

# Introduction

---

## Seeds as a Food Source

Humans have always relied on the green plant to produce the calories needed for their sustenance, either directly or indirectly after conversion by animals, and as a source of fuel and fibre. As a result of this reliance on green plants, the sun was essentially the only source of energy until the exploitation of fossil forms of solar energy ushered in the industrial revolution. Agricultural production systems became increasingly dependent upon these fossil forms of energy (coal, petroleum), but solar energy, diffuse but reliable, continued to be the primary source of our food supply (Hall and Kitgaard, 2012, p. 4). The green plant driven by solar energy will, for the foreseeable future, continue to feed humankind.

The plants utilized by humans are consumed in many different ways; for some, fresh fruits are harvested, in other cases stems, leaves, roots or tubers represent the economic yield. The entire above-ground plant is harvested in some vegetable or forage crops whereas immature fruits or seeds represent the economic yield of other vegetable crops. But the crop plants making the largest contribution, by far, to the world's food supply, are those harvested at maturity for their seed.

Seeds are important and useful because they are nutrient-dense packages of carbohydrates, protein and oil that are relatively easy to harvest, store and transport. Once the seed is dried, it can be stored indefinitely if it is kept dry and free of insects and other pests. Storage of seed is cheaper and the shelf-life is infinitely longer than plant parts that are consumed fresh. Its ease of transport provided the foundation of the global grain trade that has helped equalize worldwide supply and demand since the development of ocean-going ships (originally moved by solar energy in the form of wind). Seeds are an important source of animal feed to produce meat, eggs, milk and other animal products.

The seed is also the biological unit used to reproduce most crops; there would be little food production without adequate supplies of viable, vigorous planting seed. The slogan of the American Seed Trade Association – ‘First the Seed’ – makes it clear that our existence depends on seeds that can germinate to produce the next crop. Thus, seed has a dual function of being consumed as food or feed

and providing the means to reproduce the crop. These attributes have made the seed the foundation of agriculture since ancient times.

Many plant species have been used as sources of food, feed or fibre. Harlan (1992) compiled a 'short list' of cultivated plants that contained 352 species from 55 families. Vaughan and Geissler (1997) listed approximately 300 plant species used for food. The database of agricultural statistics (FAOSTAT) of the Food and Agriculture Organization (FAO) of the United Nations lists some 130 species in their crops category including grains, vegetables, fruits, nuts, fibre crops, spices and stimulants (coffee, tea and tobacco), but seeds are harvested from only about 35 species (FAOSTAT, 2014) and only 22 of these species are produced in substantial amounts (Table 1.1).

These 22 species represent only a few families, with 18 of them from the *Poaceae* (grasses) (nine) and the *Fabaceae* (legumes) (nine). Three of the species (maize, rice and wheat) dominate the world grain (seed) production, accounting for 76% of the 2011–2014 average production of the species in Table 1.1. If soybean, the fourth major crop, is included, the total increases to 84%. These crops account for roughly half of the calories available per capita for consumption from plant sources in 2009–2011. This proportion would increase if the seeds fed to livestock were included. It is clear that humans are fed by a very small sample of the plant species that could be used to produce food. Relying on so few crop species would seem to make our food supply vulnerable to insect or disease epidemics, but the use of multiple varieties of each crop reduces the chances of widespread crop failure (Denison, 2012, p. 3) as does the worldwide distribution of each crop. The importance of maize, rice and wheat is not a recent phenomena; Heiser (1973) pointed out that most important early civilizations were based on seeds of these crops. Truly, crops harvested for their mature seeds have served us well.

There is continuing interest in increasing the number of plant species providing our food supply. Examples of new crop species under consideration include grain amaranth (*Amaranthus* spp.) (Gelinas and Seguin, 2008), chia (*Salvia hispanica* L.) (Jamboonsri *et al.*, 2012), quinoa (*Chenopodium quinoa*), hemp seed (*Cannabis sativa* L. (Pszczola, 2012), vernonia (*Vernonia galamensis*) (Shimelis *et al.*, 2008), and potato bean (*Apios americana* sp.), a legume that produces edible tubers (Belamkar *et al.*, 2015). Attempts are also being made to develop perennial grains from conventional annual crops and exotic species. Perennial grain crops are expected to conserve soil resources by providing continuous ground cover and perhaps produce higher yield as a result of a longer life cycle (Glover *et al.*, 2010).

New crops are often touted on the basis of their superior nutritive characteristics and/or their ability to be productive on infertile or droughty soils. If these new species are, in fact, 'super crops', why were they not selected in the long domestication processes that produced the few crops that feed the world? Are the species currently used those best suited for domestication (Sinclair and Sinclair, 2010, pp. 15–23), or were they domesticated first and then simply maintained by humans' unwillingness to start over (Warren, 2015, pp. 164–167)? The relatively poor track record of new crop development schemes in recent times suggests that there may

