

Original papers

Abnormal shapes of production function: Model interpretations

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ABSTRACT

An abnormal non-monotonic shape of production function (response of obtained yield to increasing rates of mineral nitrogen fertilizers) has been observed in experimental field trials. Often, the observed effect (an inflection point, or intermediate plateau or even local undershoot of the “yield-fertilization” curve) is treated as a test distortion and will be ignored or sorted out. This article presents the authors’ efforts to interpret and to explain similar phenomenon by means of investigating two mechanistic crop simulation models – AGROSIM and AGROTOOL. It is demonstrated that an imitation model can be used as a valuable tool of scientific research, allowing for the hypothesising of alternative understandings of non-trivial natural phenomena.

1. Introduction

The search for the correct mathematical formulation of the so-called “production function” has a long history, and is a well-known problem of theoretical agro-chemistry. The production function means the response of an actual or potential yield of agricultural crops to various environmental and management factors, in particular to different rates of mineral fertilizers. For many years the experimental determination of such dose-response relationships has been a subject of investigation in multivariate field tests. One related activity is to approximate observed experimental curves by simple functional dependencies (Griffin, 1987; Status and Methods, 1961). The background of this issue has a history of over 150 years and traces its roots back to classical research by Liebig (1855), Mitscherlich (1909). Table 1 presents a short summary of existing approximations of production functions.

However, in spite of the variety of proposed functional forms, they all only describe two principal shapes of a hypothetical response curve. The first one is a monotone increasing convex function (with or without saturation, i.e. characterised by limited or unlimited growth). The second is a unimodal function reaching its maximum at the optimal rate of fertilization and having a decreasing branch for super-optimal values of argument (negative impact of higher fertilization rates). Such a qualitative nature of the production function perfectly corresponds to the intuitive idea of the principal influence of a positive limiting factor on the production process of agricultural plants.

In fact, the relative efficiency of increasing doses of fertilizers (so called NUE – nitrogen use efficiency) must be the largest for small values, where a significant deficit of the limiting factor is seen. As

fertilization doses increase, they lose their positive effect. Ultimately, very large doses can have a counterproductive influence on plant growth and development that leads to a decrease in the total yield.

Thus, typical shapes of production function (Curves 1 and 2 in Fig. 1) completely correspond to *a priori* understandings of plant reactions to possible excessive or lacking nutritional element.

At the same time, it is possible to find references to field as well as laboratory experiments which produce a more sophisticated shape of the production function curve (for wheat: Ivanova (1977); for ryegrass: Tumusiime et al. (2011); for barley: Surov et al. (1984), Emebiri et al. (2007); for rape: Seymour (2013); for cereals: Osmond et al. (2015); for nectarines: Daane et al. (1995)). In particular, this effect can sometimes be observed in test series with increasing doses of nitrogen fertilizers. The non-monotonic character of production function can be expressed by local decrease of relative NUE (inflection point), plateau-like segment or even a local minimum in the “yield-fertilization” response curve (Curve 3 in Fig. 1) appears in the medium interval of nitrogen fertilizer change.

Further increase of the nitrogen fertilizer dose leads to a return of the experimental production function to the “normal” shape. We hasten to point out that such a phenomenon is exhibited only in special, rarely occurring vegetation periods, i.e. for special combinations of environmental conditions such as abnormal early drought periods, high temperatures or other phenomena, and cannot be easily reproduced by field experiments. This in turn is often presented as an argument that the obtained results may be caused by methodological or experimental errors and, therefore, must be treated as merely test distortion. It seems, however, that the number of references to the same effect from

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Table 1
Approximations of the production function.

#	Approximation Y(X)	Author, year
1.	$Y = A \cdot X$, if $X < X_{max}$ $Y = Y_{max}$, if $X \geq X_{max}$	von Liebig (1855)
2.	$Y = A \cdot (1 - \exp(-k \cdot X))$	Mitscherlich (1909)
3.	$Y = a + b \cdot X - c \cdot X^2$	Pfeiffer and Fröhlich (1912)
4.	$Y = A \cdot \Pi(1 - \exp(-k_i \cdot X_i))$	Baule (1918)
5.	$Y = A - M \cdot R^X$	Spillman (1923)
6.	$Y = a \cdot X / (x + b)$	Briggs (1925) Rauterberg (1939)
7.	$Y = a \cdot X^{0.5}$	Boresch (1928)
8.	$Y = a \cdot X^b$	Sapehin (1923)
9.	$Y = a + b \cdot X - c \cdot X^n$	Bondorff (1924)
10.	$Y = a \cdot X^b \cdot \exp(-b \cdot z)$	Plessing (1943)
11.	$Y = a + b \cdot X + c \cdot X^2 + d \cdot X^3$	Stritzel (1958)
12.	$Y = A \cdot \exp(-z \cdot \log[(X + 1)/(m + 1)]^m)$	Boguslawski and Schneider (1962)
13.	$Y = A \cdot \log(X)$	Unknown author

independent researchers above-mentioned makes it a tendency which cannot quite simply be neglected by the agricultural scientific community.

One example coming from the authors' own experience concerns results of special field experiments with spring wheat performed at the Men'kovo Experimental Station of the Agrophysical Research Institute (St. Petersburg, Russia) in the 2012–2016 seasons of vegetation. They are presented below (see Table 2). The spring wheat cultivars “Esther” (2012) and “Darja” (2013–2016) were cultivated on sod-podzol sandy soil according to regional “good agricultural practice” for cereals production. Before sowing, nitrogen fertilizations varied from 0 to 180 kg N ha⁻¹ at increments of 30 kg N ha⁻¹. Seven test sites in a quadruple repetition each (10 × 10 m) were randomly distributed at an experimental field with a good agricultural practice. It is seen that the production function in the experiment generally takes a typical shape (convex saturated or unimodal curve) in all seasons, whereas it contains an abnormal region (local decrease of NUE) in 2013. We present two result datasets for 2013 which correspond to the experiments performed at two different agricultural fields (f1 – field with drainage system; f2 – field without drainage system). In Fig. 2 it is seen, that the production functions for both variants have well-expressed peculiarities (local plateau- or local minimum) near medium values of the argument (60 kg N ha⁻¹ for field1 with drainage system and 90 kg N ha⁻¹ for field2 without drainage system). Under the assumption that for the argument point of 90 kg ha⁻¹ the observed value is absent for the

“dashed” curve (field2) in Fig. 2, we can interpolate between the argument points 60 kg ha⁻¹ and 120 kg ha⁻¹ smoothly. The expected value will be approximately 4.2. The value observed in the experiment is 3.90 ± 0.16 (see Table 2). So, the expected value of 4.2 is out of confidence interval. Hence, the hypothesis of an existing plateau can be accepted. The same explanation can be used for the “dotted” curve (field1) in Fig. 2 for the argument point 60 kg ha⁻¹ accordingly.

