantitative, formal structure) and the phenomenal (qualities that constitute a 'world') (40). The nature of *Setaria* weed seeds and seedlings is the story of plant spatial structure (genetic, morphological) and temporal life history behaviors, instigated by functional traits, and resulting in local adaptation and biogeography. The weedy phenotype can be described in terms of its morphological structure, the embryo and specialized structures forming the seed, and the self-similar shoot tiller architecture on which reproductive inflorescences arise. The individual, self-similar seeds, form local populations (the deme) which aggregate, self-organize, into the global metapopulation. The genetic and morphological structure provides an enduring foundation for the evolution of life history behavioral adaptation: plant functions, functional traits and regulation of function. The behavioral regulation of the *Setaria* phenotype is an emergent property arising from the interaction of several morpho-physiological seed compartments (embryo, caryopsis, hull, spikelet, fascicle, inflorescence tiller). The emergent property of these interacting, self-organizing, self-similar components is seed heteroblasty: the abscission of individual seeds from a panicle, each with different inherent dormancy-germination capacities. Seed heteroblasty is the physical information forming memory of successful past seedling emergence times appropriate to a locality. It is the hedge-bet for seizing and exploiting future opportunity spacetime.

### **3. *Setaria* Seed Life History as Complex Adaptive Soil-Seed Communication System**

The nature of the weedy *Setaria* is revealed in the physical (morphological and genetic spatial structures) and the phenomenal (life history behavior instigated by functional traits). The nature of *Setaria* is the consequence of structural self-similarity and behavioral self-organization. Structural self-similarity in morphology was revealed in seed envelope compartmentalization and individual plant tillering; in genetics by local populations and *Setaria*

species-associations forming the global metapopulation. Behavioral self-organization was revealed in the self-pollenating mating system controlling genetic novelty, seed heteroblasty blueprinting seedling recruitment, and phenotypic plasticity and somatic polymorphism optimizing seed fecundity.

The consequence of structural self-similarity and behavioral self-organization has been the evolution of a complex adaptive seed-soil communication system. Weedy *Setaria* life history is represented in algorithmic form as FoxPatch, a model to forecast seed behavior. The environment-biological informational system with which weedy *Setaria* life history unfolds is represented in the seed-soil communication system.

#### **3.1. Forecasting *Setaria* Seed behavior: FoxPatch**

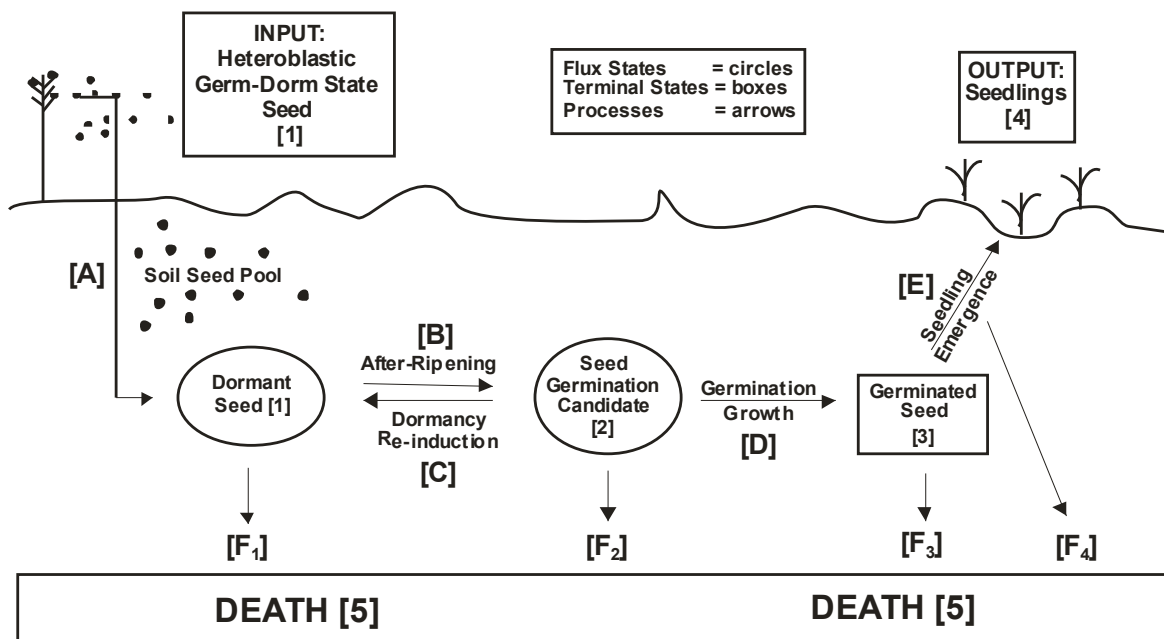
Weedy *Setaria* spp. seeds with heterogeneous dormancy states are recruited from soil pools when sufficient oxygen, water and heat accumulate over time (6). The variable timing of this recruitment is the first step in assembly with crops and other weeds in annually disturbed agricultural communities. The timing of seedling emergence is the single most important factor in determining subsequent weed control, competition, crop losses and replenishment of the soil seed pool.

FoxPatch is a computational tool to predict the behavior of individual weedy *Setaria* spp. seeds, including after-ripening, dormancy re-induction, germination and seedling emergence from the soil (5, 7, 8). It is based on intrinsic morpho-physiological traits in the seed (the germinability-dormancy state) at abscission responding to extrinsic oxy-hydro-thermal time signals it receives from the environment (5). Three rules of behavior define the interaction of individual seeds with signals from their immediate environment, and thus determine patterns of seed-seedling life history behaviors.

