

CARBON PARTITIONING IN FORAGE CROPS

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ABSTRACT

The paper describes the conceptual models used to understand the processes determining plant growth rates in response to environmental changes. A series of experiments and growth models were used at three organizational levels: the specific plant organs, the whole plant and the plant canopy. The energy conversion efficiency and the total plant carbon balance were first examined. The carbon partitioning amongst the plant parts was then studied. The energy conversion efficiency is generally understood. In modelling carbon partitioning it was first necessary to establish the carbon demand for each plant organ. The carbon partitioned amongst plant organs was then calculated in two ways. The first one based on empirical data consisted in defining which organ received the carbon prior to other organs. The second one was based on the relationship between the carbon mass of specific organs and their trophic activity. This hypothesis allowed the optimization of the carbon partitioning in order to maximize the whole plant growth rate. The opportunities to use these theoretical approaches in plant growth modelling are discussed.

1. INTRODUCTION

At the station d'Ecophysiologie des Plantes Fourragères, in Lusignan, France, the objective of our work is to explain the variations in the production of forage species in relation to growth conditions (solar radiation, temperature, water availability, nitrogen availability, atmospheric level of CO₂). The forage plants involved are grown in dense canopies with one or several species in order to harvest the total aerial dry matter.

The plants are perennial and herbaceous. Species such as tall fescue, lucerne and white clover are used. From an agronomic point of view, the rate of growth (kg/drymatter/day/hectare) of these plants, which allows them to be harvested at different stages in their biological cycle, is important.

The evolution of the plants' nutritional qualities in the course of their growth should be taken into consideration because these plants are used for animal food. Specifically, we must determine how the chemical composition of the plants is affected by the environmental growth conditions.

The preceding comments provide the framework for the particular objectives of our work as well as the levels at which our analyses should be done. It is not only necessary to globally explain the growth of the aboveground parts, but it is also necessary to breakdown this compartment into subcompartments of homogeneous nutritional quality (for example, lucerne stems and leaves).

The time scales to be considered are the production season, the regrowth period and the day. The analysis of the processes requires that the hourly period be separated to that it can later be reintegrated for a twenty-four hour period.

The conditions of a dense canopy create a particular environment for each individual plant. We are seeking therefore the reactions of the individual plant to its environment. Afterwards we try to integrate these reactions into the plant population.

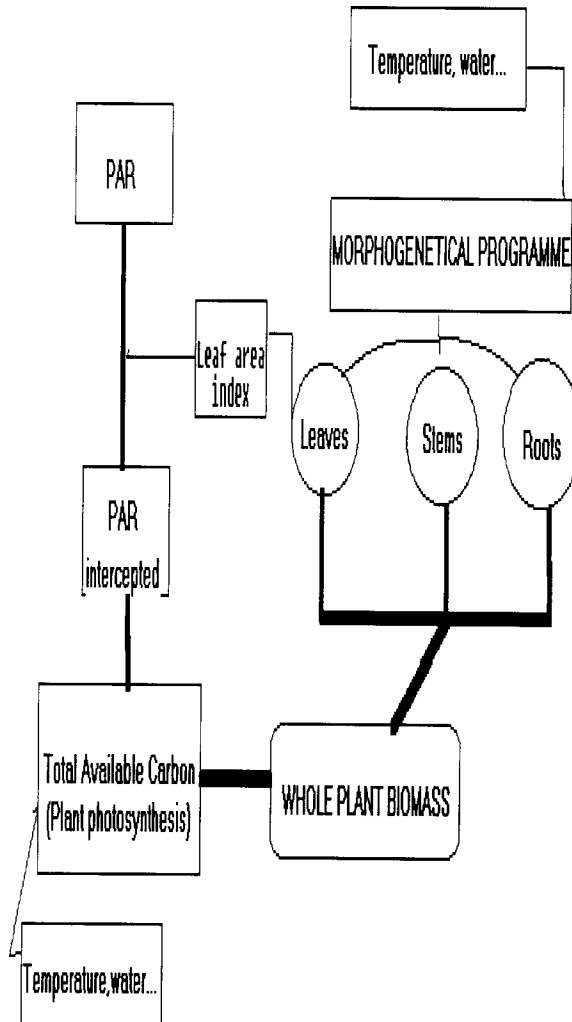


Fig. 1: Conceptual model of the growth of a forage plant such as lucerne, grass etc. showing the relationships between the environment and the plant carbon balance.

