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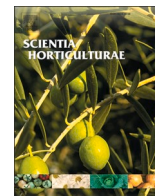
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Research Paper

Apple trees in agroforestry – Investigating the plasticity of vegetative and reproductive traits

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ABSTRACT

Agroforestry is promoted as a way to improve the sustainability of horticultural systems through plant diversification and also to mitigate climate change through carbon sequestration. It could also alleviate excessive light and temperature in high-radiation regions of the world. However, little is known about the long-term shade adaptation of the temperate fruit tree in agroforestry systems. A study was developed to investigate apple growing under walnut trees in two shade conditions compared to a full light condition. Our aim was to quantify the plasticity of traits and the covariations between traits in these three light conditions using a multiscale approach considering different scales from whole tree to annual shoot and inflorescence. Shade did not affect the height of the apple trees, while it reduced the diameter of the trunk and branches. On the other hand, the total number of growing shoots was reduced in shade, and flowering and fruiting were fewer and more irregular than in full light. Strikingly, at the whole tree scale, covariations between vegetative traits (trunk cross-sectional area versus mean branch cross-sectional area) and between vegetative and reproductive traits (trunk cross-sectional area versus total number of inflorescences) were not altered by shade. However, at the shoot scale, return-bloom was significantly reduced by shade, whereas at the inflorescence scale shade did not affect leaf number or leaf area. We propose a shade adaptation syndrome that includes not only shade intensity but also shade dynamics during the growing season and over consecutive years.

1. Introduction

Horticulture faces the challenge of contributing to healthy diets in sustainable food systems, as the two are closely linked (HLPE, 2019). It therefore contributes strongly to the Sustainable Development Goal (SDG) 2 targets on sustainable food systems, which aims to “end hunger, achieve food security and improved nutrition and promote sustainable agriculture” (United Nations Sustainable Development Goals, 2024). Considering that in an ideal planetary health regime, the half plate should include vegetables and fruits, the fruit industry has an important place in the global challenge to improve food security and nutrition in the coming decades (Willett et al., 2019). These considerations have practical implications at the farmer level, where biodiversity-based systems can provide ecosystem services such as soil fertility and biological regulation of pests and diseases, as demonstrated in annual crops (Duru et al., 2015). Biodiversified orchards have also been considered with interest in recent decades, drawing lessons from ‘integrated production’, which prioritises ecologically safer methods (Granatstein and Peck, 2017), and ‘organic farming’, which emphasises soil organic

matter and the prohibition of synthetic inputs (Weibel and Häseli, 2003). More recently, research has been developed with the aim of improving the sustainability of orchards, particularly in terms of natural pest regulation (Albert et al., 2017; Kranz et al., 2019; Simon et al., 2017) or more generally in terms of the spatial and functional organisation of the agrosystem (Lovell et al., 2018; Lauri and Simon, 2019; Lauri et al., 2020). A common basis of these systems is plant diversity, with the challenge of managing not only intraspecific (Didelot et al., 2007) but also interspecific (Granatstein and Peck, 2017) diversity, as well as the spatial and temporal design of such systems (Lauri et al., 2022). The Food and Agriculture Organization (FAO) promotes agrobiodiversity as a key lever of agroecology to facilitate the transition to sustainable agriculture and food systems (FAO, 2018; Barrios et al., 2020). The agroecology paradigm is considered fruitful for rethinking orchard design to promote not only fruit production but also other services that contribute to sustainability (Demestihis et al., 2018; Kienzle and Kelderer, 2017).

Agroforestry combines trees (including crop-producing trees), shrubs, grasses and possibly animals in the same agricultural space. It

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includes different types of intercropping systems such as 'mixed cropping', 'polyculture', 'multiple cropping' or 'alley cropping' (Gliessman, 1985). It is a relevant framework for implementing agroecological practices as it aims to fulfil different ecosystem functions, not only supporting production, but also reducing nutrient leaching, conserving soils or diversifying production (Wezel et al., 2014). It can also contribute to climate change mitigation, taking into account carbon storage below and above ground, and adaptation to climate change through microclimatic benefits in the multistrata system (Agroforestry Network, 2019).