Algorithmically, FoxPatch consists of a schema derived from the morpho-physiological traits in the seed determining its dormancy state at any time in its life history. This schema responds to soil signals in predictable ways. These predictable responses are the foundation for three seed behavior rules which together define the seed-seedling portion of the weedy *Setaria* sp. life history. Forecasting *Setaria* seed behavior relies on three separate sources of information: dormancy state heterogeneity, environmental signals and patterns of seedling emergence.

##### **3.1.1. Seed State and Process Model**

FoxPatch is a predictive tool, a formalization of what we empirically know about the *Setaria* spp. seed traits (schema) and the life history behaviors that arise from the interaction of these traits with the environments in which they thrive (behavior rules). The life history of weedy *Setaria* sp. seed is schematically represented in Figure 2.



**Figure 2.** Schematic diagram of weedy *Setaria* sp. soil seed pool behavior based on the life history of the seed (seed states and transitions between states). Life history states (terminal, boxes; flux, circles): [1] dormant seeds (DORM), [2] germination candidate seeds (fully after-ripened; CAN), [3] germinated seeds (GERM), [4] seedlings (SEEDLING), and [5] dead seeds or seedlings (DEAD). Life history processes (arrows), or transitions between states: [A] induction of dormancy and input (dispersal) of dormant seed at abscission (the seed rain), [B] after-ripening of dormant seed (AR), [C] re-induction of (2°) dormancy in germination candidates (DORM RE-INDUCT), [D] germination growth (GROW), [E] seedling emergence (EMERGE), and [F: F<sub>1</sub>-F<sub>4</sub>] death (from states 1-4).

The seed portion of the life history can also be represented by the behavioral processes leading to transitions between seed states:



Where: DORM<sub>AB</sub>, dormancy state at abscission.

### 3.1.2. Soil signal controlling seed behavior: oxy-hydro-thermal time

*Setaria* require only three resources/conditions (signals) from their immediate soil environment to germinate and emerge as seedlings: temperatures (T) favorable for germination and seedling emergence (thermal-time), adequate but not excessive soil moisture (hydro-time), and oxygen dissolved in imbibed water to support germination metabolism (oxy-hydro time). For each of these three resources/conditions there is a threshold amount an individual seed needs to germinate. Each of these three thresholds has a minimum and maximum value range within which seeds germinate. When any of these three signals is insufficient or excessive, a living seed in the soil will remain dormant. When all three signals are within their thresholds germination will occur. The conditions within all three thresholds can also be conceptualized as the germination "window" through which a seed must pass to germinate and emerge as a seedling, germination phenotype space.

FoxPatch can be expressed quantitatively by defining the environmental signal required by an individual to complete

each of the component processes, given the initial dormancy state of individuals. All viable weedy *Setaria* spp. seed in the soil obey the general seed behavior rule: The behavior of an individual weedy *Setaria* seed in the soil is regulated by the amount of oxygen dissolved in water (the oxygen-water signal) that accumulates in the seed symplast, and temperatures favorable (or not) to germination growth (the germination temperature signal), over some time period (cumulatively oxy-hydro-thermal time) (1, 3-6, 13-15, 16, 41).

All FoxPatch predictions are based on the assumption that when an individual, dormant, foxtail seed receives the minimum environmental signal required for after-ripening and germination in the soil it will emerge (barring mortality). Therefore, the parameters critical to predicting the seedling emergence of an individual seed are [1] the soil signals (T, H<sub>2</sub>O, O<sub>2</sub>) required by an individual *Setaria* sp. seed to overcome its inherent level of dormancy to after-ripen and germinate (the schema), and [2] the signals that an individual seed in the soil actually experiences and utilizes (soil signal). Provided these two critical pieces of information are available, seedling emergence predictions in FoxPatch are

based on the following:

General prediction algorithm: an individual weedy foxtail seed will change state when the minimum inherently-required oxy-hydro-thermal time signal is received from its realized environment (plus signals not causing an effect due to inefficient transduction or insensitivity).

There are two signals in the soil that interact to control weedy *Setaria* seed behavior. Both are based on temperature and moisture. The oxygen signal is OxSIG, oxy-hydro-time. The heat signal is TSIG, germination thermal time. The combined influence of these two signals on foxtail seed behavior is the oxy-hydro-[thermal]-time signal.

### 3.1.2.1. The oxy-hydro-time signal: OxSIG

One of the most striking features of the soil in the temperate regions of the globe is the diurnal fluctuation in soil temperatures that occur every day, and the ample moisture in springtime soils contains the seasonally maximum amount of oxygen immediately after thawing. This diurnal phenomena (the "big spring temperature oscillator") plays a crucial role in after-ripening and germination (15). During the cool night period water entering the seed placental pore brings with it much oxygen due to its high solubility. During the mid-day, temperatures rise and O<sub>2</sub> solubility decreases causing a de-gassing effect. The water is purged, sending a pulse of free oxygen into the seed symplast because diffusion out of the narrow pore opening is restricted. The contribution of both chronic O<sub>2</sub> availability (based on solubility alone) and acute O<sub>2</sub> availability (based on degassing with temperature change) are the two sources of the oxy-hydro signal to which *Setaria* spp. have adapted and synchronized their life history in the soil.