**Table 1.1.** World production and seed characteristics of crops where the mature seed is harvested for food or feed.

Crop		World production <sup>1</sup> (1000 t)	Harvested unit	Seed composition <sup>2</sup>		
				Carbohydrate (g kg <sup>-1</sup> )	Oil (g kg <sup>-1</sup> )	Protein (g kg <sup>-1</sup> )
<b>Poaceae</b>						
Maize	<i>Zea mays</i> L.	950,394	Caryopsis	800	50	100
Rice	<i>Oryza sativa</i> L.	733,424	Caryopsis	880	20	80
Wheat	<i>Triticum spp.</i> <sup>3</sup>	700,828	Caryopsis	750	20	120
Barley	<i>Hordeum vulgare</i> L.	138,252	Caryopsis <sup>4</sup>	760	30	120
Sorghum	<i>Sorghum bicolor</i> (L.) Moench	58,647	Caryopsis	820	40	120
Millet <sup>5</sup>	<i>Panicum miliaceum</i> L.	26,528	Caryopsis	690	50	110
Oat	<i>Avena sativa</i> L.	22,639	Caryopsis <sup>4</sup>	660	80	130
Rye	<i>Secale cereale</i> L.	14,906	Caryopsis	760	20	120
Triticale	<i>X Triticosecale Wittm ex A. Camus</i>	14,653	Caryopsis	594	18	131
<b>Fabaceae</b>						
Soybean	<i>Glycine max</i> (L.) Merrill	272,426	Non-endospermic seed	260	170	370
Groundnut <sup>6</sup>	<i>Arachis hypogaea</i> L.	41,366	Non-endospermic seed	120	480	310
Bean <sup>7</sup>	<i>Phaseolus vulgaris</i> L.	23,898	Non-endospermic seed	620	20	240
Chickpea	<i>Cicer arietinum</i> L.	12,735	Non-endospermic seed	680	50	230
Pea, dry <sup>8</sup>	<i>Pisum sativum</i> L.	11,013	Non-endospermic seed	520	60	250
Cowpea	<i>Vigna unguiculata</i> (L.) Walp.	6,661	Non-endospermic seed	570	10	250
Lentil	<i>Lens culinaris</i> Medikus	4,831	Non-endospermic seed	670	10	280
Broad bean	<i>Vicia faba</i> L.	4,332	Non-endospermic seed	560	10	230
Pigeon pea	<i>Cajanus cajan</i> L. Millsp.	4,454	Non-endospermic seed	560	20	250

Continued

**Table 1.1.** Continued.

Crop		World production <sup>1</sup> (1000 t)	Harvested unit	Seed composition <sup>2</sup>		
				Carbohydrate (g kg <sup>-1</sup> )	Oil (g kg <sup>-1</sup> )	Protein (g kg <sup>-1</sup> )
<b>Others<sup>9</sup></b>						
Rapeseed <sup>10</sup>	<i>Brassica napus</i> L., <i>B campestris</i> L.	67,789	Non-endospermic seed	190	480	210
Sunflower	<i>Helianthus annuus</i> L.	40,931	Cypsela	480	290	200
Sesame	<i>Sesamum indicum</i> L.	4,738	Non-endospermic seed	190	540	200
Safflower	<i>Carthamus tinctoris</i> L.	776	Cypsela	500	330	140

<sup>1</sup>Average of 2011 to 2014, FAOSTAT (2016). <sup>2</sup>Seed composition data from Bewley *et al.* (2013), Sinclair and de Wit (1975), Langer and Hill (1991), Hulse *et al.* (1980), and Alberta Agriculture and Forestry (2015). <sup>3</sup>*Triticum aestivum* L. most common. <sup>4</sup>Harvested grain usually includes the lemma and palea.

<sup>5</sup>May include members of other genera such as *Pennisetum*, *Paspalum*, *Setaria* and *Echinochloa*. <sup>6</sup>In the shell. <sup>7</sup>Also includes other species of *Phaseolus* and, in some countries, *Vigna* species. <sup>8</sup>May include *P. arvense* (field pea). <sup>9</sup>Rapeseed is in the *Brassicaceae*, sunflower and safflower are in the *Asteraceae*, and sesame is in *Pedaliaceae*. <sup>10</sup>May include industrial and edible (canola) types, data from some countries includes mustard (*Brassica juncea* (L.) Czern., et Coss).

not be ‘better’ species waiting to be discovered. Nearly 100 years of intensive plant breeding produced the high-yielding cultivars of today’s common crops; the need for a time investment of this magnitude in a new crop is a serious impediment to its successful deployment.

The harvested seed is a caryopsis in nine of the 22 species in [Table 1.1](#), including the major crops maize, rice and wheat. Nine of the 22 species produce non-endospermic seeds; prominent crops in this group include soybean, groundnut and bean.

Composition of the seeds of these species varies widely ([Table 1.1](#)). Nine species, the cereals, produce seeds that are high in starch ( $>600 \text{ g kg}^{-1}$ ) and low in protein ( $\leq 131 \text{ g kg}^{-1}$ ). Seeds of the traditional pulse or legume crops (seven species – bean, chickpea, dry pea, cowpea, lentil, broadbean and pigeon pea) have relatively high concentrations of protein ( $\geq 230 \text{ g kg}^{-1}$ ), high to intermediate carbohydrate levels, and very low oil concentrations. Four species (rapeseed (canola), sunflower, sesame and safflower) are classified as oil crops, with high concentrations of oil ( $290\text{--}540 \text{ g kg}^{-1}$ ) and relatively high protein levels, with safflower a conspicuous exception ([Table 1.1](#)). Soybean and groundnut fall into a class by themselves, with seeds that contain exceptionally high protein ( $310\text{--}370 \text{ g kg}^{-1}$ ) concentrations and moderate ( $170 \text{ g kg}^{-1}$ , soybean) to high ( $480 \text{ g kg}^{-1}$ , groundnut) oil concentrations.

The seeds that sustain humankind were selected over the millennia from an enormous number of potential crop species. The grass seeds, the staff of life, are major sources of carbohydrates for much of the world and are complemented by the pulses (legumes) with their relatively high protein levels (poor man’s meat) (Heiser, 1973, p. 116). These crops have fed humankind for centuries and it seems likely that we will continue to rely on them for the foreseeable future. Fortunately, the productivity of these crops has increased in step with the expanding world population.

