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Tree–Crop Ecological and Physiological Interactions Within Climate Change Contexts: A Mini-Review

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The effects of climate change are increasingly noticed worldwide, and crops are likely to be impacted in direct and indirect ways. Thus, it is urgent to adopt pliable strategies to reduce and/or mitigate possible adverse effects to meet the growing demand for sustainable and resilient food production. Monoculture cropping is globally the most common production system. However, adaptation to ongoing climate change, namely, to more extreme environmental conditions, has renewed the interest in other practices such as agroforestry, agroecology, and permaculture. This article provides an overview of ecological and physiological interactions between trees and crops in Mediterranean agroforestry systems and compares them with those from monocultures. The advantages and disadvantages of both systems are explored. The added value of modeling in understanding the complexity of interactions within agroforestry systems, supporting decision-making under current and future weather conditions, is also pinpointed. Several interactions between trees and crops might occur in agroforestry systems, leading to mutual positive and/or negative effects on growth, physiology, and yield. In this sense, selecting the most suitable combination of tree/crop species in mixtures may be best be indicated by complementary traits, which are crucial to maximizing trade-offs, improving productivity, ecosystem services, and environmental sustainability.

Keywords: modeling, ecosystem service, plant physiology, global warming, agroforestry systems, monocultures

INTRODUCTION

Multispecies systems are an ancient cropping technique that involves the simultaneous cultivation of two or more plant species within the same field (Malézieux et al., 2009; Gaba et al., 2015; Bybee-Finley and Ryan, 2018). It was estimated that agroforestry systems cover about 1 billion hectares of land worldwide (Zomer et al., 2014, 2016): 17% of agricultural systems, if more than 30% of tree cover is considered, or 46% if more than 10% of tree cover is considered (Kumar et al., 2014).

Agroforestry systems are envisaged within the European Green Deal as one of the most effective tools to mitigate and adapt to climate change (Mosquera-Losada et al., 2020), but also by their socio-ecological returns (Malézieux et al., 2009; Chapagain et al., 2020). The European Common Agrarian Policy (CAP) turnaround emerges from the evidence that previous support for the intensification of agroforestry systems (and in general to agriculture) led to many environmental problems, namely, soil and biodiversity losses as well as land degradation, and water pollution (Tsiafouli et al., 2015). In this way, mixed systems can be viewed as a nature-based solution, implying a practical application of ecological principles to agriculture, capitalizing functional biodiversity, beneficial plant interactions, and other homeostatic mechanisms (Malézieux et al., 2009). Actually, a diverse agroecosystem in genotypes, species, structures, and functions is more environmentally adaptable, resilient, and sustainable than monocrops (**Supplementary Figure 1**), especially when native species are involved (Manson et al., 2013).

Among the several types of multispecies systems, the combination of woody plants and herbaceous crops, often together with domesticated or semi-wild animals, in a range of temporal and spatial arrangements are defined as agroforestry systems (Mosquera-Losada et al., 2018). Agroforestry systems have a long tradition in tropical and Mediterranean regions (Jose, 2009; Mosquera-Losada et al., 2018; Rodríguez-Rigueiro et al., 2021). In the Mediterranean, the characteristic agroforestry systems include the oak agroforests (Portugal and Spain), agrosilvopasture mosaics (Italy), and the Valonian oak silvopastures (Greece) (Moreno et al., 2018). Several authors emphasized the pivotal role of agroforestry systems in biodiversity conservation (Mcneely and Schroth, 2006; Vodouhe et al., 2011; Montagnini, 2017; Mosquera-Losada et al., 2018, 2020; Udawatta et al., 2019; Dagar and Gupta, 2020; Rosati et al., 2020), carbon sequestration (Montagnini and Nair, 2004; Mosquera-Losada et al., 2015, 2017; Ferreiro-Domínguez et al., 2016; De Stefano and Jacobson, 2018; Udawatta et al., 2019; Dagar and Gupta, 2020), restoration of degraded ecosystems (Navas and Silva, 2016; Dagar and Gupta, 2020), and in the mitigation of climate change impacts (Lin, 2007; Bayala et al., 2008; Fernández-Núñez et al., 2010; Montagnini, 2017; Mosquera-Losada et al., 2017, 2018; De Stefano and Jacobson, 2018) by amending microclimates (Gomes et al., 2020). Agroforestry systems are also critical for rural development in low-income regions (Montagnini, 2017; Rodríguez-Rigueiro et al., 2021) by providing determinant ecosystem services such as soil fertility enhancement, prevention of soil erosion, water, wind, and pest regulation, and pollination (Rigueiro-Rodríguez et al., 2009; Kuyah et al., 2017). In this sense, mixing crops and tree species is an excellent way to increase crop yield and yield stability, especially within adverse climatic conditions (Sileshi et al., 2012; Nasielski et al., 2015).

