



Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

**Faculty of Natural Resources
and Agricultural Sciences**

Do Plants Require Nutrients in Similar Proportions?

A Possible Paradigm Shift

Joachim Nachmansohn

Independent Project at NL-faculty, SLU

The Agricultural Programme - soil/plant, Ultuna

Bachelor Thesis, 15 p

Do Plants Require Nutrients in Similar Proportions?

A Possible Paradigm Shift

Joachim Nachmansohn

Supervisor: Associate Prof. Dr. Tom Ericsson, Swedish University of Agricultural Sciences,
Department of Urban and Rural Development

Examiner: Associate Prof. Dr. Martin Weih, Swedish University of Agricultural Sciences,
Department of Crop Production Ecology

Credits: 15 hp

Level: G2E

Course title: Independent project in Biology - bachelor project

Course code: EX0689

Program/Education: The Agricultural programme - soil/plant

Place of publication: Uppsala

Year of publication: 2014

Online publication: <http://stud.epsilon.slu.se>

Keywords: plant, nutrition, nutrient, ratios, optimal, proportions, hydroponic, soilless, culture

Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Natural Resources and Agricultural Sciences

Department of Crop Production Ecology

ACKNOWLEDGEMENTS

I would like to express my greatest gratitude to the people who have helped & supported me throughout my project. I am especially grateful to my supervisor Tom Ericsson for his continuous support for the project, from initial advice & contacts in the early stages of conceptual inception & through ongoing advice & encouragement to this day. He radiates expertise, innovation and scientific rationality in the field of plant nutrition. He is a true scholar of plant nutrition.

A special acknowledgement goes to the great researchers and scholars of plant nutrition without whose sustained effort we wouldn't be able to look into these matters. I can't mention them all, however, I do want to mention Cees Sonneveld and Torsten Ingestad, whose works have been entirely necessary for this project.

A special thank of mine goes to my friend Robert Hilliard who so generously has helped me with proofreading and advice.

I wish to thank my parents, to whom I will always be indebted.

I want to express an enormous gratitude towards my wife for wholeheartedly supporting me. Without her I would be half a man, literally unable to succeed in life.

At last but not the least I want to thank my Creator, from whom all good comes and to whom all reason points. Without the help of Heaven I would never have finished this project. Finally I want to acknowledge the Creator in the grand words of Sir Isaac Newton:

”God is known from his works”

PREFACE

As an agronomist student I have encountered very different opinions and perceptions concerning the nutritional requirements of terrestrial plants. There are many aspects of plant nutrition. The area that caught my attention was the ratios of mineral nutrients in the nutrient supply and in the plants. That is, in what ratios do plants require the essential nutrients, in their uptake as well as in their tissues.

My interest was awoken for two reasons. First and foremost, I was presented with contradictions. The contradictions include different perceptions concerning what constitutes optimal nutrient ratios. It further include different opinions regarding whether or not plants in general share the same optimal nutrient ratios. On the same theme, I have met contradictory statements regarding how different nutrients affect different processes in plants. This incongruity was to be found in the oral presentations as well as in the literature of the agronomist curriculum. These contradictions are upheld by prominent professors, researchers and lecturers throughout the University. Furthermore, the University's network of farmers and plant producers as well as professional agricultural and horticultural advisers, all add to this contradictory state.

The second reason why this topic became interesting to me was because I encountered an unorthodox theory. Within the frames of the agronomist curriculum I was presented with a consistent elaborate theory that challenged most of the perceptions regarding nutrient ratios. The oddity about this theory is the perception that all plants require nutritions in the same proportions, regardless of species, habitat or morphology. Even though the perception is controversial it has received very little attention. Still, it is founded on decades of genuine research. Torsten Ingestad, the leader of the research team at the Swedish University of Agricultural Sciences (SLU), received the Wallenberg Prize in 1989, also known as the small Nobel Prize. He received the prize due to his efforts and innovation in the field of plant nutrition.

By reason of these contradictions this paper aims to study what is to be found in the literature concerning plant nutrition and required nutrient ratios. It also aims to look into the research behind the literature. This with the hope to find any sort of patterns or consensus, and if no such thing is to be found, at least evidence why assurance is not to be found yet in this field.

Joachim Nachmansohn

Gothenburg, 2013-06-07

ABSTRACT

Within the field of plant nutrition, specific nutritional requirements in plants are under constant scrutiny. In the predominant paradigm, it is held as a commonly accepted fact that different plant species have considerably different nutrient requirements, concerning the mutual proportions between the nutrients. However, the ruling paradigm shows signs of incoherence and give several examples of inconsistencies, sometimes even outright contradictions. As a result of profound research over the last four decades an elaborate contending theory have emerged. Its central hypothesis states that all terrestrial plants have the same basic nutritional requirements, concerning the mutual proportions between the nutrients, due to the same basic physiology. Foundational literature representing the predominant paradigm were surveyed. Likewise was the published materials from the research leading up to the challenging hypothesis. The issue were primarily compared through the medium of hydroponic production of soilless culture, due to the systems quantifiable properties. The results indicates that the validity of the predominant paradigm is questionable. Particularly in the light of the contending hypothesis, which stands strong under the lens of scrutiny. It were concluded that it is valid to question the legitimacy of the predominant paradigm, and that it is sensible to further investigate the challenging hypothesis.

ACKNOWLEDGEMENTS	
PREFACE	
ABSTRACT	
1. INTRODUCTION	7
1.1 Nutritional requirements	7
1.2 Nutrient ratios	7
1.3 Nutrient supply	7
1.4 Fundamental concepts explained	8
1.5. Analysis	9
1.6. Paradigm	9
1.7. Paradigm shift	10
1.8. Aims and Objectives	10
1.9. Limitations	10
2. MATERIALS AND METHODS	11
3. RESULTS	11
3.1 Challenging Theory	11
3.2. Established Paradigm	13
4. DISCUSSION	18
4.1. Initial Discussion	18
4.2. Strengths of Challenging Theory	19
4.3. Weaknesses in Challenging Theory	20
4.4. Strengths of Established Paradigm	21
4.5. Weaknesses In Established Paradigm	21
4.6. Explanations for Inconsistent Results	23
4.7. Possibilities if the challenging theory is correct	25
5. CONCLUSIONS	25
5.1 Summary Challenging Hypothesis	25
5.2. Summary Established Paradigm	26
5.3 Conclusion	26
6. REFERENCES	27
6.1 Published material	27
6.2 Unpublished material	28

1. INTRODUCTION

1.1 Nutritional requirements

In agriculture and horticulture the nutritional requirements of the crops have always had a central position in human effort to achieve optimal yields. Plant nutrition is absolutely essential if plants are to be able to grow and develop. Deficiency of nutrition can decelerate growth, inhibit development, cause damage to the plant, or even lead to plant death. An adequate nutrient supply that corresponds to the requirements of the crop is therefore necessary to achieve maximal yields with maximal quality (Marschner 1995, Mengel and Kirkby 2001, Epstein and Bloom 2005). A multitude of different elements have been found in plants through analysis. Seventeen elements were found in all plants and were later discovered to be essential. The three most common elements in plant tissue are carbon (C), oxygen (O) and hydrogen (H). They are predominantly absorbed from the carbon dioxide in the air through the photosynthesis process, and through the water uptake from the soil. The remaining fourteen are referred to as mineral nutrients, since they derive from the minerals in the soil, except for nitrogen that is derived from the air. Nitrogen (N), phosphorus (P), potassium (K), sulfur (S), magnesium (Mg) and calcium (Ca) all occur in relatively high concentrations in plant tissues, and are therefore referred to as macronutrients. Iron (Fe), manganese (Mn), Boron (B), zinc (Zn), copper (Cu), chloride (Cl), molybdenum (Mo) and nickel (Ni) all occur in considerably lower concentrations, and are hence referred to as micronutrients. (Marschner 1995, Benton 1998)

1.2 Nutrient ratios

When nutrient content of plants are determined, it is often presented as percentage of the dried biomass, or as g nutrient per g dry substance (Marschner 1986, Benton 1998). This can be problematic when different species and types of plants are to be compared. Different plants, plant parts and organs differ considerably concerning nutrient content and composition. To enable a simple, yet consistent and relevant comparison between different plants, the nutrient content can be presented as ratios describing the internal proportions in between the nutrients. Conventionally, such proportions are denoted as nitrogen ratios. Nitrogen ratios signifies that the nitrogen content is set to 100, and that the other nutrients are specified in percentage of the nitrogen content (Sonneveld 2002, Knecht and Göransson 2004).