Unfortunately, we have no unambiguous and purely agronomic explanation of this effect at the moment. But the obtained results motivated us for investigation of the observed case in more details. Indeed, sometimes similar results can be produced not in physical experiments, but in computer experiments, i.e. under the computation of eco-physiological mechanistic crop simulation models. As a result, a detailed investigation of all causal conditions and algorithms can offer a theoretical or model-based explanation for the phenomenon under consideration.

This article contains descriptions of computer-based investigations of abnormal production functions processed by means of two alternative crop simulation models. The first is AGROTOOL for spring wheat grown in 2013 at Men'kovo Experimental Station, Russia, and the second is AGROSIM for winter wheat grown in 1992 at Müncheberg Experimental Station, Germany, with extreme drought periods during spring, early summer and summer.

2. Material and methods

2.1. A description of the AGROTOOL crop model

AGROTOOL v. 3.5 is a generic crop model classified at the third production level according to de Wit's classification (de Wit, 1982). This means that the availability of water and nitrogen represents the main limiting factor in reducing potential photosynthesis-based productivity. The model consists of several independent, scalable and replaceable modules, interacting with each other at every time interval.

- **The agrometeorological module** is connected with a hydro-meteorological database that consists of all of the daily weather data required (minimum and maximum temperature, air humidity, precipitation and solar radiation characteristics).
- **The module of solar radiation and photosynthesis** calculates the daily sum of solar radiation intercepted and absorbed by plants, as well as the daily sum of accumulated assimilates due to photosynthesis and dark metabolism.

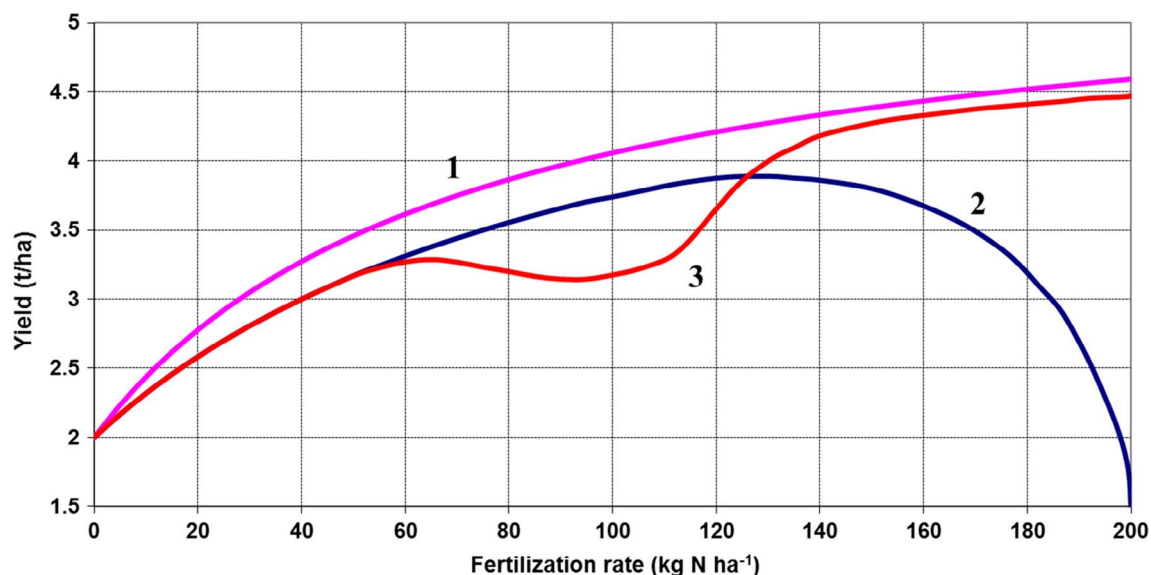


Fig. 1. “Typical” (Curves 1 & 2) and “abnormal” (Curve 3) shapes of “fertilization productivity of cereals” response curves.

Table 2

Spring wheat yields (t ha^{-1} ; mean value \pm standard error) as a function of pre-sowing N-fertilization (kg N ha^{-1}). Results from field experiments at Men'kovo Experimental Station ($59^{\circ}25'N$, $30^{\circ}02'E$) (f1 – field with drainage system; f2 – field without drainage system, LSD_{05} – least significant difference with $t_{0.05}$ critical value). Abnormal points are bold-indicated.

Year/field	N – fertilization (kg N ha^{-1})							LSD_{05}
	0	30	60	90	120	150	180	
2012	2.10 \pm 0.20	2.45 \pm 0.15	2.95 \pm 0.15	3.40 \pm 0.10	2.80 \pm 0.10	2.75 \pm 0.05	N/A	0.36
2013_f1	2.16 \pm 0.08	3.25 \pm 0.06	3.30 \pm 0.10	4.10 \pm 0.03	4.30 \pm 0.06	4.69 \pm 0.01	5.12 \pm 0.12	0.14
2013_f2	1.97 \pm 0.10	3.27 \pm 0.15	3.94 \pm 0.20	3.90 \pm 0.16	4.57 \pm 0.18	4.80 \pm 0.14	5.13 \pm 0.22	0.15
2014	2.52 \pm 0.18	2.92 \pm 0.20	3.61 \pm 0.18	3.84 \pm 0.16	4.15 \pm 0.24	4.16 \pm 0.26	3.68 \pm 0.20	0.22
2015	2.66 \pm 0.22	3.11 \pm 0.25	3.22 \pm 0.41	3.76 \pm 0.35	3.79 \pm 0.32	4.00 \pm 0.26	4.20 \pm 0.18	0.28
2016	1.76 \pm 0.12	1.98 \pm 0.14	2.26 \pm 0.20	2.42 \pm 0.26	2.71 \pm 0.30	2.93 \pm 0.30	3.27 \pm 0.28	0.9

