2. LITERATURE REVIEW

2.1. Drought: Definition, importance/perspective

Drought is a complex phenomenon and a good definition of drought in the agricultural sense should include several aspects, some of which are precipitation, soil water content, evapotranspiration (actual and potential), and stage of development and types of crops. Drought is a protracted period with a lack of or insufficient precipitation accompanied by inadequate moisture in the soil and/or atmosphere, resulting in below average crop production being possible (NOAA, 2006). This lack of rainfall, which is highly heterogeneous over years and locations, is a primary abiotic stress causing not only yield loss but yield instability as well and can frequently be accompanied and compounded by other stresses like high temperature (leading to evapotranspiration rates that are higher than the rate of water uptake by the roots), salinity, and lack of nutrient availability. Soil variation in the field can be more pronounced when soil moisture is inadequate.

In the wake of climate change drought, together with the occurrence of high temperature, is predicted to be more prevalent and more severe in many parts of the world, e.g. in Southern Africa (IPCC, 2007) and water deficits are most likely in normally less susceptible regions with temperate climate e. g. Northeast and Central Germany (Schindler *et al.*, 2007). It is also predicted that global temperature will increase by about 1,5 to 6°C (IPCC, 2007) and global evapotranspiration by 5 to 10% (OTA, 1993) in the next 100 years. Both factors are bound to compound the already complicated problem of drought. Hence, given these climate change scenarios, it is worthwhile to study yield constraints under less favourable production conditions, especially under drought as the main abiotic stress. In a recent report regarding food security, The Royal Society (2009) came to a similar conclusion, where it made a call for focussed research and funding in order to enhance food production, particularly critical under an altered, less conducive climate, increasingly degraded soils and dwindling irrigation water availability.

2.2. Gas exchange, evapotranspiration efficiency, biomass accumulation and partitioning

Gas exchange has been reported to be affected by the availability of water in the soil and by the evaporative demand of the air. The transpiration and net photosynthetic (CO_2 assimilation) rates under water replete conditions is usually high and when the extractable water in the soil is too low or the evaporative demand becomes too high, then this leads to stomatal closure (Bunting and Kassam, 1988; Sutcliffe, 1968). This closing of the stomata reduces to a larger extent transpiration but also photosynthesis. Stomatal conductance for water and CO_2 are affected directly before net photosynthetic and transpiration rates are negatively affected. As water and CO_2 use the same pores (stomata) to diffuse into and out of leaves, respectively, it is axiomatic that water has to be utilised in CO_2 assimilation, biomass accumulation and growth. It is this inevitable coupling of gas exchange which leads to the fact that water use and biomass production of cultivated plants are closely linked to each other (Ehlers, 1997).

Since the publication of the classic paper of Cowan and Farquhar (1977) on the basis of optimal function of stomata and enhancement of leaf gas exchange efficiency under diverse environmental conditions a lot of research has been carried out on different aspects of gas exchange and intrinsic or instantaneous transpiration efficiency (TE_i). In the literature TE_i has been termed, for example, simply transpiration efficiency or leaf level transpiration efficiency or even water-use efficiency. Condon and Hall (1997) point out that it should be possible to exploit genotypic variation for TE_i to ameliorate adaptation to specific environments and Franks and Farquhar (2007) emphasise that those genotypes with fast and appropriate response to environmental factors which impact on stomatal conductance (g_s), CO_2 assimilation and transpiration rates should have a higher TE_i. Since stomatal guard cells perceive and act on various signals in the aerial and soil environment so as to optimise the size of the stomatal opening thereby optimising CO_2 gain and H_2O dissipation (Jones, 1992; Cowan, 1982; Farquhar and Sharkey, 1982), stomata are importance in influencing ETE and WUE. At TE_i and WUE can be improved probably by not only decreasing stomatal aperture but also increasing CO_2 assimilation capacity (Bacon, 2004). However, at crop level there is a "decoupling effect" from the role of individual stomata like crop temperature dynamics and canopy boundary layer conductance which can be influenced by for example, leaf movements typical in some pulses like cowpeas, canopy structure, and so on. All the same, it has been suggested that TE_i based on g_s, that is the ratio A/g_s, should be a better and direct measure of the fundamental photosynthetic process since there is a process of normalisation (Medrano *et al*., 2002; Farquhar *et al*., 1989).