Agroforestry systems can also reduce evaporation (by temperature and wind reduction) (Lin, 2010), improve water and nutrient cycling and radiation protection, and increase soil organic carbon and the activity of beneficial soil organisms, leading to nutrient supply by nitrogen fixation and enhanced decomposition (Barrios et al., 2012). Additionally, plants with deep roots can lift or redistribute water to the upper layers through a process known as hydraulic lift, potentially acting as "bioirrigators" to adjacent plants (Bayala and Prieto, 2020). Biodiverse ecosystems are generally more efficient in terms of resource use (water, nutrients) and more resilient to diverse environmental stresses (e.g., weather extremes, pests, or diseases) than monocrops (Gaba et al., 2015), likely due to different traits associated with complementary functions (Lohbeck et al., 2016). Despite all the positive aspects of agroforestry systems, several ecological interactions between trees and crops (**Supplementary Figure 2**; Jose et al., 2004) can also lead to adverse effects on the physiology of both cultures. According to van Noordwijk et al. (2015), the water/nutrient use efficiency does not differ significantly between trees and C3 crops in most agroforestry systems. Being a perennial crop, trees have more developed root systems, which can explore larger soil volumes, water, and/or nutrients, thus allowing their full growth. On the other hand, tree roots can assist the weathering of saprolite or bed-rock layers inaccessible to crops and intercept water and nutrients leaching down the soil profile below the crop rooting zone. Therefore, both spatial and temporal complementarity and competition can occur (Ong et al., 2014). According to van Noordwijk et al. (1996), belowground competition occurs especially when two or more species have developed a specialized root system that directs them to explore the same rhizosphere for resources. If unsuitable combinations of species were chosen, it can result in the poor growth of both cultures (FAO and IAEA, 2008). In fact, resource competition is the most important factor for plant community diversity and dynamics as it usually reduces the marketable productivity of the system (Tilman, 1982; Schluter, 2000; **Supplementary Figure 2**). Indeed, competition or competitive behaviors can affect the plant at several levels, leading to morphological responses (plant growth), biochemical responses (plant defense), and resource allocation (Novoplansky, 2009; Yamawo, 2015). According to Jose et al. (2004), competition for nutrients is minimal in systems managed with high input of inorganic or organic nutrient supplements. Thus, competitive interactions involving water seem to be the most influential driving force of productivity in alley-cropping and silvopastoral systems. Therefore, agroforestry's effects on crop yields depend on complex interactions between trees, crops, soil, climate, and management (Bayala et al., 2012) and the balances between positive and negative interactions determine the overall sustainability and yield of the agroforests. Rosenstock et al. (2014) pointed out that the integration of N_2-fixing trees in agroforestry systems promotes excessive production of gaseous N but can improve crop yields and reduce dependence on mineral fertilization. The objectives of this manuscript were (i) to summarize the ecological and physiological processes in tree–crop interactions with respect to climate change, and (ii) to give a brief overview of process-based models for agroforestry systems.

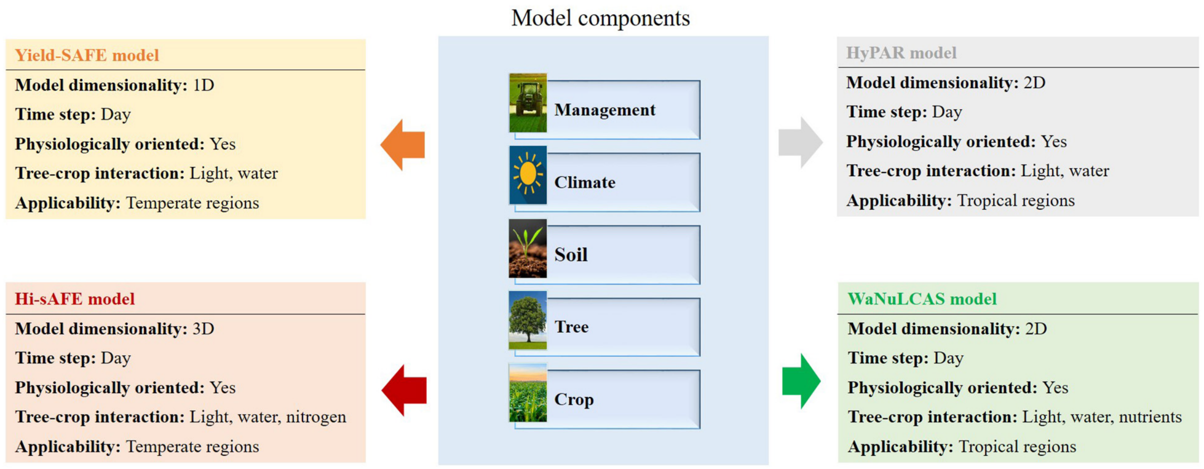
ECOLOGICAL AND PHYSIOLOGICAL PROCESSES OF TREE–CROP COMBINATIONS IN AGROFORESTRY SYSTEMS

