Plant stress—new perspectives on an old concept

## Introduction

“Definitions and terminology are crucially important. A large part of the fruitfulness of scientific thought has come from one simple fact. It is that hitherto every scientific term has had an exact definition, verbal or mathematical, universally accepted.” (Pye 1995). Contrary to the quotation above, the terms “stress” and “limitation” as used in the plant sciences do not have exact definitions universally accepted and unambiguously recognizable.

Because science often deals with unfamiliar objects and phenomena like genes, black holes and quantum entanglement, we can either (i) create a wholly new vocabulary or (ii) capture the apparent similarities between established concepts and terms in the “source domain” and reason analogically to transfer these onto a novel setting, the “target domain”; this is how scientific metaphors are constructed (Reynolds 2022). Physics is the source domain of the term “stress” that has been transferred to several target domains including biology in what Palma (2016) calls an epistemic metaphor. Epistemic metaphors when incorporated into the scientific vocabulary lose the duality of meaning ordinary metaphors have and their meaning in scientific writing and speech becomes unambiguously defined by the context in which they are used. However, the many meanings of “stress” in Biology seem to fail this test, and ambiguity of meaning has become an obstacle to communication and understanding (Jansen and Potters 2017).

As biological systems are far more complex than physical systems (**Kauffman2019?**; Kauffman and Roli 2023), multiple alternative mappings of concepts from physics to this new domain are possible. A key difference compared to mechanics is that biological systems are hierarchically organized and can be studied at different levels of organization from individual cells and their organelles to biomes (Capra and Luisi 2014). In practice, stress definitions are based on the lack of fulfilment of a condition. However, the condition and, consequently, also the criteria used to assess lack of its fulfilment varies depending on the aims of the research or activity at hand (**XXXX?**). Thus, the meaning of the term “stress”as applied to plants can remain ambiguous. To a smaller degree the same problem also affects the related concept of “limitation”.

Levine (1985) wrote “My chapter defines the concept of stress. I am not certain whether one who undertakes this task either has an enormous ego, is immeasurably stupid, or is totally mad.” In a more positive tone, Grubb (1992) in his presidential address on ecological theory tells `What I mean to indicate through the first part of my title, — ‘a positive distrust in simplicity’ — is that I not only distrust the simplest kinds of generalization, but also believe strongly that we must not simply dismiss them when they are proved wanting. Instead we must respond positively — we must be prepared to seek generalizations that are less simple and more likely to reflect the real world.’

We, a physiologist (MAKJ), an ecologist (PJA), and an agronomist (VOS), review here the different meanings with which “stress” is used in plant sciences, and contrast these meanings with current physiological, ecological, and agronomic knowledge. Our aim is not to distil a single “true” definition of stress. Instead, we explore how the multiple meanings given to the term “stress” relate to each other and to “limitation”, “stressor” and “strain” proposing a framework guided by theory and observation to classify and refine them.

## Past and current uses of the term “plant stress”

The concept of stress originally used in physics to describe mechanical forces acting on inanimate objects was transferred to target domains including psychology, physiology, and medicine, and eventually to agronomy and ecology as a metaphor describing various factors and “pressures” acting on whole organisms, on their component parts or on assemblages of organisms. Selye (1936) when introducing “stress” to biology, described the development of stress as a process with three phases: “alarm”, “resistance” and “’exhaustion”, with normal function compromised only in the last of these phases. Years later, Selye (1975) introduced the concepts of “eustress” and “distress”, likely by adapting the terms eustress and dys-stress as used in sports by Harris (1970) to contrast pleasent stress and painful or unpleasent stress. According to Selye’s use in medicine, stress events could lead to both ulterior positive effects, or “eustress”, or negative effects, or “distress”. Selye, an endocrinologist, contended that stress triggered by different stressors shared the same physiological rsponses. As we will see below, with time, and with its use with plants the meaning of “stress” broadened to encompass responses that are heterogeneous in mechanism and levels of organization.

Bidwell (1979) writes a comprehensive definition as “Normal physiology is maintained under ideal environmental conditions. However, plants seldom exist under just the right conditions. Usually something is lacking; often several factors are far from ideal. Because of the fact of competition, plants often live at the limit of their capacity to survive one or more adverse conditions. This creates considerable stress on the organism, which reacts by various biochemical and physiological mechanisms, to overcome, avoid, or neutralize the stress.” Levitt (1980) defined stress as: “Any environmental factor potentially unfavorable to living organisms.” Levitt (1980) based his proposal for “stress and strain terminology” on the use of these terms in physics. He conceded that the term “strain” as used in biology had a connotation of plastic rather than elastic strain, while he considered both as of interest. He defined in a biological sense stress as “an external factor acting on an organism” and strain as “a physical or chemical change produced by the stress”. He also states that plastic strain may be reparable while elastic strain is reversible. He used the terms “stable adaptation” for adaptation of the genotype through natural selection and “unstable adaptation” for acclimation of the phenotype. He also equated hardiness with the ability to acclimate. Contemporary with Levitt, Grime (1979), Grime (1981) linked stress, resources and disturbances to evolution and natural selection in a classification of plants into competitors, stress tolerators and ruderals (C-S-R) based on the strategies expected to contribute to fitness in environments with differences in resource abundance. We already see multiple views: Bidwell sees stress and ensuing strain as the norm, Levitt sees stress as a rather exceptional case that may cause strain or not, and finally Grime sees stress as a persistent condition in the environment that filters species but does not strain those species that pass the filter.

From the late 1980s to early 2000s, the concept of stress evolved concurrently in different biological fields and geographies. North American ecologists emphasized that simultaneous exposure to multiple stressors and limiting factors is the most common case in nature, contrasting this observation to the frequently used simplified experimental settings focusing on individual factors (e.g., Chapin et al. 1987). Winner (1991) wrote “The term ‘stressor’ can suggest that stress is caused by a single variable, however in the natural environment this is rarely the case.” In this view, “stress” comprises the states of multiple environmental factors interacting with a realized phenotype, and each of these states can potentially induce multiple strains in plants. (**BrayXXXX?**) referred to stresses as external conditions that “…adversely affect growth, development or productivity”, thus recognizing three possible criteria for diagnosis. Packham et al. (1992) instead, focusing on biomass as the criterion used, stated that “’Stress’, as it applies to plants, can be defined as the external constraints which limit the rate of dry matter production of all or part of the vegetation […]. ‘Disturbance’ may be regarded as consisting of the mechanisms which limit the plant biomass by causing its partial or total destruction.” In Europe, the frequently “loose” use for the term “stress” prompted Lichtenthaler (1998) to propose a criterion to distinguish between stress and normal responses at the physiological level, stated as: “Despite their capacity for fast acclimation of metabolic fluxes and specific adaptations as well as the development of certain stress tolerance mechanisms, plants are often exposed to sudden short-term or long-term stress events that eventually reduce cell activity and plant growth to a minimum. This can lead to severe damage ultimately causing cell death if the stress coping mechanisms or repair mechanisms of plants are overworked.” He recognized four phases: “response phase” or alarm reaction (beginning of stress), “restitution phase” or stage of resistance (continuing stress), “end phase” or stage of exhaustion (long-term stress), and “regeneration phase” or partial or full regeneration of the physiological function, when the stressor is removed. (**Koerner1999?**) challenged the frequent use of the terms stress, constraints, and limitation to describe environments with low primary production such alpine ecosystems, describing the situation as “a widespread misconception in functional ecology” arguing that the species that inhabit these ecosystems are adapted to such conditions. Based on the idea of stress as a filter, Körner (2003) concluded that “Stressful environments hardly exist” in nature, as the species that pass the “filter” can be expected to thrive. In a nuanced view of interactions, Gutschick and BassiriRad (2003) concluded that the co-occurrence of low temperature and high light intensity that leads to photoinhibition in leaves of Eucalyptus pauciflora is not a case of multiple stresses, as “neither the high light nor the subfreezing temperatures are themselves very adverse for the plant”. The recognition that fluctuations in resource availability lead to recurring temporal dynamics in plant interactions (Goldberg and Novoplansky 1997), the relevance of ecological and evolutionary theory to agricultural systems (Martı'nez-Ghersa, Ghersa, and Satorre 2000; reviewed by Denison 2012) and the role of non-cognitive sensory-based, i. e., information-based responses and communication in plant interactions (Aphalo and Ballaré 1995; **Novoplanskyxxxx?**; Callaway 2002) were described. Even if new ideas and criteria were formulated during this period, the three contrasting views from the 1970’s and 1980’s remained.

The next two decades saw significant changes in ecological theory as a result of methodological developments that allowed or forced a revised view of evolution and inheritance and the role of plasticity in fitness. Schulze, Beck, and Müller-Hohenstein (2005) focused on the individual plant, defining “stress reactions” as deviations from the “physiological normal type”, that of plants growing under optimal quantities or intensities of factors and influences and thus “maximizing physiologically achievable performance”. They recognize, however, that plants almost never find such conditions. They also state that “growth is only one of many reactions of a plant to its environment.” (**Fedoroff2010?**) discussed a systems view of the stress response in relation to stomatal guard cells. Her analysis connects responses of guard cells to knowledge on signals, structure, and function at levels of organization below whole cells while Kranner et al. (2010) recognized that stress can simultaneously trigger multiple strains in plants and that these strains can be chained. Thus, the hierarchical structure and systems views are incorporated, but with a strong focus of the individual plant as the target of stress.

More recently, Taiz et al. (2015) with a focus on physiology define stress as “any environmental condition that prevents the plant from achieving its full genetic potential.” with genetic potential defined as the maximum growth and reproductive potential based on biomass and seed number. This simple text-book definition highlights that stress in a very broad sense, encompasses all conditions in the abiotic and biotic environment of a plant that limit its growth and/or reproduction. Keddy (2017) reviews in his textbook the concept of “stress” from an ecological perspective, initially using a simple definition: ‘We will use the word stress to describe “any environmental condition that reduces the rate of production of biomass”’ but later in the book, Keddy (2017) in pp. 400-402 provides a more elaborate alternative: “When thinking about stress, it is important to separate short-term physiological effects from long-term evolutionary effects.” He also considers the evolution of risk aversion and the role of competition. Although stress is usually considered as negative, there are alternative views, more common in discussions of stress in animals and humans, that consider some stress conditions as positive (eustress) (see above) or even a requirement for normal development (Badyaev et al. 2015, and refs. therein).

Although hardening of seedlings before out-planting, priming of seeds and other similar management procedures based on intentional exposure to conditions unfavourable for growth have been in use since XXXXX times by plant growers, they have had little influence on how plant stress has been defined in physiology and ecology. At this point in time, although awareness about the complexity of biological systems had improved and the importance of the hierarchical organization of ecosystems in their function had been widely accepted, contrasting definitions of “stress” persisted,

Nowadays, on one hand, stress responses are seen as triggered by environmental conditions that are exceptional, unusual, or more generally, difficult to predict. On the other hand, “stress” is also used to describe conditions which can potentially cause strain, even in the absence of strain.

The use of conflicting criteria for normality persists to our day. The “normal” condition is sometimes taken as the potential performance of the same genotype under “optimal” growth conditions, while in other cases it is the performance of a genotype “optimally adapted” to the current environment. Although rarely explicitly mentioned, this dichotomy creates two drastically different views about stress and strain. Thus, there is a need to distinguish between utilitarian (or practical and commercial), physiological and ecological definitions of stress (Körner 2018). According to Körner (2003), “Biomass production, irrespective of the species involved, is almost always limited by one or several resources or stressors, but the suite of taxa present in a given space and time is not. This distinction, between the physiological- (process) or agronomic- (yield-) oriented meanings of limitation and stress, and the biodiversity-oriented dimension of those terms, is crucial.”

Statements indicating that stress is pervasive in nature and that plants’ growth is nearly always limited bv strain caused by environmental factors (e.g., Schulze, Beck, and Müller-Hohenstein 2005), raise questions about how meaningful it is to consider growth under optimal conditions as the “normal” reference. On the other hand, the statement that “Stressful environments hardly exist” (Körner 2003) raises questions about the levels of organization at which stress is usefully defined and whether the constrains that cause strain at one level of organization impose or not constraints at higher levels of organization.

## The changing scientific context

Gradually, the purely genetic-based view of evolution (Fisher 1958) has been expanded to encompass other information transfer mechanisms under the name of extended heredity (Bonduriansky and Day 2020). Extended heredity includes mechanisms such as maternal effects and transfer of epigenes, which even if usually persisting only for one or a few generations, are able to influence the outcome of natural selection, and consequently, the course of evolution of the genotype. Horizontal evolution (Mindell 2024) recognizes that the tree-like representation of evolution is incomplete, proposing a network representation to accommodate speciation originating from hybridization and other mechanism of horizontal gene transfer between species.

Both genotypic and environmental variation play a role in evolution through their effects on the fitness of individuals. However, due to genotypic and environmental variation, that some individuals, or even most individuals in a population are under strain, does not necessarily mean that the population as a whole is under strain or that its capacity for biological resilience is overwhelmed (Thorogood et al. 2023). That living systems can be described as systems composed of interacting parts organized hierarchically affects how we should approach their study, specially when crossing level-of-organization boundaries (e.g., Zeiger and Weinberg 1970; Capra and Luisi 2014) so that the conclusions reached are biologically and practically meaningful. However, we see this hierarchy nowadays not as tree-like, but as a network. This is not only true for evolution of species, but also for trophic networks in ecosystems and signalling networks at the cell level. This means that boundaries among levels in the hierarchy can be diffuse.

