Definitions, procedures and underlying crop physiology

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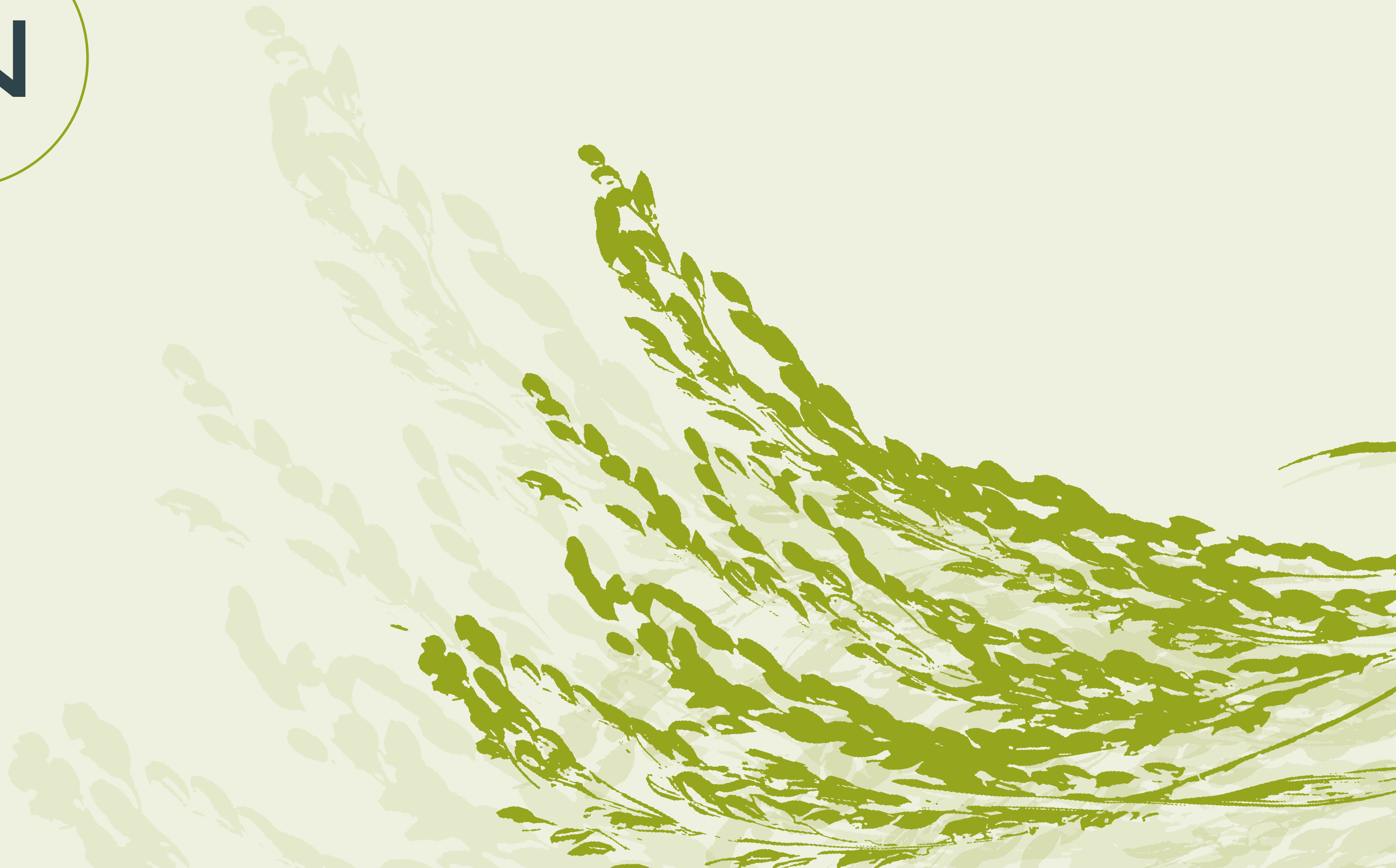

Key points

- This book aims to measure and understand crop yield increase in key crops and regions in terms of the development and adoption of new varieties and agronomic technologies.
- Farm yield (FY), potential yield (PY) and water-limited potential yield (PY_w) are defined as fundamental concepts in this chapter. The difference between PY and FY is known as the yield gap. FY is increased as the consequence of PY increase (resulting from the invention of new technology) and/or through a decrease in the yield gap (resulting from the adoption of the technology).
- FY increase is calculated from the linear regression of yield **against year** over the past 20–30 years. The linear slope is expressed as a percentage relative to the estimated FY **in the most recent year**.
- Many confounding factors, apart from adoption of new technology, can cause FY change over time. These include:
  - changes in crop location within a region
  - changes in cropping intensity or emphasis on grain quality, not yield
  - trends in levels of carbon dioxide and ozone
  - trends in the weather and the natural resource base of farming
  - shifts in regulatory policy, costs and/or prices.
- PY is measured in well-managed trials under representative environmental conditions, often conducted by breeders. PY increase is calculated as the linear regression of variety yield **against the year of variety release**, again considering releases only in the past 20–30 years. The linear slope is expressed **relative to the estimated PY of the most recent varieties.** Breeding, novel agronomic practices, and their interaction with variety, all increase PY.
- The relative progress in PY is assumed to apply to FY change for the same varieties and practices, if and when adopted on-farm. However, the maximum economically attainable FY defines a minimum yield gap of about 30% of FY.
- Key concepts in crop physiology are briefly explained since they are fundamental to explaining PY increase and understanding the limits to crop yield and input use efficiency.

Definitions, procedures and underlying crop physiology

2.1 Yields and yield gap definitions

Despite the rich general literature on measures of yield and yield progress, these terms have often been loosely used. To aid clarity throughout this book, this chapter defines the following key terms and their interpretation:

- crop yield
- farm yield (FY)
- potential yield (PY)
- record and contest-winning yields
- water-limited potential yield (PY_w)
- theoretical yield
- attainable yield
- yield gap.

The discussion relies largely on Byerlee (1992), Evans (1993), van Ittersum and Rabbinge (1997), Evans and Fischer (1999) and Connor et al. (2011).

Crop yield

'Crop yield' is the weight of grain or other product, at some agreed standard moisture content, per unit of land area harvested per crop. Standard moisture content varies between countries and crops but is 8–16% in grains. This is usually the maximum limit for marketing of grain and may vary slightly among countries—typical values are wheat (12–14%), paddy rice (14%), maize (15.5%), soybean (13%) and canola (8%). When harvest moisture exceeds the maximum limit, grain must be dried after harvest and before delivery; where harvest weather is dry, grain moisture can be 1–2% below the maximum limit. In all cases, moisture content is calculated on a fresh weight basis.[8] Complications abound (as already seen in rice). These are discussed in following chapters relevant to particular commodities. The term 'crop yield' is used in this book when greater specificity is not required.

Farm yield

The central yield figure used throughout this book is the field, district, regional or national average yield given in kilograms or metric tonnes per hectare (kg/ha and/or t/ha). This figure is reported in surveys and/or local or national statistics, and is referred to throughout this book as 'farm yield'[9] (FY). FY and many related crop statistics for all countries are collated annually by the Food and Agriculture Organization of the United Nations (FAO) and are disseminated through the publically accessible database FAOSTAT.[10] FY is expressed relative to harvested land area, noting that this area can fall well below planted area in some situations (e.g. after winter kill in winter wheat).

Although FY is quoted and used widely, it may not be as accurate as it appears, due to poor data collection, uncertain grain admixtures and other complications with data processing. With survey data, sampling error and bias can also arise.

In warm climates, more than one crop may be grown each year, so that yield per year or per day can be more important than individual crop yield. For example, Indonesian rice systems may produce three crops per year, a situation in which 'cropping intensity' (defined as the harvested area of all crops each year as a per cent of the cultivated area) is given as 300%.

Potential yield

At the high end of the yield scale it is critical to define 'potential yield'[11] (PY). PY is the yield to be expected with the best-adapted variety (usually the most recent release), with the best management of agronomic and other inputs, and in the absence of manageable abiotic and biotic stresses. Evans and Fischer (1999) provide this definition, although they use the term 'yield potential'. Many complications are hidden within this apparently simple definition but PY remains a key yardstick for understanding yield change. It may be difficult to measure, but PY and its surrogates are frequently

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[8] Grain dry weight is given by grain weight multiplied by (100 – '% moisture')/100.

[9] Some call this 'actual yield' (e.g. Connor et al. 2011). In addition, where FY is determined from the average of a population of fields or farms, this has interesting statistical properties related to distribution (normality, standard deviation, quantiles, skew, etc.), some of which arise in later chapters. Where the average comes from aggregated districts, states or countries, it is always the area-weighted average.

[10] <faostat3.fao.org/home/index.html>

[11] In this book 'yield' is retained as the noun, and 'potential' as adjective, to avoid confusion with the term 'yield potential' which appears often in published literature with various meanings.

reported in the general crop science literature—although often without adequate attention to complications.

PY is usually determined in field plots, but to be applicable to the surrounding district, the natural resource base (climate, soil type and topography) of the plots needs to be comparable (not superior) to the district. This includes consideration of any long-term management improvements (e.g. liming or tile drainage). Water supply must be adequate for PY to be determined otherwise it is necessary to instead consider 'water-limited potential yield' (PY_w), which is described further in a subsection on PY_w, below. Adequate water can come from well-distributed in-crop rainfall sufficient to satisfy most or all of the crop potential evapotranspiration (crop water use from sowing to harvest without water limitation) or from full or supplemental irrigation. Similarly, pests, weeds and diseases must be held at negligible levels through use of biocides if necessary. Finally, crops experiencing relatively rare weather damage (such as crop lodging or unseasonal frosting) are excluded from PY measurement.

Since PY is usually measured in plots, sampling errors will occur. Also, edge effects arising from extra solar radiation reaching border plants—or extra soil moisture in the case of PY_w—must be avoided, ideally by discarding the plot edges (up to a width of 25 to 100 cm, depending on crop height). If adjacent plots are harvested without discarding longitudinal edges, at the very least interplot path area must be included in the yield calculation.

PY as defined here is obtained from two sources: comparative variety trials and single variety experiments. The first source of PY data, variety trials, typically comprises well-managed experiments for the purpose of comparing new varieties against previously leading varieties (usefully called 'vintage trials'). All varieties may be present in all locations and/or years (termed a 'balanced trial'). Alternatively, multiyear unbalanced trials in which varieties gradually change over time—the situation for many breeding programs—are another source of PY information. The most useful comparative trials measure yields with fungicide protection—a good example is the wheat trials conducted by the UK Home Grown Cereals Authority (e.g. HGCA 2011). Yields from variety trials can only be considered as a true measure of PY where protection has been used, but around the world fungicide protection is not yet a common treatment in such trials. However, visible disease levels are usually reported, and if not negligible or too serious, this information can be used to correct PY.

The second source of PY data comes from careful field experiments conducted by crop physiologists, often to calibrate and/or validate crop simulation models that are largely driven by solar radiation, temperature and water supply applied to key crop physiological processes. Crop modelling is then often used to predict PY in other environments (e.g. different sowing dates, years and/or locations) and is especially useful for estimating PY across a relevant sample of seasons. Modelling accuracy has steadily improved for such purposes, but significant errors are still revealed when different models are compared (e.g. Palosuo et al. 2011). Models need to be updated for the latest varieties every few years, since breeders are steadily altering varieties (e.g. changing phasic development and improving PY). In this book, it is only when reliable measurements are unavailable that modelled yields are used to estimate PY. Thus, the primary estimates of PY and PY_w in this book are based on measured yields. However, in discussing the broader implications of these results, analyses based on modelled PY values are often cited.