2. FUNCTIONING OF A CULTIVATED FORAGE CROP

The schema described in Figure 1 is linked to the idea of the global supply and demand of carbon per plant organ, which is similar to many growth models (Thornley, 1977). It is distinguished by the definition of demand that we have chosen and by the manner in which we think this demand is satisfied amongst the different plant parts. We have described the manner in which carbon is assimilated and partitioned. The functioning is divided into two non-independent groups. The first group described the carbon entering the plant or the carbon supply. The second group defines the carbon demand as the result of the plant's morphogenesis. It presents the manner in which each plant sees its demand satisfied (Gillet, 1980; Gillet *et al.*, 1984).

3. CARBON SUPPLY

The photosynthetically active radiation (PAR) is absorbed by the leaves. The quantity of energy captured depends on the extent of the leaf area, on its optical properties and on the orientation of the leaves in the canopy (Varlet-Grancher & Bonhomme, 1979). This aspect is relatively well known today. A good estimate of the proportion of the PAR incident absorbed during one day for a cultivated population can be obtained (Figure 2, (Durand, 1987)). This type of synthetic model can be tested by using more analytical models in order to study the sensitivity to various parameters (Varlet-Grancher & Bonhomme, 1979; Gosse *et al.*, 1982).

The instantaneous photosynthetic response of the foliar surface unit to the incident PAR ((Durand, 1987), Figure 3) is characterized in a simple way by a plateau (P_{\max}) and an initial slope (α). The carbon assimilation by the plant during the day is the sum of the activities of the surface units in space (Figure 4, (Durand, 1987)) and in time. The P_{\max} and α characteristics are dependent upon the light received by the leaf. In a canopy the lower leaves are shaded by the upper leaves which remain in full light. In a dense population, this brings about a vertical distribution in the light response curve (Figure 5, (Gosse *et al.*, 1982)). It is interesting to note that this distribution is strongly related to nitrogen partitioning in the plant, which is one of the variables considered. The concentration of nitrogen in the leaves per surface unit is then distributed on the vertical axis in the same way as P_{\max} (Figure 6, (Onillon, 1988)). The leaves at the lower level, always under low light, have a lower P_{\max} but the same slope α as the upper leaves. The integration in space gives a global result similar to the one obtained with the same response curve for all the levels of leaves (Figure 7).

The weakest response to high levels of lighting of the lower leaves is mostly due to the lower level of Rubisco activity which is the essential enzyme for photosynthesis. This is shown by the lowest nitrogen concentrations in these leaves. Everything occurs as if the nitrogen partitioning in a vertical direction and the needs in assimilation potential determined by the light are precisely adjusted (integration of two time scales). Furthermore, in lucerne, it is necessary to point out that when the leaves reach the lower levels, caused by the stem growth "at the top", eighty percent of the nitrogen lost by a leaf is recuperated by the rest of the plant (Onillon, 1988).

We believe that it is necessary to interpret these experimental data as the result of a nitrogen partitioning strategy in the photosynthetic apparatus with a view to optimizing

