Ecophysiology of tropical tree crops: an introduction

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In this special issue, ecophysiology of major tropical tree crops, considered here on a broader sense and including species such as banana, cashew, cassava, citrus, cocoa, coconut, coffee, mango, papaya, rubber, and tea, are examined. For most of these crops, photosynthesis is treated as a central process affecting growth and crop performance. The crop physiological responses to environmental factors such as water availability and temperature are highlighted. Several gaps in our database concerning ecophysiology of tropical tree crops are indicated, major advances are examined, and needs of further researches are delineated.

Key words: crop growth and production, environmental stresses and physiology, photosynthesis, gas exchange, tropical tree crops

Ecofisiologia de culturas *arbóreas* tropicais: uma introdução: Nesta edição especial, examina-se a ecofisiologia de grandes culturas arbóreas tropicais, consideradas aqui num sentido mais amplo, incluindo-se espécies como bananeira, cajueiro, mandioca, citrus, cacaueiro, coqueiro, cafeeiro, mangueira, mamoeiro, seringueira e chá. Para a maioria dessas culturas, a fotossíntese é tratada como um processo-chave afetando o seu crescimento e desempenho. As respostas fisiológicas das culturas a fatores ambientes, tais como disponibilidade de água e temperatura, são enfatizadas. Várias lacunas em nosso conhecimento sobre a ecofisiologia de culturas arbóreas tropicais são indicadas, os principais avanços são examinados e as necessidades de pesquisas futuras são apontadas.

Palavras-chave: crescimento e produção de culturas, culturas arbóreas tropicais, fotossíntese, fisiologia e estresses ambientes, trocas gasosas

INTRODUCTION

Pant physiological research has a fundamental role in advancing the frontier of knowledge essential for a better understanding of plants and their interactions with surrounding environments (El-Sharkawy, 2006) for the entire or any period of the life cycle. Plant life cycle is an important aspect responsible for key differences among crops when growth and developmental strategies are considered. With regard to trees, in spite of their basic physiology being similar to that of annual species, there are some facets, such as size and complexity of organisation, making them an exciting field of diversity. The concept of a *tree* is amenable to an array of definitions, which usually involves size as well as physiognomy. Here, I have considered what is meant by tree in a broad sense according to the definition of Hallé et al. (1978) and summarised in the Merriam-Webster's Collegiate Dictionary (Mish, 1993): "… a woody perennial plant having a single usually elongate main stem generally with few or no branches on its lower part; a shrub or herb of arborescent form…". Such a definition provides a partial justification for the selection of the tropical tree crops examined here, embracing not only trees such as cashew, mango and rubber but also non-woody species such as banana, coconut and papaya (Table 1). Furthermore, for only a few tropical tree crops with greater economic importance in the world trade (e.g. citrus and coffee) there has been a relatively considerable amount of basic research on environmental physiology, but much less as compared with temperate tree crops

Table 1. Brief description of the tropical tree crops dealt with in this special issue. Unless otherwise stated, for all species, fruits are the harvestable yield. Sources: Alvim and Kozlowski (1977); León (1987); Smith et al. (1992); Schaffer and Andersen (1994); Last (2001).

Scientific name	Common name	Probable origin/Areas of cultivation/Remarks
Anacardium occidentale	Cashew	Northeast Brazil. Cultivated in lowland tropical areas. Multipurpose tree tolerating high temperatures, salinity and drought
Camellia sinensis	Tea	South-east Asia, possibly. Cultivated from tropical to temperate zones. Grows as bushes and, unlike other woody perennials, the leaves constitute the product
Carica papaya	Papaya	Lowlands of Central America and southern Mexico. Pantropical. A fast-growing, highly-productive species, usually short-lived, but can produce fruits for more than 20 years. Can reach 10 m height
Citrus spp.	Include varieties of oranges, grape-fruit, lemons and limes	Obscure; most cultivated species appear to be indigenous to the more humid tropical or near-tropical regions of China and southeast Asia; some authors have classified citrus as subtropical species. Widely cultivated in most tropical and subtropical zones. Do not tolerate frost; all species can be grown in (semi)-arid areas provided irrigation is supplemented
Cocus nucifera	Coconut	Southeast Asia. Limited to tropical lowlands, between 20°N and 20°S. A palm that grows in sunny, humid environments
Coffea arabica	Arabica coffee	Ethiopian highland tropical forest. Tropical highlands. Evolved as understory tree but open plantations generally produce more than shade plantations under high-input systems
Coffea canephora	Robusta coffee	Congo basin rainforest. Tropical lowland areas. Accounts for 34% of the world's coffee production. Together with arabica coffee, constitutes the second most valuable traded commodity worldwide
Hevea brasiliensis	Rubber	Amazonian tropical rainforest. Traditionally cultivated between 10°N and 10°S. Cultivation has been presently expanded towards higher latitudes. Latex constitutes the product
Mangifera indica	Mango	Northeastern India. Throughout tropics and subtropics. Can tolerate a relatively wide temperature range. Maximum mango yield is relatively low compared with other tree fruit crops
Manihot esculenta	Cassava	American origin, possibly from northeastern Brazil. Pantropical. High-yielding woody shrub grown as annual or biennial for its starchy roots before becoming fibrous. Unmanaged plants behave as small trees reaching about 5 m height
Musa spp.	Banana	Tropical southeast Asia. Pantropical. High-yielding perennial crop reaching up to 8 m height. Thoroughly entwined in cultures throughout the tropics and seen as ideal for agroforestry schemes. Do not thrive in areas where temperature falls below 15°C
Theobroma cacao	Cocoa	Central and western Amazon. Warm, humid tropics. Grows generally under shade with very low productivity. It is almost exclusively explored for chocolate manufacturing