Record and contest-winning yields

Sometimes crop contest-winning yields or record crop yields are considered in the scientific literature to be synonymous with PY. Even if verified independently, these yield values need to be treated with caution because they refer to very favourable circumstances (e.g. soils, weather and/or management) relative to the district or regional average conditions. With cautious interpretation, record and contest-winning yields can provide useful information, and some key examples are discussed in Section 5.2 on the US Corn Belt and Section 9.5 on modelled predictions of PY.

Water-limited potential yield

Much of the global grain crop is grown in rainfed situations where water supply from stored soil water at the start of the crop season, plus precipitation during the crop season, is much less than potential evapotranspiration (where crop water use is unlimited by water shortage). Thus for the purposes of measuring yield, it is useful to define a water-limited potential yield (PY_w). This is the yield obtained with no other manageable limitation to the crop apart from the water supply. Obviously crop yield will depend on the amount of available water, so PY_w is usually plotted relative to water supply (or use). The slope of the relationship is considered to reflect the potential 'crop water use efficiency' (or 'water productivity'), commonly reported in kilograms of grain yield per harvested hectare per millimetre of water (kg/ha/mm).

Complications can arise from variation in rainfall distribution with respect to crop development stages, but PY_w (defined as a linear function of the water supply) is a valuable and simple benchmark as argued in an in-depth review (Passioura and Angus 2010). Simulation modelling has been especially useful in dealing with expected deviations caused by variation in the distribution of water supply.

Theoretical yield

Models, such as dynamic crop simulation models, are also used to calculate yields that would result if certain physiological processes could be altered favourably within realistic bounds: such yields are here called 'theoretical yields'.

Attainable yield

In any given region, 'attainable yield' is another important yield benchmark between FY and PY (or PY_w). It is defined here as the yield attained by a farmer from average natural resources when economically optimal practices and levels of inputs have been adopted while facing the vagaries of weather.[12]

Since risk of financial loss almost always forms part of a farmer's decision to invest in increased inputs, the attainable yield definition must temper 'optimum level' with 'prudent attention to risk'. As an example this could mean input investments must be expected to return a risk premium over and beyond the cost of capital. This premium is usually low in developed countries and/or where water supply is assured, but is higher in developing countries and under rainfed conditions.

Of course attainable yield will reflect the economic circumstances of the crop and region—particularly grain prices relative to input costs, all measured at the farm gate. Although it is not easy to establish an appropriate attainable yield, general experience suggests that it will be ~20–30% below PY in situations where world prices and reasonable transport costs operate. Where this does not occur—for example, in much of Sub-Saharan Africa where infrastructure and institutions are weak—attainable yield (as defined above) may be much lower. Alternatively, where inputs and grain prices are heavily subsidised, it could more closely approach PY.

Yield gap

Because of the uncertainties surrounding attainable yield, it is easier to discuss the yield gap in terms of that between FY and PY, bearing in mind that even in the most advanced cropping situations in developed economies operating at close to world prices, FY will remain significantly below PY because of farm economic considerations surrounding attainable yield. Also it is more appropriate to **express yield gap as a percentage of FY** because when it comes to discussing food security, observed world grain production and likely increases are directly linked to FY (not PY). Other ways of estimating yield gaps are presented in Box 8.1.

General literature suggests that there is a minimum yield gap when FY equals attainable yield (as defined above), depending largely on prices. Assuming that future prices will be reasonably favourable for the farmer, this book considers that the **minimum yield gap to be 30% of FY**, meaning attainable yield is 23% below PY.[13] Any larger gap is often defined as an 'economically exploitable yield gap'. However, as shown in following chapters, the expected exploitation can be as much a task for national and local governments and agribusinesses, as one for farmers.

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[12] 'Attainable yield' is a term also defined by FAO and Connor et al. (2011), and somewhat differently by van Ittersum and Rabbinge (1997). The definition used in this book aligns more closely with that of FAO.

[13] Here, if FY equals 100, and the minimum yield gap is 30%, then PY must equal 130. Thus, the difference as a percentage of PY is 30/130 = 23%.

2.2 Measuring progress in farm yield and potential yield

Yield progress can be measured in terms of improving FY and PY.

Farm yield progress

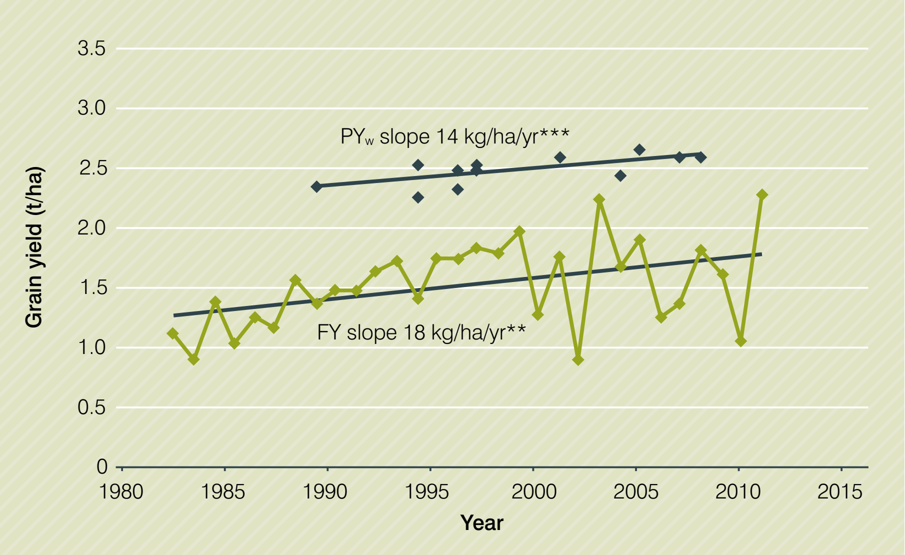
It is common to plot FY, the dependent variable, against year for given regions, states or nations. Economists look at exponential or compound rates of change (or the linear fit of log FY vs. time) expressed as annual per cent change. In contrast, crop scientists tend to calculate the linear fit of FY vs. time, coming up with a slope in kilograms (or tonnes) per hectare per year (kg/ha/yr or t/ha/yr). As change in FY over time in most cases resembles a linear relationship more closely than an exponential one (Figure 1.5), this book uses the linear slope as the basis for calculating and reporting annual rate of FY progress.

Over the last century, bilinear fits were adequate for major grain crops in most countries (Evans 1993; Calderini and Slafer 1998; Hafner 2003). Thus, slow or zero initial FY increases were replaced by rapid linear increases that often commenced in the 1950s or 1960s with the onset of modernisation of agriculture (e.g. the ‘green revolution’ in rice and wheat yields in Asia). Recently, many rising yields have slowed and some have even shown another break—this time to zero ongoing FY improvement, such as has occurred with wheat yields in parts of western Europe (Lin and Huybers 2012) including France (Brisson et al. 2010; see Section 3.8 on wheat mega-environment 11 (WME11)). In one case, maize in the USA, there has been a recent acceleration in the linear FY increase (see Section 5.2 on the US Corn Belt).

Since this book considers potential for yield gain into the future, progress is calculated using only the past 20 years (or 30 years if the data are very noisy, as with rainfed crops and/or small growing regions). This approach largely avoids the previous period of most rapid yield improvement, but also reduces the chance of picking up abrupt changes in slope (as in Lin and Huybers 2012). Linear relationships are fitted because in no case was a quadratic relationship significantly better.

Figure 2.1 illustrates a typical situation for FY progress. The linear slope and its level of significance are reported. The **standard for statistical significance** adopted throughout this book is:

- not significant (ns) for $P > 0.10$—although sometimes the observed P-value is given for the estimated slope of observed data if it is close to 0.10
- significant (*) for $0.05 < P < 0.10$
- highly significant (**) for $0.01 < P < 0.05$
- very highly significant (***) for $P < 0.01$.



$**0.01 < P < 0.05$, $***P < 0.01$

Figure 2.1 Typical plot of progress in farm yield (FY) and water-limited potential yield (PY_w) using example of spring wheat yields in Western Australia. FY is plotted against year and PY_w is plotted against year of variety release. Source: Source: PY_w from NVT (2009); FY from ABARES (2012) (see also Section 3.5)

In order to estimate the relative rate of change of yield (and crop area), throughout this book, **the linear slope (yield or area change per year) is expressed as a per cent of current FY**, estimated from the trendline in the last year for which there are statistics (usually 2009 or 2010).[14] This percentage is abbreviated to per cent rate of yield progress wherever the meaning is self-evidently an annual rate. The statistical significance is assumed to be the same as that of the linear slope, and is usually not repeated. These rules are applied also to slopes and relative rates of change obtained or calculated from other scientific literature.

Using the estimated FY for the latest year as the denominator to calculate the relative rate of progress reduces the influence of weather-induced fluctuations in FY. In the

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[14] Note that when FAO Crop Statistics refer to a given year, it is the year of harvest for all crops everywhere, with the exception of the Southern Hemisphere where it is the year of sowing of autumn-sown crops whose harvest can spill into January to February of the following year. In the US Department of Agriculture (USDA) and Australian systems, (year n to $n + 1$ notation), the first year (n) is the year of harvest of all crops except: (1) again for some late harvested southern hemisphere autumn-sown crops; and (2) for southern hemisphere summer crops, when the second year ($n + 1$) is the year of harvest. The FAO dating system is used throughout this book.

example used as Figure 2.1, the estimated FY (shown by the black trendline) in 2010 was 1.8 t/ha and thus—calculated from (18/1800) × 100—the rate of progress is 1.0%. A slope expressed relative to recent yield will also prove far more relevant to the future than a rate of progress inflated by a lower selected denominator: either the average yield of a time series or, worse still, the yield in the first year, is often used in research publications. For the same reason, where progress is linear the relative rate of increase will not be constant as in compound growth; rather, a given relative rate of progress will inevitably decrease as FY increases.[15]

Calculations in this book make no allowance for outliers or for heteroskedasticity in fitting the data, as have some authors (e.g. Finger 2010). Heteroskedasticity in this case refers to changing variance of yield with year, which is likely to be small over 20–30 years; not allowing for it should not bias the determination of slope.

Potential yield progress

PY (or PY_W) is plotted **not against year (as for FY), but against year of variety release** (see Figure 2.1). This is the first year in which farmers could avail themselves of the potential offered by that variety.[16] As with FY, the linear slope of PY vs. year of release is calculated by linear regression and shown in a figure. The rate of PY progress is given by this slope expressed as a per cent of estimated PY in the latest year of variety release (which is hopefully close to the present). In the example shown in Figure 2.1, estimated PY from the trendline was 2.6 t/ha in 2008 and the rate of progress is 0.5%—calculated from (14/2,600) × 100. Again, recently determined data have been sought to relate variety releases during the past 20 years. Where such data could not be found, longer release periods have been considered with attention to the duration of the linear relationship (i.e. consideration of whether the relationship remains linear through to the latest year of variety release).

As previously described, vintage trials—in which newer varieties are compared alongside older ones—represent the simplest situation in which to measure PY progress. Unbalanced multiyear trials have also been used to measure rate of progress, relying on recurrent control varieties that appear every year, and against which the yields of non-recurrent varieties are expressed as ratios or percentages. These ratios are then regressed against year of release. Both approaches assume that the older varieties, or the recurrent control varieties, always react in the same manner to any environmental changes over time (e.g. new disease races in unprotected trials). Obviously if varieties become more susceptible to disease with time, the rate of progress will be overestimated (see Section 3.8 on WME11, for example).