The signal controlling *Setaria* seed after-ripening, 2° dormancy re-induction, and the continuing supply of O<sub>2</sub> during the germination processes is OxSIG: the oxygen mass per water volume of seed symplast (caryopsis) per time period per seed. An individual *Setaria* seed experiences two different OxSIG's (chronic, acute) from the soil environment depending on the diurnal pattern of temperature (constant, alternating, or both). The OxSIG affecting any single seed is the summation over time of the O<sub>2</sub> received:

$$\text{OxSIG}_{\text{Total}} = [(\text{OxSIG}_{\text{Chronic}}) + (\text{OxSIG}_{\text{Acute}})]$$

The chronic O<sub>2</sub> signal (SIG<sub>Chronic</sub>) is that amount of dissolved O<sub>2</sub> (g L<sup>-1</sup>) that is diffuses into the seed symplast when the ambient temperature is constant for some time period (g L<sup>-1</sup> Time<sup>-1</sup>):

$$\text{OxSIG}_{\text{Chronic}} = (\text{OXY}_{\text{Temp}^\circ\text{C}} * \text{VH}_2\text{O}_{\text{Seed}}) * (\text{TIME}_{\text{Temp}^\circ\text{C}}) \text{ seed}^{-1}$$

Where:  $\text{OXY}_{\text{Temp}^\circ\text{C}}$ , O<sub>2</sub> solubility (g per l) at a particular temperature;  $\text{VH}_2\text{O}_{\text{Seed}}$ , H<sub>2</sub>O volume (g or ml) of a single seed symplast;  $\text{TIME}_{\text{Temp}^\circ\text{C}}$ , time (h) at a particular temperature.

We have experimentally determined the seed symplast water volume of a locally (Ames, IA, USA) adapted *S. faberi*

population (author lot # 3781; K99-40) to vary from 0.00036 to 0.00050 ml (360-500 nanoliters) per seed, depending on the immediate microsite moisture availability and temperature (Atchison & Dekker, unpublished data).

The acute O<sub>2</sub> signal (SIG<sub>Acute</sub>) is the difference in O<sub>2</sub> (g) in solution that is de-gassed (lost from solution) when the symplastH<sub>2</sub>O changes from a low to a high temperature, a process that occurs every day of the year in the soil:

$$\text{OxSIG}_{\text{AR Acute}} = (\text{OXY}_{\text{LOW Temp}^\circ\text{C}} * \text{VH}_2\text{O}_{\text{Seed}}) - (\text{OXY}_{\text{HIGH Temp}^\circ\text{C}} * \text{VH}_2\text{O}_{\text{Seed}})$$

Where:  $\text{OXY}_{\text{LOW Temp}^\circ\text{C}}$  and  $\text{OXY}_{\text{HIGH Temp}^\circ\text{C}}$  are the oxygen solubilities in H<sub>2</sub>O at the low and high temperatures, respectively.

### 3.1.2.2. The thermal signal: TSIG

Temperature (T) plays two different roles as a signal controlling *Setaria* seed behavior. The ambient temperature determines O<sub>2</sub> solubility (inversely related to T) as well as the germination growth environment. Temperature's two roles often have opposite effects on an individual seed: cool provides more O<sub>2</sub>, while inhibiting germination; warm provides less O<sub>2</sub> but promotes embryo growth.

### 3.1.2.3. Oxy-hydro-[thermal]-time: OxSIG& TSIG

The combined influence of these two signals on foxtail seed behavior is the oxy-hydro-[thermal]-time signal (chronic and acute OxSIG& TSIG). Experimentally, local soil moisture and temperature are measured at depth in the soil hourly, continuously, for accurate signal quantification.

### 3.1.3. Schema of intrinsic *Setaria* sp. seed traits

Each individual *Setaria* sp. seed possesses inherent traits, morphological and physiological, that determine how it will behave in a variety of environmental conditions it might encounter. These traits of the seed are inherited from the parent plant at abscission, and can be conceptualized as a plan for future action, a schema. The schema is a blueprint constraining an individual's unique set of reactions to local environmental conditions (biotic and abiotic), the realized phenotype. This schema is biologically complete in the sense it predicates all the behaviors an individual will perform such as after-ripening and germination. What is the schema that weedy *Setaria* sp. seed possess? In its most basic computational form it is the amount of oxy-hydro-thermal time signal required to germinate an individual seed. Experimentally this is determined by germination assays at seed abscission under optimal, controlled conditions (see dormancy induction below).

### 3.1.4. Germinability-dormancy induction

The local environment surrounding an individual *Setaria* panicle during embryogenesis, and the physiology of dormancy induction traits in developing embryos, conspire to produce a heterogeneous collection of seeds, each with potentially different dormancy states at abscission, the time they first become independent of the parent plant, seed germinability-dormancy heteroblasty. The amount of



dormancy in each seed, and the variability in dormancy quantity among individuals, is a direct display of the future timing of recruitment. The consequence of past selection and local adaptation determines the "germinability-dormancy heterogeneity bandwidth" among a cohort of seeds produced by a single successful parent plant panicle. The precise mechanisms and environmental conditions leading to particular dormancy states in individual seeds are unknown, but the role of light may be important (5, 6, 13). When this process is understood the definition of a dormancy induction rule during embryogenesis may be possible. Until that time, the quantity of dormancy induced in an individual seed at the time of abscission ( $DORM_{AB}$ ) can be experimentally determined in optimal conditions:

Initial individual seed dormancy state: The inherent dormancy state of an individual foxtail seed at abscission is defined as the minimum oxy-hydro-thermal time signal required to stimulate germination.

The initial dormancy state is experimentally determined by the minimum amount of after-ripening (AR) required for a dormant seed (DORM) to become a germination candidate (CAN), and for that CAN to germinate (GROW), in favorable (controlled, ideal) environmental conditions (e.g. AR: 4°C, moist, dark; GROW: 15-35°C alternating diurnal, moist, light). The population data is presented in frequency or cumulative distribution diagrams of AR dose versus percent germination. The signals required to after-ripen and germinate individual foxtail seeds can be expressed in a number of ways, including AR time and oxy-hydro-thermal time units.

### 3.1.5. Rules for individual weedy *Setaria* sp. seed behavior

The rules that control individual weedy *Setaria* sp. seed behavior are illustrated in its life history (Figure 2). *Setaria* sp. seed behavior is the consequence of the interaction between extrinsic local environment influences and intrinsic seed traits (the schema). These rules of behavior are the inevitable consequence of past selection and adaptation molding the *Setaria* sp. phenotypes we see in the field today. They pertain to living processes and changes in state, as opposed to the more stochastic and unpredictable factors involved in mortality.

