Summary

Soil quality affects the quality of plant products in terms of soil productivity, which in turn affects the plants’ allocation of nutrients and other resources. This allocation determines which compounds are formed in which tissues, such as protein, starch, secondary metabolites or lignin, and thus the composition of the harvested product. When soil productivity is low, as in subsistence farming or most uncultivated land, the plant’s resources are used for survival and reproduction, resulting in a small yield of material with high biological value. Medium productivity, as is typical of organic farming, induces the plant to increase the allocation of resources to defence mechanisms, it gives a higher yield of material with high amounts of anti-nutrients and higher content of protein, which the anti-nutrients make less available to herbivores such as humans. At even higher soil productivity levels, as in typical conventional farming, the plant growth is not limited by nutrient restriction, and fewer resources are used for defence. The yield reaches a maximum, and the material is easily digestible, but tends to be dominated by storage compounds with relatively low biological value. The value of plant foods for health depends on who the consumer is. For non-ruminant animal production, high productivity gives the most easily digestible feed, while ruminants equally well can use material from less fertile systems. For those human populations where most people have a choice of food available, the plants grown on soil of medium productivity are probably best for health, since their high content of anti-nutrients counteract the harmful consequences of too much and too nutritious food. However, foods grown on land with either low or high productivity provide the most nutrients per kg food, which can be an advantage for populations suffering from shortage in food availability.

X.1 Introduction

While the relations between soil productivity and yield of plant products is relatively straightforward, the effects of soil productivity on nutritional value of plant foods are subtler and far less studied. On the other hand, there is increasing interest in these relations, since if sustainable low input management strategies result in improved product quality, this could in some cases make up for corresponding reductions in yield.

Two types of studies are relevant in this respect: One type comprises basic ecological studies of the biochemical responses of plants to the growing conditions they are exposed to, with nutrient availability as the primary manifestation of soil productivity, the consequences for plant composition, and models of the general mechanisms that control these connections. They address the situation in nature and the selection pressures that originally must have caused the plants to develop adaptations to variable external influences, such as resistance to pathogens and herbivores, and cover quite wide ranges of conditions. Such basic studies and the models derived from them are useful to provide a framework for understanding and classifying the effects observed in agriculture.

The other types of studies are measurements of the composition of agricultural products from plants grown with particular experimental treatments, e.g. fertilisation. They address the comparatively small effects of management strategies within or near standard agricultural practices, primarily on those components that have traditionally been considered nutritionally
important, such as protein, minerals and vitamins (Triboi and Triboi-Blondel 2002; Bürkert et al., 1998; Lee and Kader 2000), and technical characteristics such as proteins important for baking quality of wheat (Triboi et al., 2000). A few studies also investigate the relation of soil productivity with secondary metabolites responsible for taste and colour and possibly also with effects on health (Brandt and Mølgaard, 2001).

The first part presents a general model developed to describe how plant composition is influenced by availability of resources such as nutrients (Stamp 2003). This part includes examples of how the processes known from nature are also relevant for cultivated plants. The next part will describe the consequences of these effects for nutritional value of the plant products, and how the model can be used to estimate some effects of soil management strategies on food quality, in particular in relation to sustainable agricultural systems.

X.1.1 Definitions:
Allocation: Controlling how much of a resource is used for a particular process, e.g. how much N is used for synthesis of storage protein.
Macronutrients (for humans and animals): Carbohydrate, protein (including essential amino acids, fat (including essential fatty acids)
Micronutrients (for humans and animals): Vitamins and essential minerals.
Nutrients (for plants): Primarily nitrogen, phosphorus and potassium, also other minerals.
Bioavailability: The fraction of a nutrient in a food that is available for the physiological needs of a person or animal consuming it (the consumer).
Biological value: The degree (in percent) to which a food component, e.g. protein, can be utilised for growth by the consumer. It integrates the concentration of nutrients, e.g. essential amino acids, with their bioavailability.
Nutritional value: Concentrations and bioavailability of macro- and micro-nutrients that together correspond to the physiological demands of the consumer. Nutritional value differs from biological value by taking into account differences in physiological demands, including adverse effects of excessive intake.
Secondary metabolites: Compounds made in plants, which are not involved in the cellular processes of growth and respiration. Includes colorants, fragrances, waxes, poisons etc.
Anti-nutritional factors: Compounds (secondary metabolites or proteins) in plants that reduce bioavailability of nutrients. E.g. phytate (reduces utilisation of phosphate), protease inhibitors and condensed tannins (reduces utilisation of proteins).