## Increasing Food Supplies: Historical Trends in Seed Yield

World population has increased by approximately 1000 times since the beginning of agriculture (Cohen, 1995, p. 30). The world population was roughly one billion (Cohen, 1995, p. 400) at the turn of the 19th century, when Thomas Malthus made his apocalyptic prediction (1798) that the power of population to increase is indefinitely greater than the power of the earth to provide food. The world population reached 7.3 billion in 2015, accompanied by food supplies that are, overall, more than adequate, as indicated by low grain prices in many countries, record low levels of undernourished people and rising concerns of an obesity epidemic in developed countries (FAOSTAT, 2016). Food supplies have increased since Malthus’s day more or less in step with population.

There are only six basic avenues by which food production can be increased (Evans, 1998, p. 197).

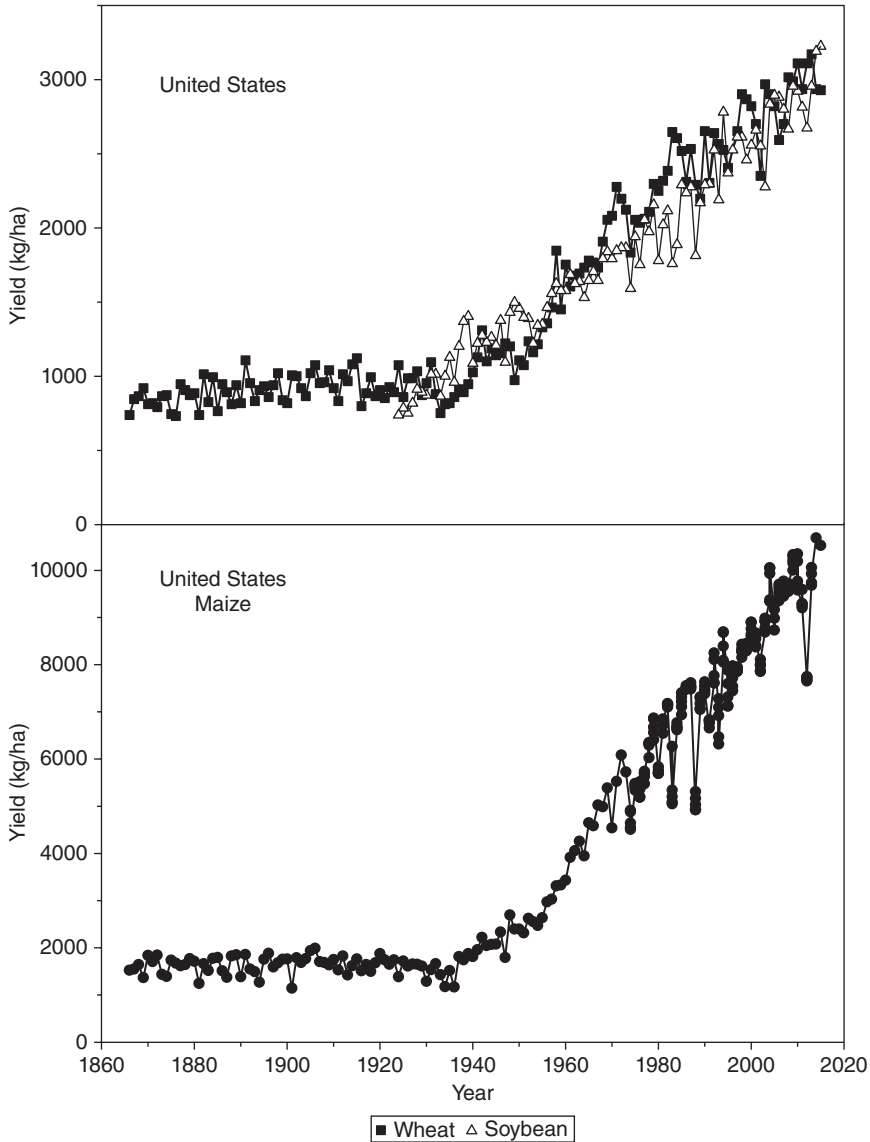
1. Increase the land area under cultivation
2. Increase the crop yield per unit area
3. Increase the number of crops per unit area per year (multiple cropping)
4. Replace lower yielding crops with higher yielding crops
5. Reduction of post-harvest losses
6. Reduced use as feed for animals.

The first four options deal with the quantity of food produced by crops, our interest in this book, but the last two would also increase the amount of food available for consumption by the world's population. Shortening the food chain by utilizing more plant and fewer animal products, and reducing waste in harvest, storage and utilization of food and feedstuffs could make significant contributions, as could reducing the land area devoted to non-food production (i.e. crops fed to cats, dogs, horses and other pets; fibre, industrial, and especially biofuel crops). All of these last options would contribute to a larger food supply without increasing the land used for crop production, yield per unit area or the inputs required to increase yield. We will come back to these non-production options in Chapter 6, but they all involve complicated economic and social issues that are mostly beyond the purview of crop physiologists and this book.

Historical increases in food production were often associated with cultivation of more land. For example, wheat and maize production in the US increased by 3.5- to fivefold from 1866 to 1920 as a result of a three- to fourfold increase in harvested area as production moved west onto new lands in the Corn Belt and Great Plains states (NASS, 2016). The shift from the use of animal power (primarily horses and mules) to mechanical power (cars, tractors, trucks) fuelled by petroleum products in the early years of the 20th century reduced the need for feed production and made more land available for food production. Increases in yield, however, played a much larger role in more recent times as the supply of unused land declined.