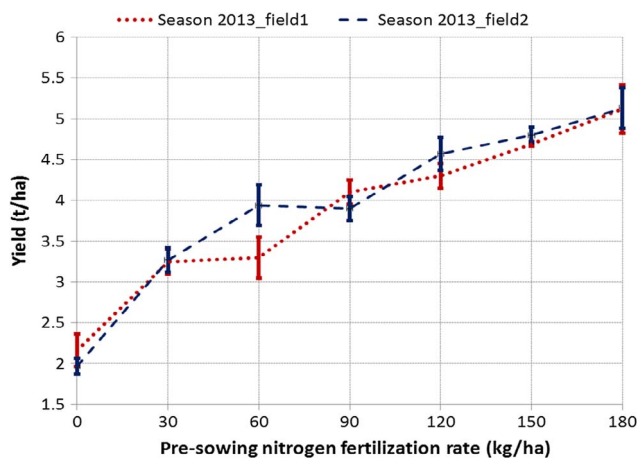


Fig. 2. Empirical production functions for field tests at Men'kovo Experimental Station in 2013 vegetation season (error bars for 5% least significant difference; field1 – with drainage system, field2 – without drainage system).

- **The module of turbulent gas exchange in the atmosphere** calculates the wind speed profile above and inside the vegetation, as well as aerodynamic resistances for fluxes of carbon dioxide, heat and water vapour.
- **The module of soil water dynamics** calculates the moisture balance in frames of multilayer presentation as a one-metre soil profile in depth. The available water content is determined taking into account rainfall intensity, plant transpiration, water evaporation from soil, percolation and moisture exchange within soil layers. The intensity of all these processes caused by water transfer is determined by water capacity in soil, so the soil's water retention curve is used for simulating these processes (Poluektov & Terleev, 2005). The relationship between volumetric moisture content and potential water capacity in soil is estimated on the basis of soil-hydraulic constants such as field capacity, permanent wilting point, saturation capacity and maximum hygroscopy (Terleev et al., 2010).
- **The module of plant growth and development** uses some specific “growth distribution” functions for performing calculations of the dry matter increase for different plant organs. The original concept of adaptive distribution key is used to define shoot-root balanced growth during the vegetative development stage. The assumptions underlying the approach are the cornerstone of the proposed explanation of the abnormal production curve. As a result, this method will be described in greater detail below. Additionally, physiological time is determined as the sum of effective temperatures, which is corrected by effects of plant water stress.
- **The module of nitrogen transfer and transformations in soil** takes into consideration the main processes determining soil nitrogen status: litter humification, ammonification, nitrification and denitrification, root nitrogen uptake, symbiotic nitrogen fixation by legumes, etc.
- **A special module** has been developed to provide the *model control*

Table 3

Functional structure of AGROTOOL model v. 3.5.

Modelling domain	Approach
Leaf area development & light interception	Detailed model based on the Monsi-Saeki approach
Light utilisation	Original model of photo-metabolism as well as dark metabolism
Yield formation	Y(PRT) – partitioning during reproductive stages
Crop phenology	$f(\text{temperature, water})$
Root distribution over depth	Exponential, based on water availability
Stresses involved	Water and nitrogen stress
Water dynamics	Richards equation in a ten-layer soil profile
Evapotranspiration	Modified Penman-Monteith approach
Soil CN model	CN transfer and interaction in plant and soil, five organic pools

of principal agronomical treatments: sowing, irrigating, nitrogen fertilizing and top dressing, harvesting. All these human impacts can be imitated both in declarative (predetermined dates and rates of actions) and reactive mode (as a formal rule based on the feedback of model state variables).

The principal methods used for the mathematical formulation of these processes are summarised in Table 3.

Two principal AGROTOOL features must be pointed out. First, it is a generic crop simulator, i.e. a single computational algorithm is used for different soils, cultures and locations, where the specificity of a currently simulated variable is controlled by a set of parameters with a predefined structure. Second, the model has an eco-physiological or mechanistic nature, i.e. a physically or physiologically based approach of process description is mostly applied, instead of empirical regression relationships having simple logical interpretations but which are on rather weak scientific ground.

AGROTOOL has a successful story of verification for different soil-climate conditions in Russia as well as in West European countries (Poluektov et al., 2000; Mirschel et al., 1999). A more detailed description of AGROTOOL can be found in various articles (Poluektov et al., 2002; Poluektov and Topazh, 2005; Badenko et al., 2014) or at <http://agrotool.ru>, an open internet resource where fully functional model versions can be downloaded.

The implementation of plant organogenesis and the method for description of carbon-nitrogen interaction in plants are closely linked to each other in the AGROTOOL computational scheme. The key question here is the principle of the distribution of primary assimilates between plant parts. It has been noted many times that such mechanisms (called “growth functions” in some references) must not have a static, but instead a dynamic character. This means that a plant has to be considered as a self-regulating system, where the shares of currently available growth resources partitioned between different vegetative and generative organs depend on the balance of the main limited nutrition elements (Reynolds and Chen, 1996; Wilson, 1988). In AGROTOOL,