It is nowadays accepted that information-carrying cues and signals play a crucial role in the regulation of the growth and development of plants (H. Smith 1981; A. Novoplansky, Cohen, and Sachs 1990; Ballaré, Scopel, and Sánchez 1990; Aphalo and Ballaré 1995; Aphalo and Sadras 2022). We have proposed that altered conditions prone to cause strain are not only dependent on the state of individual variables but also on spatially or temporally disrupted correlations among variables in the environment, because organisms have evolved to use such correlations as sources of information, including anticipation of future events or states of their environment (see, Aphalo and Sadras 2022). It has also been shown that preemptive or anticipatory responses by organisms, including plants, can be highly beneficial to fitness (Ariel Novoplansky 2016) including under exceptional “stressful” conditions. Importantly, such responses could be exploited when managing crops (Falik, Mauda, and Novoplansky 2024) and in crop breeding (Boccalandro et al. 2003). We now see plants as complex and actively regulated biological systems capable of anticipatory responses rather than as passive systems at the mercy of the environment (Aphalo and Ballaré 1995; A. Trewavas 2014; Aphalo and Sadras 2022). In fact, plants “keep a memory” within and across generations about environmental conditions they are exposed to, using multiple mechanisms, allowing memories of varied persistence. Furthermore, communication among plants through, mostly chemical, signals can play a central role in the tolerance of stress and mitigation of strain (Falik, Mauda, and Novoplansky 2024).

Evolutionary mechanisms, in a broad sense, provide the ultimate explanation of why “stress”, in each of its definitions, is or is not a frequent condition in nature. From a modern perspective, how a plant responds to an environmental condition depends not only on the genotype but also on its expression in the phenotype. Crucially, from this perspective, responses depend on the integration of both information and resource availability over a long time and the integration of information across multiple levels of organization, including the sharing of information among individuals. This clashes with the intuitive idea that when a plant is under stress its responses are mainly controlled externally but when plastically acclimating, they are controlled internally.

The definitions of stress currently in use are 30–40-year-old and still based on evolutionary, ecological and physiological understanding from those days. They have yet to incorporate the degree of complexity that nowadays is considered necessary for understanding biological systems, including plants and vegetation. The failures inflicted by the underlying complexity on naïve attempts of upscaling of physiological plant responses to higher levels of organization provide painful examples (Sadras 2020; Thorogood et al. 2023) showing that more of the exisiting complexity needs to be incorporated into “stress” theory. Below we analyse the relevance of these advances to the problem of plant stress, even asking the question of whether it is possible or not to cleanly distinguish acclimation from strain responses.

## The factors behind stress

### Time and space

Although stress is usually considered as negative, there are alternative views that consider some stress conditions as positive (eustress) (see above), a requirement for normal development (Badyaev et al. 2015, and refs. herein) and as useful in crop management (**xxxx?**). In these cases, the assessment is done at two points in time, an initially negative effect (or strain) has later in the life of the organism a beneficial effect. Furthermore, the distinction between eustress and distress depends on environmental conditions at the time the initial stress event takes place and at the time when the consequences are assessed. Although this may seem like an unusual situation, it is very common. Anticipatory acclimation that contributes to tolerance of a specific future condition has in most cases a cost, that is detrimental if this future condition is not experienced, but provides a premium if it is experienced (**XXXX?**). Thus, if the future condition, such as rainfall, can only be predicted in terms of probabilities, the categorization of a plant’s response as stressful or beneficial is only possible in retrospect, when fitness or yield is assessed. More importantly, the definition of stress becomes time- and spatial scale dependent, as what is directly detrimental for one specific individual can be indirectly favourable for the population if it benefits other individuals within it concurently or at other times. Plasticity in behaviour, function and morphology is a necessary condition for fitness in any environment subject to variation (**xxxx?**). It follows that acclimation is central to tolerance of potential stressors as well as for profiting from environmental “goodness”. We have considered that, acclimation, being a relatively slow process, to be effective has to be triggered by a signal or cue that precedes the stress event, possibly but not necessarily the potential stress causing variable (Aphalo and Sadras 2022). Obviously, the slower the response, the earlier the plant’s response has to start.

The distinction between transient vs. continuous strain is also relevant because a continuing strain normally has a negative connotation, a scenario which echoes the “exhaustion phase” in Selye (1936) original stress concept. However, strain refers to the plant-environment interaction, as continuing exposure to a potential stressor or stress can also result in transient strain thanks to acclimation in the plant overcoming it. Strain is not dichotomic, it varies continuously between two extremes that are rarely realized, at least at hierarchical levels above the individual. Thus, transient, decreasing and/or localized strains are likely to have fewer negative consequences on fitness or yield than sustained or increasing strains. Strain can even be considered in some cases positive, or even as a requirement for normal development of organisms (Badyaev 2005). Obviously, the reason behind these apparent contradictions is that a response that appears negative at one level of organization or in a short time scale, at a higher level of organization or in a longer time scale, can enhance yield or fitness.

It follows that when conditions are unfavourable or when there is a high probability that they become so, an early response such as a reduction in leaf-area or increase in the root:shoot biomass ratio accompanied by a reduction in total plant biomass are usually not an inevitable consequence of current stress but instead an adjustment to better cope with future events. A response that in the longer term of the whole life cycle is likely to be an improvement, in terms of fitness or yield, in comparison to no preemptive adjustment. This makes it difficult (impossible?) by simple observation to separate acclimation mechanisms from the direct consequences of stress at levels of organization below that used to assess fitness or yield, e.g., decreased photosynthesis and transpiration during drought because of stomatal closure.

### Plasticity and anticipatory action

Acclimation is an induced change in the expressed genotype that enhances performance under one or more environmental conditions. Acclimation in plants is implemented as a complex syndrome of multiple responses at cell, tissue and organ level, frequently difficult to disentangle into components. Modularity, or discreteness, is a ubiquitous emergent property of organismic traits that results from the universal bounded responsiveness, to genomic or environmental inputs, of the phenotype at all levels of organization (West-Eberhard 2019). Modularity in plants’ morphology allows for a given genotype to produce phenotypes that not only vary in physiology and behavior but also vary drastically in architecture, size and allometry (Niklas 1994). Plants also grow continuously almost until they die, even if long lived, and can shed parts and replace them later. In plants, acclimation depends frequently on adjustment of the size, allometry and morphology, which are slow to realize and costly to reverse. Timing of stress-sensitive growth stages, e.g., bud burst in the spring and frost hardening in the autumn in cold-climate perennials (Hänninen 2016), as well as timing of the use of resources, e.g., water in Mediterranean climates (**XXXX?**) also contribute to tolerance or avoidance of potential stress-causing events and conditions

Together with a sessile mode of life, these traits make plants very different to animals in how they cope with variable growing conditions or living contexts (Huey 2002). Acclimation in animals involves mainly regulation of metabolism, development and behaviour (West-Eberhard 2003). Acclimation plays a crucial role in plants’ tolerance of potential stress. The concept of “hardening” is older than that of stress, and familiar to most people who grow plants (**xxxx?**). The term “priming” is usually used for artificially induced favourable acclimation responses in agricultural practice. Hardening and priming are types of acclimation and expressions of plasticity. Quantitatively, phenotypic plasticity describes the amount that the expression of an individual genotype can be modified by its environment (A. J. Trewavas and Jennings 1986). These authors consider stability and plasticity of the phenotype to be opposites. Plasticity in individual phenotype tends to stabilize fitness and yield in the face of environmental variation. Acclimation is achieved through a syndrome of delicately orchestrated and coordinated concurrent responses of physiology, morphology and development, e.g., acclimation towards drought tolerance frequently depends on multiple cooperating mechanisms that help balance water supply and water use as well as mechanisms that help avoid metabolic and physical disruption by water deficits.

Awareness of the role of acclimation and plasticity in stress tolerance is not new. Whitehead (1963) when discussing effects of exposure to wind writes that “…it became clear that any genotype has some power of reacting to the environment in such a way that the changes in development can be considered advantageous to survival under those conditions.” Whitehead (1963) also discussed the possible role of plant hormones in acclimation related to the water balance of plants and the adaptive value of phenotypic plasticity.

Bidwell (1979) was aware of the complexity involved in stress-tolerance: “The effects of these factors [drought, high temperature, low temperature, and freezing] are closely interrelated. Resistance to high temperature may also involve resistance to drought, which often accompany it. Resistance to freezing appears to be largely interconnected with resistance to dehydration of tissues. The development of hardiness to one factor often confers some degree of hardiness to other stresses. As a result, the study of stress resistance has been difficult and slow, and no far-reaching general theories are widely held. We shall consider special studies of resistance to specific stresses, but it must be continuously borne in mind that stress resistance is a complex and multifaceted phenomenon; all the details must fit into any general theory before it can be accepted.” He distinguishes direct effects and conditioning effects (what we call acclimation). He considers that stress always has direct effects but that conditioning effects may or not accompany these direct effects. A. J. Trewavas and Jennings (1986) implicitly consider the problem of scaling by stating that “One unexpected feature to emerge is that processes of apparent morphological stability might hide beneath them a great deal of plasticity at lower levels of organization.”

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| Note |
| **CHECK who is he!** He also mentions parental environment effects mentioning research by H. R. Highkin (without a proper citation). The research described matches that in Highkin (1960), which is a very interesting paper, and I think still relevant!” |

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Information-acquisition by plants through sensory systems plays a key role in plant-plant interactions (Aphalo and Ballaré 1995; **NovoplanskyXXXX?**; Aphalo and Sadras 2022). Table 1 lists some of the sensory systems of plants. A role of maternal effects as well as of “memory” at a wide range of time scales, mechanistically based on epigenetic and other types of regulation, has been demonstrated for drought stress tolerance (Ariel Novoplansky 2009; Hagai Shemesh et al. 2010; Falik, Mauda, and Novoplansky 2022). The implication is that at any time in the life history of a plant how this plant responds to the environment depends not only on its genotype, but also on its physical state and how the “memory” of pasts events affects the “set-points” of the vast transduction network that regulates gene expression, plant metabolism, growth and development—from a control systems’ perspective, “decision-making” (Aphalo and Sadras 2022).

While clear evidence of airborne plant-to-plant communication mediated by emitted chemical signals in herbivory has been available for some years (e.g., Holopainen and Gershenzon 2010; Pierik, Ballaré, and Dicke 2014; Šimpraga et al. 2019), recent work has demonstrated soil-borne root-root communication in the case of drought and salinity (Falik, Mauda, and Novoplansky 2022). These signals are not only communicated between immediate neighbouring plants but are also relayed ahead by the individuals perceiving them to individuals not directly sharing soil with the initial emitter (Falik et al. 2011). Furthermore, these signals, in both cases trigger in the “receiver” responses that enhance future tolerance of the stressor experienced by the “emitter”. Although surprising in their sophistication, these mechanisms make sense from an evolutionary perspective as they can be expected to enhance fitness (Aphalo and Sadras 2022), at least in some cases, of all participants in the communication. According to (Godfrey-Smith 2014) “The evolution of cooperation has become integral to our understanding of the workings and origins of living things.”

Aphalo and Sadras (2022) proposed a model integrating resources and information as drivers of the plant phenotype. They highlight processes that can lead to pre-emptive acclimation or preparedness, while the environmental? variables acting as cues need only be good “predictors” of future conditions, thus not necessarily factors that cause strain in the plant. For example, exposure to ultraviolet-B radiation can be a cause of strain but is also a source of information for the regulation of gene expression, metabolism and growth in the absence of detectable stress (Jansen and Potters 2017).

Following exposure to a potential stressor a plant “may” or “may not” be under stress because strain depends on its current state or phenotype. In other words, strain is the result of an interaction between an organism’s phenotype and its environment, and for any variable to be called a “stressor” it must disrupt an organism’s function at a specific point in time. A fully acclimated plant will not be strained by a potential stressor, even if preemptive acclimation has required a controlled reduction in its growth rate. Maximizing growth is not necessarily adaptive in nature or profitable/sustainable in agriculture, and this is a major issue in growth-based definitions of stress (Box 2). To fully avoid strain, acclimation must precede exposure to potential stressor. On the other hand, when acclimation prevents strain at the cost of a “controlled” decrease in growth or yield, the potential stressor behaves as a limitation. From this follows, that an informational cue or signal can also limit growth and/or yield.

The success of anticipatory action towards future recurring conditions that are subject to “random” variation in occurrence and intensity cannot be evaluated deterministically. Replication in time and space is needed so that response is assessed over a multidimensional “space” that encompasses the range of environmental variation of interest. This is why extensive field trial networks are used at late steps of crop breeding. As communication among individuals and maternal effects play a role, they also need to be taken into account, e.g., using field plots instead of individual plants in pots.

### Levels of organization and interactions

Levels of organization and hierarchical organization of systems are central to contemporary biological thinking (Wimsatt 1976, 1994; Capra and Luisi 2014; **Sadras2016?**; Sadras and Richards 2016, Aphalo and Sadras 2022; Kauffman and Roli 2023; Kauffman and Roli 2023, Thorogood et al. 2023). Compositional levels of organization are defined as hierarchical divisions of biological entities ‘organized by part-whole relations in which wholes at one level function as parts at the next (and all higher) levels’ (Wimsatt 1994). In the words of Kauffman and Roli (2023) “…living things are Kantian wholes where the parts exist in the universe for and by means of the whole.” Because individuals, as Kantian wholes, propagate their offspring, their sustaining parts - lungs and kidneys in mammals – “are also propagated and evolve to function better” (Kauffman and Roli 2023). Levels ‘are constituted by families of entities usually of comparable size and dynamical properties, which characteristically interact primarily with one another’ (Wimsatt 1994). Notwithstanding cross-level interactions, (Wimsatt 1994) view highlights that molecules interact mostly with molecules (**Rietman2011?**) and plants with plants (**Harper1977?**); this partially accounts for the compartmentalized theories associated with each level. Indeed, processes can be separated into discrete classes by their time constants (**Levins1970?**). A physiological perspective challenging the cause-and-effect arrow from genotype to phenotype led to the conclusion that there is no privileged level of organisation and highlighted the importance of downward causation in the construction of the phenotype whereby higher-level properties “necessarily also causes of lower level behaviour, involving actions and interactions both ways” (Noble 2012). Below we apply these ideas in an attempt to illuminate the concepts of stress, stressor and strain.