Yield from eras closer to the beginning of agriculture 10,000 years ago provide an interesting perspective on current discussions of yield and the potential for yield improvement. Estimated maize yields in Mexico in 3000 BC were approximately 100 kg ha<sup>-1</sup>, while brown rice yields in Japan in 800 AD were 1000 kg ha<sup>-1</sup> (Evans, 1993, pp. 276–279). Wheat yield in England increased from roughly 500 kg ha<sup>-1</sup> in 1200–1400 AD to approximately 1100 kg ha<sup>-1</sup> in the 1700s and nearly 2000 kg ha<sup>-1</sup> in the 1800s (Stanhill, 1976). Wheat yields in New York averaged 1077 kg ha<sup>-1</sup> for the period from 1865–1875 (Jensen, 1978). Modern yields (2011–2014 averages) for comparison are 7593 and 4182 kg ha<sup>-1</sup> for wheat in England and New York, respectively; 6707 kg ha<sup>-1</sup> for rice in Japan; and 3146 and 9391 kg ha<sup>-1</sup> for maize in Mexico and the USA (FAOSTAT, 2016; NASS, 2016). Clearly yields have increased along with the world's population.

Documentation of changes in crop yield over a shorter time frame in the USA is shown in Fig. 1.1 for two cereals (maize and wheat) and a legume (soybean). There was relatively little change in yield of maize and wheat from 1866 to ~1940, when the advent of high-input agriculture (chemical fertilizers, herbicides



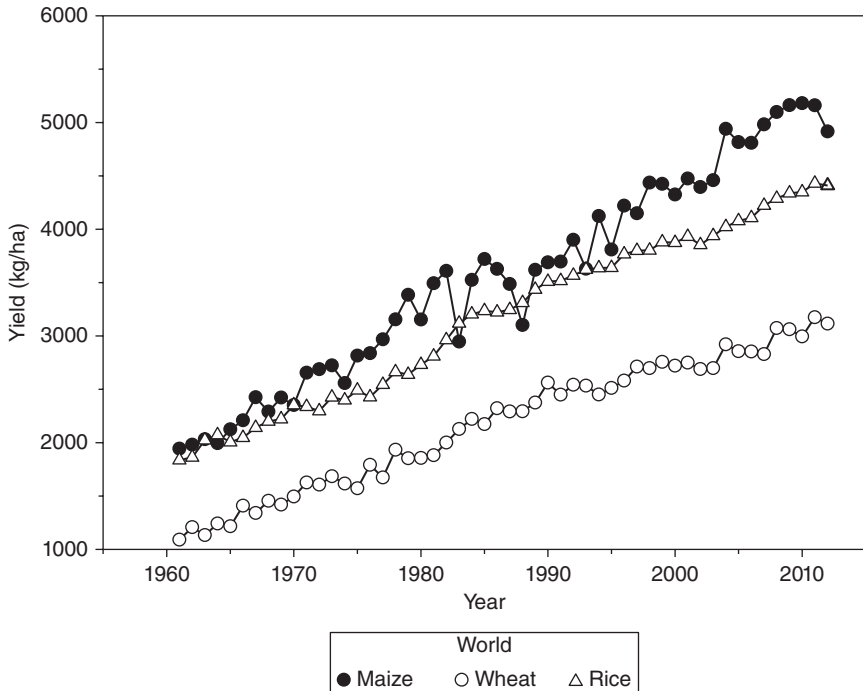
**Fig. 1.1.** Average yields of maize, wheat and soybean in the United States. Data from the National Agriculture Statistics Service (NASS, 2016).

and pesticides) combined with the use of hybridization to produce improved cultivars (hybrids in maize, but not wheat) started a steady increase in yield that has continued to the present time. Soybean yield in the USA also increased steadily from 1924; the first year that yield data were available. The three- to sixfold increases in yield of these crops in the 75 years after 1940 is truly astounding when

compared with the previous 74 years, when there was no change. The agricultural systems in place for that 74-year period were low-input systems that emphasized a mixture of crop and animal agriculture and multi-crop rotations that included legumes with manure providing much of the N input (Egli, 2008); a system that would probably fit the modern day definition of organic agriculture.

World yields of wheat, maize and rice (Fig. 1.2) also increased steadily from 1961 to 2012. World yields from earlier years are not readily available, but they probably followed a pattern similar to those in Fig. 1.1.

Any evaluation of historical yield trends leads to the question – what will happen in the future? Will the increase continue indefinitely (surely there is a maximum set by biophysical limits on the conversion of solar energy to biomass) or will it slow and eventually stop, resulting in a yield plateau? There is no clear evidence in Fig. 1.1 and 1.2 that yields are reaching a plateau. There is, however, evidence for plateaus in some crops in some production systems (e.g. wheat in France (Brisson *et al.*, 2010), rice in Korea and China, wheat in northwest Europe and India, and maize in China (Cassman *et al.*, 2010)). It is very difficult to identify yield plateaus, and many apparent plateaus in the past were only temporary cessations in yield growth. In the first edition of this book (Egli, 1998, pp. 6–7), US and world wheat yields exhibited plateaus for the last 14 (USA, 1983 to 1996) and six (world wheat, 1990 to 1995) years of record, but Figs 1.1 and 1.2 show



**Fig. 1.2.** Average world yields of maize, wheat, and rice, 1961 to 2014. Data from FAOSTAT (2016).



that these were only temporary plateaus, and yield eventually resumed its upward trend. It is always possible in any yield time series to identify short periods when there is no yield growth, but then growth begins anew and the plateau disappears. Rigorous statistical protocols to detect yield plateaus have been developed (Lin and Huybers, 2012; Grassini *et al.*, 2013), but statistical analysis cannot predict future yields and it is those yields that determine whether a plateau persists or the increase in yield resumes. Plateaus are often a result of sub-optimal environmental conditions, but they may also reflect a lack of production inputs, government policy, or emphasis on quality over yield (Fischer *et al.*, 2014, pp. 41–43) and do not always reflect fundamental limitations of the plant. Yield plateaus will seriously limit our ability to maintain adequate food supplies for an increasing world population, so the question – how long and how rapidly will yields continue to increase? – is extremely important. We will return to these issues in Chapter 6.

