Modeling agroecosystem dynamics with the metabolic pool approach

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The design of sound and sustainable management strategies requires a thorough understanding of the whole crop production system concerned. Simulation models have proved to be powerful tools to combine experimental results from various research fields and to gain insight into complex quantitive relationships. In this paper a modeling approach is discussed which describes multiple population interactions based on the flow of resources within and between trophic levels. Emphasizing the analogies, resource acquisition on any trophic level is quantified with the same functional response model. Likewise resource allocation on any trophic level follows an analogous pattern attaching decreasing priority to respiration, reproduction and growth. Furthermore, a simple expansion of the model allows to incorporate resource competition between populations on the same tropic level. A distributed delay model provides the mathematical framework to account for population development under the influence of abiotic and biotic factors of the ecosystem. Due to its simple and lucid structure, this model approach has been widely accepted in applied ecology and has contributed to an improved understanding of quantitive relationships in agroecosystems.

INTRODUCTION

Agroecosystems are managed ecosystems maintained in man-intended artificial structures (BELLMANN *et al.,* 1986). Making use of various management techniques, farmers aim to create a favorable environment for their crops and to enhance yield, i. e., to force the system into a state more profitable for man.

From a human perspective insect pests, pathogens and weeds are disturbing elements in an agroecosystem because they hamper optimal development of the crop by damaging the cultivated plants either directly or indirectly. In order to suppress the undesired competitors, a wide variety of control measures have been devised. Originally more ecologically oriented, pest control shifted to a chemical discipline with the synthesis of the first organic pesticides (HUFFAKER & SMITH, 1980). Blinded by the initial success, researchers and farmers began to focus entirely on the chemical control of individual pests, disregarding the side-effects of pesticides on natural enemies and other elements of the agroecosystems (BAUMGÄRTNER & GUTIERREZ, 1989). The unilateral reliance on synthetic pesticides and their frequent application, however, led to resistance, pest resurgence and outbreaks of secondary pests (FLINT & VAN DEN BOSCH, 1981). It became obvious that a thorough understanding of the economic and ecological aspects of the whole production system is an essential prerequisite for sound pest management strategies (DELUCCHI, 1987). The diversity and complexity of the entire agroecosystem has to be taken into account to tackle pest problems with a holistic systems oriented approach (HUFFAKER & CROFT, 1976). Moreover, emphasis has

to be given to ecological relationships rather than to organisms (GILBERT *et al.*, 1976).

Simulation models were found to be powerful tools for integrating experimental results and to provide insight into complex quantitative relationships between the various elements of agroecosystems (BAUMGÄRTNER & DELUCCHI, 1981; GETZ & GUTIERREZ, 1982; RABBINGE & BASTIAANS, 1989). They enhance our understanding of multispecies interactions and provide essential information on the systems response to changes in the environment and management inputs.

Numerous modeling approaches have been suggested in the literature over the past 25 years, all reflecting the objectives, the training and the subjective preferences of the researchers. In this paper we focus on the demographic metabolic pool model which emphasizes the relevant population interactions driving the dynamics of multitrophic systems (BAUMGÄRTNER & GUTIERREZ, 1989). Historically, the simulation of population interactions was restricted to functional and numerical responses of natural enemies to prey or host densities (BEDDINGTON *et al.*, 1976; HASSELL *et al.*, 1976). The approach reviewed here, however, has been generalized to be valid for interactions between all trophic levels, for numbers as well as for resource units. Furthermore, the model has been expanded to include not only resource acquisition between trophic levels but also competition for resources within trophic levels. As the focus here is on general principles, mathematical details will be omitted.