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[15] A 50% increase in yield over the next 50 years (e.g. from 3 to 4.5 t/ha), requires a linear increase of 30 kg/ha/yr throughout. Another way of describing this progress would be a relative rate of progress starting at 1% and falling to 0.7% in the final year.

[16] Sometimes researchers use year of first entry in widespread trials, perhaps 2–3 years before official variety release.

More recently, new statistical techniques can calculate effects from the unbalanced multiyear datasets now more common. With regular variety turnover (old varieties replaced by newer ones) over long time series, very few of the potential number of pairwise comparisons are present (e.g. <10% in Mackay et al. (2010) using multiyear Home Grown Cereal Authority (HGCA) data in the UK). Using linear mixed-model regression statistics, a coefficient for year of release can be directly fitted (e.g. Nalley et al. 2008), or variety effects can be determined and then regressed against year of release in a two-step process (e.g. Mackay et al. 2010). These procedures do not entirely reduce risk of bias due to breakdown of disease resistance with age in unprotected trials (again see Section 3.8), but bias is lessened as the residence period of varieties in the trials shortens. Again, some authors in this situation have allowed for heteroskedasticity (e.g. Nalley et al. 2008) but others do not consider this to be a significant issue (I. Mackay, pers. comm. 2012).

As explained, PY trials need to be performed under conditions representative of the target region, and such trials usually receive the best agronomic practices of the day. Advancing agronomic practice has generally contributed to PY progress, usually to the same extent as breeding,[17] and a positive interaction between the two has often delivered a major part of the progress (de Wit 1992; Evans 1993; Evans and Fischer 1999; Fischer 2009). For example, to cover two of the major interactions in modern agriculture (see Box 2.1), the rate of PY progress is higher in wheat when measured at high nitrogen levels (e.g. Ortiz-Monasterio et al. 1997), and higher in maize when measured at high plant density (Duvick 1997).[18] The balanced vintage trials mostly used for PY progress in this book were all conducted under recent environmental conditions and with the latest agronomy, even if some of the varieties involved were released (sometimes more than) 20 years ago. As a consequence, agronomy-by-variety interactions, if significant, become part of the measured 'breeding progress' in vintage trials, and are referred to in this book as such; however, the analysis misses any effect of changed agronomy on older varieties (see Box 2.1).

In the linear mixed-model approach with unbalanced datasets (see above) the agronomy-by-variety (and year-by-variety) interactions are in fact ignored and stay in the error term, but progress due to both breeding and to year (= agronomy plus any weather trends) are estimated and their sum gives PY progress correctly (see also Box 2.1). This approach is now becoming more popular; several are cited in the book, wherever possible specifying the separate components.

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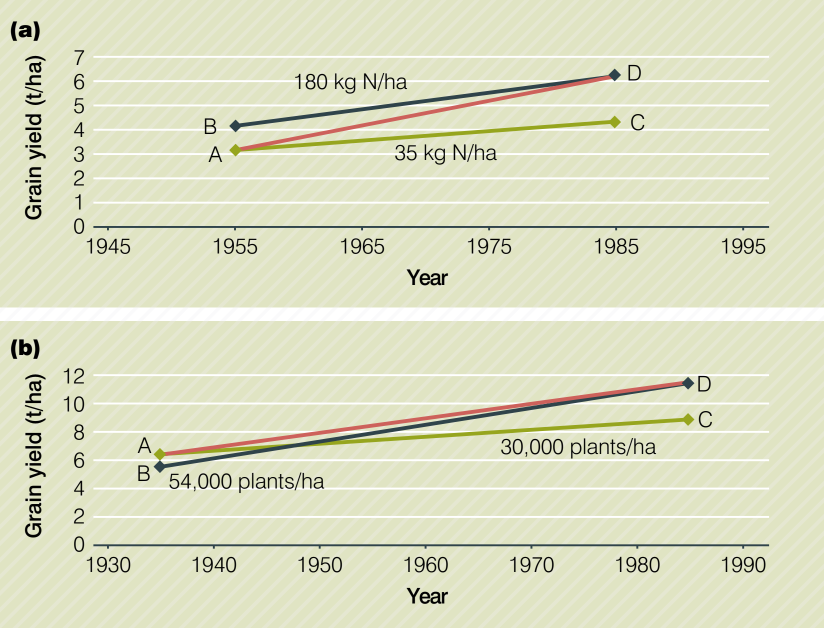
[17] Note that throughout this book 'agronomy' refers to crop management, as distinct from crop breeding.

[18] Note that it is impossible to mathematically separate the breeding and agronomic contributions in such interactions, an important point often overlooked in the attribution of progress. However, the effort taken to breed higher PY is clearly more than that required to raise the level of an agronomic input like nitrogen or seed; an entirely new agronomic intervention like conservation agriculture is, however, no effortless endeavour!

Box 2.1 Variety-by-agronomy interaction and potential yield progress

Ideally, vintage trials should be conducted under old and modern agronomy, because the examples used in the figure below show that estimates for PY progress under only modern agronomy miss the response of older varieties to changed agronomic conditions. This response could be either positive, shown in part (a) of the figure, or negative (part b). In both examples, point A represents the old variety under old agronomy, and point D represents the new variety under new agronomy: thus line AD measures true PY progress. But a vintage trial under modern agronomy would measure progress represented by BD, a lower slope than AD for the wheat example (figure part a) but a higher slope for the maize example (part b).



(a) Wheat potential yield (PY) progress at two levels of nitrogen per hectare, and (b) maize PY at two plant population densities. In each case an old and a modern variety are shown. Note: line AC represents the response to variety under old agronomy, line BD the response under modern agronomy and line AD the overall progress in PY. Source: (a) Ortiz-Monasterio et al. (1997), (b) Duvick (1997)

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Since PY trials are usually conducted under the best available agronomy for the latest varieties, yield results of latest varieties are likely to sit close to the top of their response curves. Thus when previously 'new' varieties become 'older' varieties in subsequent trials at a later date, these varieties are unlikely to respond greatly to higher agronomic input; hence the difference (or error) between lines AD and BD is unlikely to be large. It is not easy in modern agriculture to envisage an agronomic innovation that could lift yield of both old and new varieties by the same amount. However, this may be the response to increased carbon dioxide (CO_2) (see below in Section 2.4 on confounding factors), an effect that is missed by the measure of PY progress given here. To the extent that such PY progress estimation does miss agronomic innovation lifting all yields, this method underestimates PY progress and overestimates the rate of yield gap closing.

The situation is different in multiyear variety trials because yield increases not only through variety improvement but also better agronomy (and any positive interactions). This is because the trial is a measure of PY of the year of trial, not year of variety release. Linear mixed-model regression analysis can be used to separate the year effect (agronomy and/or environment change assuming no substantial change in trial locations) from the breeding effect (year of release). Again, the work of Mackay et al. (2010) with 59 years of Home Grown Cereal Authority (HGCA) variety trials in the UK provides a valuable example of this approach.

To date, however, progress through variety-by-agronomy interaction in such trials has not been separated in any of the cases cited in this book. The Mackay et al. (2010) analysis found no evidence for agronomic progress in UK winter wheat trial yields between 1982 and 2007, suggesting no significant variety-by-agronomy interaction contributing to the identified variety progress; this is common in other such analyses. However, Mackay et al. (2010) found both variety and agronomic progress between 1949 and 1981 when nitrogen levels increased notably. In this case the likely positive interaction would contribute to the estimates of both components of progress.

The estimated current values of FY and PY determined above also form the basis of the yield gap calculation. Using a current estimate for PY means that an inevitable part of yield gap is the time taken for the latest varieties (and any accompanying novel agronomy) to dominate in farm fields. Even in the best situations this lag time probably equates to around 5 years: with PY progress of 0.5% per annum (p.a.), this would inevitably lead to a small yield gap of ~2.5%. For many reasons the lag in new variety adoption can be longer—as is also common for the adoption of new agronomy—and this can partly explain much larger exploitable yield gaps reported in later chapters.

Yield gap with respect to delayed and variable variety adoption has been incorporated into some analyses of progress. For example, Silvey (1981) and Bell et al. (1995) took the breeding yield progress contained in each variety grown (relative to a standard control variety), then weighted it by the proportion of the region grown to the variety. In this way these authors built a **variety weighted index of PY** for the mix of varieties in farm fields in any year. The index was then plotted against time to estimate the relative progress that might be expected at the farm level from variety change. This process required statistics on which varieties are grown—data that are not often available—but the method does eliminate uncertainty arising from assuming that the best varieties are always adopted (after an appropriate lag). This approach is used in Section 4.2 for rice in some South-East Asian countries.

2.3 New technology, farm yield progress and yield gap closing

Many factors can be involved in the change in FY over time. The importance of each factor will change with region and crop (see Section 2.4 on confounding factors in FY change). The premise in this book is that the main driver of FY progress is the adoption of steadily improving technologies: new varieties, new agronomic or management techniques, and better timeliness and decisions by the farmer (e.g. Cardwell 1982; Bell et al. 1995). PY trials are conducted under the best current management and should therefore capture the latest in technical progress.

Furthermore, this book proposes that FY progress can be usefully divided into two components: increasing PY and closing of the yield gap between PY and FY. Figure 2.1 might indicate that the rate of increase in FY (18 kg/ha/yr) can therefore be considered the sum of the rate of increase in PY (14 kg/ha/yr) and the rate of yield gap closing (4 kg/ha/yr). This may be mathematically correct but **it is more realistic to assume that the relative rather than absolute rate of increase of PY applies to farm fields**. Thus the annual rate of FY progress of 1.0% is more usefully disaggregated into the rates of 0.5% PY increase and 0.5% yield gap closing, noting that gap closing is a negative rate of change. The critical assumption is that the relative change in FY to be expected from full adoption of PY varieties and practices is the same as the relative change in PY. This assumption has been confirmed by most on-farm testing where relative yield gains with new technologies (particularly new varieties) appear to hold up even where some management deficiencies exist. Note that this is not necessarily the case if management deficiencies are major, especially in the area of weed control. Note also that in the methodology used in this book, PY progress is always measured independently of any factors that change with time (for example, weather trends or CO_2 increase). FY remains subject to all factors that change with time (see Section 2.4), but such time trends can be used to correct changes in FY to better determine the contribution to yield progress from adopted technologies.

2.4 Confounding factors in farm yield change

Besides the major role of the discovery, development and uptake of new technologies, the following potentially confounding factors need to be considered when examining change with time in FY:

- crop area and location
- grain quality
- cropping intensity
- carbon dioxide (CO_2) and ozone
- seasonal weather
- change in the natural resource base
- government policy
- input costs and grain prices.

Crop area may change within regions, bringing the possibility of crop shifts within a region to poorer or better environments, even if there is no change in total crop area. These changes arise as land is newly cropped, old land retired, or when one crop replaces another. A key change in land use that can confound yield is the adoption of irrigation, and it is often impossible to disaggregate yield data into rainfed vs. irrigated yields. In New Zealand, for example, national wheat yields have doubled in the past 20 years but the main cause has been a shift from zero to 80% irrigated area over the period. The adoption of irrigation is better considered a land-use change, not a yield gap closing technology.

The importance of **grain quality**, through price signals to the breeders and farmers, means there can be progress in economic output with relatively less (or even without) yield progress. Economists consider this a ‘product mix’ contribution to productivity growth. This often arises because of the common negative relationship between PY and several aspects of grain quality that originate from either genetic (e.g. protein content in wheat) or agronomic (e.g. rice eating quality in Japan, as discussed in Section 4.5) influences.