Farquhar and co-workers and other researchers (e.g. Hall, 1995; Hubrick and Farquhar, 1989; Condon *et al*., 1987; Hubrick *et al*., 1986) have demonstrated that the heavier natural isotope of CO_2 ($^{13}CO_2$) as opposed to the lighter one ($^{12}CO_2$) is discriminated against so that $^{13}CO_2$ is diluted in plant tissue (assimilates) compared to the natural atmosphere, but the level of this discrimination ($\delta^{13}CO_2$) depends on the crop species and genotype, and $\delta^{13}CO_2$ is related to ETE and WUE – a low $\delta^{13}CO_2$ being generally indicative of a high ETE and WUE. This relationship remains valid whether for TE_i or ETE (Evans *et al*., 1986; Farquhar and Richards, 1984). However, low $\delta^{13}CO_2$ alone does not necessarily lead to high ETE, especially if the high ETE is as a result of low stomatal conductance (g_s) under water replete conditions. At present new methods with oxygen isotopes (H_2O^{18} and H_2O^{16}) are being used to provide supplementary information on whether high ETE genotypes identified through low $\delta^{13}CO_2$ can also have a high productivity (high WUE) under well-watered and water deficit conditions (Barbour *et al*., 2000). Nevertheless, the $\delta^{13}CO_2$ method does not allow for determination of carbon losses through respiration nor for evaporation from the soil. Besides, all these isotope-based methods are expensive especially when applied in large breeding programmes in developing countries. The situation gets complicated by the fact that high ETE generally has a productivity cost (Jones, 2004). The ETE and WUE of plants are influenced by, among other things, water availability, species, genotype, nutrition and leaf-to-air vapour pressure deficit (VPD) and because VPD depends on air temperature (Eamus *et al*., 2008; Lambers *et al*., 1998), ETE and WUE ultimately are subject to the effect of temperature during the whole ontogeny of the plant or crop.

Growth, biomass partitioning and yield are affected negatively partly by lack of water in the soil as a result of of low stomatal conductance and photosynthesis. However, there are some other processes in the plant that are more sensitive to water deficit, namely leaf cell division and growth and protein synthesis (Bradford and Hsiao, 1982). Normally this leads to thicker but smaller leaves and roots are relatively less negatively affected by low soil water potential than the shoot. Insight into effects of water deficit on the whole plant and genotypic reactions can be furnished by analysis of growth rate, whereby the relative growth rate (RGR), net assimilation rate (NAR) and allocation of dry matter (DM) to different organs (DM partitioning) (Lambers *et al*., 1989; Gifford and Evans, 1981) are useful and reliable traits. However, RGR is considered by some as being not particularly appropriate to discern the relation between physiology and growth (Lambers *et al*., 1998). Instead, carbon dioxide assimilation, leaf area, specific leaf area and leaf mass ratio, respiration and DM allocation are suggested as more meaningful parameters. The formation of agronomic yield is then influenced by environmental conditions (water nutrient and availability, temperature, light, VPD, etc) and genotype, since adaptation to environment and DM allocation to seeds (expressed as harvest index – ratio of seed DM to shoot DM) are affected by these two factors. The search for reliable morphological and physiological traits is still on-going (Richards, 2006; Araus *et al*., 2002).

2.3. Cowpeas

2.3.1 Ecophysiology, production and importance, constraints and drought research

Cowpea [*Vigna unguiculata* (L.) Walpers] is primarily autogamous (Purseglove, 1968; Summerfield *et al*., 1983; Singh, 2005) and has its origin in Africa, with latest scientific information (Padulosi *et al*., 1997) pointing towards Southern Africa as the origin of the cultivated cowpea and West Africa as the primary and the Indian subcontinent the secondary centre of diversity of cultivated cowpeas. Cowpea has various growth habits; from trailing, indeterminate and bushy types to non-trailing, erect and determinate types and can have deep roots. This species, of which many genotypes (especially the indeterminate medium to long duration types) are sensitive to effects of temperature and photoperiod (Ehlers and Hall, 1996; Wien and Summerfield, 1980; Wienk, 1963), is adapted to warm climates and needs warm soils to establish (Craufurd and Wheeler, 1999; Wien and Summerfield, 1984) and may take about 40 to 150 days to flower (de Moody, 1985).

Today, cowpea is cultivated in Africa, Asia, Australia, the Americas and southern Europe (Timko and Singh, 2008). This leguminous plant plays an important economic and agronomic role in different cropping systems because it is capable of fixing atmospheric nitrogen, a function anticipated to grow as sustainable agriculture develops (Serraj *et al*., 1999). Green leaves and pods of cowpea are used as fresh vegetables or dried to be eaten later in the dry season. The dry beans are prepared in different ways for human consumption and the haulms are used as quality fodder. Cowpeas are also utilised as cover crops and as green manure. The dry beans of cowpeas are rich in high quality protein (a good compliment for the protein-scant diet of the poor providing about 50% of plant protein in sub-Saharan Africa) and digestible carbohydrates, having an energy content almost equivalent to that of cereal grains (AATF, 2007). Dry beans have on average 20 – 27% protein, 0,4 – 3,3% fat and 56 – 66% carbohydrate (Table 1) (Singh, 1999; Fashakin and Fasanya, 1988). Cowpeas are regarded to be the principal grain legume in Africa's tropical dry savannas. Here, production is carried out on over 12,5 million hectares, with almost 200 million people consuming cowpeas and most of the production is subsistence or for sale at local markets, (AATF, 2007).