GENERAL APPROACH

Extensive modeling efforts have recently been made in order to study the dynamic interactions between a crop and its associated pest complex including insects, pathogens and weeds (GUTSCHE *et al.*, 1986; ROSSBERG *et al.*, 1986a, b; ENTWISTLE & DIXON, 1987; RABBINGE & BASTIAANS, 1989; ROSSING *et al.*, 1989; SPITTERS, C. J. T., 1989). The approaches chosen range from multiple regression equations to linked explanatory population models and therefore vary notably in analytical depth. Although these models proved their validity under specific conditions, most of them lack the complexity of real plant-pest interactions. Pest damage is described as a unilateral effect on the crop and the feedback of the host-plant on pest populations are crudely generalized, or not taken into account at all. Crop physiology is modeled in detail, while less emphasis is given to pest population dynamics and even less to natural enemies.

GUTIERREZ *et al.* (1984 and 1987) suggested a modeling approach which surmounts these shortcomings by accounting for bilateral relationships (i.e. interactions in the proper sense) between populations on different trophic levels and by paying equal attention to different populations in an ecosystem. It is based on the flow of resources such as energy, or equivalents in carbohydrates, water and mineral nutrients. GRAF *et al.* (1990b) further expanded this approach to explicitly account for interactions between populations on the same trophic level. A time distributed delay model (MANETSCH, 1976; VANSICKLE, 1977) provides the mathematical framework to describe the temporal dynamics of interacting populations. As the model makes use of the analogies in resource acquisition and allocation on different trophic levels it has a simple and lucid structure and still allows a realistic simulation of complex multitrophic systems. In the following, the basic components, that is resource acquisition, allocation, competition and ageing shall be discussed in detail. Additional features like compensation or preference

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can easily be built into the model. A description, however, would be beyond the scope of this paper.

Interactions between populations on different trophic levels: Resource acquisition and allocation

For survival, growth and reproduction any population in an ecosystem depends on resources from a lower trophic level which generates a dynamic flow of energy and material from an original source to the end of the food chain (Fig. 1).
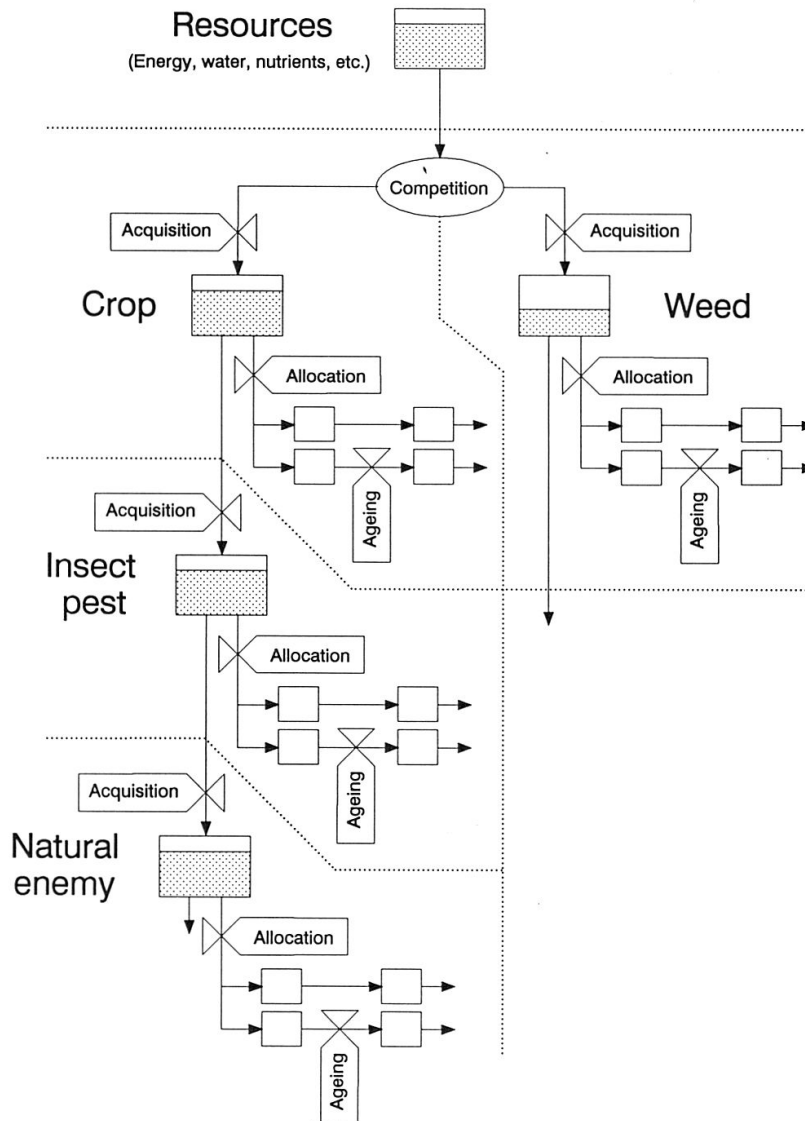
Fig. 1: Flow of resources within and between trophic levels of a model agroecosystem.