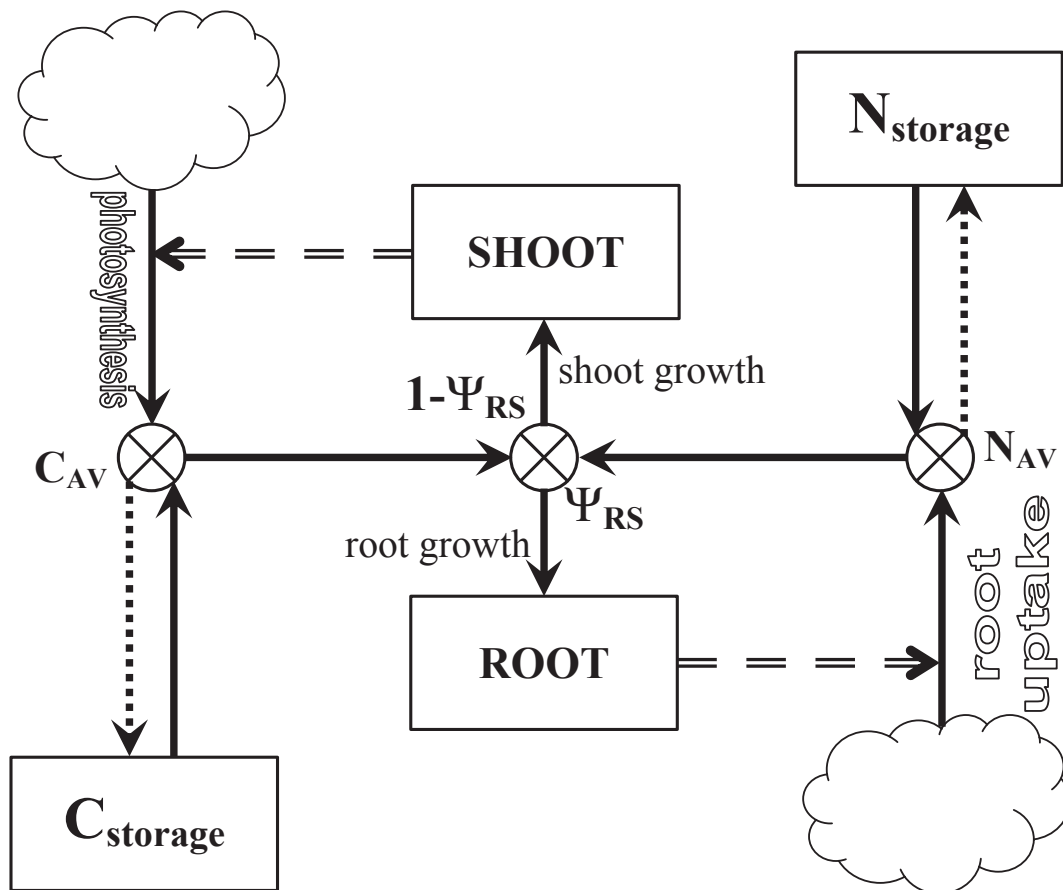


Fig. 3. Principal scheme of carbon-nitrogen interaction and plant growth in the AGROTOOL v. 3.5 crop model.

these regulatory mechanisms are described by means of an original algorithm presented in Poluektov & Topazh (2005). The principal scheme of the corresponding simulation sub-model (double component/double-flow transport model with storage pools) is shown in Fig. 3.

At every time interval, pools of labile carbon (C_{AV}) and nitrogen (N_{AV}) compounds are formed from two sources. First, new metabolites are created by vegetative organs (carbon from leaf photosynthesis and nitrogen from root uptake). Secondly, there are mobilised compounds from reserve pools (starch and nitrates – $C_{storage}$ and $N_{storage}$ correspondingly). The $C_{AV}:N_{AV}$ ratio determines the current value of Ψ_{RS} – the effective part of total growth resource in carbon units which is allocated to the root growth. The remaining available resources ($1 - \Psi_{RS}$) go to the shoot.

Next, the following approach is applied to the calculation of Ψ_{RS} . The “balanced” share value is determined in such a way as to maintain the most complete utilisation of all available assimilates (both those of carbon as well as of nitrogen). The correct allocation must provide this objective even though C:N ratios in shoot and root biomass are not equal and, therefore, different plant parts require different proportions of main construction materials to be bound in a structural biomass. However, surely this complete utilisation can only be reached for rather narrow intervals of possible values of C_{AV} and N_{AV} . In the opposite case, the whole growth resources target the organ that produces the currently limited metabolite (i.e. the shoot becomes a target of resources during a carbon deficit and the root becomes a target of resources during nitrogen stresses). In such cases, Ψ_{RS} takes one of the marginal values (0 or 1) while all remaining unclaimed assimilates (nitrogen or carbon) go to the corresponding storage pool and can be used at the next time step of model integration.

It has to be noted this procedure only takes place during vegetative

development (for example, before flowering in the case of cereals). At the generative stage of ontogenesis, genetically based rules come into force and almost all growth resources are directed to reproductive organs regardless of nutrition limitation conditions.

The abovementioned sub-model of carbon-nitrogen interaction in plants is implemented in frames of AGROTOOL comprehensive model and verified on the base of representative set of experimental data from different soil-weather samples. It can be noted that such algorithm of adaptive key of primary assimilate distribution is the only but really sufficient AGROTOOL’s mechanism for description of nitrogen stress influence on plant growth and development.

2.2. A description of the AGROSIM crop model

AGROSIM is an agro-ecosystem model for agricultural crop stands under field conditions for limited and unlimited water and nitrogen supply, where homogeneous crop stands are assumed. AGROSIM also is a model of the third production level according to de Wit’s classification (de Wit, 1982), the same as AGROTOOL. The AGROSIM model, based on plant physiology, belongs to the group of soil-plant-atmosphere-management models. AGROSIM (a) is based on modules (sub-models), (b) uses rate equations for describing process dynamics (state variables and rates), (c) utilises a minimum time interval of one day for calculations and (d) is sensitive to weather, site and management. The AGROSIM model describes the following variables: ontogenesis, assimilation, respiration, assimilate distribution, redistribution of dry matter, biomass accumulation, yield formation, leaf area dynamics, senescence of above-ground and root biomass, root exudation, evaporation, transpiration, N-uptake by plant, water and nitrogen stress factors, frost killing and frost-lifting (for catch crops only), soil water, soil temperature, soil nitrogen, and percolation. For scaling biological

time, ontogenesis (Mirschel et al., 2005) is the most important process. Unlike other agro-ecosystem models well known in the literature, in the AGROSIM model, the algorithm describing assimilation is based on the biologically active green biomass, rather than on the leaf area index. Assimilation depends on green biomass, solar radiation, photo-temperature (daily average temperature between sunrise and sunset), accumulated biomass, short-term and long-term water stress events, nitrogen stress, atmospheric CO₂-content and day length. As the basis for the description of water stress factors within the AGROSIM model, soil water dynamics and transpiration values are calculated using algorithms of the BOWET layer-oriented soil water and evapotranspiration model (Mirschel et al., 1995). Soil temperature within the AGROSIM model is calculated using the SOIL_TEM model by Suckow (1986). The soil nitrogen component of the AGROSIM model is based on a simple balance model, taking into account a nitrogen mineralisation up to 60 cm depth following Rausch et al. (1985), nitrogen fertilization, atmospheric nitrogen deposition (dry and wet), nitrogen uptake by plant and nitrogen leaching. The model needs only standard meteorological values (temperature, solar radiation, precipitation, relative air humidity and wind speed) as driving forces and generally available inputs and parameters concerning plant and soil.