The steadily increasing yields in Figs 1.1 and 1.2 were primarily the result of two basic changes. Either the plant was improved through plant breeding and selection, or the plant's environment was improved by crop management. Improvements from breeding are frequently divided into those increasing yield via defect elimination and those increasing yield in a non-stress environment (potential yield) (Donald, 1968). Defect elimination allows the farmer to 'recover' the yield that would have occurred in the absence of the defect, but does not add to the potential yield. An example of defect elimination was reported by Sandfaer and Haahr (1975) where the yield of old cultivars of barley was 26% lower than new cultivars when the evaluations were made in the presence of the barley yellow stripe virus but only 8% lower in the absence of the virus. Much of the higher yields of the new cultivars came from incorporation of virus resistance, i.e. elimination of a defect (susceptibility to the virus), and not through any change in the primary productivity of the plant. Both approaches contribute to higher yield in the farmer's field, but the relative contribution of the two is not well defined and no doubt varies among crops and cropping systems.

Both breeding and management contributed to past increases in yield and, in many cases, new cultivars were only effective when management practices changed. For example, the shorter rice cultivars that were at the heart of the green revolution produced higher yields only when they received high levels of N fertilizer (Chandler, 1969); modern maize hybrids express their superior yielding ability only when grown at high population densities (Duvick, 1984).

The traits that Duvick (1992) associated with higher yielding maize hybrids included defensive traits (i.e. defect elimination) such as resistance to premature death, stalk and root lodging resistance, shorter anthesis–silking intervals resulting in less barrenness, and tolerance to European corn borer (*Ostrinia nubilalis* Hubner). More upright leaves (probably contributing to higher canopy photosynthesis) and longer seed-filling periods (Cavaliere and Smith, 1985) probably represent direct selection for potential yield. Increasing the harvest index, the ratio of yield to total biomass, was associated with improvement in potential yield of wheat, barley (Evans, 1993, pp. 238–260) and rice (Peng *et al.*, 2000) with no change in total biomass, although more recent evidence suggests that increases are now driven

by increases in total biomass (Peng *et al.*, 2000; Shearman *et al.*, 2005). Changes in many other plant characteristics have been related to improvement of potential yield and defect elimination (see Evans, 1993, pp. 169–268 for a thorough discussion of this topic), but it is not always clear that these historical changes provide any guidance for future improvements.

Estimates of the proportion of the total yield increase coming from plant breeding range from 20 to 80% across several crops (Evans, 1993, pp. 297–307). Estimates for some of the major grain crops (maize, wheat, soybean, sorghum) in the USA suggest that from 40 to 80% of the yield increase came from plant breeding (Smith *et al.*, 2014; Schmidt, 1984; Specht *et al.*, 2014; Miller and Kebede, 1984). The total breeding effort, breeding objectives, and the quality of the environment influence progress from breeding (Evans, 1993, p. 307), so relatively low yields of some minor crops (i.e. crops grown on limited acreage, such as some grain legumes) may partially reflect limited breeding efforts. Precise estimates of the relative contributions of breeding and management are difficult and probably vary widely among crops and cropping systems. The contribution from crop management, however, will probably decrease in the future, as past improvements make the next increment in yield more difficult (Egli, 2008).

What will happen in the future is a much-debated question, a debate that focuses on three major topics with very little agreement on any of them. The three main issues are: (1) Will yields keep increasing and will the increase be adequate to feed an expanding, more affluent population? This yield question is particularly important because expansion of the land area used to produce food is usually considered an undesirable approach. (2) What effect will global climate change have on production – will reductions in production from higher temperatures and lower rainfall exceed gains from higher rainfall or from expansion of crop lands to areas where production is not currently possible (e.g. current expansion of maize production into the prairie provinces of Canada)? (3) What effect will shifting from coal and petroleum to energy sources that emit fewer greenhouse gases, such as solar and wind, have on agricultural productivity? Much of the increase in agricultural productivity in the high-input era was based on cheap energy, raising the question: Can productivity be sustained and increased with more expensive energy? These are all complex questions, and the hopes and fears they raise will be discussed in more detail in Chapter 6.

## Crop Physiology and Yield Improvement

Plant growth and the production of yield can be studied at varying levels of complexity, from the plant community to the molecular level, i.e. crop community, plant, organs, tissues, organelles, macromolecules and atoms/molecules (Thornley, 1980). Economic yield of grain crops, however, is always measured on a land area basis and must be studied as a community phenomenon, not as the product of individual plants. Consequently, agronomists have traditionally

evaluated yield at the community level. Many factors that they consider to be important, such as plant population, leaf area index and solar radiation interception, are characteristics of a community of plants, not individual plants; other important factors may be characteristics of the individual plant (e.g.  $C_3$  or  $C_4$  photosynthesis, leaf display). Characteristics that make an isolated plant productive may have no effect or a negative effect at the community level. Leaf angle is a classic example of this phenomenon; isolated plants benefit from horizontal leaves, while community productivity may be higher with a mix of horizontal and vertical leaves (Duncan, 1971).

Scientific investigations of plant growth go back at least to the work of Priestley in 1771 (plants released oxygen); Ingenhous (light required for the evolution of oxygen by plants) and de Saussure, who showed, in 1804, that plants took up mineral nutrients and  $NO_3$  from the soil (Evans, 1975, p. 12). Crop physiology, understanding the dynamics of yield production of crops, began with the work of W. L. Balls in the early 1900s on plant spacing and sowing dates with cotton (*Gossypium* spp.) communities in Egypt, **not** isolated plants (my emphasis) (Evans, 1975, pp. 13–14).