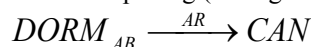
FoxPatch is based on three rules of individual weedy *Setaria* sp. seed behavior. These rules are defined by field observations of dormancy state heterogeneity among seeds at abscission from an individual panicle, as well as by after-ripening, dormancy re-induction, and germination. What particular behavior occurs is dependent on the initial state of the seed (the schema) and the rate and amount of signal accumulated. Each of these behavioral transitions is governed by a specific foxtail seed behavior rule, presented here in their qualitative forms.

#### 3.1.5.1. The after-ripening rule, and its inverse the dormancy re-induction rule

From the time a *Setaria* spp. seed is shed (typically

August-November in North America) it is exposed to moisture-temperature conditions that either after-ripen (AR) the seed (generally cool, moist) or maintain (or induce) dormancy (generally hot, dry). When sufficient AR has occurred, and the seed symplast accumulates enough oxygen (dissolved in water) over a period of time, it becomes a germination candidate.

After-Ripening (see figure 2):

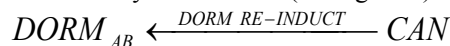


After-ripening rule: An individual dormant foxtail seed (DORM) will after-ripen when the rate of oxygen dissolved in water entering the symplast exceeds the capacity to remove that oxygen for some time period, during which the minimum inherently-required amount of oxygen has accumulated in the symplast (CAN) allowing germination (GERM) to occur at some temperature.

After-ripening prediction algorithm: An individual dormant foxtail seed (DORM) will after-ripen to a germination candidate (CAN) when the minimum inherently-required oxy-hydro time signal is received from its realized environment (plus signals not causing an effect due to inefficient transduction or insensitivity) allowing germination (GERM) to occur at some temperature.

When conditions in the field are generally hot and dry for some time (e.g. summer) the oxygen and water levels in the seed decrease and dormancy is re-induced as the effects of previous after-ripening are lost.

Dormancy re-induction (see figure 2):



Dormancy re-induction rule: An individual after-ripened foxtail seed (CAN) will reacquire dormancy when the rate of oxygen dissolved in water entering the symplast is less than the capacity to remove oxygen for some time period, during which the minimum inherently-required amount of oxygen is no longer present.

Dormancy re-induction algorithm: An individual foxtail seed germination candidate (CAN) will have dormancy re-induced when the minimum inherently-required oxy-hydro time signal is not received from its realized environment (plus signals not causing an effect due to inefficient transduction or insensitivity) preventing germination from occurring at some temperature.

Experimentally we determine AR and DORM by removing seed from the field at intervals through the year and determine the number of viable (tetrazolium assay) seeds that immediately germinate (GERM) or not (DORM) under optimal conditions.

#### 3.1.5.2. The germination candidate threshold state

Once a seed becomes fully after-ripened, saturated with sufficient dissolved oxygen in the symplast, it is poised on the threshold of germination, a germination candidate (CAN), awaiting only favorable temperature conditions to germinate. It is from the after-ripened seed pool (CAN) in the soil that seedlings are recruited. It is the least dormant seed in the soil that after-ripen the earliest in a season, and therefore

they compose the most likely germination candidates for recruitment.

### 3.1.5.3. The seed germination rule

When a fully after-ripened weedy *Setaria* sp. seed, a germination candidate, is exposed to some temperature (usually higher than that for AR) for some time it germinates.

Germination (see figure 2):  $CAN \xrightarrow{GROW} GERM$

Seed germination rule: An individual foxtail germination candidate (CAN; an after-ripened seed with sufficient free symplastic oxygen for sustained respiration) will germinate when exposed to minimally favorable temperatures for some time period.

Seed germination algorithm: An individual foxtail germination candidate seed will germinate when exposed to minimally favorable temperatures from its realized environment (plus signals not causing an effect due to inefficient transduction or insensitivity) for some time period.

Minimally favorable temperature often is a narrow temperature range that increases as the oxygen in the symplast increases (after-ripening depth).

The most complex part of FoxPatch at this time is elucidation of a quantitative function that predicts germination of a germination candidate based on both oxy-hydro (OxSIG) and thermal (TSIG) time. Two opposing forces are at work at this time: lower temperatures (e.g. 0° C liquid water) possess high oxygen solubility and inhibit germination; higher temperatures (35° is more favorable than 15° C) stimulate germination but have low

