Developments in crop ecology

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Introduction

Crop ecology studies the underlying processes of the production of high-quality food, feed and vegetable raw materials in sustainable agro-ecosystems. It focuses on the processes that determine the functioning of crops in relation to genetic, biotic and abiotic factors. It includes three basic elements:

1. crop physiology, which studies the life processes of the plant to obtain insight into the functioning of the plant at crop level in interaction with neighbouring plants and the abiotic and biotic environment. Crop physiology assesses the relative significance of basic processes for the performance of the crop in diverse production environments. It provides knowledge to allow manipulation and modification of processes, in terms of direction, rate or intensity.
2. the abiotic crop ecology, which deals with the effects of abiotic environmental factors on the functioning of cropping systems.
3. the biotic crop ecology, which deals with the interaction between crops and weeds, pests, diseases and beneficial organisms within a cropping system.

To allow quantitative analyses and decision support, crop ecology makes use of experimentation at different levels of aggregation – sub-plant, plant, crop, cropping system – and of system analysis and simulation.

In this paper we describe some of the major developments in crop ecology over the last decades, with a strong focus on the Wageningen contribution to these developments, which, by the way, was realized in close collaboration with many international research partners. We have chosen to highlight genotype × environment × management interactions (including ideotyping), stress ecology, decision support, functional biodiversity, precision agriculture, genetic engineering and metabolites for industrial use. We are aware that this set of topics reflects our personal bias and that other crop scientists may have made different choices.

Genotype x environment x management interactions

In the past decades the philosophy in crop science and plant breeding has changed from wide adaptation and homogenization of environments – with irrigated rice as the extreme example – to targeting specific genotypes in combination with specific management to the local environment. A central crop ecological question to be addressed at field level is how genotype × environment × management interactions can be optimized given the objectives set by farmer and society, including economic, environmental and socio-economic ones. Systems approaches are indispensable to quantify achievable yields of a specific genotype at different input levels in different environments. In the past decades major progress has been made in understanding these interactions between genotype, environment and management.

Genotype

Quantification of genotypic effects on crop performance is complex as plant traits of agronomically fit varieties generally differ marginally. A major genotypic trait that has been studied is phenological development rate. An interesting example is the study by Yin *et al.* (1997), who determined the optimal pre-flowering phenology in irrigated rice for several contrasting climatic conditions using the model ORYZA1 (Kropff *et al.*, 1994). Environments ranged from tropical wet and dry seasons to subtropical and temperate climates. For each environment there was a very different optimal pre-flowering period that produced the highest yield. The simulated optimal pre-flowering periods in this set of climatic conditions matched the pre-flowering period of the best varieties bred in those conditions. This indicates that crop ecological models can be used to target phenological traits of genotypes for specific climatic conditions. However, to allow effective use of crop modelling in plant breeding, the ability of crop growth models to predict yield differences among genotypes still needs to be improved (Yin *et al.*, 2000).

Environment

Potential crop production is rarely achieved, but its estimation is essential in benchmarking environments and yield gaps in specific environments (Van Ittersum *et al.*, 2003). Temperature and solar radiation influence the variation in benchmark potential yields in contrasting environments (Matthews *et al.*, 1997). Using examples for maize, rice and wheat, Muchow & Kropff (1997) showed a wide variation in potential yield, with low yields in tropical environments and high yields in temperate environments at higher latitude and altitude. In a study by Kropff *et al.* (1995) it was found that the variability in potential rice yield ranged from 6 t ha^{-1} in tropical environments (wet season, Los Baños, Philippines) to 15 t ha^{-1} at higher latitudes (Yanco, Australia). Various simulation models have explained this large difference in yield potential that was experimentally determined as well. The primary influence of temperature was on growth duration, with lower temperatures increasing the time that the crop can intercept radiation. So if for a given environment yield potential can be simulated, the yield gap with actual yield can be quantified. This was done at the International Rice Research Institute. A subsequent experimental programme showed that indeed nitrogen management needed to be improved to fill the yield gap of about 3 t ha^{-1}.