1.3 Nutrient supply

To work with concentrations in supplied nutrient solutions is a way to keep track of how much plant nutrition that is added to a culture. The concentrations of the nutrient solution in the rhizosphere creates a gradient, causing a specific uptake by the plant. The higher concentration, the higher uptake rate, and vice versa. Upholding of desirable concentrations is common in commercial greenhouse plant production, as well as in corresponding field of academic research. The aim is to find and uphold those concentrations that favors fast growth of high quality, and at the same time avoid deficient or toxic values.

Another way to add plant nutrition is by supplying amounts of nutrients over time. In such case the concentrations of the nutrients in the supplied solution is irrelevant for the nutritional requirements of the plants. Instead it is the total mass of added nutrients per unit of time that is interesting. This way of measuring added nutrients lies closer to the absolute measure of growth in a culture. Since growth is defined as increase in mass of the dry substance, the amount of nutrients measured in mass per time unit, corresponds adequately to plant growth.

1.4 Fundamental concepts explained

1.4.1 Liebig's law of the minimum

Liebig's law of the minimum refers to principle that growth within a plant be due to the access of the nutrient which the plant has least access to in relation to its requirements. Further the law states that if a plant has deficit of one nutrient it has a surplus of the other nutrients (Liebig 1940, 1955).

1.4.2. Relative growth rate R_G

Relative growth rate (R_G) is increase of mass per plant biomass and time, for example $g\ g^{-1}\ d^{-1}$. Relative growth rate is used as a tool to quantify growth rates in different plants, which is useful when comparing growth between different plants. There is often focus on the increase of biomass above soil surface. In such case R_G is defined as increase of biomass per plant biomass above soil surface and per time unit. However, since this paper studies the actual needs of the whole plant, R_G is henceforth defined as increase in mass per total plant biomass and per time unit.

Hence maximum growth is maximal R_G ($R_{G,max}$), when a plant is growing according to its own maximum genetical conditions during optimal circumstances.

1.4.3. Steady state

Steady state is required to make comparisons meaningful, when studying plant growth. The plants must have an internal unvarying condition concerning physiological processes. General surrounding circumstances must also be similar. Otherwise the correlation between plant growth and nutritional requirements can't be quantifiable. A good way to achieve a meaningful comparison between growth rates in such respect, i. e. in steady state, is to compare $R_{G,max}$ of different plants. Figure 1 displays R_G as function of the nutrient concentration in the plant (Knecht and Göransson 2004).

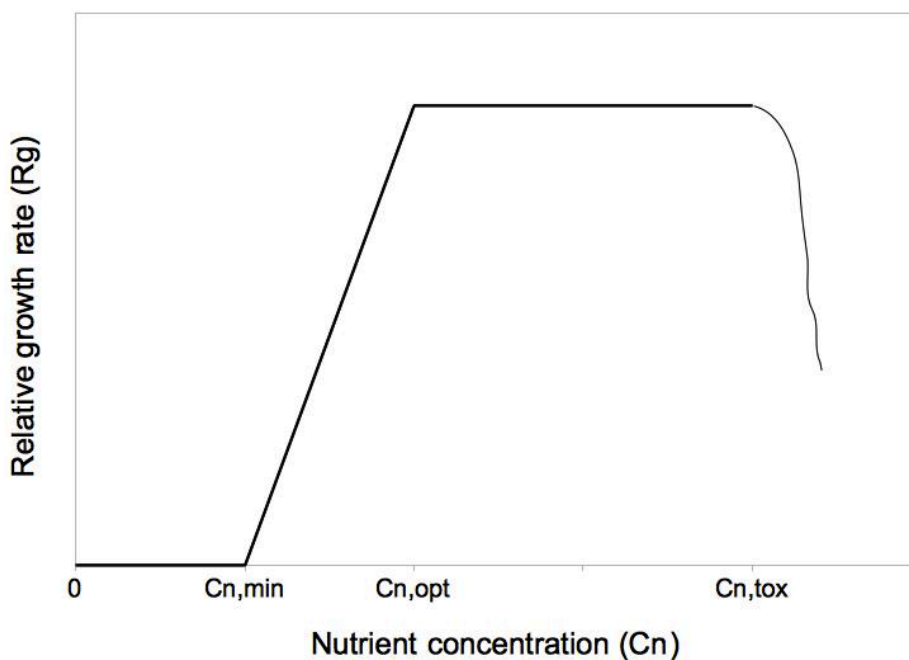


Figure 1. Definitions of growth responses in relation to nutrient concentrations in plants. The minimum concentration ($c_{n,min}$) of the nutrient is denoted “structural amount,” indicating that small amounts are required in structural compounds or to trigger mechanisms. The concentration range between $c_{n,min}$ and $c_{n,opt}$ is the response range, and concentrations above $c_{n,opt}$ are in the sufficiency range. At high concentrations ($c_{n,tox}$), nutrients become toxic and the growth rate decreases. We define this as the toxicity range. Picture with explanation are redrawn and quoted from Knecht and Göransson (2004).

1.5. Analysis

To study plant nutritional requirements analysis's of different substances are required. Obviously the applied nutrient solution needs to be analyzed in order to determine aspired nutrient proportions and concentrations. Though, it is the properties of the solution in the rhizosphere that is of central importance, since that is the solution that the plant actually assimilates. Thus, it is only the nutrient solution in the rhizosphere that can be optimal or universal regarding the concentrations and the ratios of the nutrients (Sonneveld 2002).

Analysis of plants and plant parts are somewhat different however. The nutrient composition of the tissue is determined as concentration in the plant, or as weight percentage of the dry substance. Therefore the nutrient content in plants are not defined as concentration in the generic way i. e. in mol l⁻¹, but in g nutrient g⁻¹ plant dry substance.

1.6. Paradigm

The predominant perception in the academical world is that plants nutritional needs regarding the mutual proportions of the nutrient vary according to species, physiological age and external factors (Silber and Bar-Tal 2008, Christensen and Hansson 2010).

All-purpose solutions have existed for a long time (Hoagland and Arnon 1938), and since then numerous tables of compositions have been published for different crops in soilless culture (Sonneveld 2002, Silber and Bar-Tal 2008). However, compositions for all-purpose use are considered approximative and are intended for universal use or a specific group of plants. Exact composition of the nutrient solution is still due to previously mentioned differences, such as species etc (Sonneveld 2002, Silber and Bar-Tal 2008, Christensen and Hansson 2010).

The different biochemical processes in the plant obviously requires different elements to synthesize different amino acids and other building blocks in the cells. However, certain nutrients are associated with specific properties, organs or processes in the plant. That nitrogen stimulates growth, phosphorus is favorable for the roots, blooming and fruit-setting, and that potassium strengthens plants before winter, are all examples of conventional understanding of plant nutrition (Ericsson 2006, 2007b). Perhaps this is one explanation for the dissimilar nutrient needs in between plants.

Within commercial plant production, plant cultivation consulting and fertilizer production, the same perception is predominant, that plants have different basic needs. Different compositions of nutrient solutions are used for different crops as well as for the same crops, all depending on the grower. This parallels field agriculture, as the farmer applies fertilizers according to own judgement and experience. The practice go back to old research and literature, now forgotten by most professional growers and consultants (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Alnarp, unpublished data).

The market of commercial fertilizers communicates the same perception. Fertilizers of radically different compositions are manufactured and distributed. Specially custom made fertilizer can be found for virtually any species or plant type. The motivation given for the wide span of nutrient compositions are that different plants have fundamentally different nutritional requirements (Ericsson 2006).

All these facts, perceptions and theories represents a paradigm. The collective impression of the paradigm is, not only the perception that nutrient requirements regarding the mutual proportions of the nutrients vary according to species, physiological stage etc, but also that it lacks a general consensus to what constitutes the differences, and that it reinforces contradictions. The paradigm is

well established and is still predominant in the academical world; in literature such as dissertations, books and teaching material. It is equally predominant within the commercial world among professional producers, advisers and manufacturers. This paradigm with all its implications will henceforth be referred to as the established paradigm

1.7. Paradigm shift

That all plants have the same basic nutrient requirements due the same basic physiology, and thus requires nutrients in similar proportions, is the basic thesis in the challenging theory. Extensive laboratory and field experiments combined with literature research have led up to the hypothesis that all terrestrial plants have the same basic nutrient requirements regarding the mutual proportions of the nutrients (Ericsson 2006). According to the hypothesis all plants at maximum growth and at steady state requires nutrients in similar proportions. This means that the plant has the same nutritional need throughout its growth and development (Knecht and Göransson 2004).

