Chapter 15
Limitations to Crop Productivity

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Abstract Environmental factors including water stress, nutrient deficiency, high or low temperatures, chemical (Al-toxicity, salinity) and physical soil constraints (e.g. compaction), and biotic factors reduce crop yield. Deficit of water and nitrogen, and soil constraints generally have a larger impact on canopy size and duration, hence growth reductions are closely linked with reduced intercepted radiation; radiation use efficiency is generally less responsive to stress. Extreme temperatures at critical stages usually reduce harvest index and yield. Other stresses can be neutral, positive or negative for harvest index; this depends in particular on the nature, timing, intensity and duration of stress and its relative impact on total and harvestable biomass. Yields are also reduced by the action of biotic agents such as pests, diseases and weeds. Potential yield losses to biotic stresses may be quite high but are decreased by crop protection practices.

15.1 Introduction

In Chap. 13 we have analyzed crop yield as a function of temperature and radiation interception. This "potential" yield will be higher than actual yields as other biotic and abiotic factors come into play. The main abiotic factors that reduce crop yields are water stress (already reviewed in Chap. 14), nutrient deficits, adverse chemical conditions (salinity, acidity), water excess and meteorological events (extreme high or low temperatures, hail, wind). Biotic factors are weeds, animal pests and diseases.

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F.J. Villalobos, E. Fereres (eds.), *Principles of Agronomy for Sustainable Agriculture*, DOI 10.1007/978-3-319-46116-8_15

In this chapter we'll revise the main impact of these factors on crop productivity. Some of them will be treated in more detail in specific chapters of this book (salinity, nutrient deficits, frost).

15.2 Nutrient Deficiency and Soil Related Limitations of Productivity

Deficit of water and nutrients reduce biomass by primarily reducing leaf area index and radiation interception; under severe stress radiation use efficiency is also reduced. This is because tissue expansion is more sensitive to both water and nutrient deficit than leaf photosynthetic rate. Indeed, a common short-term response of water and nitrogen stressed plants is to accumulate carbohydrates as the restriction in expansion is more severe than the restriction in photosynthesis, leading to transient excess of reduced carbon.

The effects of nitrogen supply on crop growth and yield can thus be explained in terms of its effects on interception and efficiency in the use of radiation. Nitrogen deficit reduces crop LAI by reducing tillering or branching, and leaf expansion (Fig. 15.1). Reduced leaf size of nitrogen-deficient crops is associated with reduced rates of cell division and expansion (Table 15.1). Nitrogen deficit can accelerate leaf senescence (Fig. 15.2), further contributing to reduced radiation interception and photosynthesis. Rubisco and light-harvesting proteins involved in photosynthesis represent 60 % of the leaf N content, hence the link: shortage of nitrogen → less Rubisco → less photosynthesis.

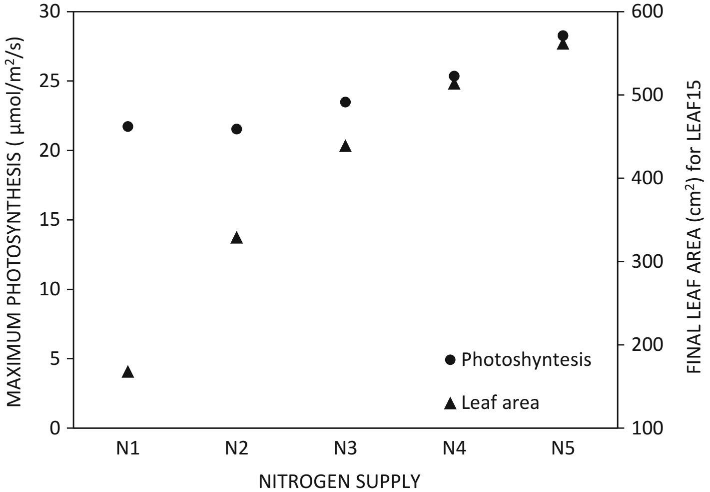

Fig. 15.1 Nitrogen deficit reduces photosynthesis and leaf size. Sunflower plants where grown under five nitrogen regimes, with extreme treatments receiving 0.25 (N1) and 7.5 g N per plant (N5) (Adapted from Connor et al. (1993) Aust J Plant Physiol 20: 251–263)