Farmers switching to earlier maturing varieties can increase **cropping intensity** (crops grown per year). Although crop yield may not increase through increased cropping intensity, productivity may benefit (e.g. many Asian paddy rice systems). Farmers who abandon intercropping practices would record higher yields for the main crop without any other change in technology. This has happened with wheat–mustard intercropping in north-western India because of rising labour costs.

At least two atmospheric gases, **CO_2 and ozone**, may cause yield change over time. The atmospheric concentration of CO_2 in parts per million (ppm) is steadily increasing, and over the past 20 years has risen at ~2 ppm/yr or 0.5% p.a. The influence of increased CO_2 on yield has been widely studied and, although the crop yield response depends somewhat on growing conditions (moisture, temperature and nitrogen), it is reasonable to assume that the yield of crops with C_3 photosynthesis (see Section 2.6 under 'Crop growth, photosynthesis and respiration') is currently increasing at ~0.2% p.a. due to CO_2 rise (Horie et al. 2005a; Tubiello et al. 2007); C_4 crops are assumed unaffected (see also Section 10.3 on direct measurement and crop modelling). Results presented in this book have not been corrected for CO_2 increase, so that observed gap-closing progress in C_3 crops (FY change less PY change) must be discounted by 0.2% p.a. to determine true technical progress on-farm.[19] Changes in ozone concentration in the lower atmosphere are much more variable in time and space, but can be high enough to reduce crop yields in some locations where modern industrial activity is intense, and thereby counter yield trends from other causes; alternatively, reducing ozone levels (e.g. with pollution control) could bias upwards estimates of yield progress resulting from technology (see Section 10.3).

Variation in **seasonal weather** causes deviations from any yield trend. Seasonal variations can also change the slope of the trendline if the changed weather correlates with year. This effect can be critical for FY determination (e.g. see Section 3.2 on WME1 and Section 10.2 on time series and climate change). Crop simulation models or simple empirical relationships permit correction for such weather changes to improve estimates of the yield slope and thus permit a better estimate of true technological change. Such weather trends may or may not be associated with human-induced climate change.

Gradual **change in the natural resource base** of cropping in a region can influence yield change. This is commonly the result of soil deterioration due to fertility or structural decline or salinisation—but equally, cropping soils can be gradually improved (e.g. through liming, applying phosphorus in excess of removal, and/or reducing tillage). Availability and quality of irrigation water can decline with overuse or poor system maintenance. Pressure from weeds, disease and pests can change as a result of new pest arrivals, pest evolution or changes in farming practice (e.g. the appearance of herbicide-resistant weeds). These changes are by definition gradual and their occurrence is often invoked as indicators of sustainability of the natural resource base of cropping when no other explanation for yield change is evident. The possibility of such impact should not be ignored, but definitive proof of such change is hard to secure. By the definitions used here, these are causes of exploitable yield gaps and are therefore manageable by proper use of technology. Often, however, the period of poor management has been decades. In such cases, management to reverse the degradation may take more than a year. Further, any particular farmer is unlikely to have caused some types of resource degradation (e.g. aquifer overuse, exotic pest invasion), and it is therefore difficult (or impossible) for one farmer to change their farm's management practice to overcome the problem.

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[19] In reality, in C_3 crops CO_2 rise lifts both PY and FY at 0.2% p.a. and does not directly affect the yield gap. The rates of change in PY estimated here do not include this effect but those in FY do, leading to the apparent yield gap closing effect due to CO_2 rise.

Farm yield can also be influenced by change in **government policy directly impacting farm practices** such as regulations and/or incentives. Limitations on the use of nitrogen fertiliser, or subsidies for low-input farming, are examples now found in western Europe (see Section 3.8 on WME11).

Farmer decision to adopt a new technology or practice is generally slow but can be strongly influenced by **input costs and grain prices** (both calculated at the farm gate) and also by availability and cost of credit. However, the allocation of already-in-use inputs by farmers responds more quickly to price shifts at the farm gate than the adoption of entirely new technologies. Economists refer to this as the price elasticity of yield (Chapter 13 'Policies and people'). Hertel (2011) estimates this elasticity as 0.2 for maize in USA, meaning that a 1% rise in prices would lift yield by 0.2%. Elasticity may be greater if input use is lower.

Finally it should be noted that when PY progress is plotted against the year of release, the PY values refer to the soil, weather and management levels under which the variety comparisons were conducted—normally meaning those of recent times. It is possible that plant breeding has unwittingly adapted varieties to some of the gradual changes discussed above (e.g. to take greater advantage of CO_2 increase, or to resist increasing salinity or ozone concentration). In analyses presented in this book, this effect is simply lumped into another positive variety-by-environment interaction contributing to breeding progress. Properly measured and calculated PY progress is not, however, inflated by the direct effect of increasing CO_2 on yield of C_3 crops, because all variety comparisons are made in the same years; if multiyear unbalanced data are used, these are corrected for the effect of year in the statistical analysis.

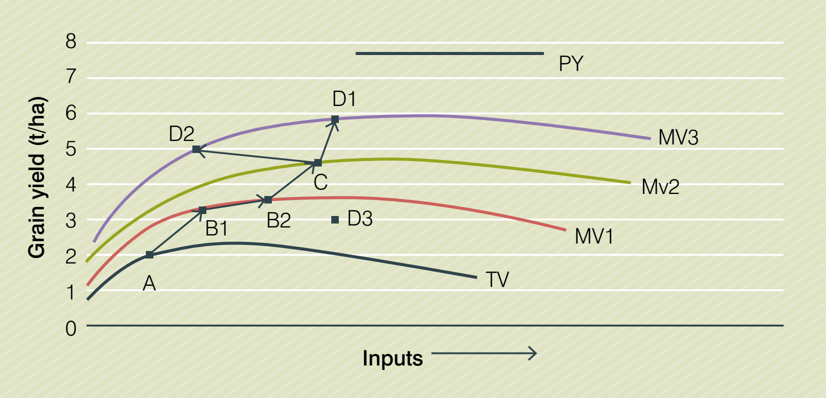
2.5 Other measures of efficiency and productivity under technical change

The next seven chapters (Chapters 3–9) deal with changes in FY and PY, the common currency of breeders and agronomists. Economists and farmers, however, look beyond yield to also consider efficiency, productivity and profit. Thus, in a finite world it is also essential to pay attention to yield per unit input, whether the input is nutrients, energy, water or labour—issues that will be covered in Chapter 11 on resource use efficiency.

Another economic measure, total factor productivity (TFP), considers productivity across all inputs. This measure is mainly useful because changes in TFP drive long-term price trends. TFP is a measure of physical output in relation to the aggregate quantity of all inputs. In this way, changes in agricultural production are disaggregated into one component relating to change in the amount of inputs, and a second relating to change in productivity. TFP is explained in Box 2.2 and further in Chapter 8 'Yield gap closing' in connection with efficiency gaps between farmers, and Chapter 12 'Trends in total factor productivity'.

Box 2.2 Efficiencies, profit maximisation and total factor productivity (TFP) under technical change

Economists define efficiency as the average cost for producing a given yield relative to the lowest cost option with the best current technology. They generally distinguish technical and allocative efficiencies. 'Technical inefficiency' refers to failure to operate at the yield frontier. 'Allocative inefficiency' refers to failure to meet the marginal conditions for cost minimisation where the marginal returns of applying an additional unit of input (the marginal return divided by the price of the input) are equal for all inputs. Profit is maximised when this marginal return is equal to the marginal cost across inputs, as determined by grain to input price ratios at the farm gate. The box figure illustrates a useful framework for identifying these economic measures as farmers adopt new varieties and practices.



Stages in the adoption of technology by farmers and effect on yield.
Source: Derived from Byerlee (1992)

The figure is derived from Byerlee (1992) using an example of the green revolution in South Asia—where, in the mid-1960s, high-yielding semi-dwarf wheat and rice varieties were first introduced. The figure plots yield against the sum of inputs (such as nutrients, seeding density, water and biocide) used after suitable adjustments for costs. TFP is the slope of the line joining any point in the figure to the origin, which will here lie to the left of the *y*-axis (because fixed inputs are not included). Four technical frontiers in time are shown, starting with the era before the green revolution shown by the curve TV for 'traditional variety', and passing to the curves MV1–3 for 'modern varieties' and technologies.

Continued next page

Continued

The PY corresponding to the final technical frontier (which is shown by line MV3) is shown some 30% above the line for MV3.

Initially, an innovative irrigated wheat or rice farmer (i.e. 100% technically efficient) could have moved from position A (on curve TV) to position B1 (on curve MV1, representing the first semi-dwarf modern varieties). Then, in what can be termed the first post – green revolution phase, the farmer could have intensified input use to attain position B2 on curve MV1, thus seeking greater allocative efficiency. The FY progress from A1 to B2 might involve an improved variety, improved fertiliser input, or their positive interaction.

In consecutive waves of technology—such as improved second and later generation semi-dwarf varieties of the 1980s and beyond (represented by frontier MV2 and finally MV3)—the farmer could move to position C and then position D1. The 100% efficient farmer could also increase TFP (input efficiency) by moving closer to the *y*-axis (point D2), but if D1 represents profit maximisation, a shift to reduce inputs to point D2 will sacrifice allocative efficiency, yield and profit.

Technically inefficient farmers will occupy positions below the prevailing technical frontier, and their efficiency is measured by the ratio (or per cent) of their yield relative to the frontier yield at their level of inputs. For example, the farmer at position D3 has the same level of inputs as another at position D1, but operates at about one-half the technical efficiency.

Establishing the technology frontier is not easy and, just as with yield gaps, site specificity and seasonal conditions influence efficiency gaps. These tend to be ignored by economists, leading to overestimations of inefficiencies (e.g. Ali and Byerlee 1991). Of course the frontier moves upwards with new technologies, but it may also shift downwards if there are serious long-term problems of resource degradation.

Yield gaps and efficiency gaps are often measuring the same things, but efficiency gaps may exist even in the absence of yield gaps. As with yield gaps, factors related to farmer characteristics and system-wide constraints explain variation in efficiency across farmers and fields. Technical efficiency relates largely to timing and technical skills in input use, and is often explained by farmer-specific knowledge and skills. However, system-level factors (such as management of irrigation systems) can also explain technical inefficiency. Allocative inefficiency can be caused by similar factors, as well as by differential risks of input use, input market failures and financial constraints.

2.6 Weather and soil parameters and physiological determinants of yield

To better understand crop yield progress—and in particular, future prospects for yield progress—this book relates yield to a number of common crop physiological concepts, considered alongside standard weather and soil parameters. Defined and described briefly below, these concepts and parameters form the building blocks for crop simulation models, to which reference is often made.

Weather parameters

The key weather parameters driving crops, and their units (and means of measurement, where appropriate) are:

- air temperature in degrees Celsius (°C)
- humidity as vapour pressure deficit (vpd) in units of kilopascals (kPa)
- solar radiation in units of megajoules per square metre per day ($MJ/m^2/d$)
- precipitation as depth of liquid water in millimetres (mm) accumulated over a given interval.

The range in **daily air temperature** is seen in the maximum (**T_{max}**) and minimum (**T_{min}**) daily temperatures. Temperature is generally summarised as **daily mean temperature** (**T_{mean}**), which is the average of T_{max} and T_{min}, and sometimes as **diurnal temperature range** (**DTR**), which is the difference between T_{max} and T_{min}.