The theory explains that the dissimilarities between the plants lies not in nutrient requirements regarding different proportions, but in their different total need thereof. It further explains differences between plants in terms of abilities opposed to varying nutritional needs. Such abilities could be skills to cope with extreme environments or competing capacities. Thus, a plant in a desert compared to a plant in a rainforest still basically requires nutrients in the same proportions (Ericsson 2006, 2007a).

According to this view recommended nutrient proportions for nutrition supply is found to be basically the same for all plants. The mutual nutrient proportions recommendable for a demand-driven nutrient supply will henceforth be referred to as recommended proportions. The theory have also extrapolated optimal nutrient proportions from experiments. Optimal nutrient ratios are defined as the ratios found in plants when all nutrients limit growth simultaneously (Knecht and Göransson 2004), in accordance with Liebig's law of the minimum. The mutual optimal nutrient proportions were found to be universal and distinguishable. The mutual nutrient proportions that makes up the actual and universal requirements of plants will henceforth be referred to as optimal proportions.

This hypothesis with its theoretical considerations and all its implications and consequences represents a challenge for the established paradigm. It will henceforth be referred to as the challenging hypothesis.

1.8. Aims and Objectives

The aim of this paper is to test the hypothesis that all terrestrial plants have the same basic nutritional requirement, in regard to if they require nutrients in similar proportions. The objective is neither to prove or disprove anything. Such aspiration would demand a vastness and profoundness far beyond what could be supplied by a bachelor thesis. Rather the objectives are to find out if there is enough evidence to support the challenging theory, and enough inconsistencies and gaps in the established paradigm to question its validity.

1.9. Limitations

Plants require different total amounts of nutrition (Voogt 2003, Silber Bar-Tal 2008). That is not in question by anyone. This paper examines required ratios in between nutrients. Thus, within the framework for this paper, plant nutrition will henceforth refer to, the mutual proportions between the 14 essential mineral nutrients, that plants require.

Certainly plant nutrition obviously includes all types of cultures and plant production. However, those cultures where the nutrient supply has maximum control are those that can control water and nutrient supply continuously. Hydroponic production in soilless culture offers a very high degree of control of the nutrient supply (Voogt 2005). Due to this, within the framework of this paper, hydroponic systems will be the main medium to study nutritional requirements and nutrient solutions. Though, the theories of plant nutrition are equally valid for any production system, since it is the need of the actual plant that is under scrutiny.

2. MATERIALS AND METHODS

The examination behind this paper are in all respects a literature study, with the minor exception of consultations with academical experts. Fundamental and basic literature concerning nutritional requirements, and nutrient concentrations and proportions, have been examined. The literature examined were mainly written from a perspective of human production, e. g. horticulture or agriculture, but also from an ecological one, i. e. from the plants perspective. Primarily scientific articles, academic books and study material, were used as materials. In a lesser extent also a few popular scientific articles have been examined.

The matter of plant nutrition requirements concerns all types of crops in any kind of culture, including all forms of nutrient supply. However, this examination is limited to matters concerning nutrient requirements regarding the mutual proportions between the essential nutrient elements.

Expert researchers and lecturers at SLU have been consulted, orally as well as through email correspondence.

Furthermore, a superficial overall examination of the commercial world have been undertaken. Commercial plant production, agricultural and horticultural consultation, and fertilizer production have been scrutinized enough to establish general trends.

All the materials have been compared mutually in the process of research to reach the aims and objectives.

3. RESULTS

3.1 Challenging Theory

There is a strong and wide evidential base for the hypothesis that all terrestrial plants share the same basic nutritional requirements, concerning the mutual proportions between the essential nutrients. Furthermore, the evidential foundation is equally strong to suggest that, these mutual ratios are constant, during the different stages of development in plants, at maximum growth ($R_{G,max}$) and steady state.

There are in both frequency and time extensive research, in the shape of laboratory and field experiments at SLU, which shows that the proportionate needs for the essential nutrients are fundamentally the same for all plants, regardless of species. A multitude of different species of great dissimilarities concerning morphology and habitat were included in the experiments. Species included in the research were birch, basket willow, poplar, alder, eucalyptus, Norway spruce, Scots pine, cucumber, tomato, blueberry, lingonberry, duckweed and the four types of grain (Ericsson 2006). The conducted research has primarily examined seedlings and young plants, and thus primarily the vegetative phase. Though, experimental research on whole life cycles have been conducted as well (Ericsson 2006). Furthermore, the same research has determined with a high degree of accuracy how these ratios are constituted (Ingestad 1979, Ingestad 1982, Ingestad and

Lund 1979, Ericsson and Ingestad 1988, Ågren 1988, Ericsson and Kähr 1993, Göransson 1993, Ericsson and Kähr 1995, Göransson 1994, Sinclair et al. 1997, Göransson 1999, 2001).

A strong evidence for the hypothesis is that it was frequently shown in laboratory experiments, that when plants were supplied with free access to nutrients, the proportions between N, P, K, Ca and Mg were similar regardless of plant species (Ericsson 1981, Ingestad and Stoy 1982, Ingestad and Kähr 1985, Ingestad and Ågren 1988). There are also similar experiments on sulfur and the micronutrients. In total, the nutritional need for all essential nutrients except Ni have been studied by Ingestad and coworkers (Ericsson 2006). However, excess uptake of nutrients does occur in plants when they are given free access to nutrients (Knecht and Göransson 2004). Therefore further laboratory experiments were undertaken, where the supply rate of the nutrients was reduced until it didn't occur any excess uptake, in accordance with Liebig's law of the minimum. This detailed laboratory research shows a theoretical optimum of the proportions between the nutrients (Ericsson and Ingestad 1988, Ericsson and Kähr 1993, 1995, T. Ericsson, Swedish University of Agricultural sciences, unpublished data). The results of the laboratory and field experiments are summarized in Table 1 (Ericsson 2006).

Table 1. Nutrient requirements of plants in nitrogen ratios, according to the challenging hypothesis at steady state and maximum growth. Column A displays nutrient content in plants at free access to all nutrients. Column B displays the nutrient content in plants when all nutrients simultaneously limits growth (i. e. at $C_{n,opt}$).

Macronutrient	A	B	Micronutrient	A	B
Nitrogen (N)	100	100	Iron (Fe)	0,7	0,4
Phosphorus (P)	13-19	8	Manganese (Mn)	0,4	0,3
Potassium (K)	45-80	30	Boron (B)	0,2	0,05
Sulfur (S)	8-9	5	Zink (Zn)	0,06	0,02
Magnesium (Mg)	5-15	4	Copper (Cu)	0,03	0,05
Calcium (Ca)	5-15	4	Chloride (Cl)	0,03	*
			Molybdenum (Mo)	0,003	*

Even though optimum ratios have been determined on a valid foundation, further verification through laboratory experiments are necessary (Göransson and Eldhuset 2001).

As table 1 displays, column A are the uptake ratios when there are free access to all nutrients. This suggests that those ratios are recommended when supplying nutrients, as a little excess uptake is a healthy safety precaution (Ericsson 2006). This is also supported by Göransson and Eldhuset (2001) as they found examples of a lower growth rate when plants were supplied with optimum nutrient ratios opposed to free access. Another consequence when comparing column A with column B is that if a plant is supplied with nutrients according to column A, and the amount supplied is deficient, it will cause nitrogen deficiency due to the fact that all other nutrients are assimilated in a small excess. Thus the challenging hypothesis specifies both recommended nutrient ratios and optimal nutrient ratios.

Further, extensive and vast literature concerning nutrient concentrations has been scrutinized with the aim to examine nutrient ratios in terrestrial ecosystems (Knecht and Göransson 2004). The proportions calculated out of the literature was found to correspond closely to the proportions determined in laboratory and field experiments. Distinctive patterns were observed, that corresponds to both theoretical predictions as well as to laboratory experiments, despite the variations in the ratios between the nutrients that occur in nature (Knecht and Göransson 2004).

Knecht and Göransson (2004) also suggests optimal nutrient ratios, which are shown in table 2. Their suggestions corresponds closely to those in table 1 by Ingestad et al.

Table 2. Suggested optimal nitrogen ratios according to Knecht and Göransson (2004). A single asterisk denotes plant supplied with nutrients at free access and a double asterisk denote birch seedlings supplied with nutrients such that no excessive uptake occurred.