Table 15.1 Nitrogen deficit reduces cell number and size, hence leaf area of sunflower

	Number of cells	Area per cell	Leaf area
	$\times 10^6$	μm^2	cm^2
High N	56	554	302
Low N	33	443	147

Data for leaf number 10 at full expansion under high or low N supply are shown

Adapted from Trapani et al. (1999) Ann. Bot. 84:599–606

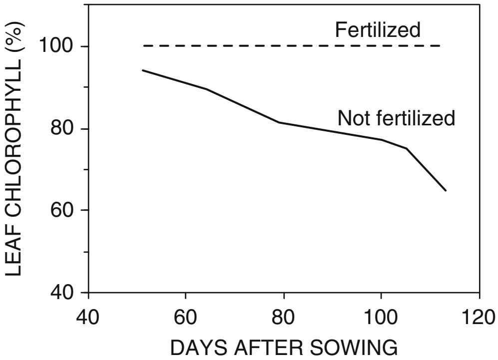

Fig. 15.2 Nitrogen deficiency accelerates leaf senescence of wheat. Leaf chlorophyll, measured in the youngest expanded leaf, is expressed as percentage of that of fertilized crops (Adapted from Caviglia and Sadras (2001) Field Crops Res 69:259–266)

The effects of water supply on crop growth and yield (Chap. 14) can also be explained in terms of interception and efficiency in the use of radiation. In response to water deficit, plants have largely irreversible responses such as reduced tillering or branching, and reduced leaf expansion. Reduced stomatal conductance and wilting are transient crop responses to water deficit that reduce both crop water use and photosynthesis. Figure 15.3 illustrates the saw tooth pattern of radiation interception in alternating dry-wet periods with transient wilting and recovery after irrigation. In addition to the individual effects of nitrogen and water, these resources often interact in complex ways. In wheat crops growing under a combination of irrigation and fertilizer regimes, RUE was 1.8 g/MJ in rainfed, unfertilized crops and increased to 2.1 g/MJ with nitrogen fertilization. Weekly irrigation did not improve RUE in unfertilized crops, but irrigation combined with nitrogen fertilization increased efficiency to 2.5 g/MJ.

In common with water and nitrogen supply, the reduction in crop growth in response to physical and chemical soil constraints is mostly mediated by reduced canopy size and interception of radiation, whereas radiation use efficiency is less responsive to stress. This is illustrated in two examples. Soil compaction is a common problem, often caused by tillage, machinery traffic, and loss of organic matter, which is reflected in increased soil bulk density. Its effects on the crop are twofold: it hinders the emergence and establishment of seedlings and slows down growth of the root system and depresses shoot growth. The effect of compaction on root growth is quantified by the penetration resistance, which can be measured with a penetrometer. For a particular soil, penetration resistance is directly proportional to the apparent density and inversely proportional to the water content of the soil.

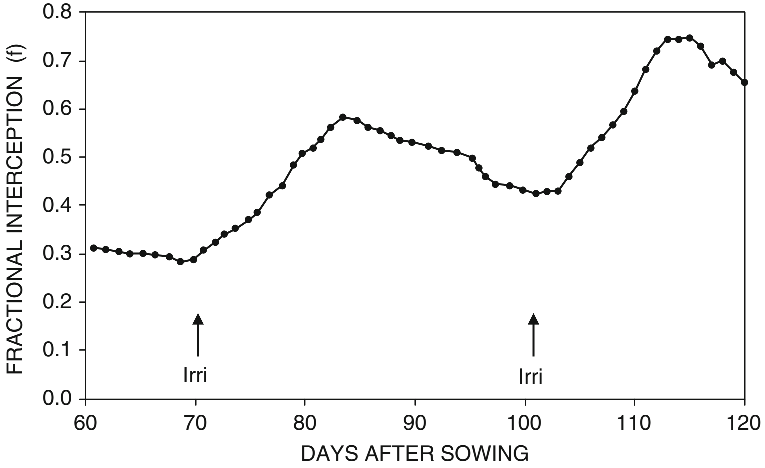

Fig. 15.3 Dynamics of fractional radiation interception of peanut crops. The saw-tooth pattern of radiation interception results from transient wilting and recovery after irrigation. During this period LAI increased from 0.5 to 2. *Arrows* show time of irrigation (Adapted from Matthews et al. (1988) Exp Agric 24:203–213)