The sun, the atmosphere and the soil represent the original sources providing a crop and competing weeds (first trophic level) with solar energy, CO_2, water and mineral nutrients. The plants supply the resources for herbivores (second trophic level), which for their part represent the resource pool for natural enemies (third trophic level). Pointing out the analogies of processes GUTIERREZ *et al.* (1987)

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considered resource acquisition on any trophic level (plants, herbivores and predators) as a predation process and generalized the Frazer-Gilbert functional response model (FRAZER & GILBERT, 1976) to quantify the flow of resources between trophic levels. The instantaneous form of this model is given in eqn. 1 as presented in GUTIERREZ et al. (1981).

$$A_i = f(r_{i-1}, d_i, s_i) = d_i \cdot \{1 - e^{-(s_i \cdot r_{i-1}/d_i)}\} \qquad [1]$$

The resource acquisition rate (A_i) on trophic level i is a function of the available resources (r_{i-1}) on the next lower level, the demand for resources (d_i) on level i and the ability of the population on level i to access the resources on level $i-1$ (s_i). Since eqn. 1 is demand and supply driven, it explicitly accounts for the interaction between trophic levels. Note that in practice two different forms of the model are applied: Resource acquisition is quantified based on the instantaneous form (eqn. 1) if resources remain constant, and the overall form (integral of eqn. 1; ROYAMA, 1971; GUTIERREZ et al., 1981; KLAY, 1987) if resources are reduced by acquisition. Solar radiation is obviously not affected by photosynthesis (A_i), which is therefore described with the instantaneous form. Here r_{i-1} stands for photosynthetically active solar radiation expressed in carbohydrate equivalents, d_i for the plant's demand for carbohydrates and s_i for light interception. As soil nitrogen is limited, potential N uptake (A_i) is quantified with the overall form, r_{i-1} standing for the soil nitrogen pool, d_i for the plant's demand for nitrogen and s_i for the proportion of nitrogen accessed in the root zone. Herbivory (A_i) is also modeled with the overall form and depends on the amount of carbohydrates or nitrogen available in attacked plant subunits (r_{i-1}), the herbivores demand for carbohydrates or nitrogen (d_i) and its ability to find the two resources (s_i). Finally predation (A_i) is a function of resources in the host population (r_{i-1}), the predators demand for resources (d_i) and the search rate (s_i).

In order to simulate gains and losses of resources on any trophic level the corresponding three variables r_{i-1}, d_i and s_i have to be estimated continuously. The quantity of available resources (r_{i-1}) is either an input from a weather data file (i.e. solar radiation) or a soil model (i.e. mineral nutrients), or it is determined by a population model on a lower trophic level (i.e. carbohydrates, nitrogen). The demand for resources (d_i) is assessed from the population and age specific potential respiration, reproduction and growth rates. The ability to access resources (s_i) is based on population characteristics and can be quantified with eqn. 2 (GUTIERREZ et al., 1987).