Plant type	Suggested optimum nutrient ratios				
	N	P	K	Ca	Mg
Deciduous plants *	100	14.6	64.6	7.0	9.4
Coniferous plants *	100	15.0	47.5	8.0	7.5
Herbaceous plants *	100	14.3	68.3	8.3	8.7
Birch **	100	8	30	2	4

However, there are anomalies from the suggested ratios. Within the field of commercial production of fruit tissue, and to some extent root vegetables, the potassium ratio are higher. In such production the potassium concentration is higher in fruit tissue compared to root, foliage or stem tissue in the plant. Thus, the potassium need is greater in the generative phase than in the vegetative phase. The nitrogen proportion of potassium is so forth greater in commercial production, than otherwise stated by the hypothesis of universal optimal ratios (Ericsson 2006).

The evidence material thus shows a consistent and coherent model, that consists with experimental measurements. The results are moreover verified through extensive frequency and generality in the experiments. Thus the evidence is reliable, quantifiable and comparable. The evidence material in support of the hypothesis is clearly strong.

3.2. Established Paradigm

3.2.1. Within the Academical world

It exists a state of consensus in the academical world that there are no optimal nutrient ratios of universal or general constitution. Nor that such notion would describe a common or generic requirement for nutrients in plants (Marschner 1995, Sonneveld 2002, Silber and Bar-Tal 2008). In the literature, in articles as well as books, there is an evident recurrence of the doctrine that the nutritional requirement regarding the mutual proportions of the nutrients depends on the species of the plant, its stage of development and external circumstances (Sonneveld and Voogt 1986, Sonneveld 2002, Silber and Bar-Tal 2008, Christensen and Hansson 2010).

There is extensive research and a multitude of laboratory experiments through which nutrient compositions have been developed. The composition of these solutions is species specific compositions, carefully balanced for certain crops during different circumstances (Adams and Massey, 1984; Van Goor et al., 1988; Savvas and Lenz, 1995, Silber and Bar-Tal 2008).

The vast multitude of known compositions all show the different nutritional requirements for different plants and different physiological age. This regardless if the nutrient ratios are examined in applied solution, the solution in the rhizosphere or the uptake concentration. This is highly relevant, since the nutrient supply is the single most important factor for the nutrient content in plants dry substance (Marschner 1995, Sonneveld 2002). The second most important factor is physiological age (Marschner 1995, pp. 466). Examples of variations in nutrient uptake between different species are presented in table 3 and 4.

Table 3. Different ratios in the nutrient uptake of tomato and sweet pepper at high yield levels of commercial nurseries (Sonneveld 2002).

Nutrient	Tomato	Sweet pepper
Nitrogen (N)	100	100
Phosphorus (P)	24	16
Potassium (K)	173	137
Sulfur (S)	25	14
Magnesium (Mg)	17	12
Calcium (Ca)	71	49

The adequate range of nutrient contents differ between plant species according to the established paradigm. Moreover, this has also been shown even in comparisons between the same organs at the same physiological age of different species (Marschner 1995, pp. 470). These variations are mainly based on differences in the metabolism and constitution between different plants (Marschner 1995, pp. 470). Table 5 displays the adequate range content in different species (Marschner 1995, pp. 471). The data given in table 5 are based on average values, and do not offer exact nutrient requirements. Table 5 also shows that data of nutrient contents in plants are more similar to the data in the challenging theory, than the data of different nutrient solutions, such as in table 3 and 4.

Table 4. Ratios of uptake concentrations of macronutrients in different greenhouse crops (Sonneveld 2002).

Nutrient	Cucumber	Sweet Pepper	Radish (summer)	Radish (winter)	Tomato	Rose	Gerbera
Nitrogen (N)	100	100	100	100	100	100	100
Phosphorus (P)	18	18	10	7	25	17	15
Potassium (K)	151	129	146	145	178	102	191
Sulfur (S)	17	14	17	12	29	18	9
Magnesium (Mg)	11	12	8	9	16	10	8
Calcium (Ca)	63	55	40	49	66	49	45

Within both research and academic educational literature on species specific nutritional requirements, emphasis on the development stage are of significance. In particular the importance of the generative stage is emphasized (Sonneveld 2002, Voogt 2003, Silber and Bar-Tal 2008). Another phase that stands out is the plantlet stage before transplanting (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Alnarp, unpublished data). Though, research shows that several factors have palpable importance for the nutritional requirements. Main factors are development stages and sub-stages such as transplanting, anthesis, blooming, fruit growth and fruit ripening. There are also other factors such as harvesting, and cycles of fruit waves. The importance of these factors for the nutrient supply is described by data in table 6 (Silber and Bar-Tal 2008).

In general, the potassium requirement increases and the nitrogen requirement decreases in the generative phase, compared to the vegetative phase (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Alnarp, unpublished data). There is also examples of an increase in the requirement for other nutrients in the generative phase. Such examples could be increased need for Ca or Mn (Sonneveld and Voogt 1986, K.-J. Alnarp, Swedish University of Agricultural Sciences, Uppsala, unpublished data).

Table 5. Ratios of mineral nutrient contents in plants, when all nutrients are in the adequate range in the plant, based on average values.

Species	Organ	N	P	K	Ca	Mg
Spring wheat	whole shoot	100	10-11	84-97	13-22	5-22
Ryegrass	whole shoot	100	12	83	20-29	7-12
Sugar beet	mature leaf	100	9-10	88-100	18-33	8-12
Cotton	mature leaf	100	8-11	47-74	17-32	10-17
Tomato	mature leaf	100	10-12	75-109	73-75	9-15
Alfalfa	upper shoot	100	9-12	71-76	29-50	9-16
Apple	mature leaf	100	8-11	50-54	59-79	9-13
Orange	mature leaf	100	4-9	50-57	125-200	10-20
Norway spruce	1-2 year-old-needles	100	10-15	37-71	26-47	7-15
Oak; Beech	mature leaves	100	8-10	50-53	16-17	8-10

Table 6. Recommended nutrient solution compositions matched to the growth phase in soilless culture in Israel, according to Silber and Bar-Tal.

Growth phase	N	P	K	Ca	Mg
<i>Strawberry in green house</i>					
Transplanting	100	39	91	113	65
Anthesis and first fruit wave	100	29	103	129	58
Second fruit wave	100	33	103	121	55
Third fruit wave	100	33	103	121	55
Fourth fruit wave	100	39	100	139	61
<i>Summer sweet pepper in green house and net house</i>					
Transplanting to blooming	100	100	141	*	*
Anthesis to fruit growth	100	100	122	*	*
Fruit ripening and harvesting	100	100	136	*	*
Fruit harvesting	100	100	136	*	*
<i>Fall-winter tomato</i>					
Transplanting	100	41	153	235	53
Blooming and anthesis	100	26	148	177	33
Fruit ripening and harvesting	100	18	126	105	24
Fruit harvesting	100	26	148	148	33

Universal nutrient solutions have been around since Hoagland and Arnon (1938). Since then a multitude has been developed and published. A draft of the most basic examples are displayed in table 7.

Table 7. Nutrient ratios in nutrient solutions recommended for universal use, for the growing of plants in hydroponic systems. Also called universal nutrient solutions (Sonneveld 2002).

Nutrient	Hoagland a	Hoagland b	Steiner	Naaldwijk
Nitrogen (N)	100	100	100	100
Phosphorus (P)	15	28	19	18
Potassium (K)	111	104	168	116
Sulfur (S)	30	14	66	57
Magnesium (Mg)	23	11	29	36
Calcium (Ca)	76	71	108	107

However, there are no universal nutrient solutions per se, but only universal compositions of nutrient solutions in the rhizosphere in the sense that most crops can be grown in it. The composition of a universal nutrient solution is merely such that, that the crops grown in it is without symptoms of deficiency or toxicity (Sonneveld 2002). Therefore, there are no universal solutions with optimal nutrient proportions with regard to the requirement of the plants as such, but rather with optimal proportions concerning the possibility of all-purpose use (Silber and Bar-Tal 2008).

3.2.2. Within the Commercial World of Plant Production

Commercial plant production is characterized by the lack of consensus regarding nutritional needs. Instead, composition of nutrient solutions for the nutrient supply are largely based on empirics and generally accepted knowledge which often lacks valid references (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Uppsala, unpublished data).

Evidence was found that indicate a lack of information in modern soilless culture practice, regarding calibrating recipes for specific crops. Even though there is research covering species specific requirements, recipes used to prepare nutrient solutions are often chosen largely at random or developed empirically (Savvas and Adamidis 1999). Hence, such practice has distinct random tendencies.