As discussed in previous sections, potential and actual stressors in nature are rarely individual environmental factors but instead combinations of factors acting jointly or sequentially. Information acquired by plants through the perception of cues and signals in the environment is combined during transduction (**XXXX?**). Acquired information and experienced stress drastically affect future responses to both informational cues and signals, and to potential stressors thanks to changes in readiness to respond and physiological, morphological and developmental acclimation. The more we learn about the molecular and physiological mechanisms of stress, the more intractable the problem appears. One difficulty, we think, is attempting to force this knowledge into two boxes by assuming that stress is distinct from normal, i.e., that there is a dichotomy. The two extreme conditions are exceptional. Realization of potential fitness or crop yield is almost never achieved in practice and death after stablishment leaving no offspring is not very common in plants, while predation on seeds and death of seedlings can be frequent. In the case of populations, complete extinction is infrequent. Most individual plants and populations function somewhere between these limits. So, if we take optimal conditions as a reference, we can conclude that nearly all plants are strained. In contrast, if we define strain as a terminal disruption leading to premature plant death or no offspring, we can conclude that strain is a very exceptional condition. Both of these views, fail to recognize that intermediate degrees of strain and the gradual transition between the extreme situations and its dynamics in time and space are the most interesting.

Hierarchical, thus asymmetrical, organization of living systems precludes upscaling and downscaling stressed states (Noble 2012, 2017; Passioura 2010, 2020). This is a feature of biological systems that affects all definitions of stress, stressor and strain. Thus, we need caution in using signs of metabolic and physiological strain (sensu Levitt) to characterize whole-organism, in our case, whole-plant strain. Similarly, signs of strain in individual plants cannot be directly used to assess strain at population, community or ecosystem levels. Stress definitions at levels of organization below the individual plant are frequently used in physiology and molecular biology, but these definitions have little in common with those at higher levels of organization. This low-level approach consists of defining one or more specific disruptions (i.e., stress or strain) in an organism’s metabolic or cellular function as a measure of stress. In many cases, criteria are based on an observable state, and thus easily quantifiable, such as for example gene expression, quantum yield of photosystem II, membrane leakage, and the total anti-oxidant capacity. In the context of reductionist biotechnology, for example, Vinocur and Altman {, 2005 #5260} define primary stresses with a focus on environmental factor, such as cold stress or salinity stress, and define a secondary stress with a focus on processes, such as osmotic stress or oxidative stress. Their conceptual framework scales up to cellular homeostasis, but not beyond. The connection between stress on individual cells and whole-plant stress is often tenuous, to the point that what is called stress at these lower levels often drives acclimation that makes possible full avoidance of stress at the whole plant and population levels. For example, enhanced drought tolerance in virus-infected plants has been attributed to increased levels of antioxidants and osmoprotectants partially mediated by increased protein hydroxylation, and interference with crosstalk between abscisic acid (ABA) and salicylic acid (SA) (**Mishraet2022?**; **Prasad2022?**; **Szczepaniec2019?**; **vanMunster2020?**). The combination of infection with tomato yellow leaf curl Sardinia virus (TYLCSV) and water deficit in glasshouse-grown tomato Moneymaker was antagonistic for stem water potential, which was -0.36 MPa in well-watered, mock-inoculated controls and dropped to -1.51 MPa under water stress with no virus, but only to -0.95 MPa in water-stressed plants inoculated with TYLCSV (**Sadras2023?**) *(Sadras et al 2023)*. Scaling down to gene expression, the effect of virus infection and drought stress was additive for the expression of three genes: SINCED1, associated with ABA biosynthesis, ABA-responsive dehydrin SITAS14 and auxin response factor SIARF8. An antagonistic interaction between virus and water regime was detected for the expression of SlCYP707A2 associated with ABA degradation. Scaling up to plant growth, an antagonistic effect between virus and drought stress was apparent for plant height, but not for plant fresh weight and root length that showed additive effects. A quantitative review with this kind of analysis reached the conclusion that “shifts in gene expression and common metabolic pathways between plant defence and response to drought stress are insightful but fall short in relevance in the absence of scaling” (**Sadras2023?**).

Density-dependence and oversimplified experimental settings further compromise scaling. Density-dependent traits such as canopy photosynthesis and crop yield do not scale from plant to stand (**Sinclair2004?**; **Pettigrew1989?**; **Pedro2012?**; **Lake2016?**). In his compilation of data on the fertility of hybrids, (Darwin 1859, 247) dismisses some observations on the grounds of experimental artefacts: “Nearly all the plants experimentised on by Gartner were potted, and apparently were kept in a chamber in his house. That these processes are often injurious to the fertility of a plant cannot be doubted”. Small pots and the imposition of sudden, severe water deficit do not allow, for example, for plant acclimation and realistic root patterns, particularly in long-lived perennials with extensive root systems. The metabolism of sunlight-grown plants does not match that of plants grown under artificial light regimes (**Annunziata2017?**); field validation is essential. Where the objective is crop improvement, the pipleline from lab to field can be reversed to an effective field to lab approach (**Thistlethwaite2020?**).

Time and its progression are important, as fitness is achieved through an individual’s life time, and in annual plants achieved only towards the end of the life cycle. As growth and development progresses, the remaining available routes for plasticity decrease, and this forces a change in strategy as a plant develops (H. Shemesh and Novoplansky 2013) *(Shemesh and Novoplansky, 2013)*. This decreasing ability for acclimation concurrent with development and growth, can make successful anticipation and early “decision making” highly beneficial to fitness. Heritability, median across cereal crops, increases from 0.31 for tiller number established early in the season, to 0.58 for inflorescence number, to 0.59 for grains per inflorescence, and to 0.79 for grain size established later in the growing season (**Sadras2012?**). This supports a hierarchy of phenotypic plasticities (sensu Bradshaw 1965): tiller number > inflorescence number ≈ grains per inflorescence > seed size. This strong hierarchy has been attributed to the differential fitness contribution from each trait, which is reinforced by the increase in interference between neighbouring plants and associated reduction in availability of resources per plant as the crop cycle progresses (**Sadras2012?**).

### Stress as maladaptation

The viewpoint that “stressful environments hardly exist” (Körner 2003) implies considering stress as caused by maladaptation at the population level. Such a definition makes stress directly dependent on local and/or global directional change of the biotic and/or abiotic environment. However, when considering individual plants, and normal genetic and environmental variation, at any point in time some genotypes in a population will have transiently higher or lower fitness than other genotypes. Individual plants may be less than optimally adapted to the current environment and thus under strain. Thus, maladaptation can be a useful criterion of stress both at individual and population levels of organization, especially for studies related to environmental change and ecology and evolution. For example, the timing of exposure to a potential stressor (e.g., drought) or benefactor (e.g., presence of pollinators) relative to phenological phases of development of wild and crop plants is crucial for fitness and yield, respectively (**XXXX?**). Already Darwin (1859) observed “…very trifling changes, such as a little more or less water at some particular period of growth, will determine whether or not the plant sets a grain”.

When considering global change, it is unlikely that a response has not been subjected to natural selection under a somehow similar although less extreme condition. Consequently, acclimation being ubiquitous will coexist with accidental responses to a challenge of novel intensity. Pre-adaptations or affordances (see Kauffman and Roli 2023) can also “happen” to help towards tolerance of environmental conditions never experienced by an individual’s ancestors making the distinction between selected-for responses and those that are purely accidental even more difficult. The situation is to an extent different when considering synthetic chemicals and pollution or foreign invasive species, as these can be qualitatively novel challenges.

A similar approach but using as measure of performance a commercially relevant quantity (such as yield) instead of fitness is applicable to crop breeding. This is so because crop breeding aims in most cases at enhanced production or stability of production in a well-defined environment, e.g., a specific geographic region or farming system. In agriculture, the role of timing is reflected in the concept of a critical-developmental-stage, which is central to crop physiology: e.g., probabilistic patterns of drought type have been developed for major crops that account for timing (relative to plant development), intensity and duration of stress inducing condition, and pairing of genotype and environment to predict stress. An ability to predict the effects on yield of stress during critical developmental periods is central to crop management *(references to follow if we include these concepts)*.

Stress definitions at levels of organization below the individual plant are frequently used in physiological and molecular biology research, but these definitions have little in common with those at higher levels of organization. The criteria frequently used are no longer directly relevant to natural selection or crop production because they assess only small portions of the complex biological systems that determine the outcomes that are relevant to evolution or to agriculture.

This low level approach consists of defining one or more specific disruptions (i.e., stress or strain) in an organism’s metabolic or cellular function as a measure to asses stress. In many cases, criteria are based on an observable state, and thus easily quantifiable, such as for example the quantum yield of photosystem II, membrane leakage, and the total anti-oxidant capacity. The connection between stress on individual cells and whole-plant stress is tenuous, to the point that what is called stress at these lower levels in many cases drives acclimation that makes possible full avoidance of stress at the whole plant and population levels. Physiological stress can have both positive and negative effects on the plant as a whole. Thus these criteria, which inform about specific mechanisms, are no substitute for the assessment of stress and strain at higher levels of organization.

The action of a stressor is easy to assess when we are strained by it. How can we decide if a plant is strained or not, when acclimation involves so many alterations to the phenotype? This question is particularly relevant where stress or acclimation responses are superficially similar, such as is the case for salinity tolerance where smaller leaves may reflect stress-mediated disruption of cell elongation, or an active acclimation response that can facilitate a decrease in transpiration (**XXXX?**). In many cases, stress has been defined based on a human-benefit perspective, e.g., a decrease in yield, or reduced growth. However, some stress adapted plants such as metallophytes also grow slowly, demonstrating that decreased biomass production cannot a priory be perceived as stress; indeed, slow growth can be adaptive in some agronomic and natural settings (Box 2). If we accept this type of definitions one needs to accept that in nature, being the growth of any plant in one way or another limited by factors external to it, all plants are under stress. Such definitions are irrelevant to the study of biological mechanisms, even if relevant to management of production systems.

Stressed humans fail to make good decisions or in extreme cases cannot make any decision (Molins, Serrano, and Alacreu-Crespo 2021; **Wu2020?**) *(Molins, Serrano, and Alacreu-Crespo 2021; Wu-et-al2020?)*. Surprisingly, this could work as a good definition of stress also for plants! A plant that grows more leaves when it is lacking water is stressed, but a plant that grows more roots is not, because it displays an adaptive response to its environment. Even a plant shedding leaves when lacking water is not necessarily stressed, as this is a good way of saving water from a plant’s perspective, at least in an “emergency situation”.

How the “goodness of a decision” can be formally assessed? For wild plants the criterion for good decision making is long-term fitness, and for crops its contribution to long-term yield, its stability and/or produce quality, i.e., the selection criteria, of natural selection and crop breeding, respectively.

## Measurement of acclimation and strain

The practical measurement or detection of acclimation and stress have been based on the measurement of a large number of different state variables in plants, their parts or their assemblages. This is natural given the complexity of biological systems and the many different potential stressors that can be present in the environment. A very frequently used criterion at whole-plant and above levels of organization has been aboveground biomass production rate, however, this criterion has no thoeretical basis and is only weakly corelated to fitness of individuals, crop yield or ecosystem stability (Box 1).

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| Slow growth could be adaptive in some natural and agricultural scenarios |
| Here we sample relationships between growth and defense, aspects of reproductive allocation, and seasonal patterns of water use to reach the conclusion that maximizing growth is not necessarily adaptive in nature or profitable in agriculture. The implication is that growth-based definitions of stress are at best incomplete and at worst flawed.  An allometric analysis of *Daphnia mitsukuri* exposed to predatory fish kairomone showed enhanced resource allocation to tail spine, a defense trait, and decreased body growth rate that did not compromise reproduction in comparison to untreated controls (Gu et al. 2021). In a set of four clones, increased resource allocation to tail spine was associated with reduced growth. This negative correlation was not interpreted in terms of a trade-off, but as a double adaptation: a larger defensive tail spine, and smaller individuals that are less conspicuous and provide less energy to the predatory fish (Gu et al. 2021). Marine planktonic crustaceans reduce feeding activity in the presence of fish kairomones and the resulting reduction in gut fullness has been proposed to be adaptive in reducing visibility to predators (Lass and Spaak 2003). However, size preference varies with predation strategy, e.g., planktivorous fish hunt visually and prefer larger Daphnia prey, whereas larvae of the phantom midge *Chaoborus* are tactile hunters and prefer smaller *Daphnia* (Lass and Spaak 2003). In the facultative symbiotic association between isopods and red wood ants (*Formica rufa* group), a smaller body size in ant associates decreases their detection by the host (Zarka et al. 2022).  Cacti combine slow growth as an adaptation to extremely dry conditions and a wide array of secondary metabolites involved in defence against biotic and abiotic stresses including alkaloids, phenolic compounds, and terpenes (Santos-Díaz and Camarena-Rangel 2019). In crowded stands, a common expectation is for the higher fitness of larger plants able to capture resources and deny them to neighbours. However, the frequency distribution of plant species body size is L-shaped within every phylogenetic lineage, and for resident species at every spatial scale – from regional floras down to local neighbourhoods (Aarssen 2015). To account for the mismatch between the expected dominance of large species and the observations, Aarssen (2015) has shifted the focus from capture of resources and growth to reproduction, whereby smaller species are more likely to reach a size threshold for reproduction in a conceptual model accounting to availability of resources and time available to reach the reproductive threshold as affected by disturbances, including herbivory.  In the context of plant domestication in the ancient Near East, slow growth is listed as an adaptation to grazing alongside thorns, toxicity, and underground storage organs (Abbo, Gopher, and Bar-Gal 2022). For annual crops relying on stored soil water, slow vegetative growth could be adaptive as a larger fraction of soil water is available during the critical period of seed set and filling; traits associated with slow vegetative growth in wheat include low hydraulic conductance associated with narrow xylem vessels in the seminal roots (Richards and Passioura 1981, 1989); higher sensitivity of plant transpiration to vapour pressure deficit (Schoppach et al. 2017), and reduced root biomass, tillering and leaf area with maintenance of stomatal conductance and photosynthesis per unit leaf area in response to dry soil (Khan et al. 2022). The implications of these traits for plant defence, if any, are unknown. In field-grown winter wheat, mechanical trimming of roots at the onset of spring growth also displaced the pattern of water use in favour of reproductive stages and increased yield in comparison to controls with intact root systems (Hu et al. 2019); root pruning increased the amount and concentration of labile carbohydrates in shoots, which play a putative role as osmotic defence against aphids (**Sadras2021?**; **Ramirez2023?**) (Sadras, 2021){Ramírez, 2023 #21197}. Imposition of mild water stress through the suspension or reduction of irrigation at the end of the growing season, known as ’drying-off”, is a common practice to increase concentration of sugar in shoot and sugar yield in commercial sugarcane fields (**Singels2021?**) {Singels, 2021 #21856}. |