More detail can be obtained with hourly temperatures, which (if not measured) can be interpolated from T_{min} and T_{max}. Temperature sums over time above a defined base temperature (**T_{base}**), below which development stops, are often calculated in units of 'degrees Celsius days'. Temperature sums can be calculated using either T_{mean}, or a daily sum that is produced by dividing the sum of hourly temperatures above the base by 24. The duration of given development periods (see below) is often a cultivar-dependent number of **growing degree days** (**GDD**).

Air humidity refers to moisture in the air, usually reported as **vapour pressure deficit** (**vpd**) given by the measured water vapour pressure of the air subtracted from the saturated vapour pressure at air temperature. Saturated vapour pressure increases as an exponential function of temperature.

Since water vapour pressure is fairly steady over the course of a day, vpd peaks at $T_{max.}$ The dewpoint is the temperature at which the air becomes saturated with the water vapour it contains; in the absence of measurement of vpd, it is often assumed that T_{min} is the dewpoint. One important aspect of micrometeorology is that leaves can modify temperature and vpd within the crop canopy. Also, transpiring leaves can be cooler (and non-transpiring leaves warmer) than the air.

The **daily solar radiation** is the total incoming solar radiation incident on a horizontal surface (**R_s**) given in units of megajoules per square metre per day (MJ/m²/d). Leaf photosynthesis over short intervals is often expressed as a function of irradiance, meaning the perpendicular component of solar radiation reaching the leaf surface expressed as power in watts per square metre (W/m²) in which one watt is equivalent to one joule per second (1 W = 1 J/s).

Measured above Earth's atmosphere, perpendicular to the Sun's rays, average solar irradiance is 1,360 W/m² (Connor et al. 2011). However, at ground level and even when the Sun is high in a very clear sky, peak irradiance is only about 1,000 W/m² for a leaf perpendicular to the solar beam. On a clear day most of the radiation is direct beam radiation from the Sun, with a small proportion (<15%) arriving as diffuse radiation (i.e. scattered solar radiation from the rest of the sky). The proportion of the total irradiance that arrives as diffuse radiation increases with cloudiness, with important positive consequences for crop photosynthetic efficiency (see below in the section 'Crop growth, photosynthesis and respiration'). Not determined by weather, the angle of the direct solar beam is also important for crop photosynthesis; the solar elevation angle is expressed relative to the horizontal and varies predictably by time of day, date and latitude.

About one-half of the solar radiation energy (direct and diffuse) occurs in wavelengths that can be used by photosynthesis—this portion, termed **photosynthetically active radiation** (**PAR**), can also be measured in units of megajoules per square metre per day (**MJ/m²/d**). The assumption made in this book is that the ratio of PAR to daily solar radiation (R_s) is 0.50 (Mitchell et al. 1998; Sinclair and Muchow 1999).

Photoperiod is determined by date and latitude, and is measured in hours and minutes. Critical for influencing the rate of development of many crops, photoperiod is closely related to day length (the interval from sunrise to sunset), but is somewhat longer because twilight, which is sensed by plants, is not included in day length.

The sum of all water reaching the ground (rain, hail and snow) is termed **precipitation** (**P**) and is measured as the depth of liquid water in millimetres (mm) accumulating over an interval (which could be a day, month, crop growing season or year). One millimetre per hectare is equivalent to 10 m³ or 10 kL of water. Irrigation is often measured in megalitres per hectare (ML/ha), with one megalitre equivalent to a depth of 100 mm of water over a hectare.

An important aspect of weather in the water balance of crops is **potential evapotranspiration** (**ET_p**), measured in millimetres per day (mm/d), or per growth interval. ET_p refers to the water that evaporates from a green crop surface completely covering the ground and well supplied with water. The value of ET_p is a moderately complex function of daily solar radiation (R_s), temperature (T), vpd and wind speed; crop type exerts little effect.

Soil properties

Soil provides physical support to crops and supplies roots with nutrients and water. Nutrients are found mostly in the topsoil (top 10–30 cm). They are largely supplied from breakdown of soil organic matter, which is measured as **soil organic carbon** (SOC) and expressed as per cent of soil dry weight (weight of soil organic matter is about 1.67 times that of soil organic carbon).

Topsoil texture is important and depends on the proportions of sand, silt and clay. Sandy topsoils are termed ‘light textured’ and have a low maximum water-holding capacity—that is, ~5% moisture by weight of dry soil, or only ~7 mm per 10 cm of soil depth (considering a sandy topsoil might have a density of 1.4 g dry soil/cm^3). At the other extreme, clay topsoils are termed ‘heavy’ and can hold much water—that is, up to 50% moisture by weight of dry soil, or ~70 mm per 10 cm of soil depth.

Total water-holding capacity of the soil profile is a critical consideration for rainfed cropping. For these purposes, water-holding capacity is usually considered in terms of **plant available water-holding capacity** (**PAWC**), measured in millimetres (mm). PAWC is the maximum amount of water that a crop (with a fully extended root system) can extract from a fully wetted and drained soil. Thus PAWC is specific not only for soil type, but also for crop type because root depth and density vary. PAWC is always less than the maximum water-holding capacity to the full root depth, because even dense root systems in the topsoil physically cannot extract all the soil water, and there are never enough roots at depth to extract all the available water. PAWC for annual crops can range from 50 mm in poor water-holding, shallow, sandy soils to >250 mm in deep silty soils (e.g. Loess soil).

Solar energy reaching the soil surface—especially when the surface is wet—causes **soil evaporation** (**E_s**) measured in millimetres (mm). Microbiological processes in the soil can also result in the release of important greenhouse gases such as CO_2 and nitrous oxide (N_2O) to the air, as well as nitrogen (N_2) and ammonia (NH_3). These gases are usually measured in grams per hectare per day (g/ha/d) or kilograms per hectare per day (kg/ha/d), but N_2 release is very difficult to measure.

Crop development

Crop development and growth are distinct and important processes. Development refers to the occurrence in time of major morphological events and periods in the life of the crop. Crop development is often termed ‘crop phenology’ and the life periods termed ‘phenophases’. The designation of periods of crop development is influenced somewhat by whether the crop is a monocot or dicot. Crops that first emerge above the soil with a single leaf are termed ‘monocots’ and examples include cereals and sugarcane. Crops that first emerge above the soil with two leaves are termed ‘dicots’ and include all broadleaf crops.

Table 2.1 summarises the development of cereals. The events and periods marked in bold are critical to the determination of yield in cereals, and divide the life cycle of all such crops (sowing to physiological maturity) into three general periods:

1. **true vegetative period** from sowing to floral initiation
2. **reproductive period** from floral initiation to anthesis (literally the release of pollen)
3. **grain-filling period** from anthesis to physiological maturity.

Table 2.1 Major events and periods in the development of cereal crops

Event or process	Definition	Comment
	True vegetative period	
Sowing[a]	Beginning of water uptake by seed	Assume soil moist
Germination	Appearance of radicle (first root) from seed	na
Emergence	First appearance of leaf above soil	na
Leaf initiation	Regular appearance of leaf primordia (microscopic bud) on apex of the main stem or shoot	Needs dissection to detect
Leaf appearance	External appearance of leaves on main stem at regular rate between emergence and last leaf appearance	Fixed number of leaves on main shoot, between 6 and ~25
Tillering	Appearance of new stems in axils of leaves on main stem (and on other tillers)	na
	Reproductive period	
Floral initiation	First appearance of floret primordia (microscopic buds) on main shoot apex (needs dissection to detect); signals end to leaf initiation on main shoot	In maize the tassel is formed at the shoot apex, the cob in a leaf axil several leaves below the final leaf
Onset stem elongation	Internodes (interval between nodes or joints) on main stem begin to elongate	na
End of floret initiation	Last floret primordia appears at apex of shoot	Many florets are initiated; few grow to complete florets
Onset inflorescence growth	Beginning of rapid accumulation of dry matter in inflorescence (spike, panicle, tassel or cob) structure	na
Meiosis	Production of haploid nuclei for pollen (in anthers) and ovule (in carpel) in developing florets	Pollen are the male equivalents, carpels the female
Final leaf emergence	Appearance of last leaf on main stem	In wheat called the flag leaf
Spike (head) emergence	Appearance of the main shoot inflorescence	Tassel in maize, panicle in rice

Continued next page

Table 2.1 Continued

Event or process	Definition	Comment
Anthesis or flowering	Appearance of first burst anthers, shedding pollen, and occurrence of pollination of the ovules (except maize)	Often known as flowering (or pollen shed in maize)
Silking (maize only)	External appearance of styles (silks) from female flowers on maize cob, receptive for pollen	Under stress in maize, silking may be significantly later than pollen shed on the same plant
	Grain-filling period	
End of inflorescence growth	Soon after anthesis and pollination	In maize the cob grows more after pollination than before
Onset grain-filling	Beginning of rapid dry matter accumulation in grain	Always some lag between pollination and onset of rapid grain growth
Grain-filling	Period of rapid grain growth	na
Physiological maturity	End of grain growth, as can be seen by changes within grain	Upper leaves may or may not still remain green
Harvest ripeness	na	Crop dry enough to mechanically harvest

a Bold text represents major events

na = not applicable

Unfortunately there are complications and confusions in the naming of these periods of crop development—sometimes the period from sowing to anthesis is termed 'vegetative' and grain-filling is considered 'reproductive' (a practice avoided in this book). Importantly, key periods for the determination of yield can be more sharply defined for individual crops and can overlap the key events of floral initiation and anthesis. Table 2.1 refers to development on the first or main shoot of the cereal plants. Many cereals have tillers, which are shoots or branches formed in leaf axils. The development stage of the tiller apices is initially a little behind that of the main shoot, but by the flowering development stage, differences between main shoots and tillers are usually small (a few days), and are negligible by physiological maturity.

Two additional periods are defined for the purposes of this book (see Chapter 9 'Increasing potential yield'), which largely determine:

1. number of grains (GN) measured per square metre of crop (#/m^2)
2. potential grain weight (GW) measured in milligrams (mg).

Depending on the crop, these two periods can occur either side of (but always close to) flowering. Note that in North America, GN and GW are often referred to as 'kernel number' and 'kernel weight', respectively.

The picture outlined in Table 2.1 is for cereals, which are determinate monocot crops—'determinate' because a floral structure terminates the main stem (and each tiller, if present). The situation is somewhat different in dicot crops, with the exception of modern sunflower, a strictly single-stemmed and determinate plant. Most other dicots—such as soybean, pulses, canola and peanut—have an indeterminant habit in which branching, leaf appearance and internode elongation overlap with stages of flowering. Branches or flowers arise as axillary buds of leaves. Floral initiation, flower appearance and anthesis can occur over an extended period (even if flowers eventually terminate the shoots); however, there are clear development events for first floral initiation and first flower opening. Reproductive development of the indeterminant dicots is thus quite asynchronous; pods form and begin to grow slowly, but flowering finishes only with a sharp onset of pod growth and seed-filling across all pods. Physiological maturity occurs relatively synchronously over all seed pods.

Finally there are root and tuber crops for which flowering is not a part of yield formation; rather, for these crops, flowering is incidental and best avoided to maximise yield. The onset of yield formation—the swelling of storage roots in cassava (and lower stem or tap root in sugar beet) and the formation of tubers in potato—usually occurs early in the life of the crop and follows similar environmental signals as (but independent from) flowering.