There is agreement in the commercial sector that plants in general have different basic nutritional requirements regarding the mutual ratios between the nutrients. However, it is not agreed exactly what specific species require. What is generally agreed or disagreed on, goes for both professional producers as well as for consultants and advisors (K.-J. Alnarp, Swedish University of Agricultural Sciences, Uppsala, unpublished data).

More importantly there is no consensus regarding what constitutes generally accepted knowledge, specifically when it comes to start values or adjustments for nutrient solutions. Although, there are some fundamental literature to consult, by for example C. Sonneveld and De Kreij, the awareness of those sources are weak due to the acceptance of what is considered general knowledge (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Uppsala, unpublished data).

Concentrations by De Kreij (1997) for cucumber, that corresponds with approximative start values in common practice within soilless culture, are presented in table 8.

Table 8. Start values for the nutrient ratios in a nutrient solution for cucumber, in mainstream commercial production, according to De Kreij.

Macronutrient	A
Nitrogen (N)	100
Phosphorus (P)	22
Potassium (K)	142
Sulfur (S)	18
Magnesium (Mg)	13
Calcium (Ca)	62

Experienced farmers and advisers have modified their own recipes out of these conventions. The development process is due to different growing circumstances, quality of water and climate. Experience of physiogenic damage and plant diseases, vary between farmers, which also influences the modification of nutrient compositions (K.-J. Alnarp, Swedish University of Agricultural Sciences, Uppsala, unpublished data).

That the nutritional need of the culture varies, is a commonly held perception. Physiological age is attributed greatest significance. As in the academical world, also here the generative phase stands out the most, but the plantlet stage also stands out (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Uppsala, unpublished data). Reasons for changing the ratio of a specific nutrient, besides accommodating an actual need per se, can also be to favor or prevent certain processes. Especially high potassium levels are associated with several good traits, such as high yields and high levels of vitamins (El-Nemer et al.). For instance nitrogen can be supplied to favor growth, and molybdenum to favor blooming. To prevent damage the ratio of a nutrient can be increased, for instance calcium to prevent pistil rot. Professional farmers strives to meet the current needs of the culture. Which is done most precise through the process of analysis of outgoing nutrient solution, drainage solution and leaf juice (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Alnarp, unpublished data). However, experienced growers are certain enough to adjust the nutrient solution through ocular inspection and timing. Therefore, most growers can decrease the frequency of analysis's needed, and do adjustments based on instinct (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Alnarp, unpublished data).

Another important aspect derives from the focus on total ion concentration. Within hydroponic production, specific and often high total ion concentrations are sought after (Sonneveld and Welles 1988, Sonneveld and Voogt 1990, Sonneveld 2002). This immediately affects the nutrient ratios. For instance in the end of the culture when the nitrogen concentration is decreased, the concentration of at least one other nutrient must be increased to uphold, the same coveted total ion concentration. A common way to do this is to add more inexpensive fertilizers, such as $MgSO_4$. By doing so the proportion of N decreases, and the proportions of Mg and S increases (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Alnarp, unpublished data).

3.2.3. Within the Commercial World of Fertilizer Production

Within the commercial world of fertilizer production there is a consensus that plants have different nutrient requirements concerning the mutual proportions of the nutrients. A great variety of species are considered to have such dissimilar nutritional requirements that all of them are dedicated with their own custom composed fertilizer with different nutrient ratios (Ericsson 2006). Bonsais, citrus plants, ficus trees, orchids, roses, cactuses, palm trees, climbers, rhododendron and summer

flowers , etc., are all samples of different species and plant types that have their own custom made fertilizer (Ericsson 2006). However, the market disagrees in how the custom made fertilizers are to be composed (Ericsson 2006). A clear example of disagreement in how to accommodate the requirements of rhododendron is displayed in table 9.

Table 9. Compositions of nutrient ratios in different brands of fertilizers that are custom made for Rhododendron (Ericsson 2006).

Product/Manufacturer	N	P	K
Bayer	100	66	73
Compo	100	15	58
Plantagen	100	22	55
Pokon	100	44	106
Pokon/super	100	114	214
Substral	100	100	150
Växa	100	44	106
Weibulls	100	18	45

4. DISCUSSION

4.1. Initial Discussion

The hypothesis that all terrestrial plants have the same basic nutritional requirements, with regard to the mutual proportions of the nutrients, is well substantiated. Likewise is the established paradigm that plants in general have different needs due to species, etc. It is undeniable that both theories are founded on extensive research and empirical data. The established paradigm has a well substantiated tradition, which is established by a long lineage of eminent scholars. Though, the challenging hypothesis does not have the same long tradition, it is not a scientific caprice based upon statistical evaluation of data of low quality. On the contrary, the research of the challenging hypothesis have been conducted with good methodology and theoretical modeling. The collection of empirical data and verifications, are for at least three decades coherent and consistent. This is why it is so strange that the two perspectives shows so different results. A comparison between the two perspectives displays obvious and big differences, which is shown in table 10.

The challenging hypothesis that plants in general require the same basic needs regarding the mutual nutrient proportions, if true, overthrows the predominant paradigm. Thus, a strong scientific foundation for the challenging hypothesis is not sufficient. Objective identification of the current paradigm's deficiencies are also necessary. Strengths and weaknesses for respective perspective must be weighted and dissimilarities must be explained.

Table 10. Comparison between the challenging hypothesis and the established paradigm. Different nitrogen ratios according to the challenging hypothesis, uptake due to species or uptake due to physiological age. A denotes recommended nutrient ratios and B denotes optimal nutrient ratios.

Nutrient	Challenging hypothesis		Uptake due to species				Uptake due to physiological age Tomato		
	A	B	Tomato	Sweet Pepper	Rose	Gerbera	Transplanting	Blooming and anthesis	Ripening and harvesting
N	100	100	100	100	100	100	100	100	100
P	13-19	8	25	18	17	15	41	26	18
K	45-80	30	178	129	102	191	153	148	126
S	8-9	5	29	14	18	9	*	*	*
Mg	5-15	4	16	12	10	8	53	33	24
Ca	5-15	4	66	55	49	45	235	177	105

4.2. Strengths of Challenging Theory

4.2.1. Hypothesis and Extent of Data

The hypothesis is very clear and specific, with a clearly defined question at issue. Moreover, it is a generic theory. Thus, all anomalies occurring are explicit arguments against the validity of the hypothesis. At least if the anomalies can't be explained. Therefore, it would seem very unlikely that a vast research material wouldn't consist of any clear rebuttals against such a hypothesis, if false. Further, the hypothesis can predict events out of a mechanistically and a physiologically theoretical reasoning (Knecht and Göransson 2004). Its predictions corresponds well with extensive experimental research (Knecht and Göransson 2004). Thus the theoretical model stands to test.

4.2.2. Methodology

The methodology is clearly quantifiable and unambiguous. One sole variable is examined individually. Namely the mutual proportions between the nutrients. The sole focus on the nutrient proportions have enabled the possibility to completely skip the use of concentrations. Instead, the nutrients were added in amounts over time, e. g. mg h^{-1} or mg d^{-1} . The research has been executed with such methodology that steady state have been kept in the plant through out its life-cycle (Ingestad 1982, Hellgren and Ingestad 1995, 1997, Ericsson 2006). Consequently, the ratios of the nutrient content in the plants represents its nutritional needs (T. Ericsson, Swedish University of Agricultural Sciences, Uppsala, unpublished data). It means that demand-driven nutrient application has the same ratios in the rhizosphere as in the plant content. The methodology provides with data of high quality, but not only that, it enables universal comparisons. Thus, data from totally different species can be compared in a completely meaningful and relevant way.

4.2.3. Horticulture in practice

The challenging hypothesis has been used in horticultural practice for more than three decades with high success. The hypothesis has been practiced as long as it has existed (Ericsson 2006, 2007a). Plant species of great variety have been grown with the same nutrient application. Regardless of species or if the plants were grown in a garden, green house or a pond, the same good results were to be found (T. Ericsson, Swedish University of Agricultural Sciences, Uppsala, unpublished data). However, it must be duly noted that this might be circumstantial, since it has not been widely used.

4.3. Weaknesses in Challenging Theory

4.3.1. Primarily Vegetative Phase

The laboratory experiments primarily addresses vegetative growth, particularly in seedlings and young plants. However, there are observations of whole life-cycles, from seed to seed, but not to the same large extent. This must be regarded as a limitation in the empirical testing of the model, and thus a weakness.