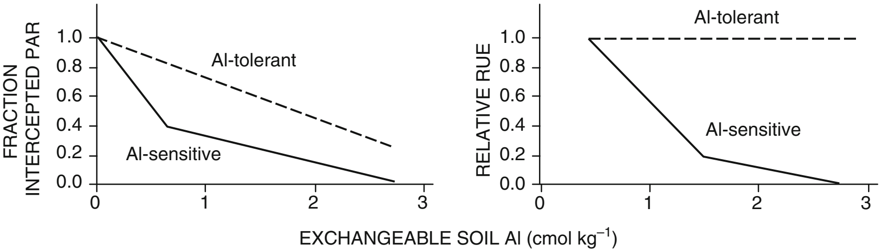

Fig. 15.4 Effects of soil aluminium toxicity on (**a**) intercepted radiation and (**b**) radiation use efficiency of wheat crops (Adapted from Valle et al. (2009) Field Crops Res 114:343–350)

Therefore the effects of compaction are more severe when the soil is dry (Chap. 17). In the Mallee region of south-eastern Australia, sandy soils often develop a compacted layer at 0.2–0.3 m depth, thus restricting root proliferation, and water and nitrogen uptake below this depth. Crops in compacted soil were compared with crops in soils were deep ripping was used to remove the constraint. Wheat yield in compacted soil ranged from 1.2 to 2.9 t/ha, and ripping improved yield up to 40 %. The reduction in yield associated with compaction was fully accounted for by the reduction in leaf area index and intercepted radiation, whereas radiation use efficiency was unaffected by soil condition. Aluminum toxicity reduces yield in acid soils ($pH<5.8$), which represent about 30 % of agricultural soils worldwide. Growth analysis of Al-tolerant and Al-sensitive wheats in southern Chile showed a marked reduction in intercepted radiation with increased concentration of Al in soils, a largely unresponsive RUE in the tolerant wheat, and reductions in RUE in sensitive wheat only at high Al concentrations (Fig. 15.4).

15.3 Climatic Accidents

We will consider the effect of extreme low temperatures in Chap. 29 and the effects of wind in Chap. 27.

15.3.1 High Temperature

In general the main effect of extreme high temperature is a reduction in HI due to reduced pollination or seed abortion. For instance, the number of grains in winter cereals decreases with canopy temperature above 31 °C. On the other hand, high temperatures will promote leaf senescence and shorten the grain filling period.

In Mediterranean climates low water availability is coincident with high temperature so low transpiration due to water stress amplifies heat stress as canopy temperature increases above air temperature.

15.3.2 Hail

Hail is a form of solid precipitation consisting of ice balls or lumps of ice which originate in strong thunderstorm clouds (cumulonimbi). The hailstones show diameters typically between 5 and 12 mm. Hail occurrence is localized, with areas affected from a few hectares to hundredths of has.

Occurrence of hail is more frequent in mid-latitudes (inland areas, elevated regions) than in the tropics despite the higher frequency of thunderstorms. Some areas where hailstorms are common are Northern India and some regions of China and Central Europe. During the year hail will occur mostly during spring and summer.