Selye (1975) tells “…the stress syndrome is — by definition — nonspecific in its causation. However, depending upon conditioning factors, which can selectively influence the reactivity of certain organs, the same stressor can elicit different manifestations in different individuals.” This view of the *stress syndrome* is an abstract one. It implies that the *stress syndrome* abstraction encompasses stress caused by different stressors and mediated by shared underlying mechanisms. We now know that the mechanisms involved vary, specially in plants, even if in some cases some underlying responses are shared. Thus, it is natural that many ways of detecting and measuring stress are in use. As these different approaches can be more or less specific to different underlying mechanisms of stress, the diagnosis or measurements based on them are likely to yield inconsistent results. In [Figure 1](#fig-indicators-of-stress) we list several of the measures used to detect and quantify stress at different levels of organization.

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| Figure 1: Diagram showing commonly used indicators of strain at different levels of organization. The rightmost column of boxes shows variables or parameters used to diagnose *strain* or the existance of stress in plants and their assemblages. |

While in many cases the detection or measurement of strain is possible at a single point in time, this is rarely possible for acclimation. The detection of stress-aleviating or stress-preventing acclimation to be reliable requires the observation of a time-course of responses, starting before strain develops. As acclimation implies a cost, distinguishing acclimation from strain and limitation is difficult. At an early stage the criteria that are used for acclimation differ to some extent from those used for stress ([Figure 2](#fig-indicators-of-acclimation)).

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| Figure 2: Diagram showing commonly used immediate indicators of acclimation at different levels of organization. The rightmost column of boxes shows variables or parameters used to diagnose *acclimation* or \_the existance of favourable plastic responses in plants and their assemblages. |

To assess if acclimation has been effective in protecting from stress, we assess strain at some point(s) in time after we assume acclimation has become effective by assessing the response to a stressor ([Figure 3](#fig-value-of-acclimation)).

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| Figure 3: Diagram showing the temporal sequence used to assess acclimation efectiveness in the context of stress as parallel time lines for *treatment* and *control*. |

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| Reaction norms and the quantification of strain |
| In the context of environmental variation, reaction norms relating the phenotype and environmental factors (Woltereck 1909) facilitate operational definitions of strain that are useful in modelling and insightful physiologically. A common modelling approach is to define the potential for a trait, e.g., photosynthetic rate, and scale the potential to account for factors such as water deficit, nutrient deficiency, or atmospheric ozone (Guarin et al. 2019) (Guarin et al., 2019). Figure 2 (left) shows the reaction norm of maize leaf expansion rate in response to meristem-to-air vapour pressure deficit. The reaction norm defines three traits: the leaf expansion rate at VPD = 0 is the intrinsic or potential rate in the absence of stress, the slope is the phenotypic plasticity, and the x-intercept is the vapour pressure deficit that completely inhibits expansion. All three traits are genotype-dependent and map to particular genomic regions (Fig. 2, right). Of particular interest in this article, nine QTL were identified for the intrinsic rate of expansion, the non-stressful condition, and six for its phenotypic plasticity, with only two of them overlapping (Reymond et al. 2003). This supports Bradshaw’s (Bradshaw 1965) early prediction of the partial independence of the genetic modulation of the trait itself and its plasticity.  *Figures 1 and 2* to be added around here. |

### The difference between stress and limitation

The use of the concept of “limitation” differs from the use of “stress/strain” discussed above in that it most frequently refers to “variables” that are quantified on a continuous scale. In many, but not all cases, they are also resources that plants use up when growing.

While stress and strain have their roots in Physics, “limitation” has its roots in economy. Its meaning is in most cases unambiguous from the context of its use: there is always a sought-after outcome and a constraint on it. This contrasts with the multiple meanings of “stress”. When stress is used as a synonym of stressor, e.g., the statement “the crop is under drought stress”, it is close in meaning to “…limited by insufficient water supply”.  
In this approach, stress is typically assessed based on the comparison of performance under two conditions, one that does not impose a persistent limitation on a target response and one that limits it. Usually the limiting environmental state is an exceptional one, and the reference a “normal” one.

In agriculture, to assess for example the impact of drought at the field-scale, frequently a comparison of crop yield is done between normal years and a drought years and across sites. This is generally only meaningful when done regionally, collecting data over several years, rather than by comparing cropping systems with markedly different average yield levels. However, for a researcher interested in a specific physiological mechanism such an approach can be inadequate as the multiple conditions can differ in too many poorly defined aspects, making necessary very long-term studies to untangle the role of individual limitations. Conversely, typical experiments in controlled conditions that drastically differ from those in the field, or that assess performance using physiological parameters, such as membrane leakage or DNA damage fail to inform about any potential cost on crop yield and/or plant fitness (Sadras 2020) (Sadras et al. 2020). However, these experiments yield publishable results in a much shorter time than long-term field trials.

As an optimal, non-limiting condition is unlikely in the natural or managed environment, using such a reference is of little practical use to agriculture or ecology (**XXXX?**; **KoernerXXXX?**). Furthermore, the definition of optimal conditions is very difficult: for example silver birch seedlings under continuous light cultivated using aeroponics with nutrient supply proportional to the growth rate can attain a relative growth rate, measured as dry mass, of 27% per day, but such conditions are unlike those in nature (Ågren and Weih 2012) *(Ågren and Weih, 2012)*. In practice, the control or reference growing environment is less limiting than the growth-limiting one, but it rarely allows the maximum potential growth rate.

In agriculture the concept of limitation has a clear meaning. For example, fertilisation and irrigation alleviate limitations, often increase crop yield, and have driven much of the sustained increase in global food production over decades (Sinclair and Rufty 2012) *(Sinclair and Rufty 2012)*. The concept of limitation leads to useful operational definitions in agriculture (Fig. 1). Based on economic analogies, ecological theory predicts that plant growth *efficiency?* is maximised when all resources are equally limiting (Bloom, Chapin, and Mooney 1985) *(Bloom et al., 1985)*. This leads to the concept of co-limitation, which is grounded on robust theory and quantitative approaches to frame the empirical evidence (**Bracken2015?**; Cossani and Sadras 2018; Elser et al. 2007; Harpole et al. 2011; Kho 2000; **Sperfeld2016?**). For example, we have gained insights on the primary production of diverse ecosystems that from the perspective of nitrogen-phosphorus co-limitation and on the seed yield of rainfed crops from the angle of nitrogen-water co-limitation (Elser et al. 2007; Harpole et al. 2011; **Sperfeld2016?**; Cossani and Sadras 2018). Scaling to three or more co-limiting factors remains a challenge (Cossani and Sadras 2018).

The usefulness of the concept of limitation breaks down when considering the ecology and evolution of plant species: “watering the desert, fertilizing the tundra, warming the alpine zone, … are commonly fatal for the plants living there, creating a completely new assemblage of species, with the former ‘limited’ ones being eliminated” (Körner 2003). The concept of limitations or constraints can be applied when considering ecosystem pools and fluxes (e.g., Chapin, Matson, and Vitousek 2011). So, usefulness of the concept of limitation depends, as one should expect, on applying it to the system of interest as a whole and its whole environment, rather than to parts within them.

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| POSSIBLE BOX |
| explaining the watering of the desert as a change or switch of limitations as competitive interactions when competition by other species is taken into account. |

One (possible?/obvious?) conclusion is that stress and strain are not binary conditions, as implicit already in Bidwell’s definitions. Both no stress and maximum stress are unusual transient situations and almost all plants whether growing in the field or in a controlled environment are in somewhere in-between situation. For strain, the situation is the same, because any classification of plant responses to environmental conditions as strain or normal would be in practice subjective or arbitrary in the choice of criteria. We next attempt to fit what we have discussed up to here into as description of plant and vegetation responses to stress as a process taking place in time and space using as starting point the phases “alarm”, “resistance” and “exhaustion/recovery” proposed in the literature.

## Response to stress as a process

Advances in plant biology have revealed a myriad of interactive effects that complicate the use of traditional stress terminology. For example, a range of novel sensors have been identified in plants (UV-B and UV-A sensors, temperature sensor, salinity sensor, nitrate sensor, calcium sensors and so on), and these may drive adjustments of function in the absence of measurable strain. *this could be expanded and citations added* In the field, where plants are exposed to multiple correlated variables, acting both as material and energy resources and sources of information, plant responses can be complex and triggered indirectly.

In addition, in the field the conditions in the environment change more happhazarly than in a controlled experiment, and this variation is what plants have adapted to. In the literature based on field measurements of plant’s photosynthesis, it is frequent to consider the conditions at some time of the day more stressful than at other times (e.g., cold nights, or hot and dry early afternoons).

Different *phases* of stress have been used when considering individual plants, as it is where their identification appears less difficult. Under gradually and steadily changing conditions, such as is frequently the case in controlled-environment experiments, these phases at first sight at least, could represent a temporal sequence of states. In this section we consider if the idea of a temporal sequence of phases is applicable to “plant stress” in and outside the laboratory.

### The “alarm” phase

The capacity to pre-emptively enter the alarm stage is one strategy among others as adaptations that avoid or resist strain under potentially strain-inducing conditions can be expressed either constitutively or conditionally in the phenotype. Conditional expression of traits can potentially be triggered in response to any condition that a plant can sense.

Much of the literature on plant stress assumes that the trigger of the “alarm” stage is incipient stress (e.g., **XXXX?**). However, this is challenged by decades of research on sensory ecology of plants suggesting that the most frequent triggers of acclimation are informational signals and cues, and that in many cases the alarm stage starts well before a plant is under strain but instead in anticipation of future potential strain (see, Aphalo and Sadras 2022). A key consideration is that the perceived signal, being a source of information, only needs to be a predictor in the statistical sense of the future unfavourable (or favourable) environmental condition. Thus, the best cue or signal is provided by a variable that is correlated with the future potential stress and available well in advance of it.

In plants, informational cues and signals related to likelihood of future potentially strain-inducing conditions are perceived mainly through light, temperature, chemical and turgor pressure receptors, although plants can also perceive gravitational, mechanical, magnetic and electrical cues (Karban 2015). Downstream of the receptors a complex signal transduction network integrates information from multiple sources, regulating gene expression, metabolism, growth, and development. Some responses are fast, but others are delayed, such as epigenetic changes affecting future responses of gene expression. Some changes are irreversible, such as the morphology of already fully expanded leaves while others are more readily reversible like the readiness of stomata to open and close (**XXXX?**).

The need to combine information and integrate it in time and space was already hinted at by Alscher and Cumming (1990) *Alscher and Cumming (1990)* when stating with respect to stress that “A successful survival strategy must, in some way, integrate external signals and induce molecular, metabolic, and physiological events. […] The processing of those [environmental] signals must involve a range of time scales and organization levels…”

Thus, the alarm stage towards future stress is frequently triggered in the absence of stress or strain. Both informational signals and spatially and/or temporarily localized strain can trigger a long-lasting “alarm” stage in a whole plant, and even in neighboring plants (**XXXX?**). Furthermore, the readiness to enter the alarm stage can depend on maternal effects, thus indirectly on the environment experienced by the previous generation(s), independently of any change in the genome (**XXXX?**). In some cases, the alarm stage can be described as readiness to acclimate (e.g., epigenes), while in other cases as preemptive or anticipatory acclimation (e.g., shoot:root ratio). The alarm trigger is rarely binary, the intensity of the signal, its duration, the concurrent and earlier perception of other signals determines frequently the extent and nature of the subsequent acclimation response, i.e., the acquired information is stored, retrieved, combined and processed (Aphalo and Sadras 2022).

After entering the “alarm phase” an alternative phenotype starts being expressed. Entering the alarm stage in relation to a potential stressor can limit growth or yield because of the cost of acclimation, not necessarily as a result of strain, as acclimation can frequently succeed in preventing physiological strain. Expressing an alternative phenotype that develops over time and can better tolerate or escape the unfavourable conditions that are likely to follow, has a net cost only in case the unfavourable conditions fail to occur. This is so, because in the presence of the unfavorable condition the cost of succesful acclimation is more than paid back by the avoided strain-caused damage or losses. Anticipatory acclimation is for the “economy” of a plant similar to taking an insurance policy for human enterprises, and can, thus, be interpreted as risk management.

Strain is the result of an interaction between an organism’s phenotype and its environment, and for any variable to be called a “stressor” it must disrupt an organism’s (or other biological system’s) function at a specific point in time. A fully acclimated plant will not be strained by a potential stressor, even if anticipatory acclimation has required a controlled reduction in its growth rate.