$$s_i = 1 - e^{-\alpha_i \cdot M_i} \qquad [2]$$

For a plant (first trophic level) s_i has to be estimated on the one hand for photosynthesis and on the other hand for nitrogen uptake. In the first case M_i and α_i stand for the leaf area index (LAI) and the light extinction coefficient, respectively. By this means eqn. 2 becomes the compliment of Beer's law, an equation suggested by MONSI & SAEKI (1953) to describe canopy light interception (s_i). In the latter case M_i means the relative root volume and α_i the nitrogen absorption coefficient. On the second trophic level M_i denotes the relative mass of herbivores and α_i the coefficient for host-plant acceptance. For a predator population eqn. 2 quantifies the prey capture rates, M_i being the relative predator mass and α_i the prey capture coefficient.

Resource acquisition is followed by allocation on the population level (Fig. 1 and Fig. 2). Resources are either used for respiration, for growth of population
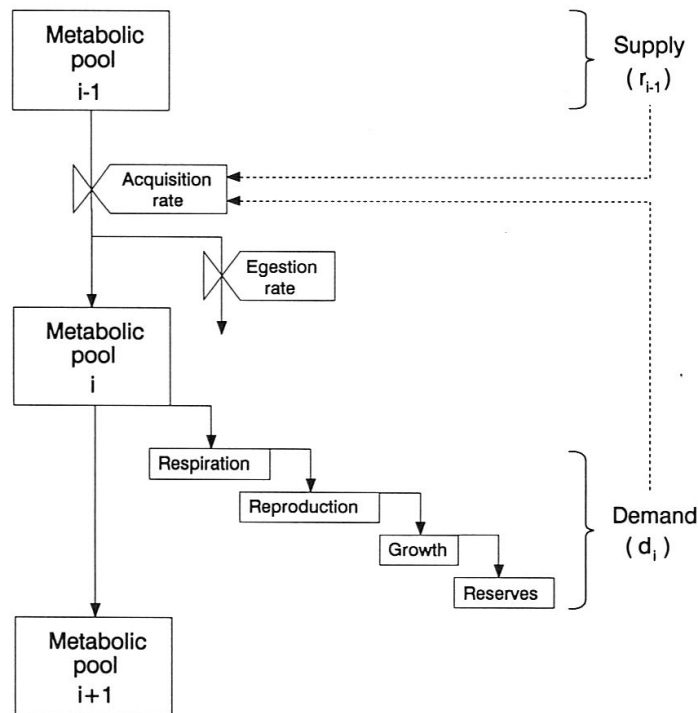
Fig. 2: Metabolic pool and allocation scheme at the population level.

subunits (e.g. plant parts) or for reproduction. JONES *et al.* (1974), GUTIERREZ *et al.* (1975) and GUTIERREZ & WANG (1976) modified the metabolic pool model proposed by PETRUSEWICZ & MAC FADYEN (1970) to describe resource assimilation in plants and later in insects (GUTIERREZ *et al.*, 1981). A population is considered as a metabolic pool which is fed by resource uptake (Fig. 2). In some populations on higher trophic levels a part of the resources taken up are lost due to egestion. The remaining part is available with decreasing priority for respiration, reproduction, growth and the accumulation of reserves. The priority scheme determines the reaction of an organism or a population to reduced resource supply, i.e. to stress. With increasing scarcity an organism will first stop reserve accumulation, then vegetative growth, then cease reproduction and finally die when respiration costs cannot be covered any more.

Obviously resource uptake on any trophic level causes resource losses on the next lower trophic level (Fig. 2). Herbivores develop at the expense of plant growth, and predators hamper the prey population build-up. It has been shown in eqn. 1 that resource acquisition is driven by supply (r_{i-1}) and demand (d_i). With increasing demand for resources on trophic level i, the losses in the source population on level $i-1$ become more severe. However, if the source population on level $i-1$ is stressed, resources for a population on trophic level i become scarce which will affect populations on level $i+1$. By this means relationships between populations on different trophic levels are modeled as dynamic interactions.