The **rate of crop development** is the reciprocal of the duration of specific development periods. It is driven strongly by a linear response to temperature, such that durations are usually a constant GDD sum above the appropriate base temperature for a given crop variety. The duration of crop development at a given temperature can, however, differ notably among crops (and among crop varieties), as many genes control the response to other environmental factors—notably photoperiod and vernalising cold (hours below ~15 °C). Longer photoperiod generally speeds development in some crops (long-day plants like wheat and barley) and slows it in others (short-day plants like rice, soybean and maize), but within short-day plants, some varieties are unaffected by photoperiod (these varieties are termed 'day neutral'). In some varieties of wheat, barley, rapeseed (including canola) and sugar beet, exposure of the plant to vernalising cold can shorten specifically the true vegetative period by accelerating the onset of floral initiation. In so-called 'winter varieties' the need for vernalisation is obligate, because without vernalisation there is no flowering; in 'facultative varieties', floral initiation is merely accelerated. Genes can also influence the GDD sum independently of photoperiod and vernalising cold.

Suffice it to say here that unfavourable photoperiods for floral inititiation will prolong the vegetative period; the number of leaves formed around the main stem will increase, and crop development will be delayed both during the vegetative and reproductive periods. The lack of vernalisation in sensitive genotypes also increases the number of leaves, but usually does not delay development after the true vegetative period. Grain-filling duration shows much smaller differences among varieties of any crop and no response to photoperiod or vernalisation.

Crop development rates become especially important when considering the effects of higher temperature as may arise with climate change. Chapter 10 on climate change expands somewhat on this subject since there are limits to the linear response of development rate to increasing temperature.

Crop growth, photosynthesis and respiration

Crop growth refers to the accumulation of dry matter (DM), which sometimes known as ‘biomass’ and is measured in weight per unit area (g/m^2, kg/ha or t/ha). DM is the sum of carbon compounds from net daytime photosynthesis plus a small proportion of other elements from the soil, less night-time respiratory loss of carbon compounds. Nitrogen and minerals from soil usually comprise less than 6% of DM, but the proportion is greater for high protein grains because of the nitrogen therein (Connor et al. 2011). **Crop growth rate** is determined as DM accumulation per day (g/m^2/d). Since roots are difficult to measure and unless stated otherwise, DM refers to above-ground parts of the crop.

Photosynthesis is the conversion of CO_2 to simple sugars by green leaves (and other green tissues) driven by energy from PAR. It is usually expressed as **net photosynthesis** because respiration (the breakdown of sugars into CO_2) continues in leaves even in sunlight. **Respiration** is an essential process for building the simple sugars from photosynthesis into the multitude of compounds found in plants (complex carbohydrates like cellulose and starch, and proteins and lipids), and for maintaining and defending the integrity of living cells. It continues day and night and for this reason is sometimes known as ‘dark respiration’.

Respiration has two components: growth respiration and maintenance respiration. **Growth respiration** can be quantitatively related to the compounds being synthesised. Thus 1.2 g of glucose is required to synthesise 1 g of carbohydrate, 2.5 g of glucose to synthesise 1 g of protein (starting with nitrate nitrogen), and 2.7 g of glucose to synthesise 1 g of lipid (Connor et al. 2011). **Maintenance respiration** is less well understood but relates to maintaining cellular processes. It is approximately proportional to the amount of living DM and highly sensitive to temperature (approximately doubling for each 10 °C increase).

Crop plants are divided into two groups according to their initial photosynthetic product. C_3 crops include wheat, barley, rice and almost all dicot crops, while C_4 crops are largely confined to tropical monocots such as maize, sorghum, millet and sugarcane. Between these two groups (C_3 and C_4), there are substantial differences in the response of leaf net photosynthesis to PAR. As seen in Figure 2.2, C_3 crops reach PAR irradiance saturation at about 200 W/m^2, but C_4 crops mostly never quite saturate in sunlight and have a higher **maximum value of net photosynthesis** (**P_{max}**) at full irradiance, given in grams of CO_2 per square metre per day (g CO_2/m²/d).[20] The light response curve for C_4 leaves also has a higher initial slope above about 25 °C. Notwithstanding Figure 2.2, there is considerable variation in P_{max} within the C_3 and C_4 groups of crop species.

Differences between C_3 and C_4 leaves reflect processes that evolved in C_4 plants over the last 40 million years to eliminate the apparently wasteful so-called **photorespiration** of C_3 leaves. In photorespiration, Rubisco (the central photosynthetic enzyme) takes up oxygen at the same site in the enzyme as CO_2, but the fixed oxygen eventually cycles back to be released in photorespiratory CO_2, thereby reducing net CO_2 uptake. C_4 crops eliminate this apparently wasteful photorespiration by a unique leaf anatomy termed 'kranz anatomy'. For initial fixation of CO_2, C_4 crops use a different enzyme, phosphoenol pyruvate (PEP) carboxylase, which has no affinity for oxygen. Rubisco remains the ultimate fixer of CO_2 in C_4 leaves, but the kranz anatomy ensures that the Rubisco is surrounded by high CO_2 concentrations released from the product of PEP carboxylation. This means C_4 Rubisco can fix CO_2 efficiently without photorespiratory wastage, as was presumably the case when C_3 photosynthesis first evolved several billion years ago, under high CO_2 and low oxygen levels.

There are other important differences between C_3 and C_4 crops. C_4 crop leaves are better adapted to higher temperatures (above ~15 °C, C_4 leaves tend to achieve higher photosynthetic rates than C_3 ones), less responsive to increased external CO_2 and more efficient with respect to photosynthesis per unit water lost (transpired) and per unit nitrogen invested in the leaf.

The last two mentioned differences between C_3 and C_4 photosynthesis serve to introduce the important (but here simplified) concepts of stomatal and mesophyll (or internal) conductance to CO_2 diffusion. 'Conductance' is the reciprocal of resistance to diffusion in gas physics. In photosynthesis, CO_2 diffuses from the air across the leaf boundary layer, through the stomatal pores into the air-filled leaf intercellular spaces, and then to the primary 'fixing' enzyme: Rubisco in C_3 plants and PEP carboxylase in C_4 plants (both located in the loose green mesophyll cells of every leaf). If the CO_2 movement in the mesophyll is assumed to also behave according to diffusion, and the CO_2 concentration is assumed to be zero at the site of initial CO_2 fixation, then the law of diffusion means that the intercellular CO_2 concentration is controlled by the stomatal relative to the mesophyll conductance. There is also a small influence of the boundary layer surrounding the leaf, but this influence can be ignored here for the sake of simple explanation.

Thus C_4 plants—with more efficient mesophyll photosynthetic machinery (i.e. higher mesophyll conductance) and a tendency for lower stomatal conductance—have under full irradiance markedly lower intercellular CO_2 concentrations of around 150 ppm (vs. 280 ppm with C_3 plants) when air CO_2 concentration is 370 ppm. This is the basis

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[20] The most common unit for P_{max} these days is micromoles of CO_2 per square metre per second (μmol CO_2/m²/s) obtained by multiplying grams of CO_2 per square metre per day (g CO_2/m²/h) by 6.31.

of the higher innate transpiration efficiency of C_4 crops. It is achieved with a lower investment in nitrogen-rich photosynthetic enzymes, the reason for higher nitrogen efficiency of C_4 photosynthesis. These concepts are also important for understanding the smaller, but possibly more important, genotypic differences within crops.

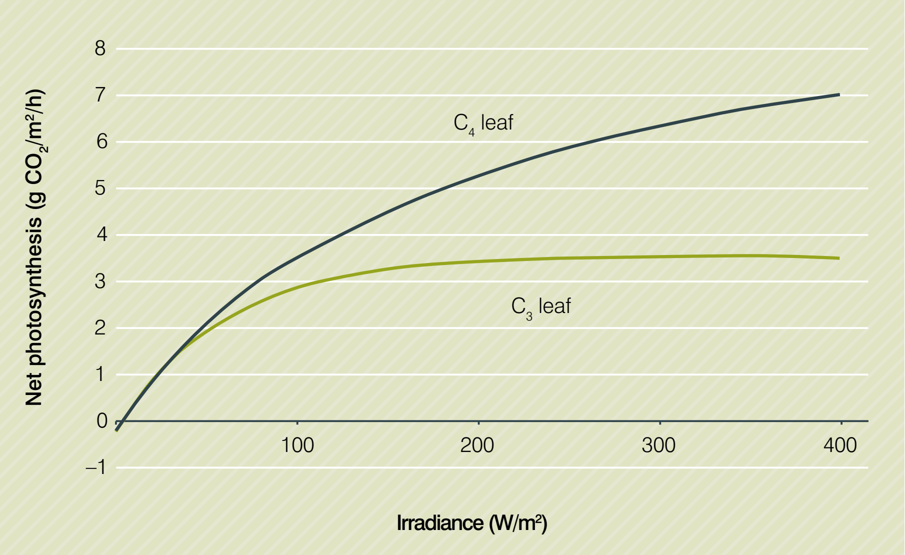

Figure 2.2 Response of leaf net photosynthetic rate to photosynthetically active radiation (PAR) expressed as irradiance. Source: adapted from Connor et al. (2011)

The leaf net photosynthetic rate vs. PAR irradiance response curve in Figure 2.2 is the principal building block for determining the photosynthesis of any crop canopy. However, the canopy comprises many leaves of different age and nutrient status (hence different photosynthetic capacity, as reflected in different P_{max} values), orientated at many angles to the vertical and illuminated by various angles of direct solar beam, which change with time. Moderately complex models can integrate all these factors if they can be measured, but crop physiologists usually take a simpler approach to the problem. To understand this, several aspects of the leaf canopy require definition.

A simplified quantification of the crop canopy is contained in the measure known as **leaf area index** (**LAI**), which is the dimensionless ratio of the area of green leaves to the area of ground (m^2/m^2); if other green parts like stems and spikes are included, this measure can be called ‘green area index’. Further, the penetration through the green canopy by solar PAR fits well a physical law: the proportion of PAR not intercepted at the bottom of the green canopy is an exponential function of the LAI (equation (1)).

equation (1) Interception of photosynthetically active radiation (PAR) by crop canopy

$$F_{PAR} = 1 - \exp(-K \times LAI) \qquad (1)$$

where

F_{PAR} is the fraction of incident PAR intercepted by the canopy

K is the extinction coefficient (a unitless parameter between 0.3 and 1.0)

LAI is the leaf area (or green area) index (m^2/m^2).

The **extinction coefficient** increases with more horizontal leaves (i.e. with lower leaf elevation angle or inclination). The more erect the display of the leaves, the greater the LAI needed to maximise PAR interception. An LAI of 4–5 is sufficient for 90% interception of daily PAR in typical monocot crops at middle latitudes ($K = 0.5$, $F_{PAR} = 0.9$). Where $LAI > 4$–5, the crop is considered to have reached 'full light interception' because any greater LAI captures little extra PAR—thus, LAI would have to double in order to reach 99% interception (or $F_{PAR} = 0.99$). Adding greatly to the use of equation (1) was the advent of portable instruments that facilitate the measurement of F_{PAR} by green canopies.