To fully avoid strain, plant acclimation must precede the potential stressor becoming an actual stressor. A variable or condition becomes a stressor when it causes strain, so if strain is avoided by successful acclimation, the variable remains as a potential stressor. On the other hand, when acclimation prevents strain at the cost of a “controlled” decrease in growth or yield, the potential stressor behaves as a limitation. From this follows, that an informational cue or signal can also limit growth and/or yield.

*POSSIBLE EXAMPLEs IN A BOX* 1) red+blue LEDs used as only source of light for plant cultivation. 2) unnatural photoperiods. 3) etc.

### Resistance phase

Not always acclimation is effective, sometimes the potential stressor(s) build up too quickly or are active for a long time and overwhelm a biological system. Conceptually, during the alarm phase “prevention” predominates and during the resistance phase “repair” predominates. However, the distiction between the alarm and resistance phases is not easy to diagnose, and conceptually acclimation and repair are not alternatives: they can coexist. The resistance phase and the alarm phase both involve active/controlled adjustment of function (e.g. metabolism) and morphology (e.g., decrease in exposed leaf area). The distinction between acclimation and repair is in practice not always easy. Although repair is restoration of an earlier state that has been disrupted while acclimation the stablishment of a new state, given that plants develop in time, repair can be observed primarily at the cell level of organization, e.g., membrane permeability restored. At higher levels of arganization, recovery from stress is rarely, if ever, described as repair, e.g., replacement of leaves consumed by herbivores by newly formed leaves. Another consideration is that in this last example, new leaves in most cases will differ from the lost ones: the new leaves will frequently have improved defenses against future herbivory. Thus repair, recovery and acclimation can coexist. Thus classifying a response as repair or acclimation is difficult.

Directly deciding about the “purpose” of a response as observed in an individual under a specific condition is philosophically questionable, as such a decision requires considering not only the realised environment but also other possible but unrealised conditions and their probabilities of occurrence. This is because “prevention” aims at mitigating future stressful conditions, that even if a real threat, may not be realised on the occasion we are studying or observing. The *interpretation* of observed plant responses is in many cases a *narrative explanation* based on function at higher levels of organization: photosynthetic rate interpreted as determinant of growth. However, this function depends concurrently on multiple responses at different levels of organization, which can overrride the causality behing the narrative explanation.

In addition to repair of damage, and protection that avoids damage or strain, there is an additional possible strategy, controlled damage/destruction. This is a very frequent approach in engineering, e.g., most electrical systems depend on fuses to prevent uncontrolled damage when overloaded. In plants, the hypersensitive response to fungal pathogens is an example (see Wheeler 1975). Thus, the damage we observe does not necessarily represent “broken machinery”, it can also represent “fuses blown as protection”. A fuse prevents uncontrolled damage but it clearly does not contribute to repairing damage or, once blown, contribute additional protection.

*Possible BOX* To build a narrative explanation about the response of a plant’s photosynthesis to the current year’s weather we need to consider the population the plant belongs to and the climate, including its variability, to which the population is adapted. As photosynthesis is constrained by other responses of the plant, the role played by photosynthesis in fitness or yield at the population level, cannot be considered in isolation from other possible concurrent responses that where limited or made possible by the observed change in photosynthesys under stress.

### Recovery or exhaustion phase

Recovery and exhaustion phases are seen as alternatives, leading to two contrasting outcomes: continuing growth and reproduction and death, respectively. But as mentioned in the previous section, while damage is being repaired acclimation can continue, and stress tolerance enhanced. Thus recovery is possible even under continuing exposure to a potential stressor, that even if remaining present stops behaving as an active stressor because of changes in the plant. So transit from the resistance phase back to the alarm phase is also possible.

Recovery involves repair of damage, but in some cases also compensatory responses, e.g., in partly defoliated silver birch sapplings the photosynthetic capacity of the remaining leaves increased by xx% (Ovaska et al. 1993). However, in most cases recovery is not complete and fitness or yield are decreased compared to plants that have not been exposed to stress.

Exhaustion hapens if both acclimation and repair are overwhelmed or innefective. A plant dies, leaves no descendence, or yields no commercially valuable produce. In contrast recovery can be partial and spans a whole range of possible outcomes.

### Conditions instead of phases

As the *phases* reviewed above do not represent necessarily a temporal sequence, we redefine them as a *classification of transient states* of the system. By doing this, we acknowledge that alarm state is not defined based on the same criterion as the other states, and that the alarm state can coexist in time with the other states even at the same level of organization.

Accepting this, frees us to consider the dynamics of stress as dependent on two processes: 1) *prevention* by anticipated acclimation accompanied by an opportunity cost ([Figure 4](#fig-acclimation-control-loop)), and 2) *repair* once strain develops and results in damage ([Figure 5](#fig-states-of-stress)).

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| Figure 4: Diagram describing *acclimation of an individual* as an adjustment of the developmental strategy in response to cues and signals informative of likely future conditions in the environment. |

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| Figure 5: Diagram describing the *state of an individual plant* based on the balance between rate of damage production and rate of damage repair. These states in most cases alternate during the course of a day and from day to day in a naturally fluctuating environment. |

In the physiological literature it is not uncommon to consider damage and repair as taking place cyclically during a day, e.g., UV-induced damage accumualted around noon being repaired in the afternoon (**XXXX?**), or low water potential and loss of turgor in the afternoon being restored at night (**XXXX?**). Some seasonal responses such as cold hardening in perennials are annually recurring acclimation responses (**XXXX?**). A case where damage and acclimation cannot be objectively distinguised is the after-effect of drought on the openning response of stomata: stomata remain “sluggish” to open even after water potential and turgor have recovered (**XXXX?**). In some cases, readiness of stomata to open never fully recovers after a drought. These examples give support to describing *states* instead of *phases*.

## A systems perspective

Levels of organization and hierarchical organization of systems play a central role in modern biological thinking (Capra and Luisi 2014; Aphalo and Sadras 2022; Thorogood et al. 2023) as well as the role of complexity (Capra and Luisi 2014). Below we apply these ideas in an attempt to untangle the concepts of stress, stressor and strain as they apply to different levels of organization using a systems perspective. The systems perspective emphasizes the role of interactions and control loops to obtain a broader view on function and its regulation (Meadows 2015).

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| Possible box (not necessarily here) |
| Giving examples on the idea/fact that: For logical clarity the condition or variable being considered as a possible stressor or limiting factor and the biological system being considered must be observed at the same temporal and spatial scales. It also follows that conclusions unless explicitly and formally upscaled or downscaled using a system’s perspective do not necessarily apply at levels above or below the one studied.  Should we cite the Spandrels’ paper? |

### The individual

As discussed in previous sections, potential and actual stressors in nature are rarely single environmental factors but instead combinations of factors acting jointly or sequentially. Information acquired by plants through the perception of cues and signals in the environment is combined during transduction (e.g., Rai, Morales, and Aphalo 2021; Podolec, Demarsy, and Ulm 2021; Sellaro et al. 2024; Casal and Qüesta 2018). Acquired information and experienced stress drastically affects future responses to both informational cues and signals, and to potential stressors thanks to enhanced readiness to respond and actually implemented physiological, morphological and developmental acclimation (Falik, Mauda, and Novoplansky 2024). Acclimation is in itself a syndrome of delicately orchestrated and coordinated concurrent responses of physiology, morphology and development. This is because the contributions of most physiological, morphological and developmental responses to fitness are interrrelated, e.g., water use, water transport, water storage, and water uptake must be in balance with each other, and building each of these capacities requires photosynthates and mineral nutrients from shared pools. Furthermore, water use is linked to photosynthesis by stomatal conductance, while the rate of photosynthesis feeds back into the pool of photosynthates. Any change in light interception, e.g., changes in the area of leaves, angle of display of leaves, white pubescence or wax deposits on the epidermis, etc., affect both transpiration and photosynthesis, but not equally. An increase in root to shoot dry mass ratio will favour not only water uptake but also the uptake of mineral nutrients. The regulation of photosynthesis takes place across levels of organization from proteins in thylacoid membranes of chloroplasts to leaf movements (Shevela, Björn, and Govindjee 2019).

The more we learn about the molecular and physiological mechanisms relevant to stress, the more intractable the problem of upscaling from these levels to levels relevant to fitness and yield appears. One difficulty, we think, is attempting to force this knowledge into two boxes by assuming that stress is distinct from normal, i.e., that there is a clear dichotomy. The two extreme conditions are exceptional. Realization of potential fitness or crop yield is almost never fully achieved in practice and death leaving no offspring rather infrequent in plants. In the case of populations, complete extinction is even less frequent. Most individual plants and populations function somewhere between these limits. So, if we take optimal conditions as a reference, we can conclude that nearly all plants are strained. In contrast, if we define strain as a terminal disruption leading to premature plant death or no offspring, we can conclude that strain is an exceptional condition. Both of these views, fail to recognize that intermediate degrees of strain and the gradient between the extreme situations and its dynamics in time and space are the most interesting.

Time and its progression are important, as fitness is achieved through an individual’s life time, and in annual plants achieved only towards the end of the life cycle. As growth and development progresses, the remaining available routes for plasticity decrease, and this forces a change in strategy as a plant develops (H. Shemesh and Novoplansky 2013). This decreasing ability for acclimation concurrent with development and growth, can make successful anticipation and early “decision making” highly beneficial to fitness.

From a mechanistic perspective, we may ask, is physiology fundamentally different in the presence and absence of strain? Strain in a plant is the result of an interaction, so it is not a state dependent only on the environment or on the plant phenotype. We think that it is most productive to think in terms of a regulation system that gradually adjusts plants’ plastic “behavior” to avoid or tolerate strain. This is like a navigation system, trying to avoid a crash and most of the time succeeding. The control system may engage in an emergency state of enhanced alertness in a crisis, but this can be interpreted as an effort to modify a set point in a control system, rather than as switch between two distinct system states.

As with many other things in biology, hierarchical, thus asymmetrical, organization of living systems precludes use of direct extrapolation for upscaling and downscaling of stressed states (Noble 2012, 2017; Passioura 2010, 2020). This is a feature of biological systems that affects all definitions of stress, stressor and strain. Thus we need to be aware that signs of metabolic and physiological strain (sensu Levitt) cannot be directly used to characterize whole-organism, in our case, whole-plant strain. Similarly, signs of strain at individual plant level cannot be directly used to assess strain at farm plot or ecosystem levels.

Currently, upscaling from gene expression and physiology in controlled environment studies to the behavior of plant populations and communities in the field is impeded by a poor (lack of?) understanding of the links among regulatory mechanisms at different levels of organization. At each level of organization, both sharing of and competition for resources and information can take place. Information and resources move both upwards and downwards across the (rather arbitrary?) boundaries between levels of organization. As these processes can contribute to fitness, they have been selected during evolution and/or crop breeding, and are thus a fundamental component of biological systems.

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| Describing complexity |
| A possible classification of problems for modelling has three categories: systems of small numbers, systems of large numbers and systems in-between these extremes (**XXXX?**). With systems of a small number of diferent agents and of possible interactions we can describe individual interactions between agents, e.g., competition between a pair of individual plants. With large numbers of agents and an even larger number of interactions among them, a probabilistic or statistical approach is most effective when the agents can be described as a population, e.g., allele frequencies in in population. Most real systems are more complex, with interactions taking place among agents belonging to different populations and a heirarchical organization with nesting of agents. In such cases a detailed description of all significant interactions and hierachical relationships is impractical or even impossible. A systems approach attemps to describe only the most important interactions ang hierarchies among agents to achieve a simplified description that can provide an approximate explaination of the behaviour of the described system under *a subset of the possible conditions in its environment*.  We may ask if the currently in fashion large language models could provide a solution. It is important to be aware that the aim of these models is only prediction, not estimation or attribution of the observed responses to causes or mechanisms (Efron 2020). They can be tought of as huge regression models not more informative than a polynomial regression. We come back round to what we discussed in relation to the possible triggers for anticipatory acclimation: a good predictor needs only be a good source of information. As with any purely empirical regression such large models can predict behaviours within the scope of the data used to train them, and given their extreme complexity cannot provide insights on the underlying mechanisms active in the real system. So, even if these models help with prediction, they do not provide mechanistic insights or directly contribute to improved understanding. On the other hand atificial-intelligence-based approaches can with tasks such as extraction of data from images, discovery of patterns in data and similar tasks that facilitate the research process. |

We think that insufficient awareness about the difficulties of scaling up has been a major source of confusion in stress physiology, especially in attempts to transfer conclusions from short-term studies under controlled environments to applications under field conditions sometimes leading to inaccurate conclusions about whole-plant’s strain based on metabolic and cell level assays of strain (the result of localized stress) or on their possible impact on produce yield or quality.

At different levels of organization it is natural to asses performance based on different variables, using different spatial and time scales. Performance at levels of organization within the organism is related to control mechanisms at metabolic, cell and organ levels. Failure of such systems to control a given low level function does not necessarily result in decreased performance at higher levels of organization and/or at longer time scales. We may define, for example, “strain” at tissue or cell levels based on an ineffective quenching of ROS, which may trigger at whole plant level a response that is inconsequential or either increases or decreases plant fitness or yield. Especially when such metabolic disturbances are transient, they may function as informational signals at the whole organism level triggering enhanced fitness compared to their absence. If we move upwards from individual plants to populations and communities, especially in natural populations with heterogenous genotypes, we face a similar challenge. To mechanistically upscale the behaviour of plants we need to understand in detail plant-plant interactions involving resources but also those related information, both signals used for plant-plant communication as well as cues derived from neighboring plant responses.