such as apple and stone fruit. Lack of fundamental research may be due partially to the fact that the majority of tropical tree crops are cultivated in third-world countries where limited resources are available for adequately exploring the diversity amongst tropical plant species. This is another reason to justify the choice of the crops explored in this special issue.

There is a great deal of pliancy in the orientation, deepness and style of each article of the present issue, but in the majority of them photosynthesis is treated as a major process affecting growth and crop performance. This is not surprising taking into account that 90-95% of plant dry mass is derived from photosynthetically fixed carbon, although straightforward relationship between photosynthesis and crop yield is not always observed (Khanna-Chopra, 2000; Kruger and Volin, 2006). It is highlighted that highly-productive species such as cassava, papaya and banana show high photosynthetic rates, which may reach values as large as 50 μmol m^{-2} s^{-1} as in cassava (El-Sharkawy et al., 1992). By contrast, slow-growing crops, such as citrus, cocoa and coffee, which have evolved as understory trees are traditionally considered as displaying very low photosynthetic rates, seldom above 10 μmol m^{-2} s^{-1}, even in the field under favourable growth conditions (DaMatta, 2003). This behaviour has mostly been associated with large diffusive, rather than biochemical, limitations to photosynthesis (Lloyd et al., 1992; DaMatta et al., 2001), which can become increasingly important particularly under stressful conditions such as drought and elevated temperatures.

Plants are frequently exposed to a variety of harsh environmental conditions which negatively affect growth and crop yield. An understanding of the responses of crops to their environment is thus fundamental to minimise the deleterious impact of unfavourable climatic conditions and to manage them for maximum productivity. Boyer (1982), for instance, argued that water supply affects productivity of trees and annual crops more than all other environmental factors combined. This aspect has been deeply explored in this issue, as for banana, cashew, cassava, coconut, papaya, and tea; however, the development of internal water deficit may be important to some crops such as coffee and mango in order to trigger phenological events such as flower bud release. Decreases in yield induced by low soil water supply may largely be associated with a decline in photosynthetic rates, either by a direct effect of dehydration on the photosynthetic apparatus or by an indirect effect by way of stomatal closure, which restricts CO_2 uptake. In addition to soil water deficits, atmospheric water deficit is also of particular relevance to tropical tree crops. This is due to the very low root hydraulic conductivity as compared with annuals, which brings about a pronounced effect of transpiration on tree water relations (DaMatta, 2003). Furthermore, for a tropical environment the range of evaporative demand on average is far higher than that of temperate zones. This implies that leaf water status changes much more diurnally in tropical trees than in many temperate trees or annuals, and leaf water deficits may occur under the high evaporative demand even without any soil water shortage, such as in banana, cocoa, coffee, papaya, and tea. Therefore, regulation of leaf water status by atmospheric conditions is relatively more important in tropical tree crops than in many other crops. Yield of crop plants under soil and/or atmospheric drought stress will largely depend on adaptive mechanisms allowing them to maintain growth and a high photosynthetic production under prolonged drought conditions. However, studies on the effects of drought on crop performance are often complicated, firstly due to the complex nature of drought stress in the field, and secondly because crop yield may be affected more directly by the smaller leaf area rather than by the decreased photosynthetic rate per unit leaf area during and following drought events.

Long diurnal periods with air temperature above 35ºC are relatively common in tropical areas. High air temperatures may steeply increase the leaf-to-air temperature difference to values above 5 to 10ºC or more, as shown for tea. Anyway, one of the major difficulties in interpreting the response of physiological processes such as photosynthesis to temperature, particularly in the field, is that increase in temperature is associated with a rise in atmospheric vapour pressure deficit. Therefore, decreases in photosynthetic rates could be due to increases in temperature per se or increases in vapour pressure deficit leading to stomatal closure, or both. However, in contrast to temperate species (see, for example, Salisbury and Ross, 1992), there seems to be a broad adequate temperature range (20-35ºC, or even above) for photosynthesis nearly corresponding to the normal temperature fluctuations frequently found in hot environments in which tropical tree crops are generally grown (DaMatta, 2003). For example, by growing cassava in a hot environment, El-Sharkawy and Cock (1990) demonstrated that maximum values of net photosynthetic rates around 30 to 36 μmol m^{-2} s^{-1} were common with leaf temperature in the range 32 to 37°C. They also pointed out that failure in adequately controlling air humidity and irradiance was responsible for the findings of several earlier reports showing cassava has lower photosynthesis and lower and narrower optimum temperatures of 25 to 28°C for maximum photosynthetic rates.