X.2 General effects of soil productivity on the allocation strategies of plants.
Most plant species adapt to differences in external factors that affect growth by adjusting the internal allocation of resources of nutrients and carbohydrates to various uses, such as growth, storage or defence. This minimises variation in yields in terms of seed production, but causes differences in composition of some plant tissues (Herms and Mattson, 1992), which in an agricultural context results in differences in biological value of plant products. Through evolution the biochemical pathways of plants are developed so that each of the relevant aspects of conditions of the site of a seedling (light, water, nutrients, soil aeration, pathogen pressure etc.), affect the corresponding reactions of the plant in a way that adjusts its allocation mechanisms to optimise its competitive ability to the circumstances (Jones and Hartley, 1999). Note that these adaptive processes depend only on those aspects of soil quality that directly influence plant growth rates in the short term (less than the lifetime of the
plant in question), such as availability of the minerals and water needed to sustain it, growth inhibiting concentrations of salt or heavy metals, and other stresses due to e.g. pathogens or pests (Herms and Mattson 1992). Since the adaptive processes provide the connection between the qualities of the soil and the composition of the plant products, other aspects of soil quality (for example the long-term stability of the soil system or its biological diversity) only affect nutritional value of plant products indirectly, through their consequences for plant nutrient availability or suppression of diseases and pests. The relevant factors are thus a subset of those that are included in definitions of soil fertility which emphasise yield (Patzel et al., 2000), since yield integrates influences during an entire growth season, while adaptive processes act on a shorter timescale (e.g. Triboi and Triboi-Blondel 2002).

X.2.1 Studies in natural ecosystems

Basic studies of plants are an important aspect of ecology, the science of the interactions of life forms with the environment. So most studies and models have been made in the context of natural ecosystems, where plants experience large variations in the availability of nutrients, light and water, spanning from semi-deserts and rainforests to marshlands and tundras. However, the ecological models are sufficiently general to also be applicable to agricultural ecosystems, where it is an advantage that they encompass the full range of variation within agriculture, from high-throughput conventional plant production, via organic systems based on a high degree of recycling, to low productivity systems in resource-deficient areas.

Several partially overlapping hypotheses have been proposed to predict a relationship between nutrient availability, plant growth rate and allocation to phenolics. The “carbon-nutrient balance” (CNB) model makes predictions about the relationship between the carbon/nutrients ratio of the plant and the fraction of relevant resources allocated to either phenolics or N-containing secondary metabolites (Bryant et al., 1983; Coley et al., 1985). Limited availability of nutrients will reduce growth (biomass accumulation) more than photosynthesis, and a surplus of non-structural carbohydrates will accumulate. These will be diverted into an enhanced production of carbon-based secondary metabolites, e.g. phenylpropanoids. The “growth-differentiation balance” (GDB) model suggests that biomass accumulation and secondary chemistry are negatively correlated. In plants growing at adequate to high nutrient availability, resources will preferentially be shunted into growth processes, resulting in a lower production of secondary metabolites (Lorio, 1986; Herms & Mattson, 1992). The two described models have been tested in many different ecosystems, and the overall predictions confirmed in a meta-analysis of a large number of studies (Koricheva et al., 1998). Stamp (2003) has reviewed the different models and integrated their common features into a general model, which is the basis for figure 1.

X.2.2 Relating ecology to agricultural systems

For the simple situation where differences in soil productivity can be expressed as different levels of overall nutrient availability, in nature this is normally primarily nitrogen, all these models provide almost identical predictions of the effects on plant composition (Jones & Hartley, 1999; Bezemer et al., 2000; Nørbaek et al. 2003). So the description in the following is not limited to any one of them, it rather serves to illustrate their common concept, and how they can be used to estimate the results of changes in soil management.