At present, the validity of the AGROSIM model has been confirmed for winter wheat, winter barley, winter rye, sugar beet and winter catch crops for different German locations. For winter wheat it also has been successfully proven for locations in the Netherlands, France, Poland, Hungary, Italy and Russia (Mirschel et al., 2004).

Detailed descriptions of the AGROSIM model have been given by Wenkel and Mirschel (1995), Mirschel et al. (2001), Mirschel and Wenkel (2007) and Mirschel and Poluektov (2010).

3. Results

3.1. Interpretation by means of the AGROTOOL crop model

The model-based production function was interrogated for the selected variables (spring wheat, Men'kovo experimental station, actual management and vegetation season 2013) where the abnormal shape (effect of local NUE decrease) was observed in reality. Investigations were carried out in the context of a specially designed multivariate computer experiment with the help of the APEX (Automation of Polyvariant EXperiments) software system developed at the Agrophysical Research Institute for multi-variant analysis of arbitrary crop models (Medvedev and Topaj, 2011; Medvedev et al., 2015). All influencing factors (“soil”, “cultivar”, “weather”, etc.) are fixed except for the factor “technology” or, more precisely, the dose of pre-sowing application of nitrogen fertilizer. This final factor varied in the interval of the investigated hypothetical intermediate plateau (60–150 kg N ha⁻¹) with an increment of 5 kg N ha⁻¹.

The obtained response curve for production function is presented in Fig. 4. The effect of intermediate plateau or even “local undershoot” having, in turn, rather strange shape, is evidently expressed. Surely, it

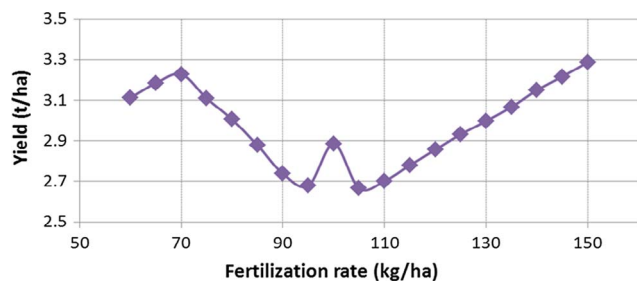


Fig. 4. The effect of the local minimum in a model-based “yield-fertilization” response curve (model: AGROTOOL; input data: actual conditions for field trial in Men'kovo Experimental Station in 2013).

does not completely correspond to the experimental results presented in Table 2 (we see well-formed local minimum instead of poorly defined inflection), so all below mentioned remarks can be considered only as a possible qualitative explanation of principal “abnormality” of production curve under chosen conditions. A clear understanding of the model algorithm allows an interpretation of this non-trivial behaviour to be proposed.

Such an explanation arises from the comparison of temporal dynamics of multiple model state variables (root biomass, Ψ_{RS} , total nitrogen uptake by roots) for different variants of nitrogen fertilization. It turns out that the principal difference takes place during a very short time interval – two to three days before anthesis (20–22 June 2013). It is reasonable to assume that these dates represent a critical period in a plant's lifecycle. Hence the impact of regulatory mechanisms is most significant in that time.

For the case under review, environmental conditions during this critical period caused the deficit of labile nitrogen to maintain coordinated plant growth for small doses of pre-sowing fertilization. Hence, all available resources are distributed to the roots ($\Psi_{RS} = 1$). Next, balanced growth ($0 < \Psi_{RS} < 1$) during the pre-anthesis time interval is possible for the variants with medium fertilization (75–85 kg N ha⁻¹). Finally, soil nitrogen content may even remain superfluous for the model plant in the case of high doses, so all resources go to shoot growth ($\Psi_{RS} = 0$) each day before flowering starts. The variation of simulated values of Ψ_{RS} during short time interval before start of anthesis (June 22) for different fertilization rates is presented in Table 4.

In spite of the brevity of the time range where the mentioned divergence occurs, it falls at the critical period of ontogenesis, characterised by an explosively high, near-exponential rate of accumulation of vegetative biomass. The achieved growth potential is high for that time. Therefore, the question of whether the root system grows or does not grow at this critical moment may cause the significant diversity in root biomass at anthesis. The relative difference between variants may reach 25–30% (see Fig. 5). This entails serious consequences after the switch to the generative development stage, where genetically conditioned limitations do not allow evaluating the weak root system. As a result, the coordinated growth cannot be further supported, and grain filling and, thereby, yield formation is depressed.

The indicated tendencies permit the qualitative and quantitative explanation of the observed effect of a partial decline in the production function. In fact, a nitrogen deficit for low doses of fertilization took place at the “proper” time. It enabled a powerful root system to be developed, which would maintain an acceptable level of nitrogen uptake during the rest of the vegetation period. Contrarily, very high doses of nitrogen leads to a relatively weak root system, but this defect can be overcome by sufficient soil nitrogen content during the whole vegetation period. Only for intermediate variants of pre-sowing fertilization were both negative factors (undeveloped roots along with an insufficient level of available soil nitrogen) present. As a result, a comparative reduction in total productivity occurred. Similar considerations make it possible to explain the presence of a small local maximum in a local undershoot of simulated production curve. It corresponds for the considered case to the partial growth of the roots at 16 and 22 June (see Table 4 also).

There is some “vaccination effect” – the nitrogen stress taking place before the critical period contributes to the formation of a powerful root system that can effectively take up nitrogen in the future. At the same time, the plants cultivated with a sparser regimen (with no nitrogen deficit before flowering) prove not to be ready for possible stress late in ontogenesis. Thus, the computer experiment with the crop model allows the non-trivial reaction of the simulated agro-ecosystem on increasing doses of pre-sowing fertilization to be “caught up” and explained. It should be noted that similar results were obtained earlier under a model-based investigation of top-dressing efficiency depending on the time and the rate of management actions (Gurin & Zaharova, 2013).

Table 4
Simulated dynamics of Ψ_{RS} values for different fertilization samples.