Agricultural intensification can be technically defined as an increase in agricultural production per unit of inputs (FAO, 2004). In several regions of the world, particularly in the Portuguese region of Alentejo, holm-oak and cork-oak agroforests (Montados) have been replaced by olive groves. However, the association between trees, crops, or pastures has multiple economic, environmental, social, and cultural benefits (Jose, 2009; Pasalodos-Tato et al., 2009; Santiago-Freijanes et al., 2018), namely by diversifying productions, income, and services, yet remaining a low input system (Lehmann et al., 2020). Diversifying the production can reduce the risks of yield losses (and yield cycles) imposed by pests, diseases, and climate change (Lin, 2011; Santiago-Freijanes et al., 2018). Agroforestry practices such as silvopasture or silvoarable with fast- and slow-growing species might help farmers to reap multiple benefits. The diversification of species can support non-productive phases of crops and exploit timber and more valuable understorey products while reducing soil erosion risks and providing shelter and protection against frost or pests (Montagnini et al., 2004; Petit and Montagnini, 2006). Providing shade can also buffer climatic extremes (van Oijen et al., 2010) by reducing the energy expended in thermoregulation, leading to higher biomass conversion and weight gain (Jose et al., 2004). Plants can perceive their surrounding environment by using the information on the distribution of essential resources (light, nutrients, and water), chemical cues (volatile compounds, root exudates, and leachates) (Novoplansky, 2009; Weston and Mathesius, 2013), or even hormones, such as abscisic acid or ethylene (Wahid et al., 2007). According to this signaling, plants display several responses to optimize their performances upon exposure to biotic stress (Pierik et al., 2013). So, woody perennials in agroforestry systems modify microclimate conditions, which, in turn, benefit livestock and wildlife (Moreno et al., 2018) and affect crops' physiology (Righi et al., 2007). Furthermore, volatile cues in a plant's environment can lead to physiological changes that alter their volatile profile, influencing the neighboring plants to respond differently, adapting to neighbors' presence (Pierik et al., 2014; Ninkovic et al., 2019).

In this context, the reduction of solar radiation, extreme temperatures, wind speed, and soil evaporation in the understory can improve water status, gas exchange, and water use efficiency by the system (Lasco et al., 2014), depending on the tree (Muthuri et al., 2009) and crop species (Arenas-Corraliza et al., 2018). Campi et al. (2009) studied the effect of tree canopy provided by *Cupressus arizonica* on durum wheat in a Mediterranean environment. They concluded that the woody tree's windbreak barrier significantly affected the water use efficiency and yield. Other work performed by Mahieu et al. (2016) in a Mediterranean agroforestry system indicated that the use of walnut trees was beneficial for chickpea growth, seed biomass, seed quality, and production due to higher mineral N availability proportioned by the trees. Recent studies in Galicia (NW Spain) have shown that the combination of broadleaf trees (*Juglans regia* L.) with wheat (*Triticum aestivum*) increased the production of this cereal compared with the tree-less areas. This might be linked to a reduction in understory light availability, which decreased the weed establishment in the understory, and the competition for light, nutrients, and water between the cereals and the weeds (Ferreiro-Domínguez et al., 2021). However, Kaushal and Verma (2003), in a study of above and belowground interactions of *Grewia optiva* and wheat, found that growth and yield of wheat were negatively affected below the tree crown while increasing with distance from the tree trunk. Therefore, tree species and crops' choice is important and should be one of the first decisions. Selection of the "right species for the right place" depends on the goals, site conditions, and species traits and should be focused on complementary traits that maximize positive and minimize negative interactions between system components (Liu et al., 2018). It is expected that different aspects of climate change (e.g., higher temperatures and atmospheric CO_2 concentration, and reduced rainfall), acting as a disturbance factor, may affect all system components and interactions between them (Luedeling et al., 2014), further complicating its management. In this sense, the selection of trees and crops better adapted to future environmental and climatic conditions (e.g., especially resistant to water, heat, and light stresses) is also extremely important in areas with drought periods, such as the Mediterranean, as was highlighted in the AFINET project by stakeholders. This selection should be based on identifying and quantifying functional traits associated with drought resistance (e.g., rooting volume, leaf arrangement, and leaf water potential).