The ecological literature generally distinguishes between resource poor and resource rich
environments (e.g. Coley et al., 1985; de Jong 1995). However, to use these models in the context of agricultural systems, it is useful to define three levels of soil productivity, low, medium and high, from their position on a curve of growth versus nutrient availability for each plant species. In this context, medium productivity will correspond to a ‘resource rich’ natural ecosystem, since in agriculture the range of productivities include additional levels that are higher than what is regularly found in undisturbed nature. Low soil productivity is a situation where the availability of nutrients is only just sufficient to keep the plant alive and reproducing. Here the addition of the limiting nutrient (normally nitrogen) will result in almost proportional increases in plant biomass production. In agriculture this is found in depleted fields with low ability to retain nutrients, e.g. resource-poor tropical agriculture (Palm et al., 2000; Bürkert et al., 1998) and some extensive pastoral systems. Medium soil productivity is found where recycling of nutrients result in a somewhat increased growth, but with diminishing returns. This is typical of most Organic Agriculture and some less intensive forms of conventional agriculture, e.g. production of grapes for high-quality wine (Chone et al., 2001). High productivity is found where further increases in nutrient input will not necessarily result in increased yields, even if plant health is not affected. It is typical of conventional vegetable production and other intensive agricultural systems (Goulding 2000; Locascio et al., 1984).

X.2.3 Comparing plants with people, to illustrate nutritional status

As a metaphor, it is useful to think of the plants in these three situations as undernourished, moderately stressed and well-fed, and to visualise this in the context of humans. Undernourished individuals (also called caloric restriction) show relatively slow development, reduced fertility, low metabolic rate and small final size. Until a few generations ago, this was the typical situation for most people, also in today’s industrialised countries. The diet of moderately stressed people provide adequate nutrients without any excess, they corresponds to the lean body type that are presently thought of as ideal. Well-fed people, presently the majority in Europe and USA, are those who consume more nutrients than the body expends, resulting in a tendency for overweight and increased risk of developing a metabolic disease at some stage of life. An important aspect of this metaphor is that for both plants and humans, normal life cycles can be sustained for generations in any of these situations, although the life expectancy and fertility will be somewhat different.
X.2.4 Description of each of the 3 nutrient availability levels

Figures 1, 2 and 3 show a model and two sets of experimental data that span and illustrate the three situations.

**Figure X.1:** Intraspecific patterns of plant defence along a resource gradient. Based on figure redrawn from Stamp (2003).

<table>
<thead>
<tr>
<th>Availability of plant nutrients</th>
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<tbody>
<tr>
<td><strong>Well-fed</strong></td>
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<tr>
<td>Plant growth rate (g per unit time)</td>
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<td>Plant mass</td>
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**Figure X.2:** The consequences of differences in soil productivity on composition of plant products, exemplified by nitrogen effects on yield and composition of rapeseeds. Based on figure redrawn from Triboi & Triboi-Blondel (2002).
Figure X.3: The consequences of differences in soil productivity on composition of plant products, exemplified by effects of different levels of green manure on yield and composition of carrots. Based on figure redrawn from Kaack et al. (2002). Open symbols are data from plants grown in 1995, filled symbols 1996.

If soil productivity is low, resulting from shortage of nutrients, the allocation mechanisms of the undernourished plants are directed towards collecting as much as possible of the scarce resources and conveying it to the next generation (Herms and Mattson 1992). The seed weight is optimised in relation to the total amount of protein that the plant can make, while a relatively low fraction of the protein is allocated to the leaves for use in photosynthesis (Jones & Hartley, 1999). The plant will have a relatively large root system that slowly produces a few thin stems with a few small leaves and sets a few seeds of normal size. In perennials, reproduction is delayed until a sufficient size has been achieved (Herms and Mattson 1992). Investments of resources for defence against pathogens and herbivores is relatively low (Loehle 1996; Matsuki 1996).

If the soil productivity is moderately high, where the plant can obtain a surplus of nutrients beyond the minimum required for survival, the plant’s growth pattern is adjusted to also engage in interactions with competitors and other adversaries (Loehle 1996). Various phytochemicals accumulate, including phenolic compounds, that make the plant less attractive to herbivores, while roots and leaves expand to collect water, nutrients and light before these resources reach the competing plants around it (Herms and Mattson 1992). The moderately stressed plant will make a strong root system, larger than the undernourished plant, and produces an even larger number of stems with medium sized leaves, resulting in a lower root/shoot ratio than when resources are very scarce (Herms and Mattson 1992;
Nørbæk et al. 2003). The plant matures quickly (Herms and Mattson 1992) and sets a relatively large number of seeds, some of which will not be able to reach the normal seed size.