Interactions between populations on the same trophic level: Competition

In a real agroecosystem a trophic level usually contains several populations competing with each other for resources from the same limited source. Weeds are competing with a crop for light, mineral nutrients and water (Fig. 1), and herbi-

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vores are competing for resources in common host-plants. Much of the current theory on competition is derived from analytical models from the Gause-Lotka-Volterra type (GETZ, 1984), or from models based on replacement experiments (DE WIT, 1960; HARPER, 1977; FIRBANK & WATKINSON, 1985). GRAF *et al.* (1990b) suggested a model expansion which allows the simulation of competitive interactions using the metabolic pool approach. Competition undoubtedly affects resource acquisition (eqn. 1) of the populations concerned ($A_{i,n}$: note, that we introduced a second subscript n denoting the population on level i). Though the demand $(d_{i,n})$ does not change, available resources (r_{i-1}) might become scarce as several populations tap the same pool. Furthermore the ability of each population to access resources $(s_{i,n})$ might be reduced due to mutual interference of the competitors.

In general the exploitation of resources on a trophic level comprising more than one population is enhanced i.e. the overall ability to access resources (s_i) increases. Solar radiation, for example, is more efficiently used if several plant populations grow on the same surface. The same is true for herbivores exploiting plant tissue or natural enemies searching herbivores. For a trophic level i with m competing populations eqn. 2 has been generalized by GRAF *et al.* (1990b) to account for this fact.

$$s_i = 1 - e^{-\sum_{n=1}^{m} (\alpha_{i,n} \cdot M_{i,n})} \qquad [3]$$

Here $\alpha_{i,n}$ and $M_{i,n}$ correspond to the parameters α_i and M_i of population n (for explanation see above) and are measures of the competitive strength of the population. The relative magnitude of $\alpha_{i,n}$ and $M_{i,n}$ obviously determines the competitive advantage, and the proportion of resources accessed by population n is therefore quantified as:

$$s_{i,n} = s_i \cdot \frac{\alpha_{i,n} \cdot M_{i,n}}{\sum_{n=1}^{m} (\alpha_{i,n} \cdot M_{i,n})} \qquad [4]$$

As $\alpha_{i,n}$ and $M_{i,n}$ are always positive numbers and eqn. 3 is a monotone increasing function with a monotone decreasing derivative (≤ 1), the ability to access resources $(s_{i,n})$ is smaller for populations suffering competition ($m > 1$) than for populations which do not have to share the resources ($m = 1$). The effect of competition is intensified with decreasing relative vigor $(\alpha_{i,n} \cdot M_{i,n})$ of the population concerned and with increasing vigor of the competitors.

Since the spatial distribution of populations and their resources have a significant influence on competition, the model habitat needs to be stratified in some cases. SPITTERS & AERTS (1983) divided the canopy formed by a crop and associated weeds into horizontal layers to account for differences in the leaf area distribution. A similar approach was used by GRAF *et al.* (1990b) to quantify the share of incident light intercepted by competing plant species. Fig. 3 illustrates the importance of plant height and vertical leaf area distribution for light competition in a crop-weed association. The tallest plant expands a part of its leaf area above the top of the next lower competitor (layer 1) which allows it to intercept part of the incident solar radiation without having to share it. In the second layer
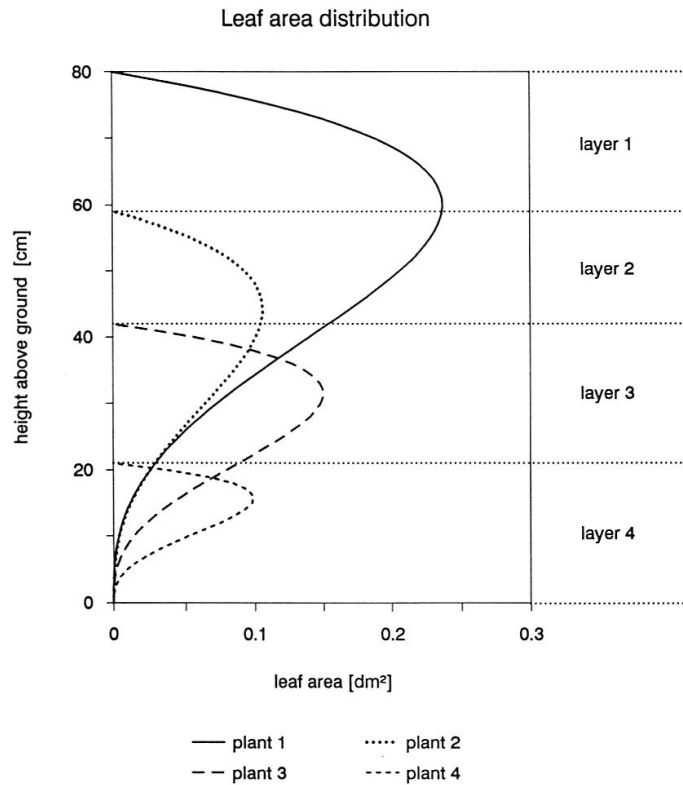
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Leaf area distribution