Agroecology and agroforestry offer complementary views of the agrosystem. Agroecology has acquired a broad meaning in recent decades, referring to either a scientific discipline, an agricultural practice, or a political or social movement (Wezel et al., 2009; Altieri, 2015). However, it is still used in its historical sense, i.e. the integration of ecological concepts in agriculture, thus focusing on the interactions between living organisms, plants and animals, in a system. Agroforestry is more specifically concerned with the spatial and temporal components of the system, i.e. the relative arrangement of plants of different biological types in relation to each other (Lauri et al., 2020).

In the tropics, cocoa and coffee trees are still mostly grown in multistrata agroforestry, that is, under shade conditions, and it is estimated that 31% of cocoa (3.41 million ha) and 40% of coffee (8.08 million ha) are grown in agroforestry systems (Somarriba and López-Sampson, 2018). Cocoa and coffee are well adapted to such systems, being sciaphilous, and much research has been done on the effects of shade on the growth and functioning of these two species in agroforestry contexts (e.g. coffee; Charbonnier et al., 2017). In temperate regions, fruit trees are considered high value trees for agroforestry (den Herder et al., 2017; Wolz et al., 2018). Several studies have been developed on mixed fruit tree-vegetable systems (e.g. Paut et al., 2021), where the fruit tree is in the upper layer. However, there is a lack of knowledge on how the temperate fruit tree would behave when grown in the shade of other trees (called shade trees) in a multistrata agroforestry system, although such knowledge is crucial for the promotion of fruit tree-based agroforestry systems (Lauri, 2021). The effects of shade trees on subcanopy environmental conditions are well documented moderating microclimatic conditions by shading from direct sunlight, reducing vapor pressure deficit (VPD) and thus limiting evapotranspiration, and reducing wind speed (Verheyen et al., 2024). However, the effects on soil moisture are more variable and less well understood (Verheyen et al., 2024). Considering that the temperature under shade trees is reduced during the day and slightly increased at night (Gosme et al., 2016), growing fruit trees in the shade of larger trees could be of interest in Mediterranean climatic regions, where excess radiation, both light and temperature, has detrimental effects on leaf function (Corelli-Grappadelli, 2003) and fruit quality (sunburn damage; Schrader, 2011).

The present study addressed this question using the example of apple (*Malus domestica* Borkh.), a major temperate fruit tree crop that extends to subtropical regions. It follows previous analyses of the establishment of young apple tree architecture (including not only branching characteristics but also organ morphology) under agroforestry conditions with walnut as a shade tree compared to full light conditions (Pitchers et al., 2019, 2020, 2021; Pitchers, 2021). These previous results illustrated some known aspects of the shade-avoidance syndrome (SAS; Ballaré and Pierik, 2017), such as an increase in specific leaf area (SLA; fresh leaf area per unit of dry mass), but also showed that other traits were not affected (e.g. internode length; Pitchers et al., 2021). Overall, these studies showed that the effects of agroforestry can be well interpreted in terms of agroforestry induced light reduction, supporting the idea that light is an important factor in plant-plant interactions (Bennett, 2021). We therefore considered that the shade-induced plasticity, i.e. the ability to develop different architectural and morphological traits depending on the light environment in its spatial (type of organ affected by shade) and temporal (period of shade within the growing season) dimensions, should be better defined for the apple, reflecting an adaptation rather

than an avoidance strategy. We will refer to this plasticity as the shade adaptation syndrome although it cannot be ignored that agroforestry may affect plant development in different ways, involving not only aerial but also below-ground interactions.

Our aim was to gain further insight into the effects of agroforestry conditions on apple tree architecture and reproductive development at different scales of organisation from the whole tree to the annual shoot and the inflorescence (Godin and Caraglio, 1998), using the same trees from three to eight years old. We addressed the following questions: 1) How does the agroforestry context affect the development of the main vegetative and reproductive traits of apple trees in successive years? 2) Do these conditions also affect allometric relationships, i.e. quantitative covariations between vegetative and reproductive traits? Furthermore, with the aim of defining a shade adaptation syndrome, can we identify some critical phases and/or specific vegetative and reproductive traits that would explain how agroforestry affects the vegetative and reproductive behaviour of the shaded apple tree?