If the soil productivity is very high, providing easy access to at least adequate amounts of all relevant resources, the plant will allocate most of its resources to growth and to competition for light (de Jong 1995). The root system will be relatively weak, the plant will make many stems with large, dark green leaves. A well-fed plant will set many seeds, most of which will continue to grow for a long time to reach the normal seed size or become even larger. However, much of the crop will be lost to herbivores and diseases, unless it is protected by the use of pesticides or other external plant protection methods, since relatively few resources are allocated for synthesis of defence compounds (de Jong 1995).

Previous studies of ecological allocation models have primarily focused on the consequences for plant fitness of its intrinsic defence mechanisms, and described the effects on plant composition as a consequence of the trade-offs between growth and defence (Herms and Mattson 1992; de Jong 1995). Most studies on the effects of management of soil productivity in agriculture are not primarily concerned with effects on susceptibility to disease, in fact it is often not mentioned at all. However, it is important to emphasise that also in agriculture differences in soil productivity result in differences in susceptibility to attacks of disease or insects: in fact moderately stressed plants consistently show less damage than well-fed ones under conditions of equal levels of inoculum (e.g. van Bruggen, 1995). As an example, when no plant protectants are used, the average yield of undamaged apples can be at least the same at low or medium levels of soil productivity as at higher levels (Lindhard Petersen & Berthelsen, 2002), since the loss of fruit to fungal diseases increases in parallel with yield (number of fruits developing) when more nutrients are made available to the trees. This effect is particularly important for organic farming, where increased disease susceptibility cannot be alleviated by just using more pesticides.

**X.3 Consequences of soil productivity for nutritional value of food and feed**

Plants grown under the three categories of soil productivity defined above (undernourished, moderately stressed and well-fed) provide products with different, predictable characteristics that are important for their use to support human or animal nutrition.

**X.3.1 Low nutrient availability**

Undernourished plants provide little biomass, although a relatively high proportion of it is as seed, corms or other reproductive organs (Lorio, 1986; Herms & Mattson, 1992, Nørbæk et al. 2003). These reproductive organs have relatively high contents of starch or oil, while the concentration of protein is low. However, the protein has a relatively high biological value (in terms of a balanced amino acid composition), since it has a low fraction of storage proteins (Jia et al., 1996). Storage proteins contain numerous repetitive units of a few amino acids, and therefore have a very low content of certain essential amino acids (Mandal and Mandal 2000), so they are of less biological value than other proteins. When phosphate availability in the soil is low, most of that which is taken up by the plant is incorporated in relevant cell components, as for the proteins relatively little accumulates in the storage form, which for phosphate is a complex with phytic acid (Barrier-Guillot et al., 1996; Raboy and Dickinson 1993). Since the association with phytate reduces bioavailability of phosphate, and also of other important minerals, such as zinc, the low fraction of phytate-phosphate ensures that
these nutrients are relatively easily available to humans and animals (Bürkert et al., 1998). The products normally have relatively high concentrations of micronutrients, since the slow growth and high root/shoot ratio facilitate the uptake of minerals (Bürkert et al., 1998), except when the soil is very deficient in a particular mineral, e.g. zinc, which then becomes limiting for plant growth (Cakmak et al., 1996).

When farmed, low productivity soils only support few people or animals in terms of basic energy needs, but provide a balanced nutrition (Ali and Harland, 1991; Bürkert et al., 1998). Note that our digestive system and that of our farm animals evolved during millions of years where this was the dominant type of plant food available (Southgate, 1991).