Fig. 3: Vertical leaf area distribution in a model plant association.

two species compete for the light penetrating the first layer, the share for each being relative to the respective leaf area in that layer. Three competing species have to be considered in the third layer, and so forth down to the canopy ground. The proportion of light intercepted by each competitor can be determined by applying eqns. 3 and 4 for all layers.

Similar approaches might be used for water and nutrient competition between plants or on any other trophic level where spatial distributions have to be taken into account.

Temporal dynamics: Ageing and population development

Once allocated to population subunits, resources are subject to ageing (Fig. 1). MANETSCH (1976) suggested a distributed delay model based on the Erlang density function to simulate ageing of a cohort with a given variance around the mean development time. A version of this model, modified by VANSICKLE (1977) to include attrition, has been widely used to describe the process of ageing, growth, mortality and migration of populations and their subunits. SEVERINI *et al.* (1990) reviewing the internal structure of the model emphasized the analogy of plant and insect development and the compatibility of this approach with demographic theory. Fig. 4 depicts a simple graphic representation of the mechanisms of the model. The ratio between the square of the development time and the variance defines the number *(K)* of age classes needed to account for the observed variability of individual development times. The amount of resources invested in reproduction determines the birth rates, an input into the first age class. Resources used for growth flow into all different age classes according to the age specific
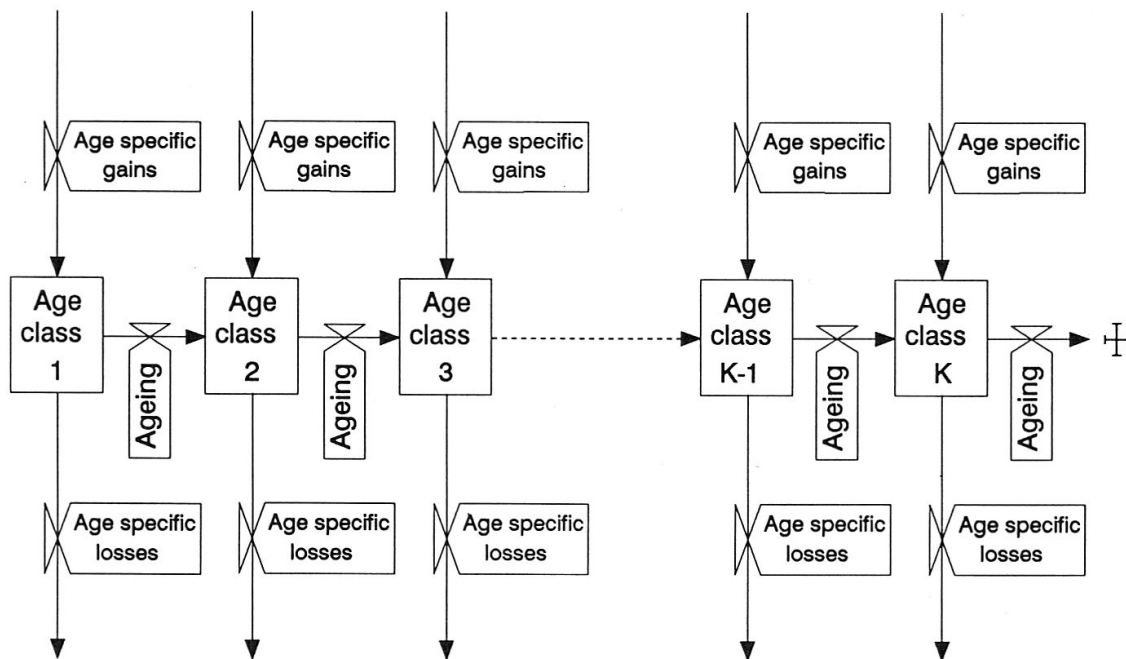
Fig. 4: Simplified graphical representation of a distributed delay model applied to plant or insect populations.