	Seeds (%)	**Hay** (%)	**Leaves** (%)
Carbohydrate	55 – 65		8 – 9
Protein	20 – 28		5
Water	7 – 12	18	85
Crude fibre	4 – 7	10	2
Ash	3 – 4	23 – 24	2 – 4
Fat	0,5 – 3	11	0,3
Phosphorus	0,146	2,6	0,063
Calcium	0,1		0,3
Iron	0,005		0,005

Table 1: Chemical composition of seeds, hay and leaves of cowpea (after Chinma *et al.*, 2008; Henshaw, 2008; Singh, 1999; Fashakin and Fasanya, 1988; Khan *et al.*, 1979; Watt and Merrill, 1975)

Cowpeas are usually produced in hot and semi-arid regions under rain-fed conditions, where rainfall is unevenly distributed in the season and over the years. Diseases, pests and drought represent the main yield limitation for cowpea, particularly in Africa, with losses due to these three constraints often amounting to as much as 90% (AATF, 2007). Almost 70% of the production occurs in Africa, where the yield is very low. The unstable and poor yields of cowpea, however, can be ascribed mainly to the inconsistent and scant precipitation which can exacerbate the occurrence of pests and diseases (Watanabe *et al.*, 1997). Nonetheless, research plots and production in North Africa, the Balkans and the USA have shown that yields from 4 tonnes (Ortiz, 1998) up to 7 tonnes (Sanden, 1993) per hectare are possible with cowpea.

Magnitude and quality of yield of crops decline due to drought and indirect drought effects (for example, disease and pest infestation (Agele *et al.*, 2006)) at various growth stages. However, there are still differing opinions on the effects of water deficiency on yield at the vegetative stage up to visible flower bud growth, but a general agreement on the negative effects during the reproductive phase (especially at flowering and podding filling) already exists (Turk *et al.*, 1980; Turk and Hall, 1980a; Hiler *et al.*, 1972) especially for determinate genotypes. Differences in results might also be caused by differences in determining the level of drought stress which is complicated by the fact that cowpeas display an isohydric behaviour (opposed to anisohydric plants like sunflower and sorghum) and control stomatal conductance (g_s) so as to maintain daytime leaf and/or shoot water status almost constant, irrespective of soil water status (Tardieu, 1996; Bates and Hall, 1981). Jones (2007) and

Tardieu (1996) points out that drought stress in isohydric plants cannot be defined well by leaf or plant water status – especially leaf water potential, except when the stress is very severe. With changes in evaporative demand or soil water content isohydric plants tend to minimise changes in leaf or shoot water status (Jones, 2004; 1983). Besides, there are two types of drought tolerant genotypes in cowpea (Mai-Kodomi *et al*., 1999a; 1999b; Singh *et al*., 1997): type 1 terminate growth but retain most of their leaves for a long time and thus conserve soil water, whereas type 2 remobilise nutrients from lower leaves leading to a relatively fast senescence of lower leaves but the tips remain alive for a longer time than those of type 1.

The knowledge of physiology of gas exchange is now being used to produce drought tolerant genotypes in cereals. The first two drought tolerant cultivars of wheat were bred based on $\delta^{13}C$, TE_i, ETE and WUE, and released in the last 10 years (Munns and Richards, 2007; Richards, 2006; Condon *et al*., 2004) in Australia. In grain legumes, however, such breeding success in this area has remained illusive. Compared with other legumes cowpea has a better adaptation to drought, although drought remains one of the major constraints to high productivity of this legume in all the major cowpea production regions of the world and drought is set to get worse subsequent to climate change. Investing, among other things, in developing drought tolerant varieties of cowpea insures against erratic rainfall and stabilises agricultural output, boosts crop productivity and can allow farmers to diversify and can immensely contribute to food security in Africa. Besides, the inclusion of legumes like cowpeas in crop rotation is increasingly being advocated in order to improve the sustainability of cereal crop production, thus reducing environmental pollution with nitrogen fertilisers and checking the increase of soil pathogens (Loomis and Connor, 1992).

In breeding, utilisation of physiological traits in screening programmes is still limited. One of the reasons is partly due to physiological traits being indirectly related to yield (Araus, 1996; Richards, 1996). Sometimes there is scant knowledge of the crop ecophysiology, particularly if breeding for yield is conducted under water-limited conditions (Araus *et al*., 2001). Besides transpiration and net photosynthetic rates, stomatal (and mesophyll) conductance is a significant gas exchange trait which has been shown to be a reliable trait linked to grow and yield (Jiang *et al*., 2006; Medrano *et al*., 2002).