X.3.2 Medium nutrient availability
Moderately stressed plants produce much higher amounts of biomass, for the vegetative parts almost proportionally more, relative to the higher availability of nutrients (Triboi and Triboi-Blondel 2002; Nørbaek et al. 2003). The products have higher concentrations of protein than those of undernourished plants, but also higher concentrations of anti-nutritional factors (Elsheikh et al., 1999), which together with a decrease in the proportion of essential amino acids reduce the biological value of protein and other nutrients for non-ruminants, such as humans, pigs, birds and most insects. The higher proportion of vegetative tissue and a relatively high cellulose content provide a sustained yield of feed with a high biological value for ruminants (Waghorn, 1990), since the rumen fermentation makes them able to compensate for the factors that reduce biological value for other herbivores. For non-ruminant farm animals, the consequence of a reduced biological value is higher feed consumption in order to obtain the same production of meat or eggs, however, on an area basis the increase in yield is always higher than the increase in feed consumption, allowing a higher total production per area (Elsheikh et al., 1999; van Houtert and Sykes 1999). However, from a management point of view, it is important to take this aspect into account on the “cost” side, when planning an initiative to improve soil productivity (Brandt and Kidmose, 2002). Both for animals and humans, the biological value of food with a high content of anti-nutritional factors can be increased after harvest by heat treatment (cooking), since most types of anti-nutritional factors are degraded by heat (Wiryawan and Dingle 1999; Elsheikh et al., 2000). So in developing countries modest improvements in soil productivity leads to an increased demand for fuel, e.g. firewood, another important item on the “cost” side for management. Additionally, a diet of plant foods with low biological value can be improved by supplementation with small amounts of animal products with a very high biological value (Roos et al., 2002; van Houtert and Sykes 1999).

While a high content of anti-nutritional factors in crops grown on soil with medium productivity can be a problem in low-income areas, where the intake of food is limited by economic constraints, there are no indications that this causes health problems in regions where the amount of food is not limiting, such as countries on transitional stages of development. The presence of anti-nutritional factors lead to excretion of part of the nutrients without digestion, and thus simulate a moderate reduction of food intake. In fact, it is well documented that for all of the many animal species tested, moderate restriction of the food intake prolongs life and reduces susceptibility to a range of diseases, both infections and non-infective disorders such as cancer (McCarter, 1995).

In addition to the effects on biological value of plant products, some anti-nutritional factors are also important for other aspects of food quality, such as taste and colour. For plant products where the quality of the final product depends on a high level of plant secondary
metabolites, it is generally observed that the best quality is found at moderate or low levels of fertilisation, corresponding to moderately stressed plants. For these products this knowledge is used to promote the cultivation at not too excessive levels of productivity. Examples are tea (van Lelyveld et al., 1990), where both the taste and the colour depend on the content of catechins, precursors of condensed tannins, which polymerise into the characteristic brown theaflavin pigments in black tea, and wine (Chone et al., 2001), where similar tannins are important for taste, and anthocyanins for colour.

X.3.3 High nutrient availability

Well-fed plants produce only slightly more biomass per area than the moderately stressed ones (Figure 1). One of the limiting factors is larger loss to insects and diseases (even when pesticides are used) (van Bruggen, 1995). The concentration of protein is highest here, and even though an increasing percentage is storage proteins with low contents of essential amino acids (Mandal and Mandal 2000), the production of essential amino acids per ha still tends to increase with increases in productivity, although not as strongly as the protein content (Bruckner et al., 1998). In very different plant species the fraction of essential to non-essential amino acids appears to decrease linearly across a wide range of soil productivities, e.g. carrots (Kaack et al., 2002) and barley (Bulman et al., 1994). However, since the levels of anti-nutritional factors decrease when plant growth is not limited by nutrient availability (de Jong 1995; Jones and Hartley 1999), the bioavailability of the macronutrients present in the plant material should be expected to improve in well-fed plants relative to nutrient limited ones. So on a dry weight basis, material from well-fed plants would be expected to sustain the highest growth rates for non-ruminant humans and farm animals. This has been found in studies with insects, that show much higher rates of reproduction on well-fed plants than on moderately stressed ones (Nevo and Coll 2001), but does not appear to have been studied systematically in actual farm animals nor in humans. A better bioavailability of protein is a clear advantage in animal husbandry, since it gives higher growth rates. However, an unfavourable amino acid composition in feed will increase the amount of protein needed, since excess non-essential amino acids are excreted as nitrogen in urine, thus increasing the environmental cost of animal production (Jørgensen et al., 1997). For minerals, the situation is different, since the phytate, which is involved in accumulation of stored phosphate, also acts as an anti-nutrient, reducing the bioavailability of several essential minerals, including zinc and iron. Combined with the rapid plant growth, which results in a relative dilution of minerals in the plant tissue, both concentration and biological value of essential minerals can decrease when soil productivity is increased (Bürkert et al., 1998). However, preliminary studies on consequences of increased plant nutrition for animal mineral nutrition (Ali and Harland, 1991) seem to not have been followed up by more definitive investigations.