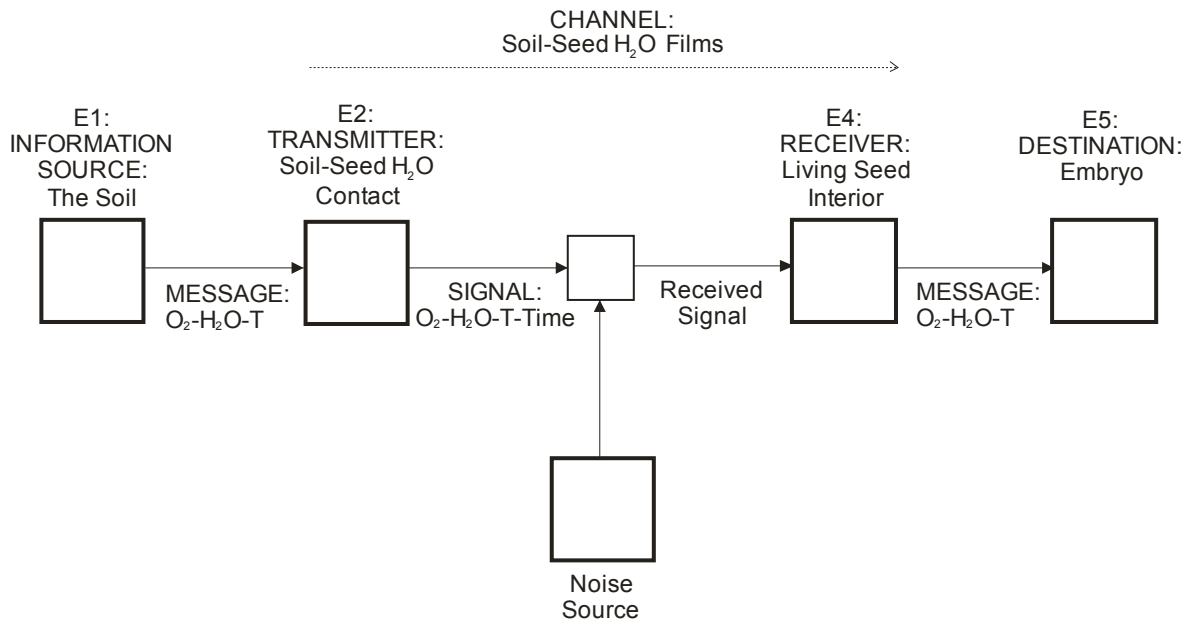
oxygen solubility. After-ripening is favored by cool, moist conditions. Germination is favored by relatively high symplast oxygen saturation and high temperatures. The correct function to predict these opposing forces will be a computational trade-off weighing their relative influences and interaction. These opposing elements provide a very powerful, yet sensitive, environment-sensing mechanism allowing *Setaria* spp. to detect very precisely favorable conditions leading to recruitment and subsequent success.

Forecasting the seed behavior of weedy *Setaria* spp. seeds in agricultural soils based on intrinsic dormancy qualities, environmental oxy-hydro-thermal-time signals, and consistent seasonal patterns of seedling emergence could provide us with a robust tool of immense value, an algorithm of the first assembly step of disturbed agricultural communities.

## 3.2. *Setaria* Soil-Seed Communication System

### 3.2.1. Shannon communication system for weedy *Setaria* seed-seedling life history

The nature of weedy *Setaria* seed-seedling life history is a complex adaptive, soil-seed communication system arising from its component functional traits (Table 1). Functional traits controlling seed-seedling behavior are physical information that has evolved in ongoing communication between organism and environment leading to local adaption. A Shannon communication system of any type must contain the five elements (E) presented in figure 1, as well as message and signal. (42)



**Figure 3.** Schematic diagram of Shannon environment-biology information-communication system for weedy *Setaria* seed-seedling life history development. Communication elements (E): E1, information source, soil; E2, transmitter, soil particle contact with seed surface water films; E3, channel, continuous soil particle-seed surface water films; E4, receiver, living seed interior from TAEL membrane to aleurone layer to embryo; E5, destination, embryo. The signal is soil O<sub>2</sub>-H<sub>2</sub>O-T-Time; the message is O<sub>2</sub>-H<sub>2</sub>O-T stimulating embryo respiration.

Weedy *Setaria* seed life history behaviors are controlled by environmental information (signals) flowing from the soil to the seed embryo. The *Setaria* seed is constructed in such a way as to be receptive to specific signals contained within the entire soil information available to it. The specific signal to which *Setaria* is tuned affecting seed behavior in the soil is the amount of oxygen and heat (T, thermal) in soil water over time, oxy-hydro-thermal time ( $O_2$ - $H_2O$ -T-Time). The message that directly controls *Setaria* seed behavior is oxygen and heat accumulating in the embryo modulating seed respiration.

The Shannon environmental-biological communication system between the soil and the *Setaria* seed contains the five elements (E) and components as schematically organized in figure 3.

### 3.2.1.1. Information source (E1): the soil adjacent to the *Setaria* seed

"The *information source* selects a desired *message* out of a set of possible messages" (Shannon and Weaver, 1949; 42)

The source of information generating the message affecting weedy *Setaria* seed life history development is the soil surrounding the individual seed in a particular locality. There are many sources of information impinging on the seed, including changing cycles of oxygen-water-heat in seasonal climate and environment, site latitude-longitude-elevation-slope-aspect, soil quality (tilth, structure, texture, compaction, organic matter, chemicals), neighboring seeds and plants, microbial and animal activity, and agricultural and other human disturbances. This information flows constantly within the soil. The soil-borne seed responds to only a limited portion of the entire soil information, the message controlling behavior. The message is heat and oxygen dissolved in soil water that the *Setaria* embryo requires for continued development, whether continued quiescence or germination. The growth and development behaviors of the embryo include 'remain dormant' or 'resume growth and development'. The message was naturally selected during *Setaria* evolution from among the larger entire set of soil information as a dependable signal stimulating-inhibiting seed germination-dormancy behaviors. The specific signal that affects *Setaria* behavior is the amount of heat and oxygen dissolved in soil water films connecting soil particles with the seed with time, oxy-hydro-thermal-time ( $O_2$ - $H_2O$ -heat-time).

### 3.2.1.2. Transmitter (E2): water film contact between soil particle-seed surfaces modulating oxygen content

"The *transmitter* changes this *message* into the *signal* which is actually sent over the *communication channel* from the transmitter to the *receiver*." (Shannon and Weaver, 1949; 42)

The transmitter converts/encodes/changes the message to produce a suitable signal. The transmitter is the water film adhering to soil particles adjacent to, and continuous with, seed exterior surfaces (hull, placental pore). The

messagesentis heat and oxygen dissolved in soil water, information is physical. The specific signal transmitted is the amount of heat and oxygen dissolved in soil water films connecting soil particles with the seed interior-exterior with time (oxy-hydro-thermal-time) received by the embryo-endosperm affecting *Setaria* behavior. The transmitter modulates the heat and oxygen content of water films that physically connect soil particles with seed surfaces and that are received by the receiver, the living tissues of the seed interior. The transmitter changes, encodes, the amount of oxygen dissolved in soil water by formation of continuous water films physically connecting soil particle-seed surfaces. Signal encoding is the change in the water film message by the morphology of the seed surface. *Setaria* seed hull surface morphology and topography accomplish these changes that encode the signal, information is physical.