Growth analysis techniques were developed in the first half of the 20th century to describe growth of plants and plant communities (Blackman, 1919; Watson, 1947, 1958). The components of growth analysis describe the accumulation of dry matter with a general goal of learning more about plant or community characteristics that regulate productivity. The absolute growth rate ( $g\ plant^{-1}\ day^{-1}$  or  $g\ m^{-2}\ land\ area\ d^{-1}$ ) provides the starting point and other growth analysis parameters deconstruct the absolute rate to better understand its regulation.

The relative growth rate (RGR,  $g\ g\ dry\ weight^{-1}$ , Blackman, 1919) describes the inherent ability of the plant to accumulate dry matter per unit of dry matter present. Photosynthesis by leaves is responsible for almost all of the dry matter accumulation by crop plants, so expressing dry matter accumulation on a leaf area basis, i.e. net assimilation rate (NAR,  $g\ m^{-2}\ leaf\ area\ day^{-1}$ , Briggs *et al.*, 1920), provides a better representation of growth capacity than RGR based on total plant weight. Since leaves are the primary source of photosynthesis, the proportion of dry weight allocated to leaves, the leaf area ratio (LAR,  $m^2\ leaf\ area\ g\ dry\ weight^{-1}$ , Briggs *et al.*, 1920) is also an important parameter.

The absolute rate of accumulation of dry matter by a crop community, the crop growth rate (CGR) expressed as  $g\ m^{-2}\ land\ area\ day^{-1}$  always refers to the growth of the crop community, never to growth of individual isolated plants. Watson (1947) defined leaf area index (LAI), the ratio of leaf area (one side only) to the ground area, as a convenient way of describing the leaf area of a crop. An LAI of 2 means that there are 2  $m^2$  leaf area per  $m^2$  ground area. The leaf area duration (Watson, 1947) interjects time into the analysis by considering how long the leaf is present. The CGR is, in its simplest form, determined by the amount of intercepted solar radiation (a function of LAI and leaf display) and its conversion by the plant into dry matter (radiation use efficiency, dry matter per unit intercepted radiation,  $g\ MJ^{-1}$  (Wilson, 1967), as shown in equation 1.1:

$$\text{Where } \text{CGR} = (\text{SR})(\text{SRI})(\text{RUE}) \quad (1.1)$$

CGR = crop growth rate ( $\text{g m}^{-2}\text{day}^{-1}$ )

SR = daily incident solar radiation ( $\text{MJ m}^{-2}\text{day}^{-1}$ )

SRI = proportion of SR intercepted by the plant community (%) and

RUE = radiation use efficiency ( $\text{g MJ}^{-1}$ ).

Growth analysis techniques provide a simple framework to help us understand the basis for differences in the absolute growth rate and productivity of individual plants or plant communities. Hunt (1978) provides a detailed summary of growth analysis techniques.

The growth analysis approach is useful because it highlights important plant and community characteristics that control productivity. The growth analysis equations remind us that differences in biomass can result from variation in simple plant or community characteristics and are not always dependent upon the inherent metabolic ability of the plant. The production of leaves to intercept solar radiation, a function of LAI, leaf area ratio, plant density and special arrangement of plants, is a key to determining CGR, so substantial differences in CGR could be completely independent of the inherent photosynthetic capacity of the plant. Variation in the growth rate of seedlings may be related to the size of the planting seed which determines the initial leaf area, solar radiation interception and the absolute growth rate without any differences in the inherent productivity (Egli *et al.*, 1990). Higher leaf area ratios will also accelerate the growth of isolated seedlings.

Crop physiologists too often emphasize metabolic aspects of growth and ignore simpler characteristics, even though they are clearly identified by growth analysis techniques. The growth analysis approach clearly differentiates between isolated plants and plant communities, a distinction that is often ignored by fundamental plant scientists. For example, large plants with many leaves and a large LAI may grow faster and yield more in isolation, but show no advantage over smaller plants in a community setting. Intercepted solar radiation (equation 1.1) of isolated plants is directly related to LAI, however, in a community solar radiation interception increases with LAI until it approaches 100% (complete ground cover); increasing LAI above this level will not increase intercepted solar radiation or CGR. A plant that produces many tillers or branches performs well as an isolated plant, but loses its advantage in a community because the extra LAI associated with the tillers or branches does not increase solar radiation interception.

Although growth analysis techniques provide a useful description of plant growth and made significant contributions to our understanding of the basic processes involved, they have a number of weaknesses that limit their usefulness. Measurements of plant dry weight are typically quite variable, especially in the field, which reduces the precision of parameter estimates and the ability to detect treatment effects. This lack of precision limits meaningful estimates of growth analysis parameters over short intervals, while average values from samples taken

at weekly or greater intervals do not provide much information about short-term environmental effects on growth.

Some growth analysis concepts, especially NAR and RGR, do not provide useful information when applied to plant communities. Once solar radiation interception by the community reaches a maximum, CGR is constant (ignoring environmental effects) (Shibles and Weber, 1965), but plant weight and LAI continue to increase. A constant growth rate combined with increasing plant weight and LAI cause RGR (growth rate per unit dry weight) and NAR (growth rate per unit leaf area) to decline. These declining rates do not provide useful information about crop growth.

The original growth analysis formulations did not deal explicitly with reproductive growth, which limited their application to understanding the production of grain yield. This deficiency was later remedied by the work of Wilson (1967) and Charles-Edwards (1982), and the development of the harvest index concept (Donald, 1962).