2. Material and methods

2.1. Study site, plant material and tree management

The study site was located in the Domaine Départemental de Restinclières, southern France (43°42'12.168 N, 3°51'29.872E; <https://umr-absys.cirad.fr/1-unite/dispositifs-experimentaux>). The soil is a silty clay (25% clay and 60% silt) deep alluvial fluvisol and the average pH is around 8.0 (Querné et al., 2017). The climate is Mediterranean with dry and hot summers (Met Office, 2024). During the experiment (2016–2023), the average monthly air temperature ranged from 6 °C in winter to 25 °C in summer. Over the same period, the average annual rainfall was 680 mm, although there was wide variation between years ranging from 466 mm to 1120 mm, with the lowest in July and August, and the highest in September to November (data collected from a nearby automated Campbell weather station).

The GAFAM (Growing AgroForestry with Apple in the Mediterranean) experiment was carried out in a walnut (*Juglans nigra* × *Juglans regia* NG23, grown for timber) plantation with 4 m between trees within a row or multiples of 4 m because the smallest walnut trees were removed in 2007 to promote the larger ones, and 13 m between rows and a legume (*Medicago sativa* L.) intercrop. The tree rows were orientated east-west. In March 2016, when the walnut trees were 21 years old, 150 apple trees (140 *Malus domestica* Borkh. 'Dalinette'; 10 *Malus domestica* Borkh. 'Story' to allow cross-pollination, both cultivars bench-grafted on Geneva® G202 C.O.V. semi-dwarfing rootstock with a tree vigour slightly higher than M.26 (CTL, 2024)), were planted as intercrops in three groups: 1) agricultural control (apple trees outside the walnut plot with 6.5 m between apple tree rows), 2) inter-row agroforestry (apple trees between two rows of walnut trees, 6.5 m from each row) and 3) agroforestry within the row of walnut trees. In all cases, apple trees were spaced 1.3 m along the row from a neighbouring apple or walnut tree, depending on the group.

Apple trees were managed according to low input organic guidelines. Woodchips were spread on the apple and walnut rows to control weeds. Drip irrigation and organic fertiliser were applied to the apple trees following technical advice from an extension service. Apple trees were trellised on a vertical support system with wires at 0.7 m, 1.4 m, 2.1 m and 2.6 m to maintain the trunk in a vertical position. All branches were left without pruning or artificial bending, except for branches below the lowest wire, which were removed to preserve as much of the natural tree architecture as possible. Apple trees were completely thinned after full flowering in 2017 and after fruit-set in 2018, two and three years after planting, respectively, to favour the establishment of the tree architecture and to avoid inhibition of flowering initiation by the current year's fruit. From 2019, fruit thinning was carried out each year after the end of physiological fruit drop, during the first two weeks of June, to maintain a crop load of 5 fruits per cm² of TCSA maintaining as much as

possible one fruit per inflorescence on all inflorescences that set at least one fruit.

In 2018, 15 three-year-old apple trees were selected in each of the three groups (agricultural control, agroforestry between rows and agroforestry within rows of walnut trees) to maximise the amount of light received (Pitchers et al., 2021). Based on this criterion, trees were generally scattered along rows of apple trees and rows of apple trees and walnut trees. These three groups of apple trees are hereafter referred to as 'full light' (FL) for trees in the agricultural control group, 'moderate light' (ML) for trees between rows of walnut trees and 'low light' (LL) for trees in the row of walnut trees.

2.2. Data collection and analyses

2.2.1. Data collected on light received by individual trees

In 2022, when the walnut trees were at full foliage (end of June), a gap fraction analysis was carried out to assess the differences in light received by each individual apple tree, now seven years old, within each previously defined group. Hemispherical photographs were taken above the apple trees using a camera (Sony NEX7-2381,723 DSLR-Compact-1289) equipped with a fish-eye lens (Lens. Cal Regent DSLR Compact, Regent Instrument Inc., Québec, Canada).

2.2.2. Data collected on vegetative and reproductive traits

Data were collected on the 45 trees, each belonging to its light modality. Measurements were made on various vegetative (trunk, branch and shoot growth) and reproductive (inflorescence characteristics and fruit-set) traits at different scales, the whole tree, the annual shoot growth and the inflorescence, and taking into account changes over the years (3 to 8). Two types of analyses were performed.

Univariate analyses were developed for the main traits characterising whole-tree vegetative growth and reproductive development on three- to eight-year-old trees, over all years or over specific years depending on the trait (Table 1).

Covariations between traits were examined to gain more insight into the effects of light modality on the plasticity of traits relative to each other at the different scales (Table 1).