### 3.2.1.3. Channel (E3): soil-seed water films

The *Setaria* communication channel is the continuous water film connecting soil particles with the seed exterior (hull, placental pore) and interior (TACL, endosperm, embryo). This water film communication channel transmits the oxygen-water-heat signal to the living seed interior receiver and the embryo destination. The capacity of this water film channel can be described in terms of the water-oxygen information it transmits per unit time from the adjacent, continuous, soil source.

### 3.2.1.4. Noise source

Introduction of noise in the communication channel means the received message exhibits increased uncertainty. The received signal is selected out of a more varied set than the transmitted set. There can be several sources of noise between the transmitter and receiver, everything that corrupts the water-oxygen signal: water film discontinuities, physical interference from soil biota and chemicals, soil structural changes, seed damage, localized areas of anomolous gas and water content/exchange.

### 3.2.1.5. Receiver (E4): the seed interior beginning with the TACL membrane continuous with the exterior water film terminating with the placental pore

"The *receiver* is a sort of inverse transmitter, changing the transmitted signal back into a message, and handling this message on to the destination." (Shannon and Weaver, 1949; 42)

The signal transmitted from exterior water films (terminating with the placental pore) are received by the seed interior by the transfer aleurone cell layer (TACL) membrane transport and diffusion equilibrating heat and dissolved gases between the exterior-interior seed compartments. Water oxygenated by the seed surface water films is the signal that is decoded by the seed interior receiver in the form of the free oxygen message available to stimulate respiration and hence embryo germination (the destination).

3.2.1.6. Destination (E5): the embryo, whose behavior is provoked by accumulation of seed interior oxygen stimulating respiration

The resumption of life history growth and development by the embryo is stimulated by the accumulation of adequate interior oxygen leading to germination and seedling emergence. Insufficient oxygen maintains or stimulates dormancy and embryo quiescence. This message is 'remembered' by the weedy *Setaria* seed in the process of evolutionary adaptation. Successfully surviving and reproducing plants arising from seed utilizing this communication system pass on these functional traits to their polymorphic progeny, each of which in turn passes on the ability to generate its own range of heteromorphic seeds appropriate to continuing local adaptation

3.2.2. *Setaria* Soil-Seed communication transmission algorithm

The *Setaria* soil-seed communication system seed behavior described above (Figure 3) can be also expressed as operations (processes) computed by seed algorithms (Table 2).

### 3.3. Seed Memory and Adaptive Evolution

Information is physical: memory resides in several

locations in the *Setaria* seed. *Setaria* seed memory has both short and long term expressions. In the short term, memory is expressed by the amount of oxygen accumulated in the seed interior. *Setaria* seed memory is the current germination-dormancy state of each living seed in a local soil pool. The seed germination-dormancy capacity is 'hard-wired' (intrinsic) to seed at birth, embryogenic seed dormancy induction. Information storage is an important component of communication. The ability of *Setaria* seeds to accumulate oxygen in the seed interior provides a message storage capability for a time interval determined by the seed's germination-dormancy capacity. Memory is expressed in the long-term by responsiveness to O<sub>2</sub>-H<sub>2</sub>O-heat messages as determined by the morpho-physiological soil-seed communication system (hull, TACL membrane, scavenger protein). Memory resides in the functional-adaptive traits that regulate all seed behaviors by transducing/transforming/encoding and decoding inorganic soil O<sub>2</sub>-H<sub>2</sub>O-heat signals over time: the threemorpho-physiological mechanisms forming the soil-seed communication system. The message is remembered: plants arising from seed utilizing this communication system pass on these functional traits to their polymorphic progeny, each of which in turn passes on the ability to generate its own range of heteromorphic seeds appropriate to continuing, successful local adaptation.

**Table 2.** Seed algorithms, operations (developmental processes), computed by weedy *Setaria* seeds during life history development by means of the Shannon soil-seed communication system.

| Soil-Seed Communication System   |  |
|--|--|
| Algorithmic Operations Computed  | Life History Developmental Processes   |
| Step 1: Acquire information from soil water source adjacent to seed (E1)               |  |
| Step 2: Transmit oxygen-water signal to seed exterior encoder and antenna              | Step 2A: Assemble transmitter encoder and antenna by adhesion of continuous water films in contact with soil particles and seed exterior   |
|  | Step 2B: Encode transmitter signal by amplifying soil-seed water film oxygen content. Change oxygen content of water films by contact with seed hull surface (e.g. increased surface area exposed to dissolve soil atmosphere gases)         |
|  | Step 2C: Seed exterior antenna transmits signal by diffusive equilibration of oxygen content throughout continuous soil-seed water film communication channel (hull, placental pore) connected to TACL membrane receiver                     |
| Step 3: Transmit oxygen-water signal to seed interior receiver                         | Step 3A: Form water films continuous with hull, placental pore and TACL membrane entrance to seed interior.  |
|  | Step 3B: Oxygen-water signal movement across seed surface facilitated by hull topography channeling to basal placental pore entrance   |
|  | Step 3C: Oxygen-water signal physically filtered by apoplastic placental pore tissues  |
|  | Step 3D: Oxygen-water signal entrance into seed interior receiver is physically restricted (tuner, resistor) to TACL membrane by continuous surrounding gas- and water-tight caryopsis coat surrounding the embryo and endosperm compartment |
|  | Step 3E: Equilibrate oxygen-water content throughout soil-TACL channel by water-gas film diffusion   |
|  | Step 3F: Equilibrate seed exterior-interior oxygen-water content by membrane-regulated diffusion   |
| Step 4: Receive oxygen-water signal in seed interior                                   | Step 4A: Accumulate oxygen-water message information in embryo-endosperm capacitor   |
|  | Step 4B: Remove oxygen in embryo-endosperm water by action of interior oxygen scavenger protein  |
| Step 5: Provoke embryo behavior with oxygen-water message at seed interior destination | Step 5A: Stimulate-inhibit respiration and embryo germination with adequate oxygen-water accumulation  |