demand. The transition rate from one age class to the next generally depends on the time step of the simulation and determines the pace of the ageing process. In particular cases ageing can also be influenced by resource availability (GUTIER-REZ *et al.*, 1981). Entities leaving the last age class account for old age mortality. Immigration, emigration and age specific mortality can be applied to any age class as gains and losses respectively. The model allows the establishment of the age structure of any population at any point in time by a simple balance of input and output in all the age classes.

MODEL APPLICATIONS

The principles of the demographic metabolic pool approach have found wide acceptance in applied ecology and have constantly been expanded and re-finded over the past 15 years. No attempt is made here to review the whole literature dealing with this subject. We will refer to investigations relevant to our own work. Originally used for modeling growth and development of cotton (JONES *et al.*, 1974; MC KINION *et al.*, 1974; GUTIERREZ *et al.*, 1975; GUTIERREZ & WANG, 1976; WANG *et al.*, 1977) the approach has been further applied in crops such as apple (BAUMGÄRTNER *et al.*, 1984), bean, tomato, cassava (GUTIERREZ *et al.*, 1987 and 1988a), peas (ROTH, 1989), rice (GRAF *et al.*, 1990a) and grapevine(GUTIER-REZ *et al.*, 1985; WERMELINGER *et al.*, 1990). All these models have been parametrized and validated with extensive field data and have proved to be useful tools to explain yield formation and phenology of the crops concerned. While the older models simply emphasized carbon assimilation and allocation, more recent models also include nitrogen dynamics (GUTIERREZ *et al.*, 1988a; GRAF *et al.*, 1990b; WERMELINGER *et al.*, 1990) to account for the effects of nitrogen on crop growth and on pest populations.

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Metabolic pool models of crops and herbivores or diseases have been linked (GUTIERREZ & WANG, 1976; GUTIERREZ *et al.*, 1983, 1984 and 1988b, c; ROTH, 1989) to study pest-plant interactions. The improved understanding of the dynamics of herbivore damage enabled the researchers to check the pest status and to revise economic thresholds previously established on an empirical base (GUTIERREZ *et al.*, 1979).

The metabolic pool approach has also been used to describe predator-prey and parasitoid-host systems (e. g. GUTIERREZ *et al.*, 1981 and 1988b; BAUMGÄRT-NER *et al.*, 1987; KLAY, 1987; GENINI, 1987). These models have been developed with the objective of quantifying the effects of predation on herbivore populations and of evaluating the potential of biological pest control.

Crop-weed interactions have been studied with an expanded metabolic pool model which accounts for resource competition between populations on the same trophic level (GRAF *et al.*, 1990b). The model describing the effects of light and nitrogen competition on rice growth and development permitted the description of the relationship between weed density and yield losses. By means of simulation, periods of strongest impact of weed competition have been identified which has facilitated the optimization of weeding strategies.