At the whole tree scale, we examined the relationships between trunk cross-sectional area (measured at 20 cm above the graft junction) and both branch cross-sectional area (measured at 3 cm from branch insertion on the trunk) and number of inflorescences. These analyses were carried out taking into account the mean values of six consecutive years for each tree (three- to eight-year-old trees).

At the shoot scale, we evaluated whether longer shoots could produce inflorescences at a higher or lower frequency compared to shorter shoots under different light regimes. Our study was based on a methodology developed in apple and mango to compare different cultivars (Lauri and Trottier, 2004; Normand et al., 2009). In the spring of each year Y on four- to eight-year-old trees, the bourse-shoots (i.e. the relay axes developed at the axil of one or more foliage leaves of the inflorescence (Fig. 6a); Pratt, 1988) developed in the previous year (Y-1) on the same trees, i.e., three- to seven-year-old trees, were randomly selected at breast height. Two data were collected from each bourse-shoot, (Y-1) shoot length and (Y) bud type, either an inflorescence again or a vegetative bud. (Y-1) shoots were grouped into 3 cm length classes (from 0.5 cm to 50 cm, with only few values above 35 cm) and the frequency of inflorescences in year Y, i.e. [Nb of inflorescences/(Nb of inflorescences + Nb of vegetative shoots)], was calculated within each (Y-1) shoot length class. At least five shoots were measured in all classes. These analyses were carried out taking into account the mean values of three consecutive pairs of years for each tree.

At the inflorescence scale, we investigated the relationship between the number of leaves subtending the inflorescence itself, known as 'foliage leaves' (Pratt, 1988) or 'primary spur leaves' (Corelli Grapadelli et al., 1994), and total leaf area, which is known to influence fruit-set (Lauri et al., 1996; Lauri and Térouanne, 1999). Yield is not presented

Table 1

Apple 'Dalinette' grafted on G202 rootstock - Vegetative and reproductive traits, and covariations between traits, analysed on apple trees belonging to three light modalities, Full Light (FL), Moderate Light (ML) and Low Light (LL), at three scales (whole tree, shoot and inflorescence) and over six to one year depending on the trait. The year of analysis (e.g., '2023') and the corresponding tree age (e.g., '8', eight-year-old tree) are given in brackets. 'Full bloom' was considered when 50% of the inflorescences had all flowers open (stage F2 according to the Fleckinger (1964) chart).

Type of analysis and Scale	Organ type Vegetative, Veg.; Reproductive, Rep.	Trait (year of analysis; tree age) Number, Nb	Period in the year of data collection
Univariate analyses			
Whole-tree	Veg.	*Tree Height (2023; 8) *Trunk Cross Sectional Area (TCSA; 2018 ↔ 2023, 3 ↔ 8)	Early Spring Early Spring
	Veg. & Rep.	*Nb of second-order branches above 0.7 m (2023, 8) *Nb of growing shoots (Veg. and Rep.; 2018 ↔ 2023, 3 ↔ 8) *Nb of inflorescences (Nb Inflor.; 2018 ↔ 2023, 3 ↔ 8)) *Flowering index ([Nb of Inflor./ (Nb of inflor.+Nb of veg. shoots)]; 2018 ↔ 2023; 3 ↔ 8))	Early Spring Full bloom Full bloom
	Rep.	*Nb of potential fruits (2022 ↔ 2023; 7 ↔ 8) *Fruit-set ([Nb of potential fruits/Nb of inflor.]; 2022 ↔ 2023; 7 ↔ 8))	After physiological drop (mid-june)
Covariations between traits			
Whole-tree	Veg.	*Trunk Cross Sectional Area vs. mean Branch Cross Sectional Area (TCSA vs mean BCSA; 2023, 8)	Early Spring
	Veg. vs. Rep.	*Trunk Cross Sectional Area vs. Nb of inflorescences (TCSA vs Nb of inflor.; 2018 ↔ 2023, 3 ↔ 8)	Early Spring & Full bloom
Shoot	Veg. vs. Rep.	*Sequence of functioning: bourse-shoot length in year Y-1 vs frequency of return-bloom in year Y (2019-2020 ↔ 2022-2023; 3-4 ↔ 7-8)	Full bloom
Inflorescence	Rep.	*Nb of leaves vs leaf area (2022; 7)	Full bloom

in this article due to recurrent, albeit uneven, codling moth infestations, which increased fruit drop during the summer and hindered relevant analyses of fruit growth and quality.