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## REFERENCES

- [1] Atchison, Bradley G. 2001. Relationship between foxtail (*Setaria* spp.) primary dormancy at seed abscission and subsequent seedling emergence. M.S. thesis, Interdepartmental Ecology and Evolutionary Biology, Iowa State University.
- [2] Dawkins, R. 1986. The blind watchmaker. Norton, New York.
- [3] Dekker, J. 1999. Soil weed seed banks and weed management. *Journal of Crop Production* 2(1):139-166. Simultaneously published in book format as "Expanding the Context of Weed Management", D. Buhler (Ed.), Haworth Press Inc. New York.
- [4] Dekker, J. 2000. Emergent weedy foxtail (*Setaria* spp.) seed germinability behavior. In: *Seed Biology: Advances and Applications* (M. Black, K.J. Bradford, and J. Vasquez-Ramos, Eds). CAB International, Wallingford, UK, pp. 411-423.
- [5] Dekker, J. 2003. The foxtail (*Setaria*) species-group. *Weed Science* 51:641-646.
- [6] Dekker, J. 2004a. The evolutionary biology of the foxtail (*Setaria*) species-group. In: *Weed Biology and Management*; Inderjit (Ed.). Kluwer Academic Publishers, The Netherlands. Pp. 65-113.
- [7] Dekker, J. 2009. FoxPatch: An evolutionary model system for weedy *Setaria* spp.-gp. seed life history dynamics. XIII<sup>th</sup> International Conference on Weed Biology, Dijon, France. Association Française pour la Protection des Plantes Annales: 117-127.
- [8] Dekker, J. 2011a. Evolutionary models of weed life history population dynamics. In: *Advances in environmental research*, Volume 10, pp. 143-165; J.A. Daniels (Ed.). Nova Science Publishers, Hauppauge, NY.
- [9] Dekker, J. 2011b. Evolutionary ecology of weeds. <http://www.agron.iastate.edu/~weeds/AG517/517Course/EEWbook.html>
- [10] Dekker, J., D. Adams, A. van Aelst, B. Dekker, J. Donnelly, and M. Haar, M. Hargrove, H. Hilhorst, C. Karssen, J. Lathrop, E. Luschei, and D. Todey. 2012a. Weedy *Setaria* seed germination-dormancy behavior: Regulatory compartmentalization. Lambert Academic Publishing, Saarbrücken, Germany. ISBN: 978-3-659-24309-7
- [11] Dekker, J., B. Atchison, M. Haar, and K. Jovaag. 2012b. Weedy *Setaria* seed life history: Heterogeneous seed rain dormancy predicates seedling recruitment. Lambert Academic Publishing, Saarbrücken, Germany. ISBN: 978-3-8454-7859-3
- [12] Dekker, J, B. Atchison and K Jovaag. 2003. *Setaria* spp. seed pool formation and initial assembly in agro-communities. *Aspects of Applied Biology* 69:247-259
- [13] Dekker, J., B.I. Dekker, H. Hilhorst and C. Karssen. 1996. Weedy adaptation in *Setaria* spp.: IV. Changes in the germinative capacity of *S. faberii* embryos with development from anthesis to after abscission. *American Journal of Botany* 83(8):979-991.
- [14] Dekker J., M. Hargrove. 2002. Weedy adaptation in *Setaria* spp.: V. Effects of gaseous environment on giant foxtail (*Setaria faberii* R. Hermm.) (Poaceae) seed germination. *American Journal of Botany* 89(3):410-416.
- [15] Dekker, J., J. Lathrop, B. Atchison, and D. Todey. 2001. The weedy *Setaria* spp. phenotype: How environment and seeds interact from embryogenesis through germination. *Proceedings of the Brighton Crop Protection Conference-Weeds 2001*:65-74.
- [16] Donnelly, J., D. Adams, and J. Dekker. 2012. Does phylogeny determine the shape of the outer seed hull in *Setaria* seeds? In: Dekker, J., D. Adams, A. van Aelst, B. Dekker, J. Donnelly, and M. Haar, M. Hargrove, H. Hilhorst, C. Karssen, J. Lathrop, E. Luschei, and D. Todey. 2012. Weedy *Setaria* seed germination-dormancy behavior: Regulatory compartmentalization. Lambert Academic Publishing, Saarbrücken, Germany. ISBN: 978-3-659-24309-7
- [17] Gunning, B.E.S., 1977. Transfer cells and their roles in transport of solutes in plants. *Sci. Prog., Oxf.* 64:539-568.
- [18] Gunning, B.E.S. and J.S. Pate. 1969. "Transfer cells" Plant cells with wall ingrowths, specialized in relation to short distance transport of solutes-Their occurrence, structure, and development. *Protoplasma* 68:107-133.
- [19] Haar, Milt. 1998. Characterization of foxtail (*Setaria* spp.) seed production and giant foxtail (*S. faberii*) seed dormancy at abscission. Ph.D. thesis, Interdepartmental Plant Physiology; Iowa State University.
- [20] Haar, M., A. van Aelst and J. Dekker. 2012. Micrographic analysis of *Setaria faberii* seed, caryopsis and embryo germination. In: Dekker, J., D. Adams, A. van Aelst, B. Dekker, J. Donnelly, and M. Haar, M. Hargrove, H. Hilhorst, C. Karssen, J. Lathrop, E. Luschei, and D. Todey. 2012. Weedy *Setaria* seed germination-dormancy behavior: Regulatory compartmentalization. Lambert Academic Publishing, Saarbrücken, Germany. ISBN: 978-3-659-24309-7
- [21] Haar, M.J. and J. Dekker. 2011. Seed production in weedy *Setaria* spp.-gp. *Journal of Biodiversity and Ecological Sciences* 1(3):169-178.
- [22] Hutchison, G.E. 1957. The multivariate niche. *Cold Spring Harbour Symposia in Quantitative Biology* 22:415-421.
- [23] Jovaag, Kari Ann. 2006. Life history of weedy *Setaria* species-group. Ph.D. thesis; Interdepartmental Ecology & Evolutionary Biology Program and Statistics Department; Iowa State University.
- [24] Jovaag, K., J. Dekker, and B. Atchison. 2011. *Setaria faberii* seed heteroblasty blueprints seedling recruitment: II. Seed behavior in the soil. *International Journal of Plant Research* 1(1):1-10.
- [25] Jovaag, K., J. Dekker, and B. Atchison. 2012a. *Setaria faberii* seed heteroblasty blueprints seedling recruitment: I. Seed dormancy heterogeneity at abscission. *International Journal of Plant Research* 2(3): 46-56.
- [26] Jovaag, K., J. Dekker, and B. Atchison. 2012b. *Setaria faberii* seed heteroblasty blueprints seedling recruitment: III. Seedling recruitment behavior. *International Journal of Plant Science* 2(6):165-180.
- [27] Kuhn, T.S. 1962. The structure of scientific revolutions.