However, the evidence material concerning the vegetative phase is very strong. In that phase, all terrestrial plants have the same basic nutritional needs, as a result of a common basic physiology. The evidence material is consistent and strong enough to assume that the nutrient requirements are the same in all vegetative growth regardless of physiological age or other circumstances. Thus, all new tissue have the same nutrient proportions.

Furthermore, this limitation to primarily focus on seedlings and vegetative growth only applies to the experimental part of the research. The vast examination of the literature rather regarded non-fertilized field conditions where the plants were acclimated and close to steady-state.

4.3.2. Deviations

There is a strong foundation for the generality of the challenging hypothesis. However, there are exceptions. Exceptions applies in principle only to production where fruit tissue is harvested. In such culture systems the fruit tissue represents a major part of the total plant biomass. Moreover, the fruit tissue is virtually the only thing that is abductured. Fruit tissue consist of more K than other tissue, which probably is due to osmotic pressure which in turn comes of higher water content (K.-J. Bergstrand, Swedish University of Agricultural Sciences, Uppsala, unpublished data, T. Ericsson, Swedish University of Agricultural Sciences, Uppsala, unpublished data). Thus it is motivated with a higher ratio of K in the nutrient supply for such production. Representative examples of such production would be greenhouse production of tomato or sweet peppers. Though it is not motivated to increase the K ratio as much as it is done within commercial production fruit and vegetables. The plants total potassium requirement does not increase dramatically, it is the proportion of K in the fruit tissue that increases considerably, compared to other tissue.

When experiments on tomatoes where executed according to the challenging hypothesis, the potassium requirement increased to approximately 80 percent of the nitrogen requirement. This is actually within the framework of recommended ratios according to column A, in table 1, though it is on the very line of boarder (T. Ericsson, Swedish University of Agricultural Sciences, Uppsala, unpublished data). Furthermore is it likely that the potassium required in the fruit tissue at least to some extent can be explained by translocation, and not just an increased demand for the plant as a whole.

Another important fact to point out is that vegetative growth continues through out the generative phase. The newly formed tissue in the meristem still has the same nutrient requirements, that is optimum nutrient ratios according to the challenging hypothesis. The deviances in the challenging hypothesis gives some recognition to the part of the established paradigm that stresses the importance of physiological age for nutritional requirements. Though, it does not show that plants in general have different basic nutritional needs. Rather, it shows that within a certain context of production there are phenomenas, which leads to anomalies from the general rule.

4.3.3. Exactness of Optimum Ratios

The scientific foundation for the exact optimum ratios is not as strong as the rest of the challenging hypothesis. The figures in column B found in table 1, which exactly renders the definitive optimum nutrient ratios, are not as rigorously tested as column A or the rest of the material. The extent of the material is not as large. Additionally, the number of species examined and compared are considerably smaller, comprising only birch, eucalyptus and spruce. They are very different compared to each other. However, they are all trees. This means an obvious limitation for the reliability of the values corresponding to optimal nutrient proportions. However, this does not mean that there is any particular reason to question the very concept of the challenging hypothesis of general optimal proportions. Rather is it an incentive to further test the hypothesis, and if possible determine more exact values.

4.4. Strengths of Established Paradigm

4.4.1. Extent

The significance of the vast extent of research and collected data, that lays the foundation of the established paradigm are undeniable. A multitude of prominent scholars and researchers have indulged in plant nutrition requirements throughout the ages, of whom most support the ruling paradigm. The tradition of agriculture, horticulture and forestry that has shaped the established paradigm is not possible to omit. It gives a tremendous weight to the established paradigm. Actually, all literature on plant nutrient requirements is incalculable. However, the framework for this paper is limited to primarily address soilless hydroponic cultures.

4.4.2. Concurrence

The concurrence is vast, concerning that plants in general have different nutrient requirements regarding the mutual proportions between the nutrients.

4.5. Weaknesses In Established Paradigm

4.5.1. Extent of Lesser Relevance

The extent of the material for the established paradigm is incredibly vast. Though, within the limitations of the framework for this paper, the extent is closer in magnitude to that of the challenging hypothesis. This is not a weakness per se, but it brings to attention that the established paradigm in this comparison does not have automatic priority through the extent of its underlying material. Actually, soilless culture in hydroponic systems have existed approximately for the same duration of time as the research and application of the challenging hypothesis. It is primarily within such systems that the research of the challenging hypothesis has been conducted. Furthermore, it is within such systems that research has most precision, and where data is most reliable, when examining nutrition needs and nutrient supply (Silber and Bar-Tal 2008). Thus, the traditions of both perspectives are equal. However, the extent of the material is still larger in the established paradigm.

Nevertheless, it is not always a precedence for a paradigm to have a long historical tradition, which includes an immeasurable extent of material, even though the data is collected scientifically. When concepts becomes generally accepted, the very vastness of the material can actually lead to ambiguity in the interpretation of data. In the same manner comparisons can become meaningless, when the data are not related to each other, as it only relates to an abstract and unverified generally

accepted concept, which creates the illusion of a relation. It is a known fact that an established paradigm has a larger margin for baseless assumptions than any challenging paradigm. This has been shown throughout history time and again. It is possible that the established perception concerning nutritional requirements of plants is nuanced by scientifically baseless assumptions.

4.5.2. Inconsequent methodology

First, steady state is not a common precondition for experiments conducted. On the contrary, the absence of it stands out, as the nutrient solutions supplied is under constant change as trials continues (Ingestad 1982). Another example of this type of inconsequence is to add the same compositions of nutrient solution to two different species as a test to find out if they have the same requirement (T. Ericsson, Swedish University of Agricultural Sciences, Uppsala, unpublished data). At a first glance it seems sensible. The problem, however, is that regardless of the actual nutritional needs of the plants, the analysis of the tissues will rather reflect the solution in the rhizosphere, the uptake capacities and possibly the capacities to reduce uptake. Steady state is absolutely necessary if the experiments are to be quantifiable and comparable (Ingestad 1982, Hellgren and Ingestad 1995, Ingestad 1997).

Secondly, when nutrient uptake and requirements are determined, both the concentrations and the ratios of the nutrients are examined simultaneously (Savvas and Adamidis 1999, Sonneveld 2002, Silber and Bar-Tal 2008). In plant tissue analysis, the importance of nutrient ratios are pointed out. However, it is also emphasized that in order to evaluate if the plants needs are met, looking at ratios alone is not sufficient (Marschner 1995, pp. 472). It is theoretically possible that a culture can show an absolute total deficiency of a nutrient even when the ratios of the nutrients in the tissue are optimal (Marschner 1995, pp. 472). However, if that would occur, the immediate question would be how that could actualize in such a state of nutrient access, or rather the lack thereof. If there were access to nutrients in optimal proportions, but in such a small absolute amount, the expectation would rather be decreased growth rate in plant, than nutrient deficiency. Carbohydrates from the photosynthesis process would be translocated to the roots in order to increase the uptake capacity (Ericsson 2007a). In the long run the plant would eventually suffer decay and expire as a result of extreme nutrient deficiency. Certainly, plants have an absolute need for nutrition, that is obvious. However, given optimum nutrient ratios, it is not essential to examine the concentrations of the nutrients as long as there is a nutrient supply and no extreme state of deficiency. Simultaneous examinations can lead to ambiguity, and ultimately to confusion of effects, due to multiple variables. Consequently, data derived from such ambiguous experiments, lacks the same comparability.

4.5.3. Economical interests

Commercial production of fruit and vegetables are often the aim of plant nutrition research. Hence, it is possible that underlying goals affects the understanding of the nutritional needs. Aims like fast growth, target quantities and wanted quality, can result in data that reflects the requirements of the producer, rather than the actual inherent nutritional needs of the plants per se. Thus empirical values could suggest ratios that favors specific goals as such. This is particularly likely when steady state is not ensured. A typical example is commercial potato production, in which it is commonly held that potatoes require more potassium than other plants in general. This is not so. When the potassium supply is increased, the potato is less likely to obtain brown spots on the peel, or turn brown at harvest or boiling. These are essential qualities to the producer, without which his crops would be unsellable. Thus it is a requirement of the grower and not that of potato. There is a similar case with rapeseed production. It is commonly held that rapeseed plants require extra sulfur. Again this is not

so. Yes, the harvested parts, i. e. the seeds, require more sulfur. However the plant as whole does not. The plant translocates sulfur when producing seeds, and does not show any increased uptake. Again there might be sought after qualities which demands a slight increase of the sulfur supply. Though, as already explained, that is not a requirement of the plant as such.