2.2.3. Data analyses

Statistical analyses were performed with light treatment (three modalities, FL, ML and LL) as an independent factor, with each individual tree as a replicate. As the assumptions for ANOVA were rarely met, all comparisons between statistical distributions for univariate analyses were made using a non-parametric Kruskal-Wallis test followed by Dunn's test for multiple comparisons.

The effects of light treatment on covariations between traits at different within-tree scales were analysed using the standardised major axis (SMA). This method of bivariate line fitting between variables

maintains, through the linear model, a global view of the general joint evolution of traits without making *a priori* assumptions about the dependence of one trait on another (Warton et al., 2006). The relationships were performed on log-transformed data and were carried out in two successive steps. First, the effect of light treatment was tested on the slope of the relationship with two alternatives, no effect or an effect. In the first case, differences were tested for the Y-intercept and for the shift along the lines with common slope. In the latter case, this indicated that the treatment affected the relationship between the two variables and no further tests were relevant (Warton et al., 2006).

All statistical analyses were carried out using Rstudio (RStudio, 2023.12.1) with R (R Core Team, 2023, 4.3.2). The following packages were used 'agricolae', 'forcats' and 'dplyr' for data exploration and management, 'dunn.test' for non-parametric comparisons between statistical distributions, 'Smatr' for SMA and 'ggplot2' for graphics. The significance threshold was set at $P < 0.01$ with Bonferroni correction where appropriate for all statistical analyses.

3. Results

3.1. Analysis of the light received by individual trees

Significant differences were found between the three groups of apple trees, with a 69% reduction in light received by apple trees in the walnut row and a 42% reduction in light received by apple trees in the walnut inter-row compared to apple trees in the agricultural control group (Fig. 1). These results confirmed the grouping of the three-year-old trees (Pitchers et al., 2021), which allowed us to analyse data on three- to eight-year-old trees.

3.2. Univariate analyses at the whole-tree scale

3.2.1. Tree size and branching

Although all bench-grafted trees were homogeneous in terms of diameter and root development when planted in the experimental plot in March 2016, ML and LL trees generally had lower and less variable TCSA than FL trees, regardless of tree age (Fig. 2a), but reached similar tree heights to FL trees at eight years of age, around 3 m (Fig. 2b). The similar number of second-order branches per tree on eight-year-old trees in the three light modalities (Fig. 2c), combined with the generally lower number of growing shoots, vegetative shoots and inflorescences,

whatever the tree age, on ML and LL trees (Fig. 2d), indicated that shade reduced the number of 3rd and 4th order shoots, i.e. branched on second-order branches, in trees under agroforestry conditions. Overall, these results on adult trees showed a significantly lower number of growing shoots and a thinner trunk in LL and ML apple trees compared to FL apple trees (Fig. 3).

3.2.2. Reproductive behavior

In all years, except for six- and seven-year-old trees, the number of inflorescences was significantly lower in ML and LL trees compared to FL trees, indicating that the shade-induced agroforestry conditions reduced the number of inflorescences per tree (Fig. 4a). On the other hand, the delayed increase in flowering index of ML and LL young trees compared to FL trees was maintained at similar levels in the three modalities for five- to seven-year-old trees, but was followed by a strong decrease in both number of inflorescences and flowering index for eight-year-old ML and LL trees, which was not the case for FL trees (Fig. 4b). As a direct consequence, although there were no significant differences in the number of potential fruits on seven-year-old trees regardless of the light treatment, partly related to the large statistical distributions, the number of potential fruits on eight-year-old trees was significantly lower on ML and LL trees compared to FL trees (−40% and −49% for ML and LL trees compared to FL trees, respectively) (Fig. 4c-d). The significant decrease in the number of inflorescences (Fig. 4a), flowering index (Fig. 4b) and number of potential fruits in eight-year-old ML and LL trees following a high flowering index in seven-year-old trees (Fig. 4d) was not observed in FL trees. This suggested that light reduction limited the potential of the apple to maintain regular flowering and fruiting compared to FL trees. However, regardless of the number of inflorescences and flowering index, fruit-set was similar between light modalities within each year and was higher on eight-year-old trees than on seven-year-old trees, suggesting that trees were able to dynamically adjust their fruiting potential to light conditions (Fig. 4e-f). These results would then show that FL trees were able to maintain high flowering and fruiting for consecutive years, whereas ML and LL trees would be more susceptible to irregular bearing, reducing the number of inflorescences after a high flowering year, even if each individual inflorescence maintained fruit-set similar to that of FL trees. Overall, therefore, our study showed that the number of potential fruits was more related to the balance between vegetative shoots and inflorescences, with a lower ability to initiate flowering after a high flowering index year in the shade, than to physiological fruit drop.

