European Journal of Agronomy 93 (2018) 27–39

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Component crop physiology and water use efficiency in response to intercropping

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ARTICLE INFO

Keywords:
Biodiversity
Functional diversity
Intercropping
Water use efficiency
Crop ecophysiology response
Sustainable agriculture

ABSTRACT

Interspecies specific interactions are generally regarded as drivers of plant productivity in multispecies agroecosystems. Complementary use of resource in diverse communities can enhance community productivity through optimal use of plant-available resources and positive interactions such as facilitation can ameliorate high abiotic stress conditions. We studied the effects on physiological response, leaf traits and water use efficiency of a multifunctional species intercropping system consisting of peanut (*Arachis hypogaea* L.), watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai], okra [*Abelmoschus esculentus* (L.) Moench], cowpea [*Vigna unguiculata* (L.) Walp.], and pepper (*Capsicum annuum* L.) planted alone or in various intercropping combinations in a low fertilizer input system in the peak of summer heat in Texas. Differences in gas exchange measurements were detected only in watermelon in year 2 of the study when okra was the dominant crop. This same year watermelon specific leaf area (SLA) was significantly higher when okra was present in a treatment and particularly in the three and four species combinations, W_{pwo} and W_{pwoc}, 27.5 and 31.0 $m^2\,kg^{-1}$, respectively, as compared to watermelon grown in monoculture, strip intercropped with peanut (S_{pw}) and within row intercropped with peanut (W_{pw}), 20.4, 20.1, and 19.8 $m^2\,kg^{-1}$, respectively. This corresponds with an increase watermelon leaf N concentration and a decrease in leaf C:N ratio in W_{pwo} and W_{pwoc} treatments. No differences in $d^{13}C$ composition, a measure of water use efficiency over the leaf lifespan, were detected across cropping system for each species. Water use efficiency based on per plant production (WUE_{yield}) indicated an increase in water use efficiency in dominant crops such as watermelon in 2011 and okra in 2012, but a reduction in WUE_{yield} subordinate crops such as cowpea and pepper both years of the study. Peanut grown in monoculture and strip intercropped with watermelon had significantly lower leaf water potential values in 2012, −2.2 and −2.1 MPa, respectively, as compared to intercropping systems increasing in level of integration ($W_{pw} = -1.1$, $W_{pwo} = -0.6$, $W_{pwoc} = -1.3$, $W_{all} = -1.1$ MPa), indicating peanut benefited from alterations to microclimate and facilitative interactions with companion crops in some intercropping systems through a reduction in plant water stress. The results from this study suggest there may be a benefit to a multifunctional intercropping system in the form of increased food production per unit of water input in dominant crops and reduced water stress for some component species. This is important to producers; showing a method to increase overall crop production without increasing water inputs.

1. Introduction

Positive interactions such as facilitation and complementarity can offset some of the negative interactions associated with plant resource competition in multispecies systems (Callaway, 1998; Hooper et al., 2005). Complementarity results from niche partitioning and a reduction of competition between species (Vandermeer, 1989; Hille Ris Lambers et al., 2004; van Ruijven and Berendse, 2005), while facilitation occurs when neighboring plants ameliorate habitat through the mitigation of abiotic stress during times of suboptimal conditions (Hooper et al., 2005; Chu et al., 2008; Zhang et al., 2012). Complementarity occurs when functionally different species differ in their acquisition of

Abbreviations: W_{pw}, watermelon-peanut within-row intercrop; S_{pw}, watermelon-peanut strip intercrop; W_{pwo}, waterrmelon-peanut-okra within-row intercrop; W_{pwoc}, watermelon-peanut-okra-cowpea intercrop; W_{all}, watermelon-peanut-okra-cowpea-pepper intercrop

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https://doi.org/10.1016/j.eja.2017.11.005
Received 24 July 2017; Received in revised form 7 November 2017; Accepted 15 November 2017
1161-0301/ Published by Elsevier B.V.

resources in either time or space (Reich et al., 2004; van Ruijven and Berendse, 2005; Tilman et al., 2006b). The stress-gradient hypothesis, which was formulated at the interspecies competition level, states there is a shift from competition to facilitation in plant communities as abiotic stress is amplified along environmental gradients (Callaway and Walker, 1997; Zhang et al., 2012). Complementary use of resources, along with facilitative interactions between species, has been cited as a reason why species are able to coexist and why plant growth and productivity are maximized in diverse natural plant communities (Hooper, 1998; Hille Ris Lambers et al., 2004; Hauggaard-Nielsen et al., 2009).

1.1. Competition and plant response

The efficiency of converting resources into biomass depends on the total amount of light intercepted by the canopy (i.e., a function of canopy size and competition for light) and the rate of net photosynthesis per unit leaf area (Lambers et al., 2008). Plants that exist in a more dense canopy, such as found in diverse ecosystems, will undergo more competition for light and, consequently, a stronger vertical light gradient (Poorter et al., 2006). Since leaves are the primary photosynthetic organs of a plant, plants respond to changes in their light environment by changing leaf morphology and altering resource allocation patterns to leaves versus other parts of the plant (Poorter et al., 2009). Plants can modify specific leaf area (SLA, leaf area per unit leaf mass), leaf area ratio (LAR, leaf area per unit plant mass), and the relative investment of nitrogen between leaf photosynthetic machinery in response to light (Evans and Poorter, 2001). For instance, shading can result in reduced leaf thickness due to reduced thickness of palisade parenchyma, thereby increasing SLA (Poorter et al., 2006). As an underlying component of relative growth rate (RGR), an increase in SLA maximizes the amount of light interception by increasing LAR (Lambers et al., 2008) and increasing a plants competitive ability. Furthermore, there is a strong positive linear relationship between SLA and leaf N concentration per unit mass. Since photosynthetic machinery accounts for more than half of leaf N content (Evans, 1989; Lambers et al., 2008), photosynthetic capacity is tightly associated with N availability and leaf N content (Evans, 1989; Loomis, 1997). Therefore, changes in leaf resource allocation and specific leaf area can be better predictors of plant growth than minor changes in net assimilation rates as photosynthetic capacity per unit leaf area is generally optimized (Potter and Jones, 1977).