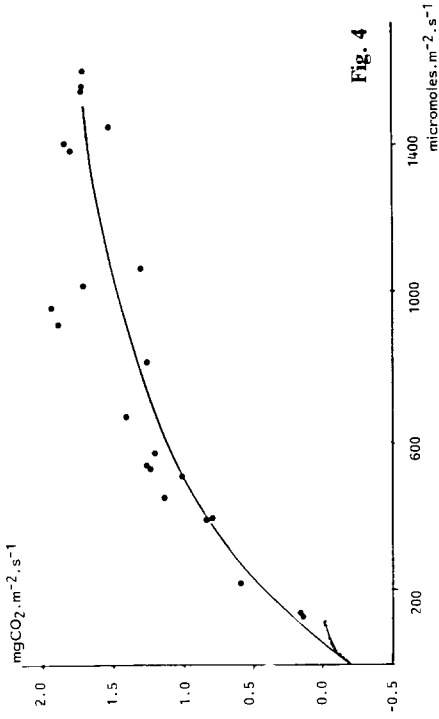


Fig. 4

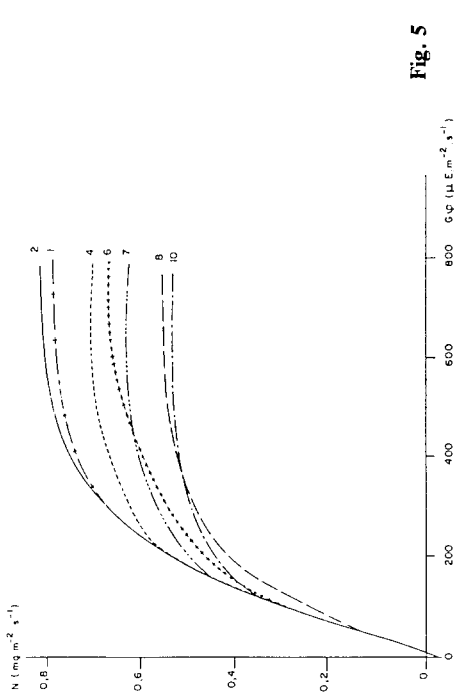


Fig. 5

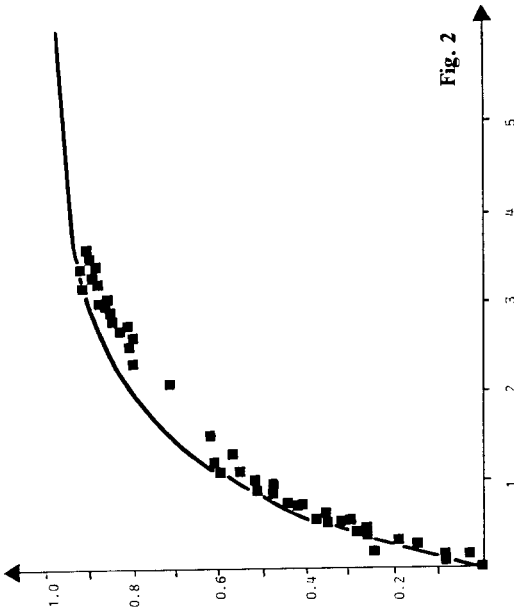


Fig. 2

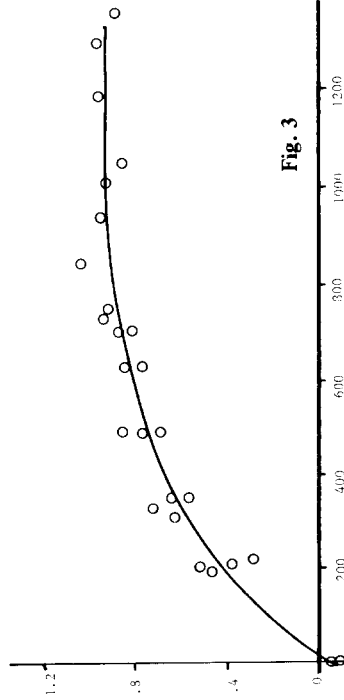


Fig. 3

Fig. 2: Efficiency of PAR interception (ratio of intercepted PAR upon incident PAR) by a lucerne crop as a function of the leaf area index (ratio of leaf surface upon soil surface). The curve is a model (Gosse *et al.*, 1982) and the symbols are measurements. (Durand, 1987).

Fig. 3: Net carbon dioxide exchange rate (in $\text{mg CO}_2.\text{m}^{-2}.\text{s}^{-1}$) in a lucerne leaflet as a function of the incident PAR (in $\mu\text{E}.\text{m}^{-2}.\text{s}^{-1}$) (Durand, 1987).

Fig. 4: Net instantaneous carbon exchange rate of a lucerne canopy as a function of the intercepted PAR for two values of the leaf area index (Durand, 1987).

Fig. 5: Net carbon exchange rates in leaves at different heights on the stem of a lucerne plant as a function of the incident PAR (Gosse *et al.*, 1982).