Fert. rate (kg N ha ⁻¹)	Simulation date							
	June 11	June 12	June 13	June 14–15	June 16	June 17–21	June 22	after
60	0.00	0.12	0.89	0.00	0.00	0.00	0.00	0.00
65	0.00	0.09	0.90	0.00	0.00	0.00	0.00	0.00
70	0.00	0.02	0.95	0.00	0.00	0.00	0.00	0.00
75	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.00
80	0.00	0.00	0.61	0.00	0.00	0.00	0.00	0.00
85	0.00	0.00	0.44	0.00	0.00	0.00	0.00	0.00
90	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00
95	0.00	0.00	0.08	0.00	0.08	0.00	0.00	0.00
100	0.00	0.00	0.00	0.00	0.06	0.00	0.26	0.00
105	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
> 110	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

3.2. Interpretation by means of the AGROSIM crop model

The AGROSIM model for winter wheat produces abnormal shapes of the production function only in very drought-stricken years characterised by special heat and drought anomalies during spring and early summer, i.e. during the vegetative growing period of winter wheat. Such extreme bad weather and growing conditions existed in 1992 in the north-eastern part of Germany. The period between the beginning of May and the end of August was characterised by very high temperatures – the four-month average was two degrees higher than average – and a precipitation deficit of more than 50% during the three months before harvest. Meteorologists called the summer of 1992 the “Summer of the 20th Century” (Gierk and Jungfer, 1993). The year 1992 should serve as a near-perfect example for explaining possible “abnormal” production function shapes in very hot and dry growing periods by the AGROSIM model using the specific weather, site and management conditions at Müncheberg Experimental Station, Germany.

For the interpretation of the simulated anomalies of the yield-fertilization curve for winter wheat caused by extreme climate stress situations during the growing period, it is necessary to describe the AGROSIM process algorithms for assimilation, for assimilate distribution, and for grain filling/yield formation in a greater detail. For the appearance of the production function anomaly caused by nitrogen

fertilization amounts, only the processes up to flowering are important. Nitrogen fertilizer after flowering mainly improves the grain quality by an increase in the grain protein content.

In AGROSIM, daily assimilation depends on the green biomass; on the entire amount of existing below-ground and above-ground biomass; on solar radiation, temperature and the atmospheric CO₂ content; and on water and nutrition uptake via the soil. In AGROSIM, only water and nitrogen uptakes are taken into account. Conversely, water and nitrogen stresses, which often are coupled to each other, decrease the daily assimilation rate. Daily assimilation shortages could be so manifest that the daily assimilation demands caused by crop maintenance respiration may not be able to be satisfied. AGROSIM introduces an assimilate pool in which all produced daily assimilates are stored. From this pool, assimilates are demanded by different processes and are distributed in a hierarchical manner: (1) for maintenance respiration, (2) for growth respiration, (3) for growth (separated into root and above-ground vegetative biomass) and (4) for grain filling. Assimilates for root and shoot growth are separated using an ontogenesis-dependent ratio. After flowering, the assimilates from the pool are available for respiration and grain filling, i.e. only those assimilates which remain after satisfying respiration process needs are available for grain filling. For days with very high water and/or nitrogen stresses, the assimilate production can be so low that it is not possible to satisfy the assimilate demand for maintenance respiration. On such days, additional

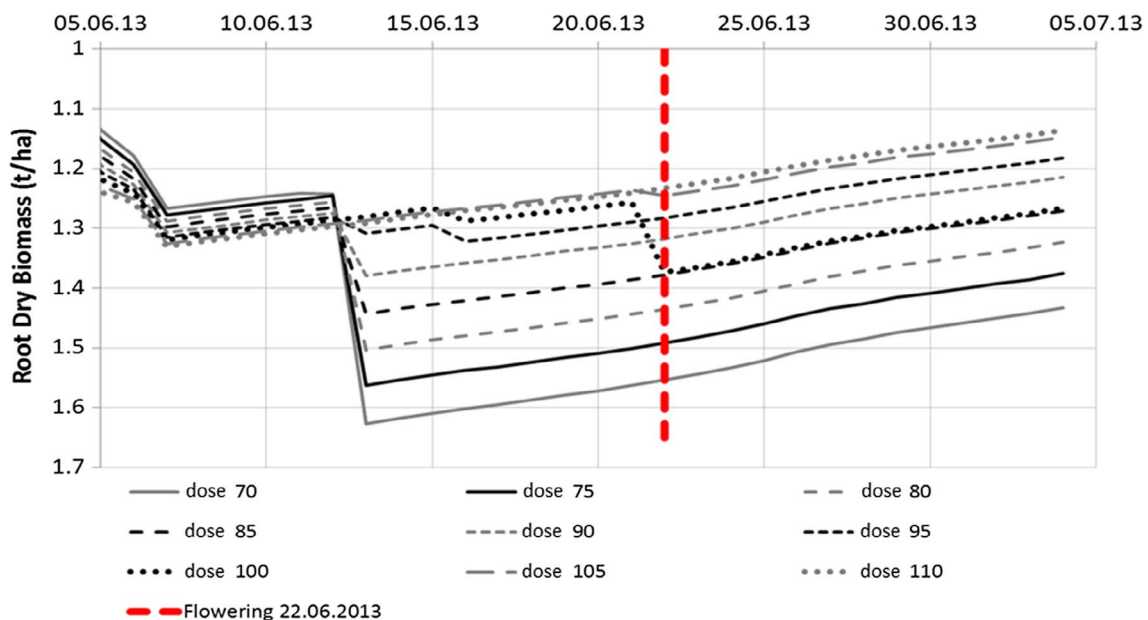


Fig. 5. Dynamics of root biomass for different simulation variants (pre-sowing fertilization intensities), computations using the AGROTOOL crop model.