Damage to the crop is due to the impact of hailstones which velocity will be proportional to size. For a 1 cm diameter hailstone, terminal velocity could reach 9 m/s while an 8-cm hailstone would fall at 48 m/s. Apart from the direct physical damage that destroys leaves or reproductive structures, wounds facilitate the infection by pathogens. The effect of defoliation due to hail on crop yield depends on the development stage when hail occurs and the level of defoliation. Partial early defoliation may be compensated by increased dry matter allocation to leaves resulting in a small reduction in yield. Full defoliation before anthesis may be catastrophic for yield. Damage to reproductive structures leads to reduced Harvest Index in proportion to the number of structures affected. Partial damage of fruits reduces their commercial value.

High value crops may be protected by covering with anti-hail nets. In field crops or extensive fruit production the main protection alternatives are:

- anti-hail rockets that use silver iodide
- ground generators that produce smoke with silver iodide
- anti-hail guns: they use shockwaves directed at the hail storm
- crop insurance

15.4 Waterlogging

High soil water content implies a limited supply of oxygen for root respiration, so root functioning (absorption, growth) is impaired. If the soil is saturated the roots decompose starting from the tips, plant stops growing and eventually it will die. Most often crops will suffer from temporal waterlogging events and will recover partially afterwards, but the poor root system will have a low capacity for water and nutrient absorption. The overall effect will be reduced yield.

Waterlogging also contributes to N losses by denitrification (see Chap. 24), the conversion of nitrate to volatile N compounds. Low N uptake will cause symptoms of N deficiency.

Waterlogging may be prevented by improving the drainage system of the field or using raised bed planting.

15.5 Biotic Factors

Biotic agents causing crop damage (generically known as pests) are weeds, animal pests (arthropods, nematodes, gastropods, rodents, birds), pathogens (fungi, bacteria) and viruses.

The effect of pests and diseases on crop growth can also be analyzed in terms of capture and efficiency in the use of radiation, and harvest index (Eq. 13.3). Insects that feed on reproductive structures, such as cotton bollworms, have a primary effect on harvest index. In extreme cases of uncontrolled infestation for example, cotton crops can accumulate large amounts of biomass with little fruit set, hence reduced harvest index and yield. Defoliators reduce leaf area and intercepted radiation, whereas some diseases can also reduce photosynthetic rate of individual leaves and RUE. Spider mites for example, pierce the leaf epidermis with needle-like mouthparts and feed on mesophyll and palisade cells, thus reducing leaf photosynthesis and RUE (Fig. 15.5). Comparisons of wheat crops protected with fungicides, and unprotected crops exposed to damage by foliar pathogens showed that growth reduction was mostly associated with reduced healthy leaf area, with a secondary contribution of reduced radiation use efficiency.

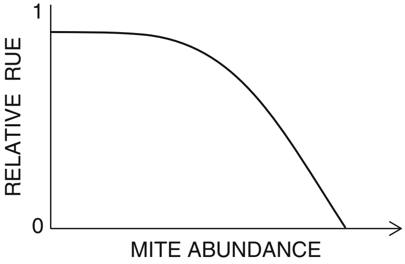

Fig. 15.5 Spider mites feed on mesophyll and palisade cotton leaves, reducing leaf photosynthesis and radiation use efficiency (Adapted from Sadras and Wilson (1997) Crop Sci 37:481–491)

15.5.1 Arthropods

Many species of insects and other arthropods are present in the agro-ecosystem but only a few are important pests, and may cause complete yield loss. Insects are six-legged invertebrates that usually undergo metamorphosis during development. Adult insects have three body regions (head, thorax and abdomen), three pairs of legs, one pair of antennae, complex mouthparts, and frequently two pairs of wings. The skin of an insect is the exoskeleton, which covers the whole body.

All insects have an egg and an adult stage. Complete metamorphosis includes four stages (egg, larva, pupa and adult). The most common, foliage-eating insect pests are larvae of *Lepidoptera* (butterflies and moths) and larvae and adults of *Coleoptera* (beetles). Aphids, leafhoppers and thrips not only feed on the crop but are also the main vector for transmission of plant virus diseases.

Many insect species are predators or parasites of other insects and are, thus, beneficial.