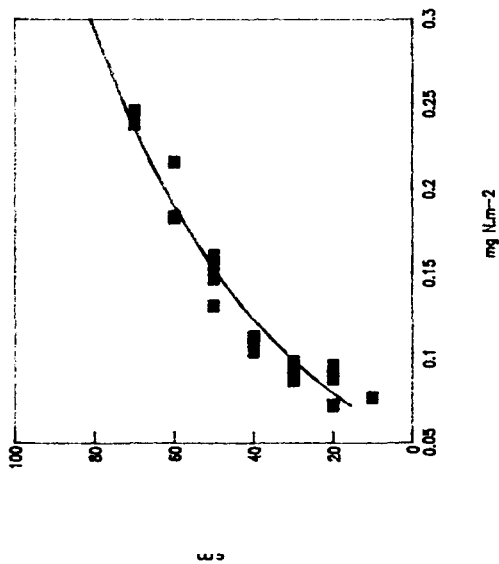
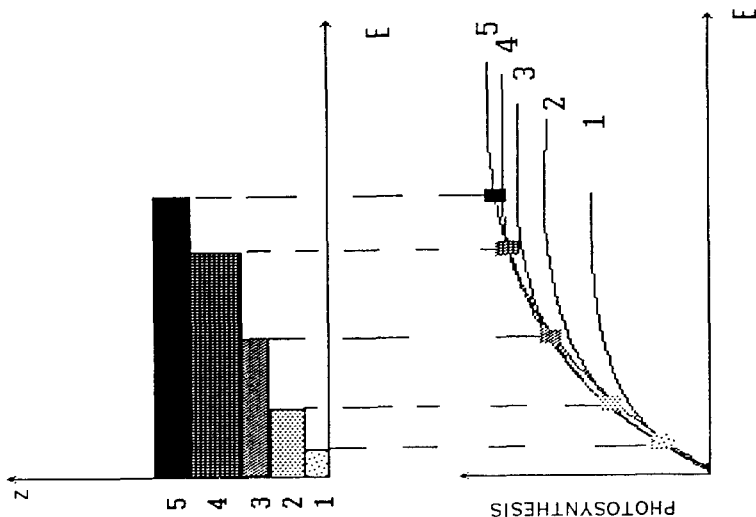


Fig. 6: Concentration of nitrogen (mg.m^{-2}) in leaves from lucerne plants growing in a dense canopy as a function of the leaf vertical position (cm height). Redrawn from data in Onillon (1988).

Fig. 7: Schematic representation of the effect of combined distributions of light (E) and P_{max} within the dense canopy of a lucerne crop on the net carbon exchange rate at each level (Z).

its functioning (Field, 1987).

With regards to the Rubisco enzyme, whose upkeep and construction results in high energy costs, one could conceive that the constraint was sufficient to determine a selection pressure. This does not tell us anything concerning the biochemical mechanisms by which the adjustment is made; but it does indicate the reasons that such mechanisms have been retained during the evolution. We think that we have not yet sufficiently developed this interpretation with a view to modelling plant growth.

4. CARBON DEMAND

Parallel to the carbon assimilation process is the growth of the different plant parts which develop according to a morphogenetic programme (Gillet *et al.*, 1984). We define morphogenesis as the dynamic acquisition of the plant form. This process is the result of the interaction between the genetic determinants and the surrounding environment. At any particular stage, one meristem is programmed to produce a particular series of organs, such as a leaf and an internode. The growth conditions (temperature, plant water status, plant nitrogen level, spectrum of solar radiation) determine the rate at which the programme can be realized. One obtains, therefore, an immaterial image of the place the plant would occupy in space. Note that it is relatively simple to measure the instantaneous morphogenesis with the help of displacement transducers; but the differences in aerial dry matter involved at the same time scale are still largely beyond reach.

The development of the plant parts requires carbon material. We are presently trying to estimate the quantity of carbon necessary for the synthesis of one mm³ of a leaf, a stem, and a root. This includes the carbon contained in a completed plant organ and the carbon utilized by the respiration during the synthesis of the structures.

It has recently become evident (Vertregt & Penning de Vries, 1987) that the energy costs of the synthesis of the plant organ were strictly connected to the level of carbon (Figure 8). This confines, therefore, the question of the estimate of the total cost of the plant organ growth to the study of the differences in dry matter densities observed and the carbon content in the dry matter.