Crop models proved to be of help in guiding research and generating quantitative hypotheses for new research. An example is the use of models to determine the damage mechanism of reducing factors such as air pollution, pests, diseases and weeds. In the example of air pollution a field experiment was conducted with a field fumigation system to determine the damage of increased [SO_2] during 3 years. Apparently a realistic [SO_2] enhancement reduced yield by more than 15%. The model included damage mechanisms such as effects on photosynthesis, respiration and leaf area development. In contrast to the dominating opinion in the 1980s not photosynthesis but earlier leaf senescence appeared to be the major damage component (Kropff *et al.*, 1989; Kropff, 1990; 1991). Similar studies have been conducted for fungal diseases (Bastiaans, 1993), viruses (Van Der Werf, 1988), pests (De Kraker, 1996) and weeds (Bastiaans *et al.*, 1997). For other examples of quantification of environmental effects we refer to the review by Kropff *et al.* (2001).

Management

Inputs in agriculture are currently under debate. There is an increasing concern on the amount of resources (land, water, energy) that are used for agricultural production, on the waste of scarce resources (phosphorus, water) that are spent on agricultural production and on the environmental pollution and land degradation that are associated with this abundant use. There is also a general awareness among scientists, farmers, governments, and the public that chemical crop protection has to be replaced by an ecological, more sustainable approach.

Optimizing crop husbandry and setting standards for cultural practices in different environments have long been the main objectives of agronomic research. As the understanding of the underlying principles grew and the tools to control the environment became more perfect, yields have increased dramatically. Crop management in high-input agriculture, however, was mostly focused on overruling variation in availability of natural resources by blanket applications of resources in abundant quantities. Farmers learned that applying enough water and nutrients made it more important to simultaneously control yield-reducing factors such as fungal diseases and pests. C.T. De Wit (De Wit, 1992) showed that despite the general acceptance of the laws of the minimum and the diminishing returns, farmers applied resources in such a way that none of the other resources was used less efficiently and most of them were actually used more efficiently. De Wit called this "best agricultural practice". The consequence of this practice is that an increase in efficiency of resource use per unit product is obtained with an increase in resource application. On a per hectare basis, however, an increase in resource application could result in environmental pollution, for example by nutrient leaching (eutrophication) or excessive influx of chemicals into the environment.

Farmers in western agriculture have been forced to reduce the input of fertilizers, water and chemical crop protectants. In some cases there was an agronomic reason to do so. The nitrogen application in sugar beet growing has been reduced tremendously in Western Europe since the early 1970s as research showed that with more nitrogen the sugar content in the fresh matter and the sugar extractability declined much more than the beet yield increased. In Dutch grassland husbandry with grazing by ruminants, nitrogen supply decreased significantly since the 1980s as farmers learned that much of the nitrogen taken up by the animal was returned to the soil by animal excretions, which had not been taken into account in the advices based on mowing experiments. In other cases (e.g. in potato) yields could still profit from additional applications of fertilizer but product quality (nitrate content in tubers), susceptibility to diseases (late blight) or environmental concerns would force farmers to restrict the fertilizer supply.

Agriculture is spending more water for irrigation than any other human activity and water is becoming increasingly scarce. With the strong increase in the world's population, especially in areas where productive agriculture without irrigation is not possible, water consumption is likely to increase to be able to feed all. Water use efficiency, however, must go up to produce more crop per drop of water. For example, farmers in China have started to grow aerobic rice to reduce water consumption, which will revolutionize their crop management.

Agriculture has also learned that consumers and governments no longer accept the wide use of chemical crop protectants. Achieving high yields without the use of chemical biocides will prove to be a challenge and will determine the research agenda of crop ecologists for many years to come.

Genotype x environment x management

To study the genotype × environment × management interactions, two major approaches can be used:

1. traditional statistical approaches in which large data sets of multilocational trials are analysed, and
2. simulation approaches in which the different performance of genotypes with different physiological, morphological and phenological traits is simulated in response to environmental factors, including management factors.