15.5.2 Plant Pathogens

Plant pathogens (fungi, bacteria, virus, nematodes, etc.) affect crop plants by altering the following processes:

- photosynthesis: destruction of photosynthetic tissue, degradation of chloroplasts, leaf senescence, yellowing, etc.
- water and nutrient transport: destruction of roots, formation of root galls and root knots, impaired root absorption, destruction or blocking of xylem tissue, damage to leaf cuticles or stomatal function (higher transpiration), altered phloem transport.
- plant respiration increases after infection which contributes to depleting the plant reserves.

– membrane permeability also increases causing leaf damage by loss of nutrients and entry of toxins
– changes in transcription and translation of nucleic acids alter plant function and structure and the synthesis of enzymes or substances involved in plant resistance.

The disease starts with a primary infection (first in the season) due to primary inoculum (spores or fungal mycelium) that overwinters. Overwintering is the ability of a pathogen to survive from one growing season to the next.

The probability of a disease epidemic is proportional to the amount of inoculum and to the proximity to its host. Primary infection occurs when the pathogen is in contact with a susceptible host under suitable conditions. The pathogens enter directly through the surface of the plant or through wounds or natural openings. Bacterial and fungal pathogens usually require free water for spore germination, so infection is favored by wet periods with high air humidity and by wet canopies.

Dissemination of the pathogen from an inoculum source to a host can occur by wind, splashing rain, runoff, insects, infected seeds or seedlings, etc. Fungi grow and spread within their host by means of mycelium, and eventually produce spores on or within the infected tissue. These spores lead to secondary infections during the season. Bacteria spread in the plant by rapidly increasing the population. Then, when fissures develop on infected tissue, the cells (secondary inoculum) are exposed to the environment and thus, dissemination may proceed.

The secondary infection cycle can be repeated many times during the growing season, depending on the biology of the pathogen and its host and environmental conditions.

15.5.3 Yield Losses Due to Pests

Two crop yield loss rates may be differentiated. The loss potential characterizes the risk that the agent exerts on crop yield in a no-control scenario. The actual losses are those occurring despite the crop protection practices. The efficacy of the crop protection practices may be evaluated as a percentage of potential losses prevented. The potential and actual loss are quite variable depending on the crop species and the region considered. Among crops the loss potential of all biotic factors worldwide varies between 50 % (wheat) and more than 80 % (cotton). Actual losses are estimated at 26–31 % for soybean, wheat, maize and cotton, and 37–40 % for potatoes and rice, respectively (Table 15.2). Overall, weeds have the highest loss potential (23–40 %) with animal pests and pathogens being less important (9–37 % and 9–29 %, respectively). Although viruses cause serious problems in potatoes and sugar beets in some areas, worldwide losses due to viruses average 6–7 % on these crops and <1–3 % in other crops. The efficacy of crop protection lies between 43 and 65 % for the different crops. Global efficacy in weed control (67–80 %) is

Table 15.2 Yield losses (%) due to pests at a global scale. Potential and actual yield losses are those occurring in a no-control and a current control scenario, respectively. The efficacy of control is the percentage of losses prevented by current control measures

		Wheat	Rice	Maize	Potato	Soybean	Cotton
Weeds	Potential	23	37.1	40.3	30.2	37	35.9
	Actual	7.7	10.2	10.5	8.3	7.5	8.6
	Efficacy	67	73	74	73	80	76
Animal pests	Potential	8.7	24.7	15.9	15.3	10.7	36.8
	Actual	7.9	15.1	9.6	10.9	8.8	12.3
	Efficacy	9	39	40	29	18	67
Pathogens and viruses	Potential	18.1	15.2	12.3	29.3	12.4	9.3
	Actual	12.6	12.2	11.2	21.1	10.1	7.9
	Efficacy	30	20	9	28	19	15
Total	Potential	49.8	77	68.5	74.9	60	82
	Actual	28.2	37.4	31.2	40.3	26.3	28.8
	Efficacy	43	51	54	46	56	65

Adapted from Oerke (2006)

much higher than that of animal pests (9–67 %) or diseases (9–30 %). These values have to be taken only as indicative as they are based on estimates of reference yields (not affected by pests).

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