
SHORT- AND LONG-TERM RESPONSES OF VEGETATION TO ENVIRONMENTAL CHANGES

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INTRODUCTION

The plant environment fluctuates at all time scales. The growth of plants can be considered as a process of capturing ephemeral radiative energy and converting it into more lasting forms.

Plants can cope with fluctuations that occur within a few seconds, but the effects of these fluctuations become only noticeable at a time scale of weeks or even longer. This short overview will discuss some important environmental and physiological processes in terms of their temporal characteristics. It is intended to be complementary to the more extensive process-based overview of Van de Geijn et al. (1997, this volume).

The diurnal and seasonal cycles in the plant environment are the most pronounced ones. Their repetitiveness has caused life to adapt to these cycles. The time scales of these cycles provide us with natural borderlines between different domains which we could call the short-term, the middle term and the long term time domain respectively. Through modelling, it is possible to connect these time domains, and indeed different levels of integration (Ehleringer and Field, 1993; Goudriaan and Van Laar, 1994; Rabbinge and Van Ittersum, 1994; Haxeltine et al., 1996).

The following course division of processes is possible according to their time scale:

- *Within a day : the short-term.*

These processes are mostly at the cellular level. They are functional processes, such as metabolism, gas exchange and nutrient uptake.

- *From a day to a season : the middle-term.*

These processes are often morphological as they refer to formation and growth of new organs, giving shape to the organism as a whole.

- *Ecosystem processes operating on the long-term.*

Soil and populations of plants and animals together form the ecosystem. Ecosystem processes relate to soil formation but also to vegetation composition and to genetic drift within the populations.

Research in these areas is often profoundly different in character. The functional process scientist tends to work in a laboratory environment, the organism scientist uses pot or field experiments involving treatment levels and periodic harvests, and the ecosystem scientist prefers the undisturbed natural environment, relying on natural variations (Walker and Steffen, 1996).

2.1 The fast processes (Intradiurnal)

a) Photosynthesis (Lawlor, 1995; Bowes et al., 1996; McMurtrie and Wang, 1993)

The light reactions of photosynthesis are among the fastest that we can measure. Excitation energy of the photosynthetic pigment is almost immediately transferred into electron transport, and subsequently into the formation of ATP from ADP and NADPH from NADP. This chemical energy will drive the formation of RubP from PGA after which the dark processes of photosynthesis can begin. The dark processes are much slower, typically they have a time coefficient of a few minutes, as follows from the duration of the post-illumination burst of photorespiration. The CO₂ response of photosynthesis is located in these dark reactions. Although these are slower than the light reactions, still the response is very fast and for all practical purposes we can call it an immediate reaction.

b) Micrometeorology and transpiration

The equilibration of leaf and canopy temperature to altered ambient conditions is a physical process that has a time coefficient of the order of one minute. Latent heat loss by transpiration plays an important role in this equilibration, and in fact it is responding equally fast. The air characteristics inside the plant canopy are closely connected to those above the plant canopy and will follow them almost immediately. Only under a nocturnal inversion may the coupling be lost, so that the micrometeorological conditions may deviate somewhat more from those above.

Soil temperature will follow air temperature at a much slower rate, and its time coefficient is rather of the order of one day (up to about 20 cm depth) or even one month (up to 1 m depth).

c) Substomatal CO₂ concentration

The diffusion of CO₂ into the substomatal cavity is a physical process. The time coefficient of this process can be estimated as the ratio of the substomatal volume and the stomatal conductance. Typical values are 0.1 of a mm air thickness per leaf area, and a stomatal conductance of 0.01 m s⁻¹, which leads to a ratio of 0.01 s. This means that substomatal CO₂ (and also water vapour) can follow the external conditions practically instantaneously. If any storage occurs, it is not in the gaseous phase.

d) Stomatal conductance (Leuning, 1995)

Transpiration is driven by radiative energy and drying power of the air, but it is controlled by stomatal aperture. The response of stomatal aperture to the environmental conditions (a physiological response) is slower than the response of leaf temperature and transpiration (a physical response). Stomatal opening is caused by a process of gaining or losing turgidity in the guard cells and apparently this process costs time, typically of the order of 15 minutes up to one hour.

e) Plant water content (Van Ieperen, 1996; Kowalik et al., 1997)

Plants, especially under dry conditions, are known to go through a diurnal cycle of water content and water potential. The reservoir of internal plant water is extremely small: if cut, a plant in the full sun will wilt within a few minutes. This can be understood by comparing rate of transpiration (up to 1 mm per hour) with the water reservoir which is at most 1 mm per ground area. A loss of 30% of this reservoir is lethal to most crop plants. This fast response means that most plants will closely follow the diurnal course of evaporative demand. If they exhibit a longer lag phase, it must be due to a larger storage/leaf area ratio which can occur after leaf abscission, by using storage water in stems and fruits (melons!) and by lags in the soil surrounding the roots.

f) Short-term assimilate reservoir

Assimilates are formed during the daylight hours, but they are being consumed all the time. The net result is an repetitive diurnal course of assimilate content, rising during the day and

decreasing during the night. Under normal circumstances the pool of assimilates is just about empty by the morning, and so the time coefficient of the use of assimilates is of the order of half a diurnal cycle period (Goudriaan and Van Laar, 1994). This is longer than the time scale of photosynthesis.

Temperature normally stimulates the consumption rate of assimilates, and so under higher temperatures the rate of decline will be faster. This increase of consumption will be accompanied by both an increase in respiration rate and an increase in the rate of conversion from assimilates into structural dry matter.