Recently, these approaches have been coupled

1. by introducing explanatory physiological process descriptions of simulation models into the statistical models (Van Eeuwijk *et al.*, 1996),
2. by using simulated yields of standard genotypes for the different environments used in the trials in the statistical models,
3. and currently by linking the approaches in an extensive study with modern genetic techniques such as QTL analysis.

Quantitative Trait Loci (QTLs) refer to genes for a quantitative trait, and QTLs have been identified in various organisms for a variety of traits. Yin *et al.* (1999a, b; 2003) conducted an integrated study to determine whether QTLs could be used to predict the traits that determine crop performance in simulation models and whether the crop model was able to explain variability in yield of different lines. A set of recombinant inbred lines, obtained from two divergent barley cultivars was used to generate an AFLP (amplified fragment length polymorphism) marker linkage map. Traits were evaluated in two growing seasons and QTLs involved in these traits were mapped and their effects estimated. The study revealed that model-input trait values could be well predicted on the basis of the DNA fingerprint patterns, specifically for traits such as pre-flowering duration, biomass partitioning, post-flowering duration and specific leaf area (Yin *et al.*, 1999b). Crop models were found to need refinement with respect to their capacity to explain yield differences between genetic lines, as source-sink relationships are not accounted for in an explanatory way.

Another area in which progress has been made in the study of genotype × environment × management interactions is the ideotyping of crop plants. The ecophysiological models that have been developed in the past decades were used to design ideotypes for crop breeding for specific environments to increase yield potential in irrigated rice by Kropff *et al.* (1995) and Aggarwal *et al.* (1997). They found that only varieties with improved sink and source characteristics resulted in an increased yield potential (see also Van Ittersum *et al.*, 2003). A further analysis of the opportunities to use crop models for plant design is given by, amongst others, Hammer *et al.* (2003).

The design of weed-suppressing varieties of crops without trade-offs with yield for preventive weed management is another area where progress has been made. The well-evaluated model INTERCOM (Kropff & Van Laar, 1993) explained the experimentally determined large differences in competitive ability between rice cultivars accurately (Bastiaans *et al.*, 1997). The model showed that competition for light is mainly determined by morphological characteristics, of which early relative leaf area growth rate, early relative height growth rate and maximum plant height were found to be the most important. The systems approach provides guidelines for the design of weed-suppressing varieties with minimum trade-offs with yield.

Stress ecology

Crops are exposed to many different types of stress, including low nutrient availability, frost, cold, heat, drought, salt, aluminium, heavy metals, pollutants, ozone, and biotic stresses. Several of these stresses affect crop performance through similar physiological effects such as plant organ temperature, reduced leaf area development or advanced canopy senescence. Combining the use of modern equipment allows the crop ecologist to analyse the crop status precisely, instantly, non-destructively and remotely. This allows him to trace the first signs of crop stress well before yield reduction has taken place. It also makes it possible to analyse the spatial and temporal variation and dynamics of stress, which can be important for detailed physiological analysis of the underlying processes, but also, for example, for the sampling of tissue showing stress-induced differences in gene expression.

A good example is the recently constructed Multiple Imaging Plant Stress (MIPS) facility of 'Plant Research International' and 'Plant Dynamics' (W.J.R.M. Jordi, Plant Research International and A.H.C.M. Schapendonk, Plant Dynamics, personal communication). It can monitor both abiotic stresses such as heat and biotic stresses such as blight infection at a very early stage. We will use heat stress to illustrate the potential of this combined use of modern equipment.

The MIPS facility can be used to define and analyse the effects of heat stress by simultaneous images of the plant organ temperature, chlorophyll fluorescence and spectral reflectance at different wavelengths. It involves:

1. thermo-imaging. The thermo-imaging system can monitor 3-D flux patterns of transpiration fluxes in response to heat. Cooler canopies are associated with canopy temperature depression, resulting in higher yield. Thermography makes the visualization of differences in surface temperature possible by detecting emitted infrared radiation. This allows, for example, to assess the (genetic basis of the) association between heat tolerance and effective temperature decrease by transpiration. Such an association may be a powerful and robust selection criterion for heat tolerant genotypes.
2. fluorescence and photosynthesis regulation. Fluorescence induction kinetics can be used to evaluate the electron-transport rate and photochemistry in plants exposed to heat stress. By combining the techniques of thermo-imaging and fluorescence lifetime imaging, processes that are related to stomata behaviour and processes that are related to photosynthesis can be distinguished.
3. spectral reflectance. Measuring changes in spectral reflectance can be used to monitor long-term changes in pigment composition, which may reflect long-term differences in photosynthetic capacity caused by senescence in response to stress.