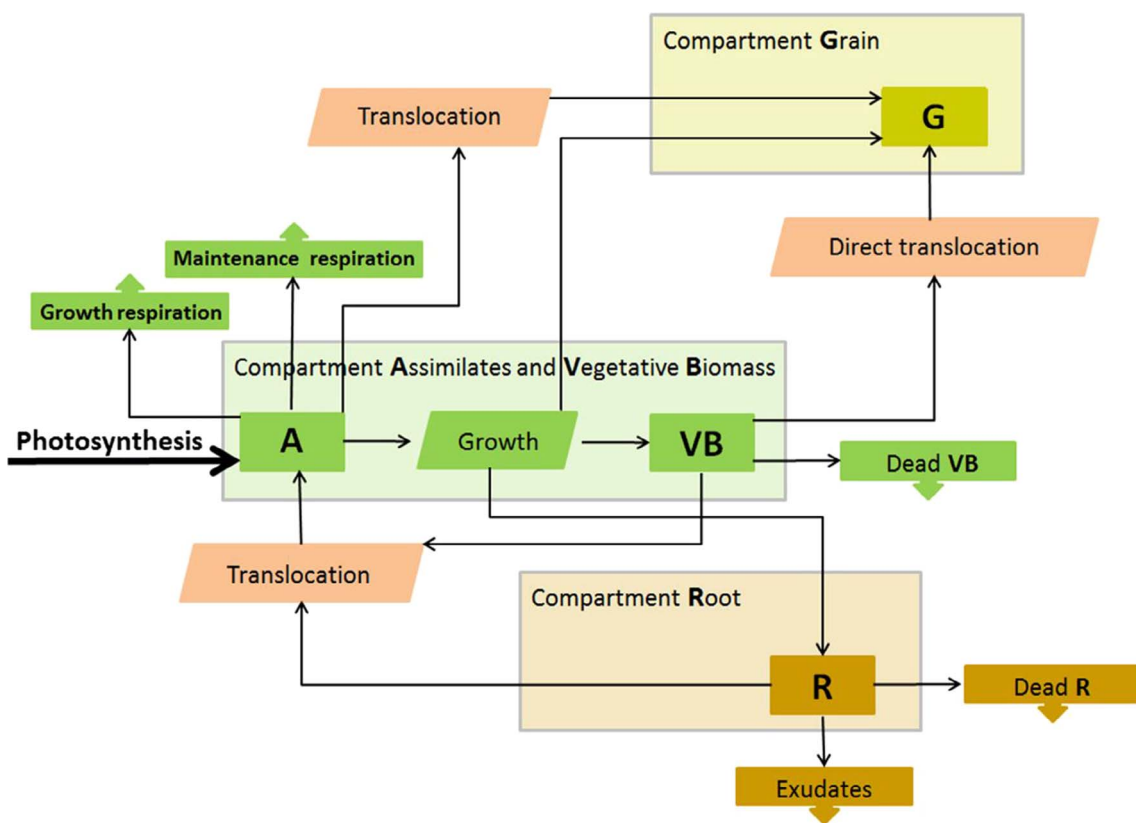


Fig. 6. Overview schema for the source, sink, distribution and translocation processes for biomass and their interactions within AGROSIM.

translocations of biomass from the root and from the shoot will be activated to satisfy maintenance respiration demands, i.e. the root and shoot biomasses will be reduced by these translocation rates. There is no root and no shoot growth and also no grain filling on such days.

Biomass accumulation during vegetative growth directly influences the ear and grain number dynamics per square metre. The ear number dynamics in AGROSIM depends on pre-existing vegetative biomass and on its daily growth rates; this is active between the beginning of shooting and the beginning of flowering. Based on the variety-fixed grain number per ear, AGROSIM calculates the grain number dynamics per square metre, taking into account the ear number and the daily water and nitrogen stresses, including possibilities after flowering. Water and nitrogen stresses are one reason for reducing the grain number per ear and consequently for reducing the grain number per square metre. Not in every case can this grain reduction be compensated for by an increase in thousand-seed weight during grain filling.

Fig. 6 gives an overview of the source, sink, distribution and translocation processes for biomass and their interactions within AGROSIM. A detailed description of all processes and model algorithms is given in Wenkel and Mirschel (1995).

A simulation using AGROSIM for winter wheat at Müncheberg, Germany shows that the high stress events regarding water and nitrogen levels caused by high temperatures and long drought periods in 1992 would very negatively affect biomass accumulation, ear and grain number dynamics and yield formation. AGROSIM simulation experiments with different nitrogen fertilizer amounts for 1992 with high and interacting water and nitrogen stress events up to the flowering stage resulted in a grain yield curve which had a local slowdown of the yield increase notwithstanding continuously increasing N-fertilization rates (see Fig. 7).

An analysis of causes for this local slowdown in yield increase, under the extreme stress situations in 1992, is only possible on the basis of a complex analysis of the interplay between soil and plant.

For all fertilization variants taken into account and simulated by

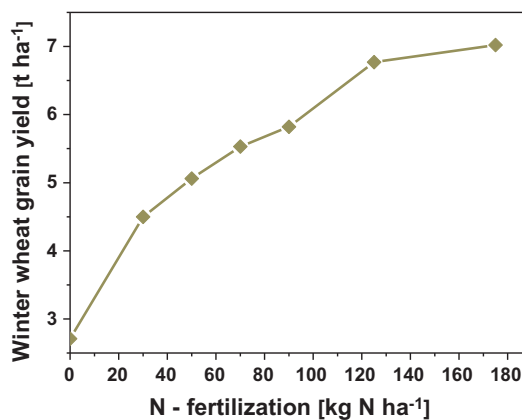


Fig. 7. Winter wheat grain yield in relation to N-fertilization simulated by AGROSIM for the dry year 1992 at Müncheberg Experimental Station.

AGROSIM from spring to the beginning of the drought period, the root biomass is developed in such a manner that the soil volume is occupied by roots big enough for an adequate water and nutrition supply for the winter wheat crop stand. For the N-fertilization variants higher than 90 kg N ha⁻¹, the soil nitrogen content is higher, and in these cases, the crop stand is oversupplied in terms of nitrogen. In the AGROSIM model, for such cases luxury storage of nitrogen within the biomass is present. This means that the nitrogen content in the biomass is significantly higher when compared to the ontogenesis-dependent nitrogen content threshold for the occurrence of plant nitrogen stress. In these cases, there is an additional nitrogen reservoir (luxury reservoir) in the crop stand which may help to bridge possible future nitrogen stress situations caused by an insufficient nitrogen supply via the soil. This is described in the AGROSIM model; the nitrogen stress value is calculated taking into account the ontogenesis-dependent threshold for nitrogen

Table 5
A summary of model-based interpretations.