MODELING TREE–CROP INTERACTIONS IN AGROFORESTRY SYSTEMS

Agroforests are complex systems whose management depends on their components and the interactions between them (Lehmann et al., 2020). Climate change will alter the interactions among components (Luedeling et al., 2014), which will inevitably affect the sustainability (Mbow et al., 2014) and productivity of the agroforestry systems (Jose et al., 2004) while contributing to climate change mitigation (Mbow et al., 2014). The growing need to consider the inherent complexity of agroforestry systems has fostered an increased interest in modeling approaches. The development of modeling tools that can incorporate multiple objectives, alternatives, and interests might be of great help for farmers, landowners, researchers, and policy-makers. These tools can integrate very diverse and complex interactions, typical of agroforestry systems, at a relatively low cost, effort, and time, for assisting in management decisions (Ellis et al., 2004). However, this is a very challenging task. When trees and crops are grown together, several changes occur over time and space, mainly in response to biophysical interactions, environmental conditions, and management options (e.g., the exact arrangement and placement of trees and crops). Integration of all these issues in modeling approaches is also challenging since models should represent processes accurately, and at the same time, be easy to use.



Yield-SAFE model
Model dimensionality: 1D
Time step: Day
Physiologically oriented: Yes
Tree-crop interaction: Light, water
Applicability: Temperate regions

Hi-sAFE model
Model dimensionality: 3D
Time step: Day
Physiologically oriented: Yes
Tree-crop interaction: Light, water, nitrogen
Applicability: Temperate regions

HyPAR model
Model dimensionality: 2D
Time step: Day
Physiologically oriented: Yes
Tree-crop interaction: Light, water
Applicability: Tropical regions

WaNuLCAS model
Model dimensionality: 2D
Time step: Day
Physiologically oriented: Yes
Tree-crop interaction: Light, water, nutrients
Applicability: Tropical regions

FIGURE 1 | Overview of the most used agroforestry models, in relation to model components, model dimensionality, time steps, integration of physiological process, tree–crop interactions, and applicability.

Several models have been developed for a wide range of environmental conditions, agroforestry practices, and purposes in recent years. Such models can be organized into six categories according to their goals (Burgess et al., 2019): (i) allometric models – models for estimating aboveground biomass and volume; (ii) models for describing the environmental impact of agroforestry practices on soil carbon, soil nutrients, and water flow (e.g., CO2FIX and SCUAF models); (iii) models for exploring tree and crop growth (e.g., ALWAYS, HyPAR, WaNuLCAS, Yield-SAFE, and Hi-sAFE); (iv) models for describing aboveground canopy architecture (e.g., AMAP model), belowground architecture (e.g., FracRoot), or both (e.g., NOTG model described by Simioni et al., 2016), i.e., architectural models; (v) models for assisting whole-farm decision-making (e.g., ARBUSTRA, Farm-SAFE, and Forage-SAFE), and finally, (vi) landscape models – models for determining the effect of agroforestry systems at the landscape scale. Most existing models present inadequate flexibility and require numerous parameters, many of which are hard to obtain, making model calibration and validation difficult (Luedeling et al., 2016). Under such circumstances, the risk of making maladaptive decisions is much higher, limiting model adoption, and application. Furthermore, most of the models mentioned above ignore the interactions within agroforestry systems, indicating that they are unlikely to capture their complexity adequately. In this sense, the model's accuracy will inevitably be affected (Mishra et al., 2021). The need to correctly address the complex dynamics of tree–crop interactions and predict responses beyond known conditions has fostered process-based models instead of empirical ones (Oreske, 2003). Such models can simulate physiological processes involved in growth in response to abiotic factors such as soil, climate, or management (Luedeling et al., 2014). Among the many models that consider the interactions between trees and crops and include physiological oriented high-resolution approaches, the most relevant are WaNuLCAS – a model for water, nutrient, and light capture in agroforestry systems (van Noordwijk and Lusiana, 1998), Hi-sAFE, developed in the EU SAFE project (Silvoarable Agroforestry for Europe) that explores the competition between trees and crops for light, water, and nitrogen (Dupraz et al., 2019), Yield-SAFE, also created under the SAFE project, is designed to describe tree and crop yields (van der Werf et al., 2007), and HyPAR, which combines the continuous-canopy forest (Hybrid) and crop (PARCH) models, taking into account the competition for light and water (Mobbs et al., 1998). The overall characteristics of these models are presented in **Figure 1**.