The combination of these three non-destructive techniques will yield diverse information on the physiological response of a crop to stress. The overall picture will allow the researcher to assess the behaviour of the crop plants both at short notice and for the long term. The study of these physiological responses may give guidance to analyse stress tolerance more effectively. It will also enable the farmer to make decisions on proper counter-measures at a much earlier stage.

Decision-making

The use of advanced crop ecological knowledge may be applied at higher levels of the hierarchy of the agro-ecosystem to design ecologically sustainable systems of management of pests, diseases and weeds. Designing strategies to control yield-reducing factors should include prevention, decision-making and control.

Land use systems can be re-designed in such a way that the spatial and temporal distribution of crops of the same species is less conducive to the spread of the disease or pest. Regional distribution of crops can be regulated to prevent the severe occurrence of pests and diseases, especially those that are air-borne. Farming systems can be designed in such a way that the chances of re-infection or spread are minimal, for example by surrounding fields of easily infected crops by ecological safe-havens for antagonists, natural enemies and other beneficial organisms. Crop rotations can be widened to reduce the level of infection with soil-borne pathogens or weeds. Cropping systems can be diversified by mixed cropping, strip cropping, varietal mixtures, enhancing associated biodiversity in the system, or even by including and maintaining natural, disease- or pest-suppressing elements in the farming system.

Other important instruments for prevention are farm hygiene, the synergistic and antagonistic effects that occur in a cropping system, cultural practices supporting these effects, the optimization of inputs to improve the natural resistance of the crop or to increase the damage threshold, and breeding for tolerance and resistance.

If despite all prevention methods taken, problems do occur it is crucial to make a wise decision on crop protection. There are three major types of decision making in crop protection:

1. strategic decisions, taking into account the long-term developments and effects;
2. tactical decisions, focusing on the effects of management of a crop over an entire growing season;
3. operational decisions, concentrating on what to do when and how in the field.

Until recently the emphasis in agriculture was strongly on the last type. Operational decisions on control of biotic stresses have been changed by the introduction of the damage threshold concept. Only in cases when the damage reaches (or is expected to reach) a certain economic limit, application of a biocide is advisable. Operational decisions, however, should not only include the immediate effects on the current crop, also the mid-term and long-term effects are relevant. This is for example the case in weed control, where not only the immediate competition between crop and weed plant is relevant, but also the production of survival structures by the weed as they threaten future crops. In this way the operational decision becomes a tactical or even a strategic one.

To be able to make decisions in a rational way, the severity of the infestations must be known. The type of biotic stress determines when this knowledge must be available. For soil-borne diseases this is before the growing season, for seed-borne pathogens this is at planting or sowing and for air- of water-borne pathogens this is during the growing season. Warning systems have been designed to produce information on the severity of the threat, for example for late blight in potato. To be able to make a decision on economic grounds, criteria must be defined, based on the objectives, planning and risk attitude of the farmer. Knowledge on the (possible) severity of the infestation can help to predict crop yield loss, quality loss, and future losses resulting from an increase in population of the pathogen or pest. Decision-making should also weigh the efficacy of control methods, which depends on the technology available and the timing of application, as well as the possible side effects of the control method. Much progress has been made in designing the information technology to allow the farmer to make such decisions.