Monteith (1977) proposed that crop growth rate be related to daily intercepted PAR, and crop DM accumulation to the cumulative daily intercepted PAR, finding that the slope of this relationship tended to be a stable number across the crop life cycle and reasonably stable for any crop across environments. This slope is defined as the **radiation use efficiency** (**RUE**) measured in grams of dry matter produced per megajoule (g DM/MJ). Notwithstanding limitations fully discussed in Mitchell et al. (1998), Monteith's (1977) ideas have subsequently become the basis of much relatively simple modelling of crop growth and yield under non-water-limiting conditions (equations (2) and (3)).

equations (2) and (3) Daily crop growth rate and accumulated crop growth. Source: Monteith (1977)

$$dDM/dt = PAR_i \times RUE \qquad (2)$$

where

dDM/dt is the dry matter accumulated daily ($g/m^2/d$)

PAR_i is the daily intercepted photosynthetically active radiation; in other words, daily incident PAR given by ($0.5 \times R_s$), multiplied by F_{PAR}

RUE is radiation use efficiency measured in grams of DM produced per megajoule of PAR intercepted (g DM/MJ).

$$DM = \sum PAR_i \times RUE \qquad (3)$$

where

DM is dry matter accumulated (g/m^2) over some period

$\sum PAR_i$ is the accumulation in daily time steps of intercepted PAR over the same period

RUE is as given in equation (2).

With progression from CO_2 uptake in photosynthesis to DM accumulation in RUE, dry weight of the initial sugar product (from photosynthesis) will be only 68% of the mass of CO_2 fixed because of oxygen released by photosynthesis. In addition, (dark) respiratory losses must be subtracted and minerals added. Finally, since RUE usually refers to above-ground DM, no account is made for net translocation of DM to roots. Early in the crop life cycle, DM investment in roots is significant—starting at root/shoot DM ratios of 0.5 to 1.0—but by anthesis in grain crops, this ratio is usually less than 0.15, after which there is little root growth.

Despite these caveats, many measurements subsequent to Monteith (1977) confirmed that RUE is a relatively robust crop-specific parameter (Mitchell et al. 1998; Sinclair and Muchow 1999; Stöckle and Kemanian 2009) very useful in crop modelling. Obviously canopy net photosynthesis—and by inference, RUE—is equal to the sum of net photosynthesis across all leaves in the canopy, but only some are exposed to the full solar beam perpendicular to the leaf surface (giving P_{max}). Many leaves in a canopy receive low levels of irradiance because they are at oblique angles to the solar beam and/or due to degrees of shading within the canopy. The situation under cloud, when diffuse radiation dominates, is even more complex.

It is obvious that leaves in a canopy operate at various levels of efficiency with respect to PAR depending on where they sit on the curve in Figure 2.2 and that this efficiency changes throughout the day. Nevertheless, three important general points are apparent:

1. Canopy photosynthesis does not saturate at high light—unlike individual leaves (Figure 2.2)—therefore canopies reach higher net photosynthesis rates per square metre than sunlit leaves (e.g. up to 10 g/m^2/h).
2. Canopy RUE responds to change in P_{max} of the constituent leaves, other things equal. Detailed canopy models suggest that if leaf P_{max} increases by 1%, RUE in a wheat canopy at LAI = 6.5 will also increase but by a lesser relative amount depending on solar elevation (~0.2–0.4% according to Day and Chalabi 1988).
3. Most sun angles in most cropping environments are such that canopies with erect leaves are likely to achieve higher RUE, other things equal.

Thus C_4 crops, with higher P_{max}, show generally higher RUE values than C_3 crops. For growth before grain-filling under optimal conditions, the following general average RUE[21] values and ranges were reported by Mitchell et al. (1998) and confirmed in Sinclair and Muchow (1999):

- maize (C_4) 3.3 g DM/MJ (range 2.3–4.1)
- wheat (C_3) 2.7 g DM/MJ (range 2.4–3.1)
- rice (C_3) 2.2 g DM/MJ (range 2.0–2.5)
- soybean (C_3) 1.9 g DM/MJ (range 0.9–2.7).

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[21] Note this refers to above-ground DM and was more correctly termed as the ‘radiation conversion factor’ in the thorough review by Mitchell et al. (1998). However, RUE is now the accepted term, and RUE is always expressed in this book relative to PAR.

Ranges in crop RUE, or within-crop variation, may seem to challenge the validity of RUE as a concept—especially as all the reported ranges related to well-managed and well-watered crops. Such challenge is countered by ease of RUE measurement and application of RUE in simple models to disaggregate crop growth into major and independent components (as in equation (3)). Also there is a reasonable (if empirical) understanding of RUE variation, attributed largely to environmental factors (i.e. higher RUE values with a higher proportion of diffuse radiation, or lower vpd). There have been few reports of effects due to variety in side-by-side comparisons, except that RUE tends to decline during grain-filling in older varieties. The generally lower RUE for soybean probably reflects the larger respiratory load associated with nitrogen fixation, and (during grain-filling) the higher energy content of soybean seed arising from high oil and protein content.

Regarding RUE and leaf inclination, again detailed canopy photosynthesis models provide evidence favouring erect leaves. Photosynthesis of a leaf at high irradiance is at or close to PAR saturation and thus uses PAR inefficiently (Figure 2.2). Erect leaves reduce the angle of incidence of the solar radiation—and hence the effective irradiance seen by the leaf—so PAR is used more efficiently. An early example is the canopy modelling of Loomis and Williams (1969), which shows the advantage of vertical leaves (leaf angle 90°); LAI needs to be greater than 3 to benefit from this effect, otherwise F_{PAR} may be too low. An ideal canopy would have erect leaves at the top, with less-erect leaves at depth. Small leaves and green structures, with relatively larger penumbral effects, also have the beneficial effect of scattering sunlight deeper into the canopy.

Crop growth, partitioning of dry matter and determination of potential yield

As the crop canopy is built, the products of photosynthesis are distributed by a process called ‘partitioning’, by which DM is distributed among major crop parts. Figure 2.3 illustrates this for irrigated spring wheat in north-west Mexico. Crop development (or phenology) is shown on the *x*-axis to set the temporal framework within which partitioning occurs.

As well as total DM production, Figure 2.3 shows the **partitioning of DM** into key crop parts. Thus crops first produce leaves (with an area to DM ratio of 200–300 cm^2/g DM, depending on crop) in an exponential phase of growth until 100% PAR interception is approached (40–60 days after sowing under irrigation and high fertility). After the crop has reached full light interception, total DM accumulation becomes strictly linked to incident PAR and RUE—that is, extra leaves produced beyond this point will not much increase the proportion of light interception, because interception is already above 90%, a situation which continues until leaves start to senesce towards the latter half of grain-filling.

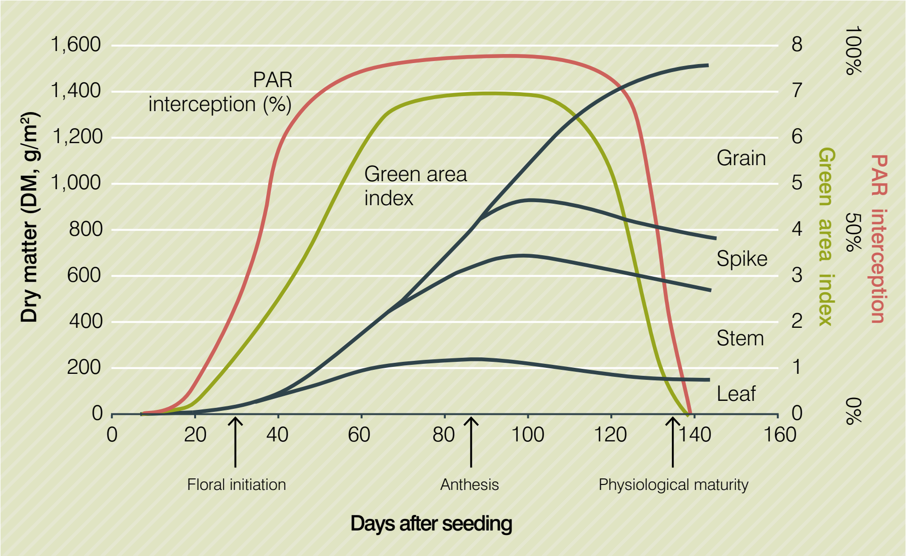

Figure 2.3 Evolution of green area index, photosynthetically active radiation (PAR) interception (%) and dry matter (DM) accumulation in crop parts as a function of days after seeding in spring wheat. Example for spring wheat grown under irrigation and high fertility in north-western Mexico. Crop parts are shown as the cumulative dry weights of leaf, stem, spike and grain. Source: adapted from Fischer (1984)

Stems begin to grow soon after floral initiation and then (some 20 days before anthesis) the spike (or inflorescence) also becomes an important sink (destination) for DM. Accumulation of grain DM begins soon after anthesis in Figure 2.3, reflecting the warm environment of north-west Mexico. Towards the later stage of crop development (in the latter half of grain-filling), the downturn of trendlines for stem and leaf suggests sources for some of the final grain DM. Studies with radiocarbon (^{14}C)-labelled carbohydrates confirm that DM accumulation in later grain-filling occurs largely through translocation of stored carbon compounds to the grain. This process is known as the contribution of pre-anthesis stored carbohydrate (and protein) to grain yield, commonly expressed as a percentage of total DM at anthesis or, alternatively, percentage of the grain yield.

A key outcome in Figure 2.3 is the **harvest index (HI)**, which is the ratio of grain DM, or yield (g/m^2), to final total crop DM above ground (g/m^2) at physiological maturity (often called 'biomass') expressed as a percentage or dimensionless ratio. As with RUE, HI is a robust crop parameter. HI depends on crop and variety, but less on environment under good management. HI is easy to measure, provided all senesced crop parts can be collected at physiological maturity, and provides a measure of breeding progress to which it is frequently referenced.

As with crop development, the exact pattern of crop growth varies among crops and varieties under the influence of the genetics-by-environment interaction, but the general pattern is similar for all grain crops. Thus the simple relationship of PY to DM and HI becomes useful to understanding yield changes in all grain crops (equations (4) and (5)).

equations (4) and (5) Potential yield (PY) as a function of dry matter (DM) accumulation

$$\mathbf{PY = DM \times HI} \tag{4}$$

in which DM (final dry matter in this case) can be substituted by equation (3) to give:

$$\mathbf{PY = \sum PAR_i \times RUE \times HI} \tag{5}$$

where

PY is potential yield in grams per square metre (g/m^2) at zero grain moisture in this equation

$\sum PAR_i$ is the cumulative intercepted photosynthetically radiation given in megajoules per square metre (MJ/m^2)

RUE is radiation use efficiency given in grams of dry matter per megajoule of PAR intercepted (or simply g/MJ)

HI is the harvest index, the ratio of grain dry weight to crop dry weight (above ground) at physiological maturity.

Equation (5) is the most common simple model of PY, and it is used as the basis for discussing breeding and agronomic progress in this book. Reference is also often made to P_{max} (and sometimes stomatal conductance) as surrogates for RUE when the latter may not have been measured.

Numerical components of grain yield

Before leaving the general physiology of PY determination, it is useful to present another simple model for grain crops that is used by many physiologists as equation (6).

equation (6) Potential yield (PY) as a function of numerical yield components

$$\mathbf{PY = GN \times GW} \tag{6}$$

where

PY (commonly in this case) is grain dry weight in grams per square metre (g/m^2)

GN is grain number, the number of grains per square metre of land area

GW is grain weight, the dry weight of individual grains in grams (g), but also often reported in milligrams (mg).

As with equation (5), the relative physiological independence of the components (in this case, GN and GW) makes equation (6) useful for understanding causality of PY; GN is usually the dominant determinant. An added advantage is the ease with which GW can be measured, and that grain number can be estimated from yield divided by GW (provided that errors are small). There is little advantage, however, in dissecting GN into its traditional numerical components (e.g. plants per square metre, inflorescences per plant and/or grains per inflorescence) because of their strong interdependence.