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| Crop breeding and upscaling (Possible BOX) |
| The analysis presented here shows that natural-selection- and breeding-selection as reference together with a scaling approach that incorporates the hierarchical structure of biological systems can avoid many of the weaknesses of the ill-defined concepts and terminology frequently used to describe biological stress in plants. In this box we describe how it applies to crop breeding for stress tolerance.  For example, a crop breeder is ultimately interested in yield, and aims at reducing strain quantified based on yield. To a breeder biological strain assessed based on fitness is irrelevant while it can be the main interest on an ecologist. Both, breeder and ecologist, maybe interested in strain as well as in acclimation at cellular level, but only in relation to their contributions to responses at the higher levels of organization, quantified using the measures of performance they are interested in.  As Alscher and Cumming (1990) Alscher and Cumming (1990) wrote, “…it is quite obvious that information obtained from molecular and biochemical characterizations of plant stress cannot legitimately be applied to whole organisms directly and certainly not to organisms growing in the field.” We hope our attempt at summarizing, organizing and connecting different definitions of stress, will contribute to the realization of the integration across disciplines that Alscher and Cumming (1990) already envisaged three decades ago and the book edited by (J. A. C. Smith and Griffiths 1993) attempted in relation to water stress.  From a mechanistic perspective, we may ask, is physiology fundamentally different in the presence and absence of strain? Strain is the result of an interaction, so it is not a state of the environment or a state of the plant. We think that it is most productive to think in terms of a regulation system that gradually adjusts plants’ plastic “behavior” to avoid or tolerate strain. This is like a navigation system, trying to avoid a crash and most of the time succeeding. The control system may engage in an emergency state of enhanced alertness in a crisis, but this can be interpreted as a shift in a set point of a control system, rather than as a distinct system. |

Views vary on whether stress is to be considered a normal, even necessary condition for development (Badyaev et al. 2015, and refs. therein), or as an exceptional condition with mainly negative consequences (Jansen and Potters 2017). In part this relates to levels of organization and the need to distinguish between metabolic-, cell-, organ-, individual- or even population-level challenges to performance including its dependence on “decision making” (sensu Aphalo and Sadras 2022). Furthermore, homeostasis at each of these levels works at different spatial and temporal scales. The word stress is used also at even higher levels of organization, communities, ecosystems, and the biosphere. At these higher levels of organization stability and resilience are emergent properties of very complex systems, with natural selection indirectly affecting them (Godfrey-Smith 2009; Thorogood et al. 2023).

It is relevant to consider how the concepts of eustress and distress (see Jansen and Potters 2017) can be interpreted from a hierarchical viewpoint. Körner (2018) writes “Levitt (1960) has distinguished between conditioning stress or ‘eustress’, which, despite it being potentially harmful for some individuals, it increases the long-term fitness of a species, and ‘distress’, conditions in which environmental constraints become increasingly destructive.” While Levitt considered individuals and species, two levels of organization, an equivalent hierarchical relationship exists between cells or tissues and whole plants. For a plant, fitness is the relevant measure of performance , and stress on cells, tissues or organs can increase (eustress), decrease (distress) or be inconsequential for the plant as a whole.

Eustress triggers adaptive acclimation, while distress disrupts homeostasis or triggers mal-adaptive responses, at the plant level of organization. So more broadly, distress can be stress on lower levels of organization that induces stress at a higher level of organization and eustress can be stress that either takes place at lower levels of organization and/or is transient and that helps mitigate or avoid strain, or even enhance performance, at higher levels of organization or over the lifetime of an organism. Jansen and Potters (2017) consider the strength of the stress as the determinant of it behaving as eustress or distress. However, as discussed above stress is not a property inherent to the stressor but instead determined by the character of the plant’s response, in other words, stress, as well as eustress and distress are emergent properties originating from the interaction between a plant and its environment during a time period relevant to the measure of performance of interest. When Badyaev et al. (2015) consider stress as a normal, even necessary condition for normal development in animals, they imply that stress at a short temporal scale is needed for a normal development observed at a longer time scale and lifetime fitness. The propagation of a strain event defines distress, while acclimation triggered by a transient strain event that ameliorates or avoids later stress events and, thus, enhances fitness defines eustress (Fig. 1).

### Selection of stress tolerance

Traits associated with stress resistance (e.g. avoidance or tolerance) have arisen as a result of exposure and selection under potential stress-inducing conditions during previous generations, and this process is reflected in the plant genome. At the population level, this process comprises directional selection, appearance of novel traits but also potentially local extinction (Badyaev 2005), (acute) stress events play an important role in evolution. From an evolutionary viewpoint, stress is a condition compromising reproduction and survival, from which it might be concluded that plants are very seldom under stress in their natural environment, i.e. such plants are either adapted to, or extinct in that environment. However, while this simplification may be theoretically correct in the case of some extreme (life or death) stress-conditions, it does not apply to more realistic “transient” and/or “quantitative” stress conditions where a balance between stress resistance and associated fitness cost (trade-off) will determine survival as well as performance measured as fitness. However, the hypothetical exposure to “life or death” stress conditions provides a key insight by highlighting that stress at individual or population (but not necessarily physiological) level can be defined as the result of lack of adaptation or miss-adaptation to a specific condition. Then, at two levels of organization, individual and population, we can dispense with definitions of stress based on disruption of physiology and/or homeostasis. This view is consistent with Körner (2003), who writes “Stressed plants are commonly those which are unfit for a given situation…”. As the latter plants will be impaired in their reproduction, they can be assumed to go locally extinct, leading Körner (2003) to state that “Stressful environments hardly exist”.

Second, numerous studies have documented an increase in phenotypic and genotypic variance under stress, and it is suggested that this variance is a source of novel adaptations under changed environments (XXX).

Yet, for stress-induced modifications to have evolutionary importance they have to be inherited and persist in a sufficient number of individuals within a population. This requires individuals with altered genotypes to survive stress and reproduce; thus stress-induced variation has to be accommodated by an organism without drastically reducing its functionality.”

Plasticity itself, is under both natural selection and plastic regulation (metaplasticity sensu Ariel Novoplansky 2009). Anticipatory or pre-emptive acclimation is crucial for fitness, as demonstrated by phenological research in many plant species (e.g., Hänninen 2016) as well as research on competition for light and shade avoidance (Aphalo and Sadras 2022; Sellaro et al. 2024). It is also important to keep in mind that extreme stress events, that repeat at very long-time intervals can select for “risk avoidance” behavior (H. Shemesh and Novoplansky 2013), thus, what may appear as suboptimal behavior in the short term, maybe beneficial on a longer time scale by ensuring the survival of the population.

A central question in stress biology is how organisms can prepare for exposure to extreme environmental change? It can be argued that the organism’s ability to mount an appropriate reaction to a stressor requires (advance/early) recognition and evaluation of the risks and limitations imposed by a likelihood of exposure to an extreme environment in the future. Mechanistically, the physiological consequences of exposure to the environment determine the necessary “countermeasures”. In turn, this raises the question about the role in plants of “recollections” of having been exposed to a stressor, or to cues and signals of its high likelihood, on an earlier occasion. Distinct from traditional evolutionary perspectives, new breakthroughs have been made in characterizing plant “memory” within the current generation, and in some cases recent past generations, as reflected in the epigenome and phenome (Yan et al. 2020; Aphalo and Sadras 2022).

Badyaev (2005) contends that “The response to stress depends crucially on prior experience and a ‘memory’ of response to a stressor. Generally, repeated exposure to a particular stressor favors the evolution of mechanisms that suppress an organism-wide stress reaction and, instead, activate stress-specific responses”. We can think of these responses as being pre-emptive, and triggered in advance of stress, or palliative and triggered by, possibly incipient, stress. As discussed by Aphalo and Sadras (2022) pre-emptive acclimation can be triggered by sensing of cues (see section XXX) and/or signals in the environment probabilistically correlated with high likelihood of future exposure to a potential stressor. The putative future stressor variables or conditions can also behave as informational cues before they become stressors. Thus, this creates a novel stress perspective, with important consequences for “stress concepts”. Rather, than the “traditional” (**xxxx?**) perspective whereby mainly strain in individual cells, tissues or organs gives rise to signals, such as the release of hormones or ROS, that convey information to other parts of the plant that subsequently respond in ways that contribute to whole-plant fitness, there is an additional pre-emptive adaptive response which decouples “adaptive stress-responses” from actual strain.

## Conclusions

Stress is an abstract concept describing the consequences of a deviation away from a “normal” (or alternatively “target”) state of a biological system. In practice, stress is used to describe a whole set of conditions that have in common some properties but can differ in others, including their causes, mechanisms and consequences. Stress is a generic concept, like fruit in Botany, that includes not only fruits from different plant species, but also different types of fruits such as accorns, drupes, grains, etc.

Even statements like “plants are under drought stress” or “… under heat stress” specify only the cause, not the mechanism or the consequences or type of strain triggered. “Oxidative stress in mesophyll cells triggered by prolonged exposure to high temperature and strong light” starts to narrow down into a small set of conditions and consequences, still dependent on the exact temperature, spectral irradiance, exposure time and plant phenotype and genotype.

Even as an abstraction, “stress” is used by different researchers from different perspectives, mostly dependent on the level of organization and type of function being described. Like the term “fruit”, the terms “stress”, “stressor” and “strain” are extremely useful in describing generalities about stress, but are too ambiguous to be used unqualified when describing specific cases.

A stressor is a stressor, by definition, only as a result of an organism’s responses, rather than intrinsically. An organism’s responses to the environment are adaptive or not depending on the context where they are triggered in, i.e., most responses of organisms are not inherently favorable or negative. Their contribution to fitness or crop yield are circimstantial.

The difference between “eustress” and “distress” is one of valuation: eustress is a good stress while distress is a bad stress. The mechanisms do not necessarily differ, and the same stress event can be labeled as eustress or distress if evaluted at different points in time or using different criteria. As a binary classification based on a continuous valuation scale it represents an oversimplification prone to hide nuances. On the positive side, it makes clear that “bad” stress observed at one point in time can be beneficial at a later time, and that stress at a lower level of organization can be beneficial at higher levels of organization.

A major diference exists between natural and managed biological systems. When studying a natural system we attempt to infer the normal condition based on our knowledge of the functioning of the system. There is a danger of being arbitrary or teleological in this inference, but we look at the system from a holistic perspective and as objectively as possible. In this case we can conclude that biological stress makes sense in the light of evolution and environmental change. In managed systems, the target is that set by the human manager, and it can be even an economic one. This is an utilitarian perspective on stress and its use makes sense only for human enterprises.

As Körner (2003) emphasizes, it is crucial not to apply a utilitarian definition of stress in ecology. For example, a crop breeder is ultimately interested in yield, and aims at reducing strain quantified based on yield. To a breeder biological strain assessed based on fitness can be irrelevant while it can be the main interest for an ecologist. Both breeder and ecologist, maybe interested in strain at cellular level, but only in relation to its contribution to responses at higher levels of organization. In this case, breakdown of strict physiological homeostasis is not the correct criterion to use for defining plant, population or crop stress.

A given response to a given informational signal can make a positive or negative contribution to fitness depending on future, yet to be realized, environmental conditions. Furthermore, at the time of response, these future environmental conditions cannot be predicted with certainty, at best they can be assigned a probability of being realized at a future time.

Responses mediated by sensory mechanisms responsive to the external environment and those triggered by the state of metabolism are not necessarily as different as they initially appear. In most cases, responses to the state of metabolism, and even to damage, also involve sensors responsive to the internal environment of the cell and signaling triggering adjustments in regulatory mechanisms and gene expression.

When considering populations growing in a heterogenous environment, their performance integrates the responses of individuals and the variation in the environment. Different individuals may have different genotypes and individuals of the same genotype will express different phenotypes based on the local environment they are exposed to. Exploitation of small-scale environmental variation relies on phenotypic plasticity (see Grime 1994).

A further distinction is important: acclimation describes responses that have been realized (implemented), while memory, describes changes is the readiness to respond or the nature of a future response to a specific stimulus or a combination of stimuli (Aphalo and Sadras 2022). This distinction is important from the viewpoint of investment of resources: Acclimation consumes resources while memory modifies the “rules” applicable to future “decisions” about the use of resources. Plasticity is a more abstract concept, describing the hability to express different phenotypes from the same genotype, irrespective of mechanisms (*IS THIS CORRECT?*).

Any response, independently of the mechanism that triggers it, can have both immediate and/or delayed consequences relevant to fitness. We consider those responses that have a delayed favorable effect on fitness as leading to anticipatory acclimation. The same response can have an immediate effect in addition to contributing to acclimation. Acclimation can also be pre-emptive or triggered by proxies correlated with a given environmental challenge or bounty (Aphalo and Sadras 2022). Given the variability of the environment in time and space and the variation in the genotype, epigenome and phenotype of the members of a population of plants, wild or cultivated, statistical probabilities are involved. The ability to thrive in a variable and ever changing environment is selected for as a direct consequence of the existence of variability in the environment where selection takes place.

In nature, stress will rarely cause a disruption such that all regulation is rendered ineffective, and almost never acclimation based on the sensing of non-stress conditions will be inconsequential to performance under subsequent stress conditions. Both strain and acclimation are quantitative traits and mechanistically syndromes. Thus, neither stress nor acclimation are binary responses, they have to be described and measured as continuous. A no stress condition is in most cases a fiction, in nature almost always there will be deviations from the normal, and deviations can exist at any level of organization.

Levels of organization and temporal and spatial scale all play crucial roles in biology, from biochemistry all the way up to ecology and evolution (Godfrey-Smith 2009; Capra and Luisi 2014). The multiple feedback loops and interactions inherent to all living systems give rise to difficult-to-predict emergent properties and behavior at higher levels of organization. So, it is necessary not to confuse stress at the cellular level with stress at whole-plant level or stress at whole-plant level with stress at population level or crop field level. Upscaling of “stress” is difficult, and frequently even counterintuitive.