In a further step towards better insight into multitrophic agroecosystems, GUTIERREZ *et al.* (1988b) investigated the cassava ecosystem in Africa with a metabolic pool model which includes carbon, water and nitrogen dynamics and interactions between the crop, pests, predators and parasites. With this work the authors made a major contribution to the optimization of the Africa-wide Biological Control Programme (HERREN *et al.*, 1987) and helped explain the success of the introduction of exotic natural enemies.

CONCLUSIONS

The metabolic pool model has proved to be a powerful tool in agroecosystems analysis, surmounting some of the short-comings of other modeling approaches. As it respects the analogies of resource acquisition, allocation and competition on different trophic levels, it has a relatively simple and transparent structure. Due to its simplicity it is able to handle the overall population dynamics of multitrophic systems in a realistic way, without exceeding a manageable size.

Interactions between populations on the same or on different trophic levels are considered by resource competition and acquisition respectively. Resource uptake on any trophic level implies losses on the next lower level. Since acquisition is driven by supply and demand, it changes with the size of the source (e. g. plant, herbivore) as well as with the size of the sink (e.g. herbivore, predator). If the demand is not covered by the supply, a population gets stressed, which also affects populations on the next higher trophic level. Competition is seen as a restriction of access to resources and consequently it reduces acquisition rates.

The demographic structure of the model provides a dynamic base for the implementation of age-specific population characteristics like intrinsic mortality, fecundity and migration. Special physiological features like carbon or nitrogen recycling in plants can easily be included as the age structure is accounted for in the model.

A further advantage of the metabolic pool model is the fact it needs relatively few population specific parameters, unlike most of the physiologically based approaches. The basic parameters like temperature and food dependent

development rates, life spans or potential growth, reproduction and respiration rates can be estimated in simple field or laboratory experiments. Standard life table analyses and energy budgets can provide the required data.

In general the metabolic pool approach represents a useful theoretical framework for the formulation of realistic models of simple to highly complex systems. These models are likely to substantially contribute to the further improvement of our understanding of dynamic interactions in agroecosystems, a prerequisite for the design of sound management strategies.

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ZUSAMMENFASSUNG

Ein umfassendes Verständnis der landwirtschaftlichen Produktionssysteme bildet die Grundlage für die Erarbeitung von ökologisch vertretbaren und nachhaltigen Bewirtschaftungsformen. Da sich empirische Methoden für das Studium komplexer Systeme nur beschränkt eignen, werden zunehmend Simulationsmodelle entwickelt, um Forschungsergebnisse aus verschiedenen Bereichen zu kombinieren und mehrdimensionale quantitative Beziehungen besser zu verstehen. In dieser Arbeit wird ein Modell-Ansatz vorgestellt, der Interaktionen zwischen mehreren Populationen eines Agro-Ökosystems als Fluss von Ressourcen innerhalb und zwischen den trophischen Stufen beschreibt. Die Aufnahme von Ressourcen erfolgt auf allen trophischen Stufen nach analogem Muster und wird deshalb mit derselben funktionellen Reaktion quantifiziert. Auch die populationsinterne Verteilung der Ressourcen verläuft nach analogen Prinzipien. Sie erfolgt sowohl in Pflanzen als auch in tierischen Organismen nach der Prioritätenfolge Respiration, Reproduktion, Wachstum. Eine einfache Erweiterung des Modells ermöglicht ausserdem die Simulation der Konkurrenz um Ressourcen zwischen Populationen auf derselben trophischen Stufe. Ein Modell zur Beschreibung zeitverteilter Prozesse bildet den mathematischen Rahmen für die Simulation der Populationsentwicklung unter dem Einfluss abiotischer und biotischer Faktoren des Ökosystems. Dank seiner einfachen und klaren Struktur stiess dieser Modell-Ansatz auf grosses Interesse im Bereich der angewandten Ökologie und trägt unbestritten zu einem besseren Verständnis quantitativer Beziehungen in Agro-Ökosystemen bei.

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