There are few results in this area. Figure 9 gives an example of the differences in the density of the lucerne stems having been harvested from experimental plots with two levels of water supply. The differences with size and time are slight (100 ± 10 mg/cm³). Drought tends to increase the density. The analyses of carbon content of these samples are still to be completed.

Thus, we have a dynamic definition of carbon demand. We could express it in mg of carbon per mm³ of plant organ and per growth day for each plant part. It is also known what has entered the plant due to photosynthesis; thus it is possible to compare the costs of the effective realization of the whole potential programme and the supply of carbon evaluated using the photosynthesis model.

On the one hand, one possesses a description of the morphogenesis in terms of size and space utilization. In order to translate this volume growth into mass growth and thus into carbon costs, one must acquire an estimate of the dry matter density. On the other hand one knows the quantity of carbon available due to the measurement of photosynthesis. If the necessary carbon quantity is equal to the supply, the volume is effectively filled.

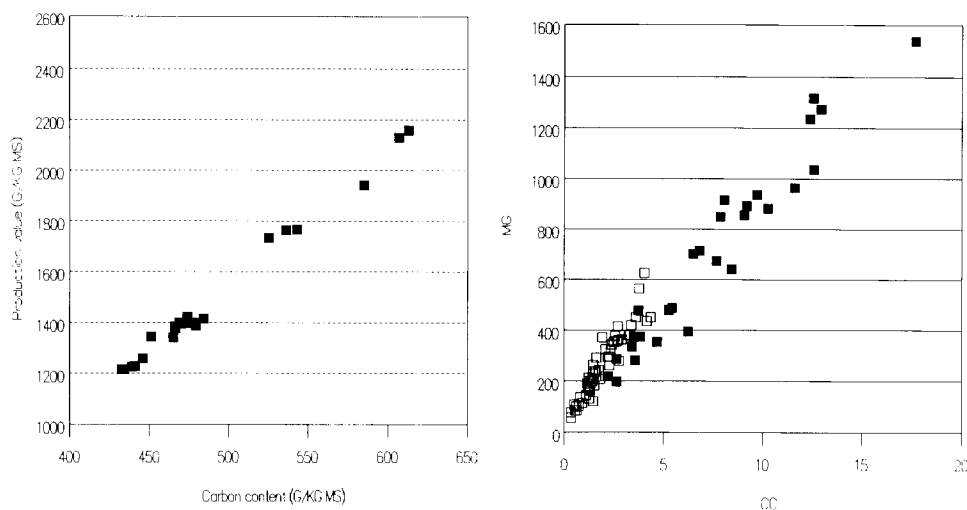


Fig.8 : Total carbon costs of the tissue production (expressed in mg of glucose equivalents) as a function of carbon content of the tissue dry matter (Vertregt and Penning de Vries, 1987).

Fig.9 : Stem dry matter as a function of stem volume in a lucerne canopy for dry (open symbols) and well watered (closed symbols) crops. The slope provides an estimation of the mean stem density (Durand unpublished data).

Otherwise only a fraction is realized, the carbon becoming the limiting factor of morphogenesis.

Note that until now, this type of approach has already been done by considering the carbon demand per surface unit (Volenc & Nelson, 1984). We are obligated to consider the volumes in order to really separate that which is attributed to morphogenesis and that which is attributed to the materialization of these volumes.

5. CARBON PARTITIONING: PRIORITY PLANT ORGANS

If we have a method of calculating the carbon demand (morphogenesis \times carbon mass/plant organ volume), we are unable to infer the actual growth unless the supply is equal to this demand. In numerous cases, we are far from this; the demand is superior (negative carbon balance, senescence) or inferior (role of the plant reserves). It is necessary, then, to have rules which make the calculation of carbon partitioning possible. Numerous models can provide a solution to this question.

We have retained two possibilities regarding carbon partitioning. Firstly, the carbon is divided up according to a pre-established hierarchy, but the rules cannot be revealed except by experimentation (the manipulation of the supply and the demand as independently as possible). Secondly, the carbon is divided up according to a known adaptive strategy.