Upholding sought after total ion concentrations in the nutrient solution is very central in hydroponic production (Sonneveld and Welles 1988, Sonneveld and Voogt 1990, Sonneveld 2002). Thus, the price of the nutrient composition affects the nutrient solution, since different fertilizers vary in cost. In the end of the culture the N ratio is often decreased. Instead $MgSO_4$ is often added to the solution, simply because it is a cheap fertilizer. This method provides with a high total ion concentration for a lesser price. Thus two goals are achieved, the sought after total ion concentration is upheld, and the budget for plant nutrition is decreased. This reasoning is, however, considerably flawed. Maximal economical efficiency can't be accomplished solely by the tuning of the total ion concentration. Maximal economic efficiency, rather comes as a result of giving the plant exactly the nutrients it needs, in correct ratios, when it needs it. Then the nutrient supply corresponds to the nutrient uptake, instead of accumulation in the circulation water or as leakage in drainage water.

4.5.4. Theoretical modeling

The perception that plants basic nutritional requirements are different due to species, physiological age and external circumstances is not so much founded on theoretical models. Rather is it based on conclusions of weighted aggregated data.

Neither is the theory generic like the challenging hypothesis. Meaning that even when similarities are shown, data needs not to be interpreted as if the nutritional requirements actually are similar, but that similarities were circumstantial. In turn, this means that the established paradigm is harder to falsify.

Furthermore, reasons have been found that arise suspicion to a form of empiricist trial-and-error methodology against theoretical modeling (Ingestad 1982, 1997, Savvas and Adamidis 1999). As a result empirically founded descriptions of the nutrient requirements in plants can operate well in practice. The risk, however, is that its data reflects, not the actual nutrient requirements of the plant, but a function within given but unknown and undefined parameters.

4.6. Explanations for Inconsistent Results

4.6.1 Introduction

If the different results from the two perspectives do not lie in that plants have different basic nutrient requirements, then what is the reason, or the reasons, for the dissimilarities? There is differences in between plants that can explain this, which becomes clear when the example of nature is understood correctly.

4.6.2. Total Requirement

The total absolute demand for nutrition differs considerably between various species (Ericsson 2006). This is not due to that the nutritional needs fundamentally differs. On the contrary, it is founded on the fact that every newly formed cell have the same basic physiology. Same basic physiology means same basic nutritional requirements. The difference between species is due to how fast the plant can form new cells. The total nutrient demand differs between the species due to growth capacity. In turn, the growth capacity is primarily controlled by the plants ability to

assimilate light radiation from the sun. Consequently, it is often plants with thin leaves that has the greatest growth capacity. Thus, it is morphology and not physiology that causes variety in the total demand for nutrition. It is, however, well known that plant species significantly differ morphologically.

4.6.3. Adaptability

Plants adaptability differs significantly between different species. Likewise does habitats and its nutrient contents differ considerably. This is, however, not an indication that the nutritional needs differ between the species. Instead is it the ability to master different soil chemical and physical conditions, which varies from species to species (Ericsson 2006, 2007). This means that different species have different capabilities to accommodate its nutritional requirements concerning different external circumstances. Different species are simply adapted to different habitats, and have different capacity to compete depending on where they grow.

A typical example of this is how different plants are adapted to different pH and calcium content in the soil. The calcium content in the soil varies significantly due to high or low pH. Those species that grows in soils with a high calcium content, does not have a higher demand for the element. Rather such plants are tolerant to high calcium content in the soil. It means that such plants have mechanisms that enables uptake of nutrients that due to the high pH of the soil is bound hard.

4.6.4. Nutrient uptake ability

Plants nutrient uptake capacity is generally oversized, and needs not to be used at its maximum to accommodate the nutritional requirements of the plant (Ingestad 1982). Nutrient uptake capacity is not governed by the plants nutritional needs. Rather is it a survival mechanism that makes the plant take up nutrients in excess, in order to prevent a potential future deficit. Furthermore is it an ability to compete. If one species takes up all accessible nutrition in the soil, no other species can grow there. The capacity of the roots to take up nutrients does, consequently not, reflect the very nutrition requirements of the plant, but the soil solution and the plants ability to compete.

4.6.5. Antagonism and synergism

Antagonism and synergism with different concentrations is another important aspect. Ions with equal charge can affect the uptake of one another. For instance is the Mg^{2+} uptake disturbed by high concentrations of Ca^{2+} due to the same charge. The best way to avoid such disturbances is to supply nutrients in the proportions that the plants actually requires (Ericsson 2007a). Thus, when working with concentrations as opposed to ratios and amounts over time, the risk for antagonism increases. Consequently can antagonistic uptake be confused with uptake based on actual requirement of the plant.

4.6.6. The Role of Nitrogen

When nutrients are supplied in recommended ratios according to the challenging hypothesis, nitrogen functions as the growth limiting nutrient. This does, however, not mean that the plants suffers from nitrogen deficiency. There won't be any nitrogen deficiency symptoms when the uptake of nitrogen and other nutrients harmonize with the growth, which it does if nutrients are supplied in amounts per unit of time in recommended proportions (Ericsson 2007a). Thus, the nitrogen access can be growth limiting without causing any negative deficiency injury. In this sense a slight limit in nitrogen access creates a balance between income and outlay in the plant. Excess sugars from the photosynthesis can be utilized for blooming, defense chemicals, energy storage and recompense to mycorrhiza and beneficial microorganisms (Ericsson 2007a).

4.7. Possibilities if the challenging theory is correct

4.7.1. Simplicity

The challenging theory provides a grossly simplified approach towards supplying nutrients within green house cultures. The nutrient supply will be very similar regardless of plant species, physiological age, season or external factors. Only small adjustments will be necessary due to small variations in the need of Potassium, and due to a few other exceptions. Thus, when providing the actual requirements of the plants, there will be no need to adjust the nutrient ratios in the irrigation water. The only real matter that remains is to accommodate the total demand of nutrients required by the culture, which is very simple.

4.7.2. Effectivity

The nutrient efficiency increases dramatically, due to supplying the actual requirements of the culture. The actual requirements of the plants concerning the nutrient ratios, is equivalent to the uptake. Consequently, it means that the culture will have no excess uptake of a certain nutrient. Neither will there be any accumulation in the substrate of a certain nutrient. Thus, optimizing fertilization will become easier. Furthermore, fertilization and the supplying of nutrients will become cheaper. It will be so regarding both the amount of fertilizer used, as well as the management required. In the same sense it also prevents leaching of nutrients into the environment, which otherwise would cause pollution.

4.7.3. Amount per unit of time

Correct ratios of the nutrients supplied meets the need of the plants. Thus, to supply nutrients according to the total demand is a matter of amount. The total nutrient demand should be met through amount per unit of time (Ingestad 1982). It should be measured in mass per time unit. Since the nutrient ratios are known as well as stable, there is no need to keep track of concentrations. Thus, management is simplified further as a consequence of the challenging theory.

4.7.4. Enabling new habitats in hydroponics

The challenging hypothesis enables virtually any plant species to be cultivated in hydroponic cultures. Since all plants share the same basic nutritional needs, there is no reason to assume that variety in habitats and abilities postulates anything else than controlled temperature and irrigation.

5. CONCLUSIONS

5.1 Summary Challenging Hypothesis

In summary the challenging theory has a profound scientific foundation, as well as many strong points. It provides with a good theoretical model, based on universally accepted biology and plant physiology, and it can predict events with good accuracy. It can explain why it shows results different from the established paradigm. Extensive material of data collected over a long time is coherent and consistent. Beyond scientific validity and credibility, the hypothesis also provides many benefits if true, of which simplification of plant nutrition theory and application is the most important. Further benefits are increased economic efficiency, prevention of environmental pollution and no build up of unbalanced accumulations in the nutrient circulation system. The challenging hypothesis appears valid, strong and with strong arguments.

5.2. Summary Established Paradigm

In summary the established paradigm has a profound scientific material with strong implications from its large bank of data, but it has a flawed model. That model cannot satisfactorily explain, in terms of biology or plant physiology, neither differences in data and nutritional needs, nor the inconsistencies. Its methodology has a weaker case than the challenging hypothesis. It has considerable weaknesses and many gaps. The established paradigm appears inconsistent and insufficient regardless of its great foundation. Even the most moderate scrutinization of the established paradigm would lead to, no matter how established, conventional and empirically verified, the raise of many questions concerning its accuracy and validity.