From an actionable perspective, as stress-triggered responses have much in common to anticipatory responses and to constitutive traits affording stress tolerance and stressors are not inherently different to other environmental conditions, shouldn’t we simply integrate all research on responses to environmental variability under the same umbrella? Even if this is the case, unambiguous definitions for limitation, stress, stressor and strain that fulfil the requirements of epistemic metaphors (sensu Palma 2016) are needed. These terms describe abstract concepts that need to be carefully qualified when used to describe specific cases or situations. Otherwise, ambiguities and apparent contradictions are generated in the scientific discourse.

Aarssen, Lonnie W. 2015. “Body Size and Fitness in Plants: Revisiting the Selection Consequences of Competition.” *Perspectives in Plant Ecology, Evolution and Systematics* 17 (3): 236–42. <https://doi.org/10.1016/j.ppees.2015.02.004>.

Abbo, Shahal, Avi Gopher, and Gila Kahila Bar-Gal. 2022. *Plant Domestication and the Origins of Agriculture in the Ancient Near East*. Cambridge University Press. <https://doi.org/10.1017/9781108642491>.

Ågren, Göran I., and Martin Weih. 2012. “Plant Stoichiometry at Different Scales: Element Concentration Patterns Reflect Environment More Than Genotype.” *New Phytologist* 194 (4): 944–52. <https://doi.org/10.1111/j.1469-8137.2012.04114.x>.

Alscher, R. G., and J. R. Cumming. 1990. *Stress Responses in Plants: Adaptation and Acclimation Mechanisms*. Vol. 12. Plant Biology. New York: Wiley-Liss.

Aphalo, Pedro J., and Carlos L. Ballaré. 1995. “On the Importance of Information-Acquiring Systems in Plant-Plant Interactions.” *Functional Ecology* 9 (1): 5–14. <https://doi.org/10.2307/2390084>.

Aphalo, Pedro J., and Victor O. Sadras. 2022. “Explaining Preemptive Acclimation by Linking Information to Plant Phenotype.” *Journal of Experimental Botany* 73 (15): 5213–34. <https://doi.org/10.1093/jxb/erab537>.

Badyaev, Alexander V. 2005. “Role of Stress in Evolution.” In *Variation: A Central Topic in Biology*, edited by Benedikt Hallgrímsson and Brian K. Hall, 277–302. Elsevier. <https://doi.org/10.1016/b978-012088777-4/50015-6>.

Badyaev, Alexander V., Erin S. Morrison, Virginia Belloni, and Michael J. Sanderson. 2015. “Tradeoff Between Robustness and Elaboration in Carotenoid Networks Produces Cycles of Avian Color Diversification.” *Biology Direct* 10 (1): 45. <https://doi.org/10.1186/s13062-015-0073-6>.

Ballaré, C. L., A. L. Scopel, and R. A. Sánchez. 1990. “Far-Red Radiation Reflected from Adjacent Leaves: An Early Signal of Competition in Plant Canopies.” *Science* 247 (4940): 329–32. <https://doi.org/10.1126/science.247.4940.329>.

Bidwell, Roger G. S. 1979. *Plant Physiology*. 2nd ed. New York: Macmillan.

Bloom, A. J., F. S. Chapin, and H. A. Mooney. 1985. “Resource Limitation in Plants: An Economic Analogy.” *Annual Review of Ecology and Systematics* 16 (1): 363–92. <https://doi.org/10.1146/annurev.es.16.110185.002051>.

Boccalandro, Hernán E, Edmundo L Ploschuk, Marcelo J Yanovsky, Rodolfo A Sánchez, Christiane Gatz, and Jorge J Casal. 2003. “Increased Phytochrome b Alleviates Density Effects on Tuber Yield of Field Potato Crops.” *Plant Physiology* 133 (4): 1539–46. <https://doi.org/10.1104/pp.103.029579>.

Bonduriansky, Russell, and Troy Day. 2020. *Extended Heredity: A New Understanding of Inheritance and Evolution*. Princeton: Princeton University Press.

Bradshaw, A. D. 1965. “Evolutionary Significance of Phenotypic Plasticity in Plants.” In *Advances in Genetics*, 115–55. Elsevier. <https://doi.org/10.1016/s0065-2660(08)60048-6>.

Callaway, R. M. 2002. “The Detection of Neighbors by Plants.” *Trends in Ecology and Evolution* 17: 104–5.

Capra, Fritjof, and Pier Luigi Luisi. 2014. *The Systems View of Life*. Cambridge University Press. <https://www.ebook.de/de/product/26316581/fritjof_capra_pier_luigi_luisi_the_systems_view_of_life.html>.

Casal, Jorge J., and Julia I. Qüesta. 2018. “Light and Temperature Cues: Multitasking Receptors and Transcriptional Integrators.” *New Phytologist* 217 (3): 1029–34. <https://doi.org/10.1111/nph.14890>.

Chapin, F. S., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. “Plant Responses to Multiple Environmental Factors.” *BioScience* 37 (1): 49–57. <https://doi.org/10.2307/1310177>.

Chapin, F. S., P. A. Matson, and P. M. Vitousek. 2011. *Principles of Terrestrial Ecosystem Ecology*. 2nd ed. 2012. Springer.

Cossani, Cesar Mariano, and Victor O. Sadras. 2018. “Water–Nitrogen Colimitation in Grain Crops.” In *Advances in Agronomy*, 231–74. Elsevier. <https://doi.org/10.1016/bs.agron.2018.02.004>.

Darwin, Charles. 1859. *On the Origin of Species by Means of Natural Selection*. London: John Murray. <https://archive.org/details/onoriginofspecie1859darw>.

Denison, R Ford. 2012. *Darwinian Agriculture: How Understanding Evolution Can Improve Agriculture*. Princeton University Press.

Efron, Bradley. 2020. “Prediction, Estimation, and Attribution.” *Journal of the American Statistical Association* 115 (530): 636–55. <https://doi.org/10.1080/01621459.2020.1762613>.

Elser, James J., Matthew E. S. Bracken, Elsa E. Cleland, Daniel S. Gruner, W. Stanley Harpole, Helmut Hillebrand, Jacqueline T. Ngai, Eric W. Seabloom, Jonathan B. Shurin, and Jennifer E. Smith. 2007. “Global Analysis of Nitrogen and Phosphorus Limitation of Primary Producers in Freshwater, Marine and Terrestrial Ecosystems.” *Ecology Letters* 10 (12): 1135–42. <https://doi.org/10.1111/j.1461-0248.2007.01113.x>.

Falik, Omer, Shachar Mauda, and Ariel Novoplansky. 2022. “The Ecological Implications of Interplant Drought Cuing.” *Journal of Ecology*, September. <https://doi.org/10.1111/1365-2745.13991>.

———. 2024. “The Ecological Implications of Interplant Drought Cuing.” *Journal of Ecology* 111: 23–32. <https://doi.org/10.1111/1365-2745.13991>.

Falik, Omer, Yonat Mordoch, Lydia Quansah, Aaron Fait, and Ariel Novoplansky. 2011. “Rumor Has It...: Relay Communication of Stress Cues in Plants.” *PLoS ONE* 6 (11): e23625. <https://doi.org/10.1371/journal.pone.0023625>.

Fisher, Ronald A. 1958. *Genetical Theory of Natural Selection*. Dover Publications Inc.

Godfrey-Smith, Peter. 2009. *Darwinian Populations and Natural Selection*. Oxford New York: Oxford University Press.

———. 2014. *Philosophy of Biology*. Princeton: Princeton University Press.

Goldberg, D, and A Novoplansky. 1997. “On the Relative Importance of Competition in Unproductive Environments.” *Journal of Ecology* 85 (4): 409–18. <https://doi.org/10.2307/2960565>.

Grime, J. P. 1979. *Plant Strategies and Vegetation Processes*. Wiley. <https://books.google.fi/books?id=75nwAAAAMAAJ>.

———. 1981. “Plant Strategies in Shade.” In *Plants and the Daylight Spectrum*, edited by H. Smith, 159–86. London: Academic Press.

———. 1994. “The Role of Plasticity in Exploiting Environmental Heterogeneity.” In *Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Belowground*, edited by M. M. Caldwell and R. W. Pearcy, 1–19. San Diego: Academic Press. <https://doi.org/10.1016/b978-0-12-155070-7.50006-8>.

Grubb, P. J. 1992. “A Positive Distrust in Simplicity — Lessons from Plant Defences and from Competition Among Plants and Among Animals.” *Journal of Ecology* 80: 585–610.

Gu, Lei, Yang Xu, Tingting Yang, Shanshan Qin, Lu Zhang, Yunfei Sun, Yuan Huang, and Zhou Yang. 2021. “Predator-Induced Allometric Changes in the Tail Spine Length ofDaphnia: A Distinct Resource Allocation Strategy.” *Journal of Plankton Research* 43 (6): 884–93. <https://doi.org/10.1093/plankt/fbab063>.

Guarin, Jose Rafael, Belay Kassie, Alsayed M. Mashaheet, Kent Burkey, and Senthold Asseng. 2019. “Modeling the Effects of Tropospheric Ozone on Wheat Growth and Yield.” *European Journal of Agronomy* 105 (April): 13–23. <https://doi.org/10.1016/j.eja.2019.02.004>.

Gutschick, Vincent P, and Hormoz BassiriRad. 2003. “Extreme Events as Shaping Physiology, Ecology, and Evolution of Plants: Toward a Unified Definition and Evaluation of Their Consequences.” *New Phytologist* 160 (1): 21–42. <https://doi.org/10.1046/j.1469-8137.2003.00866.x>.

Hänninen, Heikki. 2016. *Boreal and Temperate Trees in a Changing Climate*. Dordrecht: Springer Nature. <https://doi.org/10.1007/978-94-017-7549-6>.

Harpole, W. Stanley, Jacqueline T. Ngai, Elsa E. Cleland, Eric W. Seabloom, Elizabeth T. Borer, Matthew E. S. Bracken, James J. Elser, et al. 2011. “Nutrient Co‐limitation of Primary Producer Communities.” *Ecology Letters* 14 (9): 852–62. <https://doi.org/10.1111/j.1461-0248.2011.01651.x>.

Harris, Dorothy V. 1970. “On the Brink of Catastrophe.” *Quest* 13 (1): 33–40. <https://doi.org/10.1080/00336297.1970.10519674>.

Highkin, H. R. 1960. “The Effect of Constant Temperature Environments and of Continuous Light on the Growth and Development of Pea Plants.” *Cold Spring Harbor Symposia on Quantitative Biology* 25 (0): 231–38. <https://doi.org/10.1101/sqb.1960.025.01.023>.

Holopainen, Jarmo K., and Jonathan Gershenzon. 2010. “Multiple Stress Factors and the Emission of Plant VOCs.” *Trends in Plant Science* 15 (3): 176–84. <https://doi.org/10.1016/j.tplants.2010.01.006>.

Hu, Changlu, Victor O. Sadras, Guoyan Lu, Runze Zhang, Xueyun Yang, and Shulan Zhang. 2019. “Root Pruning Enhances Wheat Yield, Harvest Index and Water-Use Efficiency in Semiarid Area.” *Field Crops Research* 230 (January): 62–71. <https://doi.org/10.1016/j.fcr.2018.10.013>.

Huey, R. B. 2002. “Plants Versus Animals: Do They Deal with Stress in Different Ways?” *Integrative and Comparative Biology* 42 (3): 415–23. <https://doi.org/10.1093/icb/42.3.415>.

Jansen, Marcel A. K., and Geert Potters. 2017. “Strees: The Way of Life.” In *Plant Stress Physiology*, edited by Segei Shabala, 2nd ed., xi–xiv. Wallingford: CABI.

Karban, Richard. 2015. *Plant Sensing and Communication*. Chicago: The University of Chicago Press.

Kauffman, Stuart A., and Andrea Roli. 2023. “A Third Transition in Science?” *Interface Focus* 13 (3). <https://doi.org/10.1098/rsfs.2022.0063>.

Keddy, Paul A. 2017. *Plant Ecology*. Cambridge University Press. <http://www.ebook.de/de/product/26311639/paul_a_keddy_plant_ecology.html>.

Khan, Faisal, Yupeng Feng, Jairo A. Palta, Yinglong Chen, Victor O. Sadras, and Kadambot H. M. Siddique. 2022. “Selection for Yield over Five Decades Favored Anisohydric and Phenological Adaptations to Early-Season Drought in Australian Wheat.” *Plant and Soil* 476 (1): 511–26. <https://doi.org/10.1007/s11104-022-05543-w>.

Kho, Ramun M. 2000. “On Crop Production and the Balance of Available Resources.” *Agriculture, Ecosystems &Amp; Environment* 80 (1–2): 71–85. <https://doi.org/10.1016/s0167-8809(00)00135-3>.

Körner, Christian. 2003. “Limitation and Stress Always or Never ?” *Journal of Vegetation Science* 14 (2): 141. <https://doi.org/10.1658/1100-9233(2003)014[0141:lasaon]2.0.co;2>.

———. 2018. “Concepts in Empirical Plant Ecology.” *Plant Ecology & Diversity* 11 (4): 405–28. <https://doi.org/10.1080/17550874.2018.1540021>.

Kranner, Ilse, Farida V. Minibayeva, Richard P. Beckett, and Charlotte E. Seal. 2010. “What Is Stress? Concepts, Definitions and Applications in Seed Science.” *New Phytologist* 188 (3): 655–73. <https://doi.org/10.1111/j.1469-8137.2010.03461.x>.

Lass, Sandra, and Piet Spaak. 2003. “Chemically Induced Anti-Predator Defences in Plankton: A Review.” *Hydrobiologia* 491 (1–3): 221–39. <https://doi.org/10.1023/a:1024487804497>.