In spite of the limitations of growth analysis approaches, they provide a useful theoretical framework to guide our thinking about crop productivity. These concepts should not be forgotten in the current high-tech crop physiology research environment. In fact, the vestiges of growth analysis can be found in many current descriptions of crop growth, including the widespread use of CGR and radiation use efficiency.

In the middle of the 20th century, physiologists began to shift their emphasis to lower levels of complexity, to the organ level or below (Boote and Sinclair, 2006), as they investigated basic plant growth processes such as photosynthesis, nitrogen fixation, nitrate reduction and assimilate transport. This shift was probably partially driven by the inability of growth analysis techniques to address more fundamental questions about plant growth raised by a deeper understanding of plant metabolism. The availability of simple infra-red gas analysers to measure CO<sub>2</sub> concentrations opened the door to extensive study of single-leaf (Hesketh and Moss, 1963) and canopy photosynthesis (Larson *et al.*, 1981). The underlying assumption of this approach was that studying the fundamental metabolic processes involved in plant growth would lead to a better understanding of the yield production process. It often proved difficult, however, to relate information about the basic functioning of a process to the growth of an intact plant or a plant community.

In theory it should be possible to integrate information across all levels, from the molecular level to the plant community but this has proven to be difficult and may be practically impossible (Thornley, 1980; Sinclair and Purcell, 2005). Even using knowledge of the biochemistry of plant processes to predict canopy photosynthesis or CGR seems beyond the realm of possibility. The problem may be one of complexity; crop growth and yield are the end result of many individual plant processes and cycles operating over time, making it difficult to integrate knowledge of them together in a useful fashion. Some would argue that not enough is known about the processes to put them together; more research is needed and then yield can be explained, starting at the molecular level. Another possibility may be that

the usefulness of information of processes at lower levels is limited by the dominance of whole plant–plant community characteristics in determining yield.

W.G. Duncan, one of the original crop modellers, addressed this dilemma when he described the study of the pieces of the photosynthetic apparatus as ‘something like being given the pieces of a good watch in a box and then being asked what time it is’ (Duncan, 1967, p. 309). Duncan was making the point that basic knowledge of an individual process, in this case photosynthesis (i.e. light reaction, Rubisco, etc.) does not necessarily provide any useful information about the functioning of the plant community, i.e. canopy photosynthesis and the production of yield.

The focus on basic plant growth processes was followed by renewed interest at the whole plant–plant community level (Boote and Sinclair, 2006), which may have reflected our inability to integrate knowledge from lower levels to the whole plant or plant community level. Current research has again shifted to lower levels (Boote and Sinclair, 2006), probably driven by developments in molecular biology with its focus on specific genes and their role in regulating plant growth. Boote and Sinclair (2006) suggested that this cycling between a narrow focus at the gene level and whole plant and plant community studies will continue in the future. This cycling may eventually blur the difference between basic knowledge and its significance in the yield production process.

The complexity of the yield production system and the inability to integrate knowledge from basic levels to the functioning of the plant community stimulated interest in the development of crop simulation models. These models were visualized as tools to understand how the bits and pieces of the system contributed to the functioning of the community. The first models took a very simplistic approach to crop growth; for example, one of the first models (Duncan *et al.*, 1967) simply calculated the daily photosynthesis of a crop community as a function of photosynthetic system ( $C_4$  or  $C_3$ ), leaf area, leaf display (leaf angle) solar radiation and a solar radiation–single leaf photosynthesis response curve. One of the contributions of this simple model was to quantify the effect of leaf angle on canopy photosynthesis, a relationship that was much debated at that time, and to show that vertical leaves only increased canopy photosynthesis at high LAIs (Duncan, 1971). These findings illustrate one of the key functions of a model – the ability to evaluate relationships that are very difficult to test experimentally (Boote *et al.*, 1996). De Wit (1965) also made significant contributions to the early development of crop simulation models and, from those early beginnings, the models developed to the point where they ‘grow’ crops from planting to maturity. These models eventually included water relations, mineral nutrients, respiration, partitioning, and temperature effects and produced estimates of yield often expressed as the number of seeds per unit area and seed size (weight per seed). Some models were included in a systems package (e.g. the DSSAT family of models, Jones *et al.*, 2003) that made it possible to conduct multi-year comparisons of various management strategies; in short, they were sophisticated tools for studying management and environmental effects on crop growth and yield. In recent years, crop simulation models provided insights into the potential effects of climate change on crop yield (Asseng *et al.*, 2009), insight that would be very difficult to obtain experimentally.

Crop simulation models made contributions to our understanding of the yield production process, but I don't think they had the impact envisioned by the early pioneer modellers. Models have rarely contributed great insights into the fundamental processes controlling grain yield. The ability to manipulate individual processes and relationships with no limitations would seem to be a crop physiologist's dream, but it hasn't been as useful as expected. In spite of the ability of models to evaluate the effect of management practices on yield for multiple locations and years, applied agronomists continue to laboriously evaluate the same practices in field experiments year after year. Models would seem to be the perfect adjunct to the development of precision agriculture practices, but again they seem to have had only marginal impacts.

One limitation to the use of crop simulation models is that they are still too simplistic to capture all important aspects of the yield production process. A simplistic representation of a complicated process does not necessarily provide a strong basis for in-depth investigations of that process. I think the impact of crop models is also limited by a lack of interaction between crop physiologists (experimenters) and modellers. Crop physiologists designing experiments to answer questions raised by modellers, and modellers testing hypotheses to sharpen the focus of crop physiologists (Passioura, 1996) has not, in my opinion, occurred on a wide scale, certainly to a lesser degree than the interactions between theoreticians (equating a crop simulation model to a theoretical description of crop growth) and experimenters in other disciplines. This interaction and the entire modelling endeavour may have been limited by the absence of funding streams for the explicit development of models to study yield production in grain crops.