	Necessary conditions	Key considerations
AGROTOOL interpretation	Non-optimal conditions (cloudiness etc.) for carbon assimilation in the short time interval before anthesis	<ul style="list-style-type: none"> • Root growth is hindered in a critical time window (a few days before flowering) for the cases of significant fertilization doses to maintain the balanced plant development. • As a result, a relatively weak root system forms up to the point of switching to the generative development phase and cannot be increased later. • This causes nitrogen stress during the rest of vegetation for medium doses of applied nitrogen.
AGROSIM interpretation	Increased water and nitrogen stress conditions for daily photosynthesis during vegetative growth in spring, early summer and summer	<ul style="list-style-type: none"> • Insufficient supply of maintenance respiration needs by daily assimilation for plants with medium nitrogen fertilization amounts induces a biomass translocation from roots and vegetative biomass to the assimilate pool. • As a result, root and green biomasses as well as water and nitrogen supplies via the root system are reduced; a luxury reservoir of nitrogen in the crop does not exist for medium nitrogen fertilization amounts. • Consequently in this case, ear and grain numbers are reduced and cannot be increased before harvest. • The grain filling rate is limited by a lower grain number that results in an overall yield reduction.

content in the biomass on the one hand and the degree of its shortfall on the other.

During the drought period in 1992, the maintenance respiration demands for existing biomass can be met by the daily assimilation rates for the nitrogen fertilization variants lower than 90 kg N ha^{-1} . As a result, these variants do not activate their assimilating translocation processes from root and vegetative biomasses to the assimilate pool. Compared to higher nitrogen fertilizer variants, the ear and grain numbers calculated for the lower nitrogen fertilizer variants are lower; this is caused by the lower vegetative biomass of these variants.

In the nitrogen fertilization variant of 90 kg N ha^{-1} , the accumulated biomass is higher before the start of the drought period compared to the lower nitrogen fertilization variants. This higher biomass resulted in a higher maintenance respiration demand. In 1992, AGROSIM calculated water and nitrogen stress factors that greatly reduced the daily assimilation rates for this nitrogen fertilizer variant. In this variant, the calculated nitrogen stress factor could not be compensated for by the crop stand because a luxury storage reservoir of nitrogen did not exist in this variant. As a result of all these factors, daily assimilation rates are reduced in such a manner that it would not be possible to supply the maintenance respiration demands. Here, AGROSIM activates biomass translocations not only from the above-ground vegetative biomass, but also from the root biomass. A reduced root biomass means a reduced rooting soil zone, i.e. a reduced root activity in the soil and, in consequence, a reduced nitrogen supply via the soil. The root exudation rates for soil micro-organisms are also reduced. As a result, the allocation of plant-available soil nitrogen by micro-organisms is decreased. This consequently means that the result of all these processes is a reduced biomass accumulation and, in turn, the grain number per square metre is still less than that of the lower nitrogen fertilizer variants because of higher nitrogen stresses. The consequence is that in the nitrogen fertilization variant of 90 kg N ha^{-1} , both the grain number per square metre and accordingly the daily grain filling are reduced; this results in a lower grain yield.

For the higher nitrate fertilization variants, a luxury reservoir for nitrogen in the crop stand biomass develops. This is the reason that in 1992 – for a short time in any case – the crop stand would be able to compensate for soil nitrogen stress events using its own nitrogen reservoir in the accumulated biomass. This resulted in a lower total stress for the crop stand in the higher nitrogen fertilization variants, and a relatively higher part of the maintenance respiration demand could be covered by the daily assimilates produced by photosynthesis. Based on this, in the higher nitrogen fertilization variants, the translocations from root and vegetative biomasses into the assimilate pool are lower. Compared with the nitrogen fertilization variant of 90 kg N ha^{-1} , this means a lower reduction of the active root biomass, a bigger or more

intensively rooted soil volume, higher root exudates for soil micro-organisms and a lower reduction in vegetative biomass. All these result in a smaller reduction in grain number and in higher levels of grain filling after flowering, and finally in a lower yield reduction.

4. Discussion & conclusions

We have suggested two different exploratory theories as interpretations of the effect of possible abnormal shape of production function. They are both based on an assessment of alternative mechanistic crop models. Table 5 presents a brief comparative summary of these model interpretations.

In the main model complexes both mechanistic agro-ecosystem models AGROTOOL and AGROSIM are structured similarly, but in the individual processes and algorithms taken into account they clearly differ in certain respects. Not only are the algorithms in both models different, but the explanatory rationales for the anomalies in the fertilizer-dependent production functions are as well. Nevertheless, in both models the main reasons for the anomaly are reductions in root biomass and reductions in root activity induced by nitrogen-related stress events. In AGROTOOL, the root system is decreased permanently, which means a nitrogen stress for the rest of the vegetation phase. In AGROSIM, on the other hand, a decreased root biomass during vegetative biomass growth results in a reduced grain number for the rest of the growing period up to harvest. High stress events can further reduce the grain number.

Surely, both proposed interpretations can provoke reasoned doubts. The results obtained from simulations can reflect the specific features of the models themselves, but do not concern the real object being simulated. Moreover, one can treat them as model artefacts or induced defects of an applied method of numerical computations. In particular, robust temporal discretisation of the models (with time intervals of one day) affects the conclusions to a great extent. Finally, it is always better to have a single unambiguous interpretation, rather than several interlocking hypotheses. However, principal qualitative conclusions drawn with the help of model consideration seems to be reasonable and can be a good starting point for later experimental as well as model-based researches. With other words, models are useful because they allow us to identify situations which have some unexpected behaviour (“abnormal” production function) and to interpret this behaviour more in detail.

Recently, the traditional view on the role and place of mathematical simulation models in agro-ecology and crop science has been changing significantly. Comprehensive theoretical models including a detailed description of all basic processes in a “soil-plant-atmosphere-management” system are still being developed. Nevertheless, the scope of their

possible application has converged bit by bit to rather narrow subject researches (Affholder et al., 2012). At the same time, simple regression models have once again returned as useful tools for many practical applications, such as for precision agriculture or in agricultural meteorology. The main advantages of such models are the simplicity and efficiency of their calculations coupled with a guarantee of obtaining interpretable and reasonable results for any input data. This benefit often prevails over considerations about scientific accuracy.

There are, however, possible objectives of model development outside of just practical applicability and utilitarian purposes. One of these would be the ability to use the model as a tool of purely scientific search, i.e. in theoretical investigations. Here, we note that the stability and predictability of the simplest regression models becomes rather disadvantageous. On the contrary, the complexity and structural richness of comprehensive mechanistic models can be understood as preferable. The research presented above demonstrates the potential ability of simulation approaches to be sources of new knowledge.

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