Based on the information obtained the following questions must be answered: (1) is control needed?, (2) if yes, when and where is control needed?, (3) how should control take place? An economic risk assessment, based on threshold information, should provide the answer to the first question. In many cases control can be local or site-specific (based on proper diagnostic tools and intensive observation), but timing of the control measures (depending on the techniques used) is essential for success. Control techniques are rapidly developing, the current chemical methods are being replaced by mechanical or biological tools. Currently, self-learning systems are being developed that create site-specific knowledge and thus help to design site-specific management options. Optical techniques for weed control and control of pests and diseases that cause clearly visible above-ground plant symptoms or other techniques based on other non-invasive measurements (similar to the ones earlier described for abiotic stress) may come within reach in the near future. Whatever control method is selected, control should take place with precision, with a high efficacy and preferably with as little biocides as possible.

Crop models can be used to explore and design options for decisions, both at regional scale (agro-ecological zonation, land use evaluation), at farm scale (prototyping of farming systems, design of cropping systems and of crop rotations, trade-offs between economic and environmental objectives) and at crop level (decision support for crop managers, for example relating to fertilizer application, irrigation and crop protection) and thus contribute to the innovation in agriculture. For overviews see Hammer *et al.* (2003) and Van Ittersum *et al.* (2003).

Functional biodiversity

Agro-ecosystems with increased biodiversity generally encounter fewer pest problems than agro-ecosystems based on monoculture crops. In agro-ecosystems, various options are available to obtain an increased diversity of functional groups: e.g. increased crop rotation (increased spatial and temporal crop diversity), mixed cropping and the establishment of a diverse field margin vegetation. Diversification in and around crops may lead to improvement of the life support function and of the regulation of pests, diseases and weeds, and thus reduces pesticide usage. However, hard data illustrating this hypothesis and explaining the mechanism of regulation are lacking, although insight into the working mechanism of pest, disease and weed regulation is crucial for implementation of this life support function.

In the past decade many crop ecological studies have been conducted to explore these complex systems. Examples are the use of mixed crops to increase the weed suppressing ability of the cropping system (Baumann *et al.*, 2002; Akanvou *et al.*, 2001) or the evaluation of the role of vertebrate and invertebrate weed seed predators (Westerman *et al.*, 2003), originating from newly created habitats in field margins. However, while diverse vegetation in field margins may have an insect pest regulatory effect and a weed seed predation stimulus, it may also enhance the weed pressure if weedy plant species can develop and produce seeds. Type and management of the boundary vegetation determine stability and associated risk through their effect on plant competition relationships (Kleijn, 1997; Schippers, 2000). In general these studies revealed that quantitative understanding of the complex plant-plant interaction as generated in the weed studies (INTERCOM, Kropff & Van Laar, 1993) is an essential basis for optimizing intercropping systems.

Large-scale farmer-participatory research on the effects of increasing functional biodiversity in arable farming is currently under way (J.C. Van Lenteren, personal communication).

Precision agriculture

A novel example of the use of models for water and nutrient management is provided by precision agriculture. A decision-support system for arable farming systems in the Netherlands is being developed with a primary focus on operational decisions and soil related variability. Bouma *et al.* (1999) have designed a forward looking approach for N fertilization that enables farmers to respond in a pro-active way to possible deficiencies in nitrogen and to possible crossings of environmental threshold values for groundwater pollution. The system they designed consists of a soil database, management units and real-time simulation. The soil database is created by sampling the soil in a grid pattern, of which the grid density depends on the spatial variability in the field. Primary data (e.g. layer structure, bulk density, organic matter content) are stored in the data base and secondary data such as hydraulic characteristics are derived using so-called pedo transfer functions. The increasing availability of these functions makes expensive measurements redundant. Spatial resolution at which precision agriculture is implemented can vary greatly. Equipment is currently being developed for precision at the sub-metre level (Stafford 1997; Robert *et al.*, 1994). However, the level of spatial detail of the basic database determines which level of precision is proper. Models can be used to distinguish between land units that significantly differ in soil characteristics. These land units can form the basic management units. Real-time simulations can be performed using proper site-specific soil and weather data. They can indicate the need for fertilizer and irrigation. If the models are not well calibrated, soil and plant measurements may be needed.