As mentioned, there is a **critical period for grain number determination**: that period of 20–30 days leading up to and shortly following flowering. Potential GW is determined by events at and after flowering. The critical GN period is demonstrated by the increased sensitivity of GN to environmental change (e.g. solar radiation) during this stage of crop development, and further aids yield analysis by linking GN to equation (2) and Figure 2.3. Thus grain number has been related to one or more of the following traits:

- crop growth rate in the critical period for grain number—that is, from 20–30 days before flowering to 10 days afterwards in determinate crops or, in maize, from 15 days before silking to 15 days afterwards
- ability of the variety to partition photosynthetic products to the developing reproductive organs in this critical period—along with crop growth rate, partitioning ability determines dry weight of inflorescences
- ability to build many fertile florets per unit inflorescence dry weight.

It is notable that the critical period for grain number (at least in wheat and rice) is also when the aforementioned water-soluble carbohydrates are being accumulated in stems for later translocation to the growing grains. Therefore grain number and grain weight in such crops may not be as independent as originally proposed because carbohydrate availability per floret around flowering also affects the survival of florets (Slafer et al. 2009) and potential weight of grains, at least in wheat (Calderini et al. 2001).

Determination of key yield components in relation to flowering holds well for determinate crops (like wheat, rice or maize), but may seem less clear-cut in indeterminate crops (like soybean, rapeseed or pulses) with long flowering periods. Nevertheless, the determination of grain number in soybean (e.g. Slafer et al. 2009) and canola (Mendham and Salisbury 1995) does seem to fit this model relating grain number to DM accumulation during flowering.

Reference to grain number raises one final important notion with respect to photosynthesis: that of **source–sink relations**, a term commonly used by crop physiologists. The source is considered to be the photosynthetic tissue (but can also include temporary storage tissues), while the sink is the growing organ to which the products of photosynthesis are being translocated. During grain-filling the sink clearly comprises the grains growing to reach some given potential size. It is often argued that during this period, crop photosynthesis can actually be limited by the grain sink (or demand) for the products of photosynthesis. This appears to be the case when there is a large photosynthetic area relative to the number of grains; artificially decreasing the photosynthetic area can increase the photosynthetic rate of the remaining leaves, or artificially increasing grain number in novel experiments can have the same effect. It remains uncertain whether sink limitation of photosynthesis can occur before grain-filling. The relative stability of RUE before grain-filling suggests that such sink limitation at that time is unlikely, but RUE is often observed to decline during grain-filling.

Determination of water-limited potential yield

Some changes to the above schema for PY determination are needed to deal with performance under water-limited conditions (i.e. PY_w). Water limitation implies insufficient supply of water for crop evapotranspiration (ET) to reach the maximum for the particular crop (i.e. ET_p). For water-limited crops, total ET may lie between 5% and 80% of ET_p.

For PY_w determination, again it is easiest to relate DM production to the limiting resource, which in this case is water. A simple expression, coming originally from Passioura (1977), facilitates this and lies behind much of the simulation modelling of PY_w (equation (7)).

equation (7) Simple expression of water-limited potential yield (PY_w). Source: Passioura (1977)

$$PY_w = T \times TE_1 \times HI \tag{7}$$

where

PY_w is the water-limited potential yield measured in kilograms per hectare (kg/ha)

T is transpiration (amount of water transpired by the crop) measured in millimetres (mm)

TE_1 is transpiration efficiency, measured in kilograms dry matter (DM) produced per hectare per millimetre of transpiration (kg/ha/mm)

HI is the harvest index.

Furthermore, a simple but useful and robust variant of equation (7) was developed for wheat crops in South Australia by French and Schultz (1984) (equation (8)).

equation (8) Water-limited potential yield (PY_w) from water supply, transpiration efficiency and harvest index. Source: French and Schultz (1984)

$$PY_w = (ET - E_s) \times TE_1 \times HI \tag{8}$$

where

PY_w is the water-limited 'potential' yield in kilograms per hectare (kg/ha), using kg units to accommodate the common units for transpiration efficiency (TE)

ET is evapotranspiration (crop water use) measured in millimetres

E_s is soil evaporation in the crop from seeding to physiological maturity

TE_1 and HI are as defined for equation (7). Note that French and Schultz (1984) originally called $TE_1 \times HI$ the 'maximum water use efficiency', but this term has since come to mean many things and is not used in this book.

ET is equal to transpiration (water consumed through the plant) plus evaporation from the soil (E_s). ET of a field crop is only weakly dependent on crop leaf area index (LAI) as long as the soil surface is wet. This is because the solar radiation that reaches an unshaded wet soil surface (i.e. in the absence of a growing crop, crop residue or mulch) will drive as much soil evaporation as would have occurred as transpiration if the soil surface had been shaded by leaves. Thus transpiration and soil evaporation are relatively independent, but the latter decreases markedly when the soil surface dries. Note than transpiration (T) in equation (7) equates in equation (8) to ET less E_s.

French and Schultz (1984) set E_s at 110 mm, a reasonable assumption for many soils and annual crops. E_s is essentially a loss to the crop. For wheat in southern Australia at the time, French and Schultz (1984) found that the maximum slope ($TE_1 \times HI$) for yield vs. ET attained by the best crops was ~20 kg grain/ha/mm. Note, however, that the original French and Schultz equation (from which equation (8) is derived), defines a 'grain yield frontier' (at 12% grain moisture) attained by farmers with the best varieties and management; strictly speaking, this 'frontier' is the water-limited attainable yield (as defined in Section 2.1), which may lie somewhat (~30%) below true PY_w as defined for this book.

Equation (8) was developed to demonstrate a target water-limited attainable yield for farmers, but, as reviewed by Passioura and Angus (2010), the equation proves valuable as a simple model for understanding PY_w given that the three components (i.e. ($ET - E_s$), TE_1 and HI) remain relatively independent. Equation (8) emphasises the notion that water supply is central to PY_w, as reflected in the ET term (discounted by E_s). Thus equation (9) offers a description of ET.

equation (9) Determination of evapotranspiration (ET) by water supply

$$ET = \Delta S + P - \text{losses} \qquad (9)$$

where

ΔS is equal to the change in millimetres (mm) in soil water between seeding and physiological maturity, thereby picking up the contribution of any soil water stored in the fallow period prior to seeding. ΔS can reach (but never exceed) the plant available water-holding capacity (PAWC) for the particular crop–soil combination if seeding occurs into a 'full' profile of soil water

P is precipitation in millimetres (mm) during the crop cycle

losses refer to precipitation in millimetres (mm) lost to deep drainage below the root zone or surface run-off during the crop cycle.

In concluding discussion of crop physiology through simple equations, determination of transpiration efficiency (TE) is now explored. Apart from water supply, TE is the main factor in equation (8) that links PY_w to climate. Crops transpire water largely through open stomata in their leaves. This is an inevitable consequence of opening stomata to permit CO_2 uptake for photosynthesis, a process that exposes the water-saturated inner leaf surfaces to water loss to the atmosphere. TE is linked to the ratio of CO_2 taken up to water lost, but the CO_2 uptake is converted to weight of carbohydrate photosynthesised to calculate TE. As for RUE, TE is also subject to upper limits. The limit is higher for low intercellular CO_2 concentration of the photosynthesising leaves, and is separately modified by the relationship between transpiration rate and the prevailing dryness of the air (equation (10)).

equation (10) Inverse relationship between transpiration efficiency (TE) and the prevailing dryness of air in crop canopies. Source: Tanner and Sinclair (1983)

$$\mathbf{TE_2 = k/vpd} \tag{10}$$

where

TE_2 is the dimensionless ratio between weight of dry matter accumulated to that of water transpired (reciprocal of the longstanding transpiration ratio).[†]

k is a crop-dependent efficiency factor between vpd and TE_2, given in pascals (Pa). It is negatively related to the intercellular CO_2 concentration in the leaf, which (being less than ambient CO_2 concentration) determines the rate of diffusion of CO_2 into leaves.[‡]

vpd is vapour pressure deficit given in pascals (Pa). It refers to the appropriate daytime average vpd (when stomata are open) and is about two-thirds of the daily maximum vpd (Stöckle and Kemanian 2009). Since the intercellular spaces of the leaves are always saturated with water vapour, vpd determines the gradient for water diffusion out of the leaf.

[†] Dimensions given to TE in equation (7) (kg/ha/mm) conveniently convert to a dimensionless weight ratio simply by dividing by 10,000 (because 1 mm of transpiration over 1 ha is 10,000 kg of water). Thus 50 kg/ha/mm (a typical value for DM production) becomes 0.005 kg/kg or simply 0.005 (a transpiration ratio of 200).

[‡] Apart from being higher for C_4 than C_3 crops, k is considered to be relatively stable for each crop and hence is a valuable term for crop models.

The lower intercellular CO_2 in C_4 leaves means a greater gradient for CO_2 diffusion into the leaf, causing higher k and TE_2, other things equal. Thus the value of k is about 9 Pa for maize and sugarcane, 6 Pa for wheat and rice and 5 Pa for soybean (Sinclair 2010). Since the original work of Tanner and Sinclair (1983), it has been recognised that stomata tend to close in response to increasing vpd—this decreases intracellular CO_2 concentration and thus k increases as daytime vpd increases across the whole range of values encountered (e.g. 0.5–3.0 kPa). Therefore, the decline in TE_2 with rising daytime vpd is somewhat less than equation (10) would predict (Kemanian et al. 2005). This is not the same as stomatal closure in response to soil water shortage, which also increases TE_2 (other things equal), but it can be difficult to distinguish between the two responses.

Important general considerations for crop transpiration efficiency are the spatial variation in vpd (increasing markedly from humid to arid regions), and the seasonal march in vpd (lowest in mid winter or in the wet season; highest in midsummer or the dry season).

Harvest index (HI)—the last component in the water-limited conditions shown in equation (8)—becomes less stable and tends to be lower because water becomes scarce during grain-filling. Thus transpiration is often constrained at a time when TE is lower due to vpd increase during grain-filling, and grain growth and HI suffer in a reasonably quantifiable way (Sadras and Connor 1991). Other aspects of water limitation bearing on HI, such as the sensitivity of grain number to water shortage, are introduced in Section 9.6.

Agronomic studies often refer to water productivity or water use efficiency (WUE), given as yield per unit of water use (kg/ha/mm). It is important to define water use in this context: it is commonly ET but can refer to other measures (e.g. water supply such as rain or irrigation).

2.7 Concluding remarks

To cover the broad principles of crop physiology in a few pages inevitably cuts many corners, but the aim is to provide a foundation for much of the following discussion of yield progress and prospects. The interested reader is referred to Sadras and Calderini (2009) and Connor et al. (2011) for greater detail. The terms introduced here (and a few others that appear elsewhere in this book) are listed in the Glossary.

Chapters 3–7 move to looking at the yield performance of individual crops to seek the genetic, agronomic and socioeconomic factors behind yield progress. This is facilitated by defining (at the outset of each single commodity chapter) the **major mega-environments** around the world in which the commodity is grown. This is a term developed by the International Maize and Wheat Improvement Center—otherwise known as *Centro Internacional de Mejoramiento de Maíz y Trigo* (CIMMYT)—to facilitate research targeting maize and wheat, but it is a useful tool for all crops. Mega-environment is a commodity-specific term, and refers to broad (but not necessarily contiguous) areas facing similar agroecologies in terms of weather, abiotic and biotic stresses, and cropping system requirements for the crop under consideration.