5.3 Conclusion

It is therefore concluded that the evidence in favor of the challenging hypothesis is sufficient, and that the evidence that shows the established paradigm inconsistent, incoherent and weak, is strong enough, to question the ruling paradigm. The evidence material is not sufficient to settle the case, nor provide any final evidence. However, it strongly indicates that the established paradigm is questionable, and that the challenging hypothesis is a valid alternative. Thus it is finally concluded that it is scientifically accurate to seriously question the legitimacy of the ruling paradigm. Henceforth, research with a complete new approach is requested. Requested research should address two aspects; the validity of the challenging theory, especially regarding optimal nutrient ratios, and the inconsistency of the ruling paradigm. The approach should be to examine the very nutritional needs of the plants per se in steady state at maximum growth.

6. REFERENCES

6.1 Published material

- Adams, P. and D.M. Massey. 1984. Nutrient uptake by tomatoes from recirculating solutions, pp. 71-79. In: ISOSC, Proceedings 6th International Congress on Soilless Culture, Wageningen, The Netherlands.
- Ågren, G.I. (1988). Ideal nutrient productivities and nutrient proportions in plant growth. *Plant Cell Environ.* 11:613-620.
- Benton, J. (1998). *Plant Nutrition: Manual*. Boca Raton: CRC Press.
- Christensen I, Hansson T 2010 Gödsling i slutet odlingsystem i växthus – underlag till utbildningsmodul. Rapport 2010:15. Tillväxt Trädgård, SLU. Publicerad i Epsilon, Alnarpsbiblioteket
- El-Nemer, M.A., M.M.H. Abd El-Baky, S.R. Salman and W.A. El-Tohamy. (2012). Effect of Different Potassium Levels on the Growth, Yield and Quality of Tomato Grown In Sand-Ponic Culture: *Australian Journal of Basic and Applied Sciences*, 6(3): 779-784, 2012 ISSN 1991-8178
- Epstein, E. and Bloom, A.J. (2005) *Mineral Nutrition of Plants: Principles and Perspectives* (2nd edn). Sunderland, MA: Sinauer Associates.
- Ericsson, T. 1981. Effects of varied nitrogen stress on growth and nutrition in three *Salix* clones. *Physiol. Plant.* 51:423-429
- Ericsson, T. (2006). Hemträdgården: *Ett enda gödselmedel och gröna fingrar - ger lyckat växtodlande*, (3), pp. 42-46.
- Ericsson, T. (2007a). Hemträdgården: Näring - upptag, tillgänglighet och brist, pp. 33-36.
- Ericsson, T. (2007b). Hemträdgården: Näring - de livsnödvändiga näringsämnena, pp. 33-36.
- Ericsson, T. and T. Ingestad. (1988). Nutrition and growth of birch seedlings at varied phosphorus addition rate. *Physiol. Plant.* 72:227-235
- Ericsson, T. and M. Kähr. (1993). Growth and nutrition of birch seedlings in relation to potassium supply rate. *Trees* 7:78-85
- Ericsson, T. and M. Kähr. (1995). Growth and nutrition of birch seedlings at varied relative addition rates of magnesium. *Tree Physiol.* 15:85-93
- Göransson, A. (1993). Growth and nutrition of small *Betula pendula* plants at different relative addition rates of iron. *Trees.* 8:31-38.
- Göransson, A. (1994). Growth and nutrition of small *Betula pendula* plants at different relative addition rates of manganese. *Tree Physiol.* 14:375-381.
- Göransson, A. (1999). Growth and nutrition of *Betula pendula* at different relative supply rates of zinc. *Tree Physiol.* 19:111-116
- Göransson, A. (2001). A technique for quantitative trace element and micronutrient studies in plants. *In Trace Elements in the Rhizosphere*. Eds. G.R. Gobran, W.W. Wenzel and E. Lombi. CRC Press, Boca Raton, NY, pp. 697-700.
- Göransson, A. and T.D. Eldhuset. (2001). Is the (Ca + K + Mg)/Al ratio in the soil solution a predictive tool for estimating forest damage? *Water Air Pollut.* 1:57-74
- Hellgren, O. and T. Ingestad. (1995). A comparison between methods used to control nutrient supply. *Journal of Experimental Botany*, Vol. 47, No. 294, pp. 117-122
- Ingestad, T. (1979). Nitrogen stress in birch seedlings. II. N, K, P, Ca and Mg nutrition. *Physiol. Plant.* 45:149-157.
- Ingestad, T. (1982). Relative addition rate and external concentration; driving variables used in plant nutrition research. *Plant Cell Environ.* 1:443-453.
- Ingestad, T. 1997. A shift of paradigm is needed in plant science. *Physiol. Plant.* 101:446-450.
- Ingestad, T. and G. I. Ågren. 1988. Nutrient uptake and allocation at steady-state nutrition. *Physiol. Plant.* 72:450-459
- Ingestad, T. and M. Kähr. 1985. Nutrition and growth of coniferous seedlings at varied relative nitrogen addition rate. *Physiol. Plant.* 65:109-116
- Ingestad, T. and A.-B. Lund. (1979). Nitrogen stress in birch seedlings. I. Growth technique and growth. *Physiol. Plant.* 45:137-148.

- Ingestad, T. and V. Stoy. 1982. Mineral nutrition of wheat, rye, barley and oat seedlings in nutrient solutions. *Swed. J. Agric. Res.* 12:185-192
- Knecht, M. F. and A. Göransson. 2004. Terrestrial plants require nutrients in similar proportions. *Three Physiology* 24:447-460
- Liebig, J. 1840. *Die organische Chemie in ihrer Anwendung auf Agrikultur und Physiologie*. Friedrich Vieweg und Sohn, Braunscheig, Germany, 352 p.
- Liebig, J. 1855. *Die Grundsätze der Agrikultur-Chemie mit Rücksich auf die in England angelstellten Untersuchungen*. 2Nd Edn. Friedrich Vieweg und Sohn, Braunscheig, Germany, 107 p.
- Marschner, H. (1995). *Mineral Nutrition of Higher Plants*. 2. Ed. London: Academic Press.
- Mengel, K. and Kirkby, E.A. (2001). *Principles of Plant Nutrition*. Bern: IPI
- Silber, A. and Bar-Tal, A. (2008). Nutrition of Substrate-Grown Plants. In: Lieth, J.L. & Raviv, M. (eds), *Soilless Culture: Theory and Practice*. London: Elsevier BV, pp. 290-339.
- Sinclair, A.G., J.D. Morrison, C. Smith and K.G. Dodds. (1997). Determination of optimum nutrient element ratios in plant tissue. *J. Plant. Nutr.* 20:1069-1083.
- Sonneveld, C. (2002). Composition of Nutrient Solutions. In: Savvas, P. & Passam, H. (Eds), *Hydroponic Production of Vegetables and Ornamentals*, Athens Greece: Embryo Publications, pp. 179-210.
- Sonneveld, C. and W. Voogt. (1986). Supply and uptake of potassium, calcium and magnesium of spray carnations (*Dianthus caryophyllus*) grown in rockwool. *Plant and Soil* 93:259-268.
- Sonneveld, C. and W. Voogt. (1990). Response of tomatoes (*Lycopersicon esculentum*) to an unequal distribution of nutrients in the root environment. *Plant and Soil* 124:251-256.
- Sonneveld, C. and G.W.H. Welles. (1988). Yield and quality of rockwool-grown tomatoes as affected by variations in EC-value and climatic conditions. *Plant and Soil* 111:37-42.
- Savvas, D. and F. Lenz. 1995. Nährstoffaufnahme von Aubergine (*Solarium melongena* L.) in Hydrokultur (Nutrient uptake by eggplant (*Solanum melongena* L.) in soilless culture). *Gartenbauwissenschaft* 60(1):29-33.
- Van Goor, B.J., A. De Jager, and W. Voogt. 1988. Nutrient uptake by some horticultural crops during the growing period, pp. 163-176. In: ISOSC, *Proceedings 7th International Congress on Soilless Culture*, Wageningen, The Netherlands.
- Voogt, W. (2003). Nutrient management in soil and soil-less culture in the Netherlands: Towards Environmental goals. *Proc. 529 Int. Fret. Soc.*
- Voogt, W. (2005). *Fertigation in Greenhouse Production: Fertigation Proceedings: Selected Papers of the IPI-NATESC-CAU-CAAS International Symposium of Fertigation Beijing/China*

6.2 Unpublished material

- Bergstrand, K-J. (2013). E-mail correspondence. Agr. Dr., Associate professor, Alnarp, SLU
- T. Ericsson, Oral communication, Associate professor, Department of Urban and Rural Development, Uppsala, SLU