Haverkort *et al.* (2003) have designed precision tools for improved use and efficiencies of water and nitrogen in potato. Their system is based on precise measurements of the nitrogen status of crop and soil, the water status of the soil, weather forecasts and the simulation model LINTUL-Potato. They have identified how much nitrogen a potato crop must contain before the end of a crucial time window to be able to perform at the desired level. If this quantity of nitrogen is not yet reached nitrogen supplementation is needed. Irrigation must take place before water is depleted from the soil at a critical level. Moisture depletion in the soil must therefore be monitored. Timing and amount of irrigation follow from the moisture depletion rate, as influenced by the proportion of ground covered by a green canopy and the evaporation rates predicted on the basis of weather forecasts.

Much is also expected from site specific weed management techniques because it is well known that the spatial pattern of annual and perennial weeds is typically aggregated (Wallinga, 1998). The spatial distribution of weeds provides a starting point for determining the perspectives of controlling only where necessary. Knowledge about this spatial distribution can be obtained by going out to the field and observe the spatial positions of the weeds. It can be derived theoretically that weeds occur in patches and that patches remain stable over time using the individual based model of annual weeds that occur endemically on an arable field with homogeneous abiotic conditions (Wallinga, 1998). Starting out from randomly distributed individuals, the spatial configuration of the individual weeds rapidly settles down into a clustered pattern. This pattern is rather stable in the sense that the 'type' of clusters remains the same over time, and also in the sense that the positions of clusters show strong correlation in time, i.e., the position of clusters does not change very much over time (Wallinga, 1998). There is also some experimental evidence that indeed weed patches remain stable over time (Wilson & Brain, 1991). The aggregated pattern creates the potential for spraying only the weed patches, thereby reducing the amount of herbicide applied (Mortensen *et al.*, 1993). Engineering approaches have tried to develop a technology to support such a weed control (Miller *et al.*, 1995). The potential reduction in herbicide use varies from 30–70% with weed infestation level and spatial pattern of weeds (Kropff *et al.*, 1997).

Genetic engineering

The rapid developments in life sciences have also affected crop production. Although our ability to convert genomic data into useful information relevant to crop ecology is still very limited (see e.g. Wilson *et al.*, 2003) genetic engineering has already yielded new cultivars with specific, useful traits. The role of genetically engineered crops in the production of food, feed and industrial raw materials is potentially enormous, provided the consumers are willing to accept this technology. The area of genetically modified crops grown in the world has increased very rapidly over the recent years and is already well above 50 Mha per year. Table 1 summarizes the important crop traits that can be modified by genetic engineering.

Genetic engineering of resistance against weeds, pests and diseases is very important. Weed control can be optimized by making crop plants resistant to certain herbicides. Resistance against viruses is for example based on genes encoding for viral coat proteins or ribosome inactivating proteins (Sonnewald & Herbers, 2001).

Tolerance to abiotic stress resistance may be induced by inserting genes encoding for osmoprotectants. Hybrid seed production can be made more effective by manipulating pollination based on influencing cellular integrity in the pollen or on inhibiting cellular functions required for pollen development.

Many quality traits of crop plants are apparently easily manipulated. Changing levels of low-molecular sugars, micronutrients and vitamins have already been achieved (Sonnewald & Herbers, 2001). Control of physiological disorders (e.g. blackspot in potato) is possible. For many agricultural products the biochemical composition can be changed by manipulating enzymes, proteins and other factors in the pathways. Post-harvest behaviour (e.g. fruit softening or sprouting) can be manipulated as well.

Especially promising is the manipulation of production of secondary metabolites. This can be achieved by making pathways more efficient. Polymers have been changed or novel polymers have been incorporated, whereas levels of antinutritional factors can be reduced. Industrial uses of crop products have become feasible and bioremediation of soils and water have been made more efficient.

Scientists also aim to influence sink-source relations, ontogenesis and morphogenesis, and to increase yield, but these developments can only be achieved on the long run.