We have begun to work with the former which allows us to use a simple crop model on the one hand, and offers an analytical framework on the other hand. The limitations of this approach favour the use of the latter for work we want to conduct in the future.

5.1. Hierarchic partitioning (Figure 10)

The idea of a hierarchy between plant organs is a result of the observation of experimental results concerning the partitioning of the dry matter between different plant organs. All of the plant components do not have access to the whole carbon supply as easily as some of the others. When growth is affected by a limiting condition (drought, insufficient nitrogen or water supply), it is noted that certain plant parts are more sensitive than others. Likewise, when the carbon becomes limiting (defoliation, shade), the partitioning is changed in favour of the photosynthetic organs.

With lucerne, we were able to establish a hierarchy between the maintenance of the actual biomass and the growth of new leaves, new stems and new roots which decrease in priority. Similarly, in perennial grasses, the growth of the root parts ceased after defoliation. The carbon partitioning in such a system is carried out simply by satisfying the demand of each type of organ in a sequential manner, by order of priority.

It is clear that this approach has its limitations. To begin with, it is impossible that the partitioning is always done this way (the growth of roots being necessary for the growth of leaves). The argument born from the observation of the different partitioning (*i.e. a posteriori*) may be criticized when it becomes a question of determining a hierarchy *a priori*.

To attempt to understand the manner in which these hierarchies are activated, it was necessary to analyze the manner in which the environmental variables were perceived by the plant. Through bibliographical references and with the help of adapted experiments we realized that it was not the variations in the carbon flow that were perceived but the correlated variables. For example, shade reduces the quantity of fixed assimilates but also modifies the spectral composition of light which changes the morphogenesis and

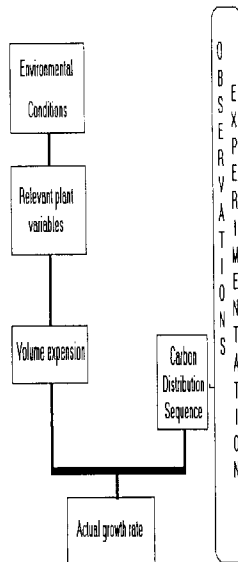


Fig. 10: Conceptual schema of rules of carbon partitioning in a predefined hierarchical manner.

consequently the carbon partitioning. The plant receptor is the phytochrom which directs the morphogenesis. It is important to note that the phytochrom does this before any significant change in the plant carbon balance. The case of regulating the water flux through the plant is analogous. In numerous cases, we find an anticipated process for growth limiting conditions (Piaget, 1967).

5.2. Adaptive strategies (Figure 11)

We return, henceforth, to the schema in which the functioning of the plant is depicted as a system (robot) possessing the ability to acquire a partial knowledge of its environment: to translate it on a physiological level and to direct the carbon partitioning in relation to this information and predefined objectives. It is by virtue of this that the notions of supply and demand have introduced those of investment and savings. The study of examples allows us to show the interest of these steps.

When the incident radiation on most of the leaves of a fescue plant diminishes due to self-shading, the plant no longer produces new leaves (it no longer invests in new leaves), but rather promotes the extension of existing leaves. This type of behaviour allows the individual plant to better resist the extended shade than those plant genotypes which multiply their leaves and which in a meadow population are in the shade and end up by presenting a negative carbon balance. The most recent results obtained by one member of our group on a large range of meadow species confirm this theory (Varlet-Grancher, unpublished data).

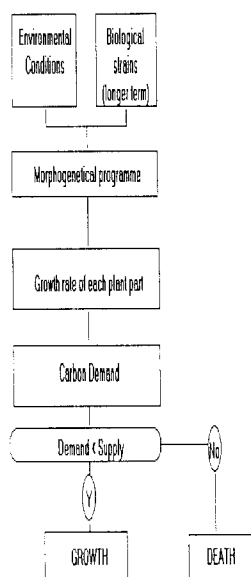


Fig. 11: Conceptual model based on the interaction between the plant morphogenesis (viewed as a way of anticipating climatic changes) and the environmental signals affecting plant growth.