We now have a much better understanding of how crop plants grow and produce yield, thanks to the efforts of crop physiologists, other plant scientists, and modellers, than we had in the middle of the last century when yields started their rapid increase (Figs 1.1, 1.2). Our understanding of the yield production process will, no doubt, continue to improve; the challenge is to use this understanding to improve our crop production systems in the face of an uncertain future.

## **The Seed: an Integral Component of the Yield Production Process**

A fairly detailed understanding of crop growth and the production of yield is now available at the community level. Crop physiologists and modellers, however, have been slow to consider the seed as an explicit component of the system, but the seed cannot be ignored because only the dry matter accumulated by the seed is harvested for yield. It is worth noting that vegetative growth, before the seeds start accumulating dry matter, is just a preliminary activity; at the beginning of seed growth, no yield has been produced, it is all produced during the seed-filling period. Granted, leaves, stems and roots provide the synthetic capacity to feed the seeds, but all storage materials that give seeds their value (oil, protein, and starch) are synthesized largely in the seed from raw materials produced in the leaves. This



synthetic capacity makes the seed a critical component of the yield production system in grain crops. Consequently, including the seed in the yield production process will lead to a more complete understanding of the system.

The seed has a dual function in agronomic crops, it serves, as planting seed, to regenerate the crop, and it is the organ harvested for economic yield. Of course, the growth and development of the seed on the plant are the same if the ultimate fate of the seed is to be planted in the soil to produce the next crop or if it is to be eaten or processed for food, feed or industrial purposes. The two seeds, planting seed or grain, however, are not equal from a crop management viewpoint. The attributes of quality are not the same and consequently the management practices for producing high-quality planting seed are not always the same as those used to produce seed for grain. Planting seed must be genetically pure, viable and vigorous; traits not important for seed produced for grain. My focus in this book is on grain yield and the role that the seed plays in determining yield. I will not consider the essential role of the seed as a regenerator of the crop because this role has been covered at length by other authors (e.g. McDonald and Copeland, 1997; Copeland and McDonald, 2001; Bewley *et al.*, 2013).

Many formulations of the production of yield describe the accumulation of dry matter by a crop community and then simply partition or allocate some portion of this dry matter to the harvested fraction, for our purposes, the seed (Wilson, 1967; Charles-Edwards, 1982; Sinclair, 1986). This approach emphasized that yield was not solely a function of the ability of the crop to accumulate dry matter, but also a function of how much dry matter was allocated to the reproductive fraction. Unfortunately, this allocation was represented by a simple ratio at maturity that did not provide any mechanistic insights into the yield production process.

Growth analysis techniques emphasized understanding the processes involved in the production of dry matter and largely ignored the processes regulating the accumulation of dry matter by the seed. Division of yield production into the production of assimilates by the source and utilization of those assimilates by the sink included seeds in the evaluation, but the sink (seed) was too often assumed to be a simple receptacle for assimilate produced by the leaves. The seed was directly involved in investigations of yield components – plants per unit area, pods per plant, seeds per pod and weight per seed for a grain legume. Relationships among these components were studied to learn more about how the plant produced seed yield. Much of this research, however, represented a statistical search for relationships among components and contributed little to our understanding of yield production. Yield component compensation – when changes in one component were frequently associated with changes in the opposite direction in another component with no change in yield – gave yield components a bad reputation. I will attempt a fresh look at yield components in later chapters that will, hopefully, improve their reputation.

Although past investigations that included the reproductive fraction of the plant have not been particularly useful, it is my thesis that the processes involved in determining the proportion of the total biomass that ends up in the seed, i.e. grain yield, cannot be understood at a mechanistic level without considering the growth



and development of the seed. Accumulation of dry matter by the plant community is the fundamental basis of crop yield, but it is not the only important process. The ability of the individual seed to accumulate dry matter is also important; after all, it's the seed that is harvested for yield and it should not be surprising that the ability of the seed to accumulate dry matter is an important consideration in understanding the yield production process. I believe the key to understanding many important yield formative processes (determination of seeds per unit area, seed size, source–sink relationships) is to include the characteristics of the seed in the analysis.

My objective in this book is to consider the production of yield by grain crops from the perspective of the individual seed. This will be accomplished by investigating the characteristics of growth and development of the individual seed, the regulation of growth and development and the influence of the environment and plant characteristics on growth and development. This information will be used to develop a mechanistic understanding of the role of the seed in the production of yield by grain crops.

My focus in this book will be primarily at the level of the organ, plant and plant community. I will not investigate seed growth at lower levels; the extensive information on the physiology and biochemistry of the processes underlying seed growth and the potential involvement of hormones will not be covered. There are two reasons for these omissions. First, these topics are already covered in great detail in other publications (e.g. Bewley *et al.*, 2013), so no particular purpose would be served by repeating that information here. Second, and perhaps more importantly, these topics, in my opinion, provide little useful information about the role of the seed in the determination of crop yield.

When one considers the great diversity in shape, colour, size and composition of seeds harvested from grain crops, the objective of this book may seem hopelessly ambitious, requiring, at best, several volumes. Fortunately, this is not so, because, as we shall see, the important characteristics and general patterns of seed growth are remarkably uniform across the species listed in [Table 1.1](#), and perhaps across most plant species bearing orthodox (non-recalcitrant) seeds. This uniformity will make it possible to develop concepts describing the role of the seed in the production of yield that will apply to all grain crops.