Table 1. Important crop traits to be modified by genetic engineering (changed after Keller & Hütter Carabais, 2001)

Agronomic traits	Weed control (based on herbicide resistance of crop plants)
	Insect pest resistance
	Resistance to diseases (viruses, bacteria, fungi, nematodes)
	Tolerance to environmental stress (e.g. heat, cold drought, salt, aluminium, heavy metals)
	Increased nitrogen fixation
Breeding traits	Hybrid seed production
Quality traits	Enhanced nutritional quality of food crops (e.g. contents of vitamins, micronutrients, proteins)
	Delayed ripening of fruits
	Control of sprouting
	Changes of colour, flavour, texture
	Modification of oil, starch and protein composition
	Elimination of toxic or anti-nutritional components
Industrial uses	High values chemicals
	Modified and speciality oils
	Recombinant or engineered proteins including industrial enzymes
	Production of pharmaceuticals (e.g. antibodies, vaccines)
	Renewable non-food products (e.g. plastics, fuels)
	Bioremediation

Crop modelling can contribute to enhancing integration of molecular genetic technologies in crop improvement by its capability to bridge the gap between genotype and phenotype (Hammer *et al.*, 2003).

Primary and secondary metabolites for industrial use

Plant materials can provide primary or secondary metabolites for industrial use. Primary metabolites include fibre, oil, starch or carbohydrates, and proteins. Secondary metabolites are for example dyes, flavours and medicines.

The industrial use of agricultural products declined when alternative raw materials, especially from petro-chemical industries, became available. Nowadays, there is a renewed interest in agricultural raw materials as they may be more sustainable. The economic feasibility of the production of raw materials from arable farming, however, is poor, especially in Europe, mainly because of high costs of labour, land and other production factors. This provides a challenge to crop ecologists to design technologies to produce agricultural raw materials that are economically competitive. The example of hemp shows that very high yields can be produced at low costs and with very little burden on the environment (Struik *et al.*, 2000).

Primary metabolites

Crops for bulk production of primary metabolites should have at least the following characteristics (Struik & Venturi, 2000):
1. a high and stable dry matter production, as made possible by a long life cycle,
2. high light conversion efficiency, low costs of dry matter conversion, and high stress resistance;
3. a high harvest index, i.e., a high proportion of usable dry matter and a high content of desired components;
4. a high resource-use efficiency, at least for water and nutrients;
5. a high and stable quality;
6. a minimum requirement for energy during cultivation, harvest and storage, and an environmentally friendly crop husbandry.

Bulk production is efficient when the agronomically most efficient crops are grown at large scale in areas with high yields, low prices of arable land and low labour input and labour costs. Only very efficient industrial crops producing C5 or C6 molecules, like sugar beet, sugarcane or cellulose crops low in lignin such as hemp, may be used for that purpose (Struik *et al.*, 2001).

Bulk production becomes more attractive if the raw material can be used in systems for integrated plant conversion, based on biocascading (Struik *et al.*, 2001). In that case, a crop can be used for several processing steps each yielding a specific compound. In this way a wide range of products can be obtained. Examples are biocascading of grass, sugar beet or hemp.

Secondary metabolites

Secondary metabolites often play a vital role in the physiology of the crop but can also be valuable for man. Examples are biocides, repellents, flavours, medicines and dyes. These compounds are often complex and synthesized through complex pathways in specific crops. Commercially interesting examples are the anti-malaria drug artemisinin from *Artemisia annua* and the anti-cancer drug taxol from taxus. Breeding can help to increase the contents and proper crop management can change the physiology of the crop to increase yields of the desired compounds. An intense interaction between crop ecology and metabolomics (i.e., the powerful molecular technology whereby the entire metabolite composition of an organism is analysed) can help to identify new options to produce precious secondary metabolites and to increase efficiency of their production by improved crop husbandry.

Final comments

Crop ecology has developed from a empirical, qualitative science into a science that makes direct use of the latest insights from life sciences, uses quantitative hypotheses and tools, and is predictive at different levels of aggregation, from sub-plant to cropping and farming system. The research agenda has changed tremendously over the last 50 years, as a result of opportunities provided by scientific and technological progress but also – and perhaps even more so – because of socio-economic demands towards agriculture. The challenge farmers face to feed a rapidly increasing number of people with continuously less good arable land, increasingly scarcer resources and more and more strict regulations for maintaining a license to produce will keep the pressure on crop ecologists to come up with innovative solutions for highly complex problems.

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