3.3. Covariations among traits

3.3.1. At the whole-tree scale, the relationship between TCSA and both BC SA and number of inflorescences

Considering the mean values over the six years of the study, there was a positive relationship between TCSA and both mean BC SA and number of inflorescences per tree with a common slope and the same intercept between the three light modalities (Fig. 5a-b). As expected from the univariate analyses, there were significant differences in the shift along the common slope, with ML and LL trees having lower values of TCSA, mean BC SA and number of inflorescences per tree compared to FL trees.

3.3.2. At the shoot scale, the relationship between the length of a shoot in year Y-1 and the frequency of return-bloom on this shoot in year Y

The relationship between the length of a bourse-shoot in year (Y-1) and the frequency of flowering in year Y (Fig. 6a) was significant and positive only for FL trees, suggesting that an increase in the length of the bourse-shoot on these trees increased return-bloom, at least slightly and up to the values obtained in our study for the longer bourse-shoots (see Materials and Methods, section 2.2.2.; Fig. 6b). However, there were no significant relationships between return-bloom and bourse-shoot length in ML and LL trees. These results suggest that if the local vegetative

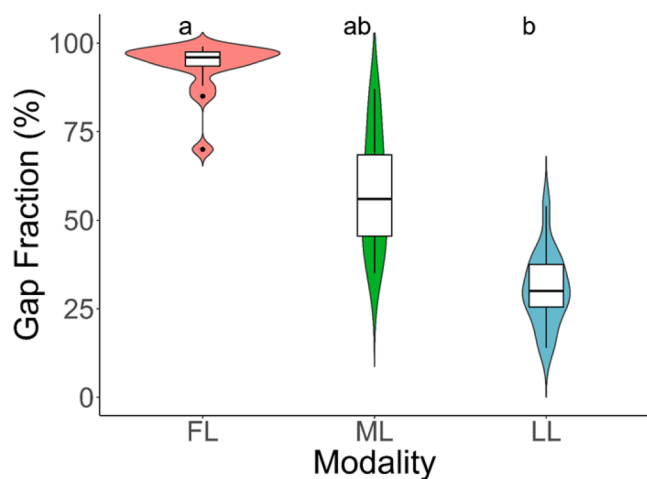


Fig. 1. Apple 'Dalinette' grafted on G202 rootstock, seven-year-old trees – Gap fraction (%; fraction of visible sky; median and interquartile interval; $n = 15$) over apple trees according to light modality. FL (Full Light), ML (Moderate Light) and LL (Low Light). The width of the violin graph is proportional to the number of values. Different lowercase letters above the violin graphs indicate statistically significant differences between the light modalities at $P < 0.01$.