In contrast to the use for production animals, a high content and digestibility of energy and protein is not necessarily advantageous for human food. In societies such as the European and the North American (USA/Canada) food intake is generally in surplus. In fact, numerous epidemiological studies show that people who eat food with a relatively high content of anti-nutritional factors, such as fruits and vegetables, have a reduced risk of important diseases such as cancer, diabetes and cardiovascular disease (La Vecchia 2001; Williams et al., 1999; Ness and Powles 1997). Taken together with studies showing that high intake of food with very high biological value, such as meat (protein) and fat (energy) increase the risk of the same diseases (Greenwald 1999) this indicates that here the ability of non-nutrient secondary metabolites to prevent cancer and cardiovascular disease is more important for
health than the supply of even more energy and nutrients (Brandt & Mølgaard, 2001). This is reflected in the official food recommendations, which urge the population to reduce as much as possible the consumption of foods with high biological value (Levi et al., 1999), including refined grains and saturated fat. In contrast, for people who are subject to involuntary dietary restriction (who cannot afford or obtain sufficient food), food with a high biological value is an advantage from a health point of view.

X.3.4 The difference between organic and conventional plant production and the effect on the health of consumers

Organic plant production generally provides moderate nutrient availability, compared with the high levels in conventional farming. Partly because it is relatively expensive to provide high amounts of organic plant nutrients, partly because those farmers who strike the right balance have the healthiest crops with the smallest risk of pests and diseases, and therefore have the best basis for a good economic outcome. Typical differences in content of oil, starch, protein, vitamins and secondary metabolites are 10-20% (with more of oil, starch, vitamin C and defence related secondary metabolites, and less of protein and carotenes). The reduction in risk by increasing the intake of fruits and vegetables has been calculated by van’t Veer et al. (2000), and from their formulas it can be calculated that a 10-20% increase in consumption of fruits and vegetables will reduce the risk of both cancer and cardiovascular disease by 3-6%. Together these two diseases are responsible for about 60% of all deaths in countries such as the UK, where most people have more nutrients in their diet than what is best for them (FSA 2007). There is reason to believe that most or all of this health benefit is due to the secondary metabolites in the fruits and vegetables (Brandt et al. 2004). To determine how much this matters for health, it is useful to think of the effect of the production system as making the food more or less concentrated. For example, for fruit and vegetables, there is 10-20% higher concentration of secondary metabolites in organic products than in conventional ones, so from the perspective of the effect on health, changing from conventional to organic food corresponds to increasing the intake of fruits and vegetables by 10-20%. So if everyone changed from conventional fruits and vegetables to organic ones, without changing the amount of each food, we would expect to see the mortality rates reduced by 2-3%. Pesticide residues are not a health problem for consumers in countries where the control with these substances is effective (Brandt 2007), but in places with less stringent control, this effect will be even larger.

X.4 Conclusion

Differences in soil productivity is one of several types of stress, that affect the allocation of nutrients and energy in plants, and thus lead to predictable differences in the contents and bioavailability of nutrients in products harvested from them. While consistent trends have been found for the effect of soil productivity of single aspects of nutritional value, such as protein content or synthesis of anti-nutritional factors, only little is known about the resulting effects on nutritional value. In particular since the needs of humans and animals depend on the availability of supplementary food items and general nutritional status. Increased soil productivity increases protein content of plants, but decreases the percentage of essential amino acids. And intermediate values of soil productivity induce the highest levels of anti-nutrients, which tend to decrease bioavailability of protein and energy for non-ruminants such as humans, but have little effect on ruminants. Anti-nutrients are important for plant health, and may benefit humans as well by reducing the risk of diseases such as cancer. Increases in content and bioavailability of nutrients, which increase productivity of farm animals, are not
always advantageous to health of humans, since we tend to eat more than what is good for us, when we have the opportunity.

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