Manipulation of microclimate for increasing the efficiency with which resources are used in agriculture has received renewed attention the last few years. In agroforestry and inter-cropping systems taller plant canopies may alter not only the radiation, but also air humidity and temperature around understory crops. Seedlings of many tropical tree crops grow better under shaded conditions than in full sunlight (e.g. cocoa, tea), perhaps because they are subjected to photoinhibition, and/or have large root resistances to water uptake resulting in early stomatal closure (Huxley, 2001). During the juvenile phase of tree crops, inter-cropping with fast-growing tree crops such as cassava, papaya and banana is often successfully used. This allows not only improved light capture and biomass production per unit land area but also improved growth as a result of a more favourable water status. In fact, it may be suggested that shading, provided it is not excessive, may be advantageous for tree crop cultivation in the tropics considering that: (i) photosynthesis in several tropical tree crops is irradiance-saturated below full sunlight; (ii) in the tropics during most of the year incoming radiation is high and may lead to photoinhibitory damages, particularly when associated with water shortage; and (iii) improved microclimate leads to a buffering of air humidity and soil moisture availability, thereby allowing maintenance of leaf gas exchange for longer. Other reasons for maintaining shade trees with perennial crop plantations include the income provided by their fruit and/or timber (or latex if rubber is the dominant species), increasing awareness of the environmental costs associated with high-input monocrops, and biodiversity maintenance. Indeed, a growing body of evidence suggests that whenever correctly managed, inter-cropping and agroforestry schemes will become a promising alternative for sustainability in tropical agriculture, as highlighted here for crops such as cocoa, coffee, rubber, and tea.

FUTURE SCOPE

There is an increasing trend in expanding tropical agriculture towards marginal and degraded lands where water shortage and unfavourable temperatures already constitute major constraints to crop yield. The scientific community has long been aware of the impact of the environment on plant productivity, and this aspect of plant biology has recently become a greater political and public concern in the wake of discussions surrounding global climate changes (Chapple and Campbell, 2007). In any case, large areas of valuable irrigated land are facing crop conversion problems because either they are allotted to less valuable annual crops or critical salinisation problems (roughly one-fourth of world-wide irrigated land involved); Janssens and Subramanim, 2000. Considerable areas with currently sufficient water will experience in a near future some degree of water shortage, *e.g.* India and parts of China (Wallace, 2000). The use of appropriate perennial crops in combination with adequate irrigation to exploit saline lands may be successful where annuals would normally fail. In addition, perennial crops may help to buffer the farmer's production against year-to-year oscillations in yields from rainfed annual crops. In effect, in the latter half of the last century, most particularly in the last decade, the proportion between annual and perennial crops evolved more in favour of the latter. There is also an expectation that the proportion of perennial crops to annual crops will continue increasing during this new century (Janssens and Subramaniam, 2000). Most of this increase involves tropical and subtropical tree crops. Needless to say there are uncountable tropical species with potential agricultural use whose domestication remains unfulfilled.

As occurs with most tropical plant species the gaps in our knowledge on ecophysiology of tropical tree crops are incommensurable, though significant advances have occurred in the last years. The bulk of research has slowly been shifted from more observational studies on plant growth and developmental responses to physiological processes, as can be seen when examining the current papers dealing with banana, citrus, coffee and mango, for example. Unfortunately, however, physiological research concerning tropical tree crops has been restricted to a few laboratories throughout the tropical/subtropical countries where those crops are chiefly grown. To date, significant fundamental research has been conducted using potted plants without the appropriate calibration in the field, which can lead to a waste of time and resources since in most cases results cannot be extrapolated, or simulated by crop modelling, to describe what may occur in natural environments (El-Sharkawy, 2006; Long et al., 2006). Even under field conditions, much emphasis on ecophysiology of tropical tree crops has been focused at the leaf level without advancing substantially towards the canopy level. Furthermore, part of the available information obtained in field conditions is known on the grounds of empirical experimentation rather than scientifically based, with predominantly observational results and no mechanistic and functional links. With a few exceptions, the use of isotope techniques, fundamental biochemical and molecular studies, multiscale analyses, and crop simulation models have not yet been the major goals in basic and applied research in tropical tree crops. From the above, the deep understanding of the physiology of currently cultivated tropical trees and its impact on subsistence and commercial agriculture is a challenge to be met within the near future.

Hopefully, this special issue will not only highlight some recent advances in ecophysiology of tropical tree crops, but also may serve as a stimulus for further efforts in this important challenging field of research. As yet we are awaiting that the new tools in genetics, biochemistry and molecular biology, that are just beginning to be explored in major crops such as coffee and citrus, can also be expanded towards other tropical tree crops. It must be emphasised, however, that if significant benefit to the farmer is to be attained, crop performance must be also evaluated under the naturally changing tropical environmental conditions. After all, yield improvement under such conditions is the major goal to be achieved.

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