The WaNuLCAS and the Hi-sAFE models are the most commonly used in tropical and European regions, respectively (Dupraz et al., 2019). WaNuLCAS is a dynamic model that has been used in a wide range of agroforestry systems ranging from hedgerow intercropping [e.g., maize (Hussain et al., 2016) and sugarcane (Pinto et al., 2005)] to fallow-crop mosaics or even isolated trees in parklands (van Noordwijk and Lusiana, 1998). Apart from successfully simulating soil erosion and runoff, nutrient dynamics, and carbon sequestration (Pansak et al., 2010), the WaNuLCAS model may also be used to answer questions related to vulnerability and adaptation associated with climate change mitigation (Luedeling et al., 2014). In turn, the Hi-sAFE model is a mechanistic 3D model that explores the interactions between the above and belowground components that govern the dynamics of light, water, and nitrogen (Dupraz et al., 2019). Simulations using the Hi-sAFE model proved to be a powerful tool for examining different agroforestry designs, management strategies, and environmental variation, including climate change (Dupraz et al., 2019). Compared to the WaNuLCAS model, the Hi-sAFE is easier to use, but it cannot predict long-term dynamics (Malézieux et al., 2009). For more details in both agroforestry models, please see van Noordwijk and Lusiana (1998); Malézieux et al. (2009), and Dupraz et al. (2019).

FINAL CONSIDERATIONS

Agroforestry systems have high landscape and ecological values and are strategic for biodiversity conservation and the livelihood of farmers, especially in tropical and Mediterranean regions. However, there is an urgent need to enhance their productivity and resource-use efficiency in the context of increasing populations and limited land. The selection of tree/crop combination is crucial for the success of agroforestry systems. Many researchers explored the potential mutual benefits to gain a better understanding and enable sustainable use of various species in agroforestry. However, one of the major obstacles to the widespread use of agroforestry systems is insufficient knowledge about the interactions between trees and crops, ranging from competition to facilitation. Therefore, more effort should be put into the characterization of species involved, for example, concerning their tolerance to shade, drought, heat, pests, diseases, and compatibility with other species, to reverse the negative impacts and maximize the positive influences of trees on crops. Since this requires dealing with trade-offs that depend on the environment, considering envisaged environmental changes in the near future is of particular importance. A change in aboveground resource availability necessarily changes the struggle for belowground resources and thus the relation between trees and crops. However, such effects are not well documented. Therefore, it will be of paramount importance to increase our knowledge of key processes that determine belowground interactions, such as root expansion and nutrient dynamics, and environmental dependencies.

To prepare agroforestry systems for more extreme conditions related to climate change, it might also be necessary to: (a) test new species combinations or management options; (b) to study improved crop technology that minimizes competition and maximizes facilitation; and (c) to breed and genetically modify plants to increase productivity and nutritional quality. Moreover, the development of agroforestry models capable of simulating the complex interactions between trees and crops at aboveground and belowground levels under future climate conditions, although difficult to achieve, should be a research priority. Similarly, the integration of physiological parameters, such as photosynthesis or transpiration, is a significant challenge but should be considered in modeling. With climate change, shifts in distribution and impacts of biotic constraints (pests, diseases, and invasive species) are an increasing concern, so these aspects should also be accounted for when modeling. A key future challenge of modeling agroforestry systems will be to balance the trade-offs between model complexity and the variety of interactions that are possible to simulate.

AUTHOR CONTRIBUTIONS

BG: conceptualization and writing – original draft and review and editing. MM and SP: writing – review and editing. MM-L and MS: conceptualization and writing – review and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.661978/full#supplementary-material

Supplementary Figure 1 | Advantages and constraints associated with agroforestry systems in comparison to monocultures.

Supplementary Figure 2 | Ecological interactions and potential effects on species. + and − denote positive and negative effects, respectively. 0 denotes no effect (adapted from Jose et al., 2004).

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