Levine, Seymour. 1985. “A Definition of Stress?” In *Animal Stress*, 51–69. Springer New York. <https://doi.org/10.1007/978-1-4614-7544-6_4>.

Levitt, Jacob. 1980. *Responses of Plants to Environmental Stresses*. 2. ed. Vol. 2. Water, radiation, salt and other stresses. New York: Academic Press.

Lichtenthaler, Hartmut K. 1998. “The Stress Concept in Plants: An Introduction.” *Annals of the New York Academy of Sciences* 851 (June): 187–98. <https://doi.org/10.1111/j.1749-6632.1998.tb08993.x>.

Martı'nez-Ghersa, MA, CM Ghersa, and EH Satorre. 2000. “Coevolution of Agricultural Systems and Their Weed Companions: Implications for Research.” *Field Crops Research* 67 (2). <https://doi.org/10.1016/S0378-4290(00)00092-7>.

Meadows, Donella. 2015. *Thinking in Systems*. Chelsea Green Publishing Co. <https://www.ebook.de/de/product/7353874/donella_meadows_thinking_in_systems.html>.

Mindell, David P. 2024. *The Network of Life: A New View of Evolution*. Princeton: Princeton University Press.

Molins, Francisco, Miguel Ángel Serrano, and Adrian Alacreu-Crespo. 2021. “Early Stages of the Acute Physical Stress Response Increase Loss Aversion and Learning on Decision Making: A Bayesian Approach.” *Physiology & Behavior* 237 (August): 113459. <https://doi.org/10.1016/j.physbeh.2021.113459>.

Niklas, K. J. 1994. *Plant Allometry: The Scalling of Plant Form and Process*. Chicago: University of Chicago Press.

Noble, Denis. 2012. “A Theory of Biological Relativity: No Privileged Level of Causation.” *Interface Focus* 2 (1): 55–64. <https://doi.org/10.1098/rsfs.2011.0067>.

———. 2017. “Evolution Viewed from Physics, Physiology and Medicine.” *Interface Focus* 7 (5): 20160159. <https://doi.org/10.1098/rsfs.2016.0159>.

Novoplansky, A., D. Cohen, and T. Sachs. 1990. “How Portulaca Seedlings Avoid Their Neighbors.” *Oecologia* 82: 490–93. <https://doi.org/10.1007/BF00319791>.

Novoplansky, Ariel. 2009. “Picking Battles Wisely: Plant Behaviour Under Competition.” *Plant Cell and Environment* 32 (6): 726–41. <https://doi.org/10.1111/j.1365-3040.2009.01979.x>.

———. 2016. “Future Perception in Plants.” In *Anticipation Across Disciplines*, edited by Mihai Nadin, 57–70. Cognitive Systems Monographs. Berlin: Springer. <https://doi.org/10.1007/978-3-319-22599-9_5>.

Ovaska, J., S. Ruuska, E. Rintamaki, and E. Vapaavuori. 1993. “Combined Effects of Partial Defoliation and Nutrient Availability on Cloned Betula Pendula Saplings .2. Changes in Net Photosynthesis and Related Biochemical Properties.” *Journal of Experimental Botany* 44 (265): 1395–1402. <https://doi.org/10.1093/jxb/44.8.1395>.

Packham, J. R., D. J. L. Harding, G. M. Hilton, and R. A. Stuttard. 1992. *Functional Ecology of Woodlands and Forests*. London: Chapman & Hall.

Palma, Hector. 2016. *Ciencia y Metaforas. Critica de Una Razon Incestuosa*. Prometeo Libros.

Passioura, John B. 2010. “Plant-Water Relations.” John Wiley & Sons, Ltd. <https://doi.org/10.1002/9780470015902.a0001288.pub2>.

———. 2020. “Translational Research in Agriculture. Can We Do It Better?” *Crop and Pasture Science* 71 (6): 517. <https://doi.org/10.1071/cp20066>.

Pierik, Ronald, Carlos L Ballaré, and Marcel Dicke. 2014. “Ecology of Plant Volatiles: Taking a Plant Community Perspective.” *Plant, Cell & Environment* 37 (8): 1845–53. <https://doi.org/10.1111/pce.12330>.

Podolec, Roman, Emilie Demarsy, and Roman Ulm. 2021. “Perception and Signaling of Ultraviolet-b Radiation in Plants.” *Annual Review of Plant Biology* 72 (1): 793–822. <https://doi.org/10.1146/annurev-arplant-050718-095946>.

Pye, David. 1995. *The Nature and Art of Workmanship*. Revised ed., repr. London: Herbert Press.

Rai, Neha, Luis O. Morales, and Pedro J. Aphalo. 2021. “Perception of Solar UV Radiation by Plants: Photoreceptors and Mechanisms.” *Plant Physiology* 186 (3): 1382–96. <https://doi.org/10.1093/plphys/kiab162>.

Reymond, Matthieu, Bertrand Muller, Agnès Leonardi, Alain Charcosset, and François Tardieu. 2003. “Combining Quantitative Trait Loci Analysis and an Ecophysiological Model to Analyze the Genetic Variability of the Responses of Maize Leaf Growth to Temperature and Water Deficit.” *Plant Physiology* 131 (2): 664–75. <https://doi.org/10.1104/pp.013839>.

Reynolds, Andrew S. 2022. *Understanding Metaphors in the Life Sciences*. Cambridge University Press. <https://doi.org/10.1017/9781108938778>.

Richards, R. A., and J. B. Passioura. 1981. “Seminal Root Morphology and Water Use of Wheat II. Genetic Variation.” *Crop Science* 21 (2): 253–55. <https://doi.org/10.2135/cropsci1981.0011183x002100020012x>.

———. 1989. “A Breeding Program to Reduce the Diameter of the Major Xylem Vessel in the Seminal Roots of Wheat and Its Effect on Grain Yield in Rain-Fed Environments.” *Australian Journal of Agricultural Research* 40 (5): 943. <https://doi.org/10.1071/ar9890943>.

Sadras, Victor O. 2020. “Agricultural Technology Is Unavoidable, Directional, Combinatory, Disruptive, Unpredictable and Has Unintended Consequences.” *Outlook on Agriculture* 49 (4): 003072702096049. <https://doi.org/10.1177/0030727020960493>.

Santos-Díaz, María del Socorro, and Nancy Gabriela Camarena-Rangel. 2019. “Cacti for Production of Metabolites: Current State and Perspectives.” *Applied Microbiology and Biotechnology* 103 (21–22): 8657–67. <https://doi.org/10.1007/s00253-019-10125-5>.

Schoppach, R., D. Fleury, T. R. Sinclair, and W. Sadok. 2017. “Transpiration Sensitivity to Evaporative Demand Across 120 Years of Breeding of Australian Wheat Cultivars.” *Journal of Agronomy and Crop Science* 203 (3): 219–26. <https://doi.org/10.1111/jac.12193>.

Schulze, Ernst-Detlef, Erwin Beck, and Klaus Müller-Hohenstein. 2005. *Plant Ecology*. 1st ed. Book Pedro Viikki Science Library: Springer.

Sellaro, Romina, Maxime Durand, Pedro J. Aphalo, and Jorge J. Casal. 2024. “Making the Most of Canopy Light: Shade Avoidance Under a Fluctuating Spectrum and Irradiance.” Journal Article, Peer-reviewed. Edited by Madhusmita Panigrahy. *Journal of Experimental Botany*, August. <https://doi.org/10.1093/jxb/erae334>.

Selye, Hans. 1936. “A Syndrome Produced by Diverse Nocuous Agents.” *Nature* 138 (3479): 32–32. <https://doi.org/10.1038/138032a0>.

———. 1975. “Confusion and Controversy in the Stress Field.” *Journal of Human Stress* 1 (2): 37–44. <https://doi.org/10.1080/0097840x.1975.9940406>.

Shemesh, Hagai, Adi Arbiv, Mordechai Gersani, Ofer Ovadia, and Ariel Novoplansky. 2010. “Anticipating Future Conditions via Trajectory Sensitivity.” Edited by Hans Henrik Bruun. *Plant Signaling & Behavior* 5 (11): 1501–3. <https://doi.org/10.1371/journal.pone.0010824>.

Shemesh, H, and A Novoplansky. 2013. “Branching the Risks: Architectural Plasticity and Bet-Hedging in Mediterranean Annuals.” *Plant Biology (Stuttgart, Germany)* 15 (6): 1001–12. <https://doi.org/10.1111/j.1438-8677.2012.00705.x>.

Shevela, Dmitry, Lars Olof Björn, and Govindjee. 2019. *Photosynthesis: Solar Energy for Life*. Edited by null null and Lars Olof Björn. Singapore: World Scientific Publishing Co Pte Ltd.

Šimpraga, Maja, Rajendra P. Ghimire, Dominique Van Der Straeten, James D. Blande, Anne Kasurinen, Jouni Sorvari, Toini Holopainen, Sandy Adriaenssens, Jarmo K. Holopainen, and Minna Kivimäenpää. 2019. “Unravelling the Functions of Biogenic Volatiles in Boreal and Temperate Forest Ecosystems.” *European Journal of Forest Research* 138 (5): 763–87. <https://doi.org/10.1007/s10342-019-01213-2>.

Sinclair, Thomas R., and Thomas W. Rufty. 2012. “Nitrogen and Water Resources Commonly Limit Crop Yield Increases, Not Necessarily Plant Genetics.” *Global Food Security* 1 (2): 94–98. <https://doi.org/10.1016/j.gfs.2012.07.001>.

Smith, H. 1981. “Light Quality as an Ecological Factor.” In *Plants and Their Atmospheric Environment, 21st Symposium of the British Ecological Society*, edited by J. Grace, E. D. Ford, and P. G. Jarvis, 93–110. Oxford: Blackwell Scientific Publications.

Smith, J. A. C., and H. Griffiths. 1993. *Water Deficits: Plant Responses from Cell to Community*. Oxford: Bios Scientific Publishers.

Taiz, Lincoln, Eduardo Zeiger, Ian M. Moller, and Angus Murphy. 2015. *Plant Physiology and Development*. Edited by Eduardo Zeiger, Ian Max Møller, and Angus Murphy. 6th ed. Sunderland, Mass.: Sinauer Assoc.

Thorogood, Rose, Ville Mustonen, Alexandre Aleixo, Pedro J. Aphalo, Fred O. Asiegbu, Mar Cabeza, Johannes Cairns, et al. 2023. “Understanding and Applying Biological Resilience, from Genes to Ecosystems.” *Npj Biodiversity* 2 (1). <https://doi.org/10.1038/s44185-023-00022-6>.

Trewavas, A. 2014. *Plant Behaviour and Intelligence*. Oxford University Press. <https://books.google.fi/books?id=6Pk5BAAAQBAJ>.

Trewavas, A. J., and D. H. Jennings. 1986. “Introduction.” In *Plasticity in Plants*, edited by D. H. Jennings and A. J. Trewavas, 1–4. Symposia of the Society for Experimental Biology. Cambridge: The Company of Biologists.

West-Eberhard, Mary Jane. 2003. *Developmental Plasticity and Evolution*. Oxford University Press. <https://www.amazon.com/Developmental-Plasticity-Evolution-Mary-West-Eberhard/dp/0195122356?SubscriptionId=0JYN1NVW651KCA56C102&tag=techkie-20&linkCode=xm2&camp=2025&creative=165953&creativeASIN=0195122356>.

———. 2019. “Modularity as a Universal Emergent Property of Biological Traits.” *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 332 (8): 356–64. <https://doi.org/10.1002/jez.b.22913>.

Wheeler, Harry. 1975. *Plant Pathogenesis*. Berlin New York: Springer-Verlag.

Whitehead, F. H. 1963. “The Effects of Exposure on Growth and Development.” In *The Water Relations of Plants*, edited by A. J. Rutter and F. H. Whitehead, 235–45. New York: John Wiley & Sons.

Wimsatt, William C. 1976. “Reductionism, Levels of Organization, and the Mind-Body Problem.” In *Consciousness and the Brain*, 205–67. Springer US. <https://doi.org/10.1007/978-1-4684-2196-5_9>.

———. 1994. “The Ontology of Complex Systems: Levels of Organization, Perspectives, and Causal Thickets.” *Canadian Journal of Philosophy Supplementary Volume* 20: 207–74. <https://doi.org/10.1080/00455091.1994.10717400>.

Winner, William E. 1991. *Response of Plants to Multiple Stresses*. Edited by H. A. Mooney, W. E. Winner, and E. J. Pell. Physiological Ecology. San Diego: Academic Press.

Woltereck, R. 1909. “Weitere Experimentelle Untersuchungen Über Artveränderung, Speziell Über Das Wesen Quantitativer Artunterschiede Bei Daphniden.” *Verhandlungen Der Deutschen Zoologischen Gesellschaft* 19: 110–72.

Yan, Yan, Frederick L. Stoddard, Susanne Neugart, Michal Oravec, Otmar Urban, Victor O. Sadras, and Pedro J. Aphalo. 2020. “The Transgenerational Effects of Solar Short-UV Radiation Differed in Two Accessions of Vicia Faba l. From Contrasting UV Environments.” *Journal of Plant Physiology* 248: 153145. <https://doi.org/10.1016/j.jplph.2020.153145>.

Zarka, Jens, Frederik C. De Wint, Luc De Bruyn, Dries Bonte, and Thomas Parmentier. 2022. “Dissecting the Costs of a Facultative Symbiosis in an Isopod Living with Ants.” *Oecologia* 199 (2): 355–66. <https://doi.org/10.1007/s00442-022-05186-9>.

Zeiger, B. P., and R. Weinberg. 1970. “System Theoretic Analysis of Models: Computer Simulation of a Living Cell.” *Journal of Theoretical Biology* 29: 35–56. <https://doi.org/10.1016/0022-5193(70)90117-7>.