Changes in leaf-level traits (LMA: leaf mass per unit area or the reciprocal of SLA), gas exchange and water-use efficiency (WUE) have been found to be associated with growth habit in row crops such as soybean and wheat (Tanaka et al., 2008; Barrios-Masias et al., 2014). The morphological and anatomical changes that occur at the leaf-level can affect chlorophyll content and, consequently, stomatal conductance and photosynthetic rates (Makoi et al., 2010; Barrios-Masias et al., 2014). As previously discussed, photosynthetic activity is linked to efficient plant nitrogen uptake and partitioning within a leaf, which is, in part, influenced by growth habit (Evans and Poorter, 2001). However, there is a tradeoff between high leaf N and leaf longevity, wherein leaves with greater N:C ratios have a shorter lifespan (Field and Mooney, 1986). In addition, since leaf N content is positively correlated with photosynthesis and stomatal conductance (Niinemets and Kull, 1998; Reich et al., 2003; Hikosaka, 2004), photosynthetic rate per unit N is tightly coupled with water use efficiency in some species (Sage and Pearcy, 1987). Moreover, sustained high photosynthetic rates are, in some instances, correlated with higher crop yields (Ainsworth et al., 2002; Ainsworth and Long, 2005).

1.2. Plant response to intercropping

Intercropping has become an important management strategy for enhancing crop resource use efficiency and maximizing plant productivity through the deliberate manipulation of interspecific species interactions (Vandermeer, 1989; Li et al., 1999; Andersen et al., 2007; Hauggaard-Nielsen et al., 2009). Intercropping has been found to have both positive and negative effects on net assimilation rates and plant growth (Hooper and Vitousek, 1998; Andersen et al., 2005). Intercropping with functionally dissimilar species may lead to an increase in leaf area index (LAI) and overall light interception (Bilalis et al., 2010; Salau et al., 2014), thereby capturing more available light but also potentially creating a more dense canopy leading to increased competition for light.

Most intercropping studies have limited their approach to simplified two-species systems (Andersen et al., 2007). Further, the majority of studies conducted in temperate regions have focused on legume-cereal intercropping systems (Zhang and Long, 2003; Gao et al., 2009; Hauggaard-Nielsen et al., 2009; Dahmardeh et al., 2010; Gao et al., 2010). Makoi et al. (2010) found that photosynthetic rates and WUE (as measured by isotopic discrimination) decreased in cowpea when intercropped with sorghum at different planting densities and those decreases were especially pronounced at high densities. Su et al. (2014) also observed a decrease in photosynthetic rate in soybean seedlings when intercropped with maize. In contrast, Pinheiro and Filho (2000) observed an increase in maize photosynthetic activity when intercropped with cowpea as compared to monocropped maize. There was a decline in cowpea photosynthesis, however. They also observed an improvement in water relations in both crops as measured by leaf water potential. They attributed both the improved water relations and lower net photosynthesis measurements in intercropped cowpea to facilitative environmental modifications from shading by maize. Light interception is important as plants grown under higher irradiances tend have higher photosynthetic rates and stomatal conductance (g_s) values, but lower WUE (Evans and Poorter, 2001; Tanaka et al., 2008; Barrios-Masias et al., 2014). Other studies have found higher photosynthetic rates associated with two-species intercropping systems (Gomez-Rodriguez et al., 2007; Ahmad et al., 2013).

In summary, there is little agreement on how intercropping may impact component crop physiology and water use owing to the variability in species response and to the dynamic interactions between species. Studies have primarily been limited two-species systems and there is a gap in our understanding of how component crops will respond physiologically to a functionally diverse intercropping system and how this may alter the water use efficiency of component crops. In addition, there is little mention of leaf-level acclimation in existing intercropping studies. Therefore, the objectives of this study were threefold: 1) to quantify changes to photosynthetic parameters and leaf-level traits induced by intercropping, 2) to evaluate the effects of functionally diverse intercropping on water use efficiency, and 3) to assess the impact of this intercropping system on component species water status. We hypothesized that a functionally diverse cropping system would enhance water use efficiency of component species through niche partitioning and complementarity of resource utilization and that this system would reduce plant stress in crops during the peak of summer through facilitative interactions in a low fertilizer input organic system consisting of peanut, watermelon, okra, cowpea and pepper.

2. Materials and methods

2.1. Study area

Plots were established at Texas A&M University's Horticulture Farm (30°37′N, −96°22′W) in Bryan, Texas during the 2011 and 2012 growing seasons. Management consisted of a low fertilizer input and organic approach. Average monthly air temperatures for this area from May to October ranged from 28 to 39 °C for the maximum and 15–26 °C for the minimum in 2011 and 27–37 °C and 15–25 °C in 2012 (NOAA/NCDC; Fig. A.1).