- University of Chicago Press, IL.
- [28] Loewenstein, W. 1999. *The touchstone of life: molecular information, cell communication, and the foundations of life.* Oxford University Press, New York.
- [29] Narayanaswami, S. 1956. Structure and development of the caryopsis in some Indian Millets. VI. *Setaria italica*. *Botanical Gazette* 118:112-122.
- [30] O'Brien, T.P. 1976. Transfer cells. In: *Transport and transfer processes in plants*; Eds. I. F. Wardlaw and J. B. Passioura. Academic Press, Inc. New York. Pp. 59-63.
- [31] Pate, J.S. and B.E.S. Gunning. 1972. Transfer cells. *Ann. Rev. Plant Physiol.* 23:173-196.
- [32] Rominger, J.M. 1962. *Taxonomy of Setaria (Gramineae) in North America*; Volume 29. Illinois biological monographs, University of Illinois Press, Urbana.
- [33] Rost, T.L. 1971a. Fine structure of endosperm protein bodies in *Setaria lutescens* (Gramineae). *Protoplasma* 73:475-479.
- [34] Rost, T.L. 1971b. Structural and histochemical investigations of dormant and non-dormant caryopses of *Setaria lutescens* (Gramineae). Ph.D. Thesis, Iowa State University, Ames.
- [35] Rost, T.L. 1972. The ultrastructure and physiology of protein bodies and lipids from hydrated dormant and nondormant embryos of *Setaria lutescens* (Gramineae). *Amer. J. Bot.* 59:607-616.
- [36] Rost, T.L. 1973. The anatomy of the caryopsis coat in mature caryopses of the yellow foxtail grass (*Setaria lutescens*). *Bot. Gaz.* 134:32-39.
- [37] Rost, T.L. 1975. The morphology of germination in *Setaria lutescens* (Gramineae): The effects of covering structures and chemical inhibitors on dormant and non-dormant florets. *Ann. Bot.* 39:21-30.
- [38] Rost, T.L. and N.R. Lersten. 1970. Transfer aleurone cells in *Setaria lutescens* (Gramineae). *Protoplasma* 71:403-408.
- [39] Rost, T.L. and N.R. Lersten. 1973. A synopsis and selected bibliography of grass caryopsis anatomy and fine structure. *IA State J. Res.* 48:47-87
- [40] Sacks, Oliver. 1998. *The man who mistook his wife for a hat, and other clinical tales.* P. 129. Touchstone, NY.
- [41] Sareini, H T. 2002. Identification and characterization of the major seed peroxidase in *Setaria faberii*. M.S. thesis, Molecular Biology and Biochemistry Department, Iowa State University, Ames.
- [42] Shannon, C.E. and W. Weaver. 1949. *The mathematical theory of communication.* P.31. University of Illinois Press, Urbana.
- [43] Wang, R.L, J. Wendell and J. Dekker. 1995a. Weedy adaptation in *Setaria* spp.: I. Isozyme analysis of the genetic diversity and population genetic structure in *S. viridis*. *American Journal of Botany* 82(3):308-317.
- [44] Wang, R.L, J. Wendell and J. Dekker. 1995b. Weedy adaptation in *Setaria* spp.: II. Genetic diversity and population genetic structure in *S. glauca*, *S. geniculata* and *S. faberii*. *American Journal of Botany* 82(8):1031-1039.
- [45] Willweber-Kishimoto, E. 1962. Interspecific relationships in the genus *Setaria*. *Contrib. Bio. Kyoto Univ.*
- [46] Wilson, R.G. Jr. 1980. Dissemination of weed seeds by surface irrigation water in western
- [47] Zee, S.-Y. 1972. Vascular tissue and transfer cell distribution in the rice spikelet. *Aust. J. Biol. Sci.* 25:411-414.
- [48] Zee, S.-Y. and T.P. O'Brien. 1971. Aleuron transfer cells and other structural features of the spikelet of millet. *Aust. J. Biol. Sci.* 24:391-395.