2.2 The middle term processes (from one day to one season)

The processes at this time scale are crucial for yield formation.

The methods of study often rely on periodic harvests, which has serious implications for the accuracy of measurement. A growth rate can then only be found by comparing organ sizes derived from different individuals at subsequent moments in time. The intrinsic variability between individuals necessitates smoothing from replicated observations, while securing statistical requirements. Because of this disadvantage, it is a challenge to devise experimental methods for non-destructive measurements (Van Ieperen, 1996). Spatial size is easier to measure non-destructively than biomass or water content.

The time scale of growth of individual leaves is about one week, considerably longer than the time scale of assimilate turnover. This means that an adaptation of leaf area is necessarily slower than the immediate response of growth to altered environmental conditions. The necessary buffering can occur through storage of assimilates in stems (Grüters et al., this volume) or in the leaves, leading to relatively fast changes in specific leaf area. In spring time, the relative growth rate of leaf area is stimulated by temperature at about 0.01 per degree day. Growth of roots is stimulated by abundance of above ground factors such as radiation and/or CO₂ concentration (Van de Geijn et al., this volume).

Adaptive processes within the lifetime of a plant may occur. So-called downregulation of photosynthetic capacity as a reaction to elevated CO₂ has been observed, but does not always occur.

In annual plants with a determinate growth pattern, the formation of sinks is limited to a relatively short period. If the conditions are good in this period, sinks are usually formed in great abundance. Competition between the growing sinks for assimilates or nutrients will later cause abscission and abortion, such that a balance is obtained between the total size of the source and the sink. Plant varieties exhibit large differences in these ratios between different organs, which makes plant breeding an extremely powerful tool in shaping the right variety for the right environment (Evans, 1993). Some of the flexibility of plant growth comes from variability in rates of development for different phases of growth. There are early varieties and late varieties, some respond strongly to photoperiod and other varieties are day-neutral. The large importance of photoperiod was once more shown in the excellent review of Junttila (1996). Some varieties have a strong apical dominance so that there are almost no branches or tillers (sunflower, maize), others have a strong inclination to tillering. The strongly tillering plants are much more flexible in their adaptation to planting density. The growth of the root system has a large effect on the ability of the plants to extract soil water and soil nutrients. The performance of simulation models is critically dependent upon the correct representation of the processes within the soil domain.

2.3 The long term processes (longer than one season)

Trees, grasses and other perennial plants are influenced in their growth habit by their life history and the conditions in the previous growing season. The modelling of the trans-seasonal effects is quite complicated and has to deal with bud formation in autumn, of

storage pools of assimilates and nutrients in stems, stolons, bulbs or roots. The processes of formation and breaking of dormancy are critical, but poorly understood (Kramer, 1996; Cumming and Burton, 1996).

It is not just the individual, also the complex structure of a forest as a whole will influence its functioning (Shugart, 1984; Prentice and Leemans, 1992; Pacala et al., 1995).

Beyond the life of the individual plant or tree, the ecosystem composition is strongly influenced by climate. Numerous studies appeared on this topic (Holdridge, 1947; Box, 1981; Woodward, 1987; Bugmann, 1996; Bugmann, 1997; Kienast, 1991; Prentice et al., 1992). Ecosystem change may exert a feedback on climate (Smith et al., 1992; Neilson, 1993). Prolonged climatic change will cause a genetic drift in the population of a single species, and a change in species composition of ecosystems as a whole (Jackson et al., 1990; Huntley et al., 1997). In forests, it may take hundreds of years before the species composition has adapted to the new climate (Bugmann, 1997).

Soil formation is a slow process, even on the time scale of ecosystems (Lal et al., 1995; Rounsevell and Loveland, 1994). Decomposition of plant litter (Cadish and Giller, 1997) is one of the main causes of soil formation. Elevated CO₂ may alter its rate, and with it the rate of nutrient cycling (Comins and McMurtie, 1993; Van Ginkel et al., 1996).

3. Prediction of long term responses

Borderlines of species distribution (Bonan and Sirois, 1992; Emanuel et al., 1985; Huntley et al., 1997) can be matched empirically to climatic borderlines, such as the forest-grassland boundary in Western Canada (Hogg, 1997). The borderlines of species distribution are the final result of the battle of competitive forces over a period of many years, but rare events of very short duration may still be decisive. A severe frost once in a lifetime may wipe out sensitive species that would otherwise have gained ground. This means that fast processes can be instrumental to understand a long term outcome. The prediction of such events, even if their character is known, is not a simple matter.

The matching of climatic boundaries and ecosystem boundaries may become different when the climate alters. In addition to a separate effect of climate change, elevated carbon dioxide can be expected to induce a reduction of the moisture requirement of forests, and thus cause a gradual increase of forests at the expense of grasslands. The world-wide increase of nitrogen cycling may have completely different and still unforeseen consequences.

For agro-ecosystems the effects of climate change are better understood. Modelling has been strongly developed for agricultural crops (Plentinger and Penning de Vries, 1996; Porter, 1993; Porter et al., 1995; Van Diepen et al., 1989; Van Keulen and Seligman, 1987; Van Laar et al., 1992; Goudriaan and Van Laar, 1994; Kartschall et al., 1996; Kartschall et al., 1995; Ingram, 1996; Matthews et al., 1995; Hunt and Pararajasingham, 1995; Kropff et al., 1994; McCown et al., 1996). The above mentioned processes for the different timescales are mostly included in the available models. Pests and diseases complicate the modelling of crop growth, and the prediction of the outcome of climate change (Goudriaan and Zadoks, 1995).

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