When a dense lucerne population (closed canopy) is irrigated and is supplied with appropriate fertilization, one observes that a number of individual plants die and that a stable population is only reached when the density is such that the plants are isolated from one another. In the preceding situation, the demand of the aerial plant parts is first satisfied (investment) which brings about an incomplete reconstitution of root reserves (saving) and causes the plant to be weak during the period following defoliation. The plant dominated in such a manner presents a negative carbon balance. Everything occurs as if the plant, which is grown far from the environmental conditions where the species originated (area where density of tall plants is low for lucerne), present a rigid behaviour and in this case is not adapted to perennality in a dense canopy. The mechanism which is in place when a plant grows in isolation and has an abundant seed production becomes dangerous if the plant is grown in a competitive situation when the reproductive phase is made impossible. The latter is due, in this case, to the harvest which precedes the fructification.

The idea of investment contains the notion of risk and suits this type of situation. A white clover plant with similar carbon levels can increase the size of the limbs, the petioles or the internodes creeping on the soil surface. Shading of individual plants either naturally or artificially created, stimulates the extension of the existing organs while inhibiting the formation of new plant parts. This corresponds to an exploration strategy in a single direction until a lit area is encountered. Here again, the cost of the axis extension is not profitable unless the apex reaches a lit zone which is highly probable in the geographical zone where the species has evolved.

Note that the correlation between different signals is sometimes strong enough so that the plant can react to a signal in order to react to another environmental variable. For example, the plant responses to photoperiod are undoubtedly a way of anticipating temperature changes. In an analogous manner, the interruption of the leaf extension process, even when irrigated during the summer, in certain dormant varieties of tall fescue, reduces the evaporative surface of the plant and therefore anticipates the climatic water demand generally superior to the soil water availability at this time. In order to increase the merit of this approach to carbon partitioning, we must overcome two difficulties. On the one hand, there is a danger of assigning *a priori* an adaptive role to one aspect of the plant physiology. We do not know all the signals perceived by the species that we study. It is therefore possible that we are misled by assigning the objectives to a particular type of functioning which is in reality neutral or evinces previous conditions (fossil growth habits). Similarly, such functioning unexplainable today in adaptive terms will perhaps become explicable if we find an unknown plant ability to respond to a signal.

On the other hand, it is necessary to formalize the whole process of carbon assimilation and partitioning within the plant using an adaptive strategy. This formalization has yet to be done. In order to do this, it is necessary to define the objectives relevant to the plant, such as space utilization, sexual reproduction and perennality. It may eventually be necessary to combine different objectives.

It is also necessary to translate these objectives into physiological functions which implies an understanding of the relationship between the size of a plant part and its particular functioning. This has been widely accomplished for the leaves and carbon assimilation. It has not been done for roots and nitrogen supply.

Finally, we must establish the responses of morphogenesis to relevant variables.

6. INTEGRATION OF ORGANIZATION LEVELS

This type of conceptual model allows the researcher to integrate acquired knowledge at different organization levels. It is not always necessary to know the physiological mechanisms (molecular, cellular) of the plant which are the translation of the perceived physical signals. Thus, even if the reaction of the leaf extension to drought goes through Abscissic Acid metabolism, it can be sufficient, at a certain scale to know the objectives of the regulation (optimizing the water losses in relation to carbon gains). If it is a question of improving plant responses to environmental changes, it is actually the mechanism that needs to be modified.

Inversely, all mechanisms at the molecular level are perhaps not subject to the adaptation to the various climatic ranges that we encounter. Thus, the flow rate within the phloem is not likely variable compared to the kinetics of the loading and unloading (Passioura, 1977). Similarly, the variations of the *in vitro* activity of the Rubisco are without doubt largely utilized within the plant canopy in natural conditions precisely to adapt the activity to the available solar energy at each level. If we want to increase the efficiency of solar conversion, we now know that it is not solely a question of obtaining a more efficient Rubisco, but also of ascertaining that the partitioning of this molecule is optimized by the plant.

7. CONCLUSION

We attempt to use the integration of different biological levels of organization in forage plants. Models are a privileged way of realizing this. We have progressed unequally. We estimate that we should soon be able to transform the plant functioning schema into a growth model, by considering the plant not out of time but situated in the unfolding of environmental events to which the plant responds in the expectation of the continuation of the development of its morphogenetic programme.

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