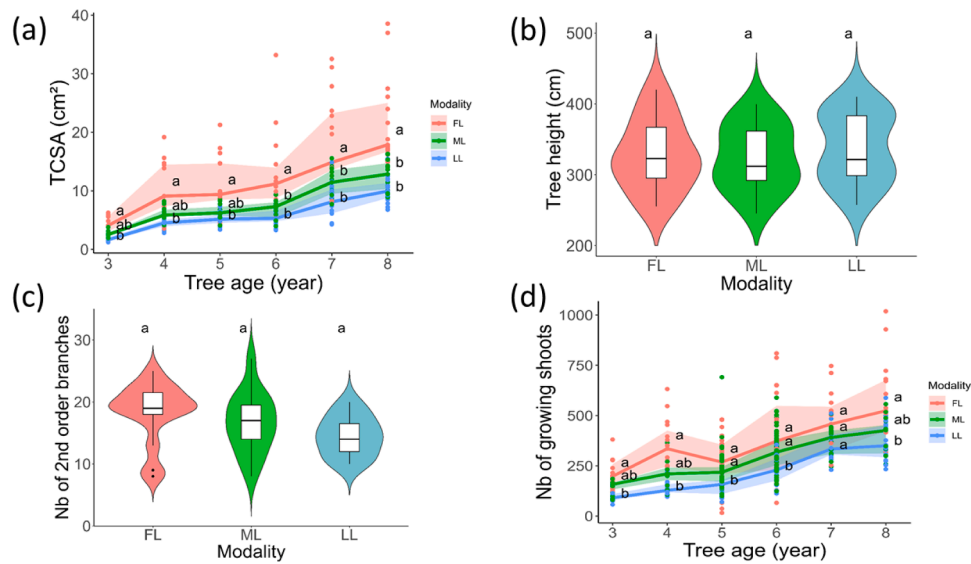


Fig. 2. Apple ‘Dalinette’ grafted on G202 rootstock - Effects of the light treatment (FL, Full Light; ML, Moderate Light; LL, Low Light) on tree size and growth (medians with interquartile intervals). (a) changes in TCSA of three- to eight-year-old trees, (b) height and (c) number of second-order branches per tree of eight-year-old trees, and (d) number of growing shoots either vegetative shoots or inflorescences and associated bourse-shoots on three- to eight-year-old trees. Medians with the same lower case letters are not significantly different at $P < 0.01$ ($n = 15$). (a)(d) comparison is made for each year. (b)(c) width of the violin is proportional to the number of values.

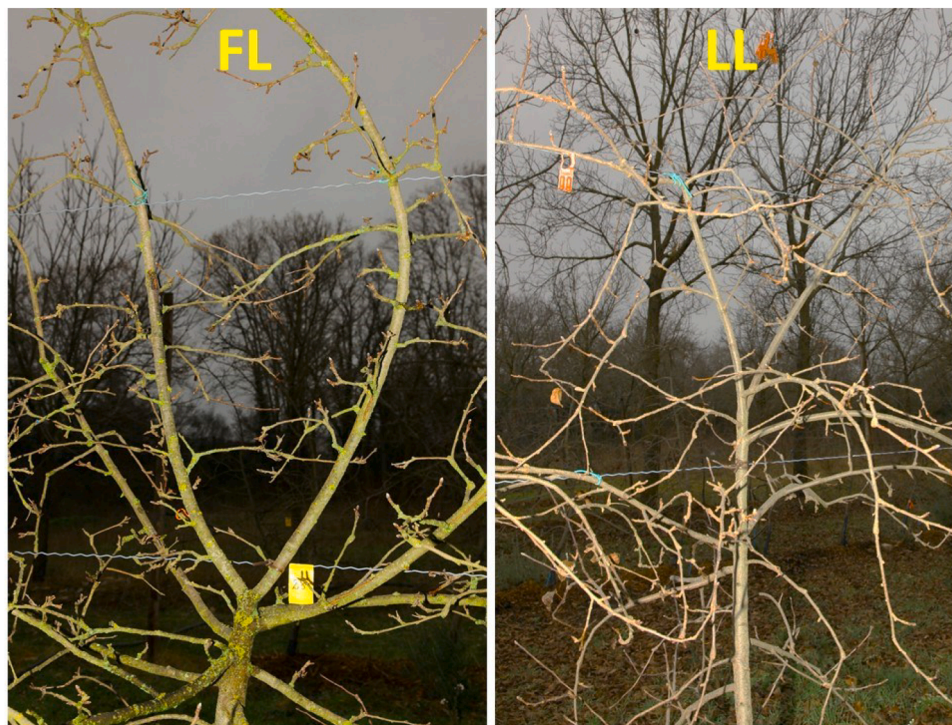


Fig. 3. Apple ‘Dalinette’ grafted on G202 rootstock, eight-year-old trees - Effects of the light treatment on branching density and shoot morphology of apple trees in full light (FL) and low light (LL) modalities.

context was well related to flowering initiation, i.e. the close relationship between the length of a bourse-shoot and the behaviour of its apical bud, under full light conditions, this was not the case under lower light conditions.

3.3.3. At the inflorescence scale, the relationships between the number of leaves and leaf area

At the scale of individual inflorescences, light treatment did not affect the relationships between number of leaves and total leaf area

(same slope and intercept) (Fig. 7). Furthermore, there was no significant shift along the common slope, indicating that inflorescence size did not vary between light modalities.

4. Discussion

Our results on the growth and flowering of apple trees in agroforestry with walnut trees as overhanging trees were interpreted in terms of the light gradient received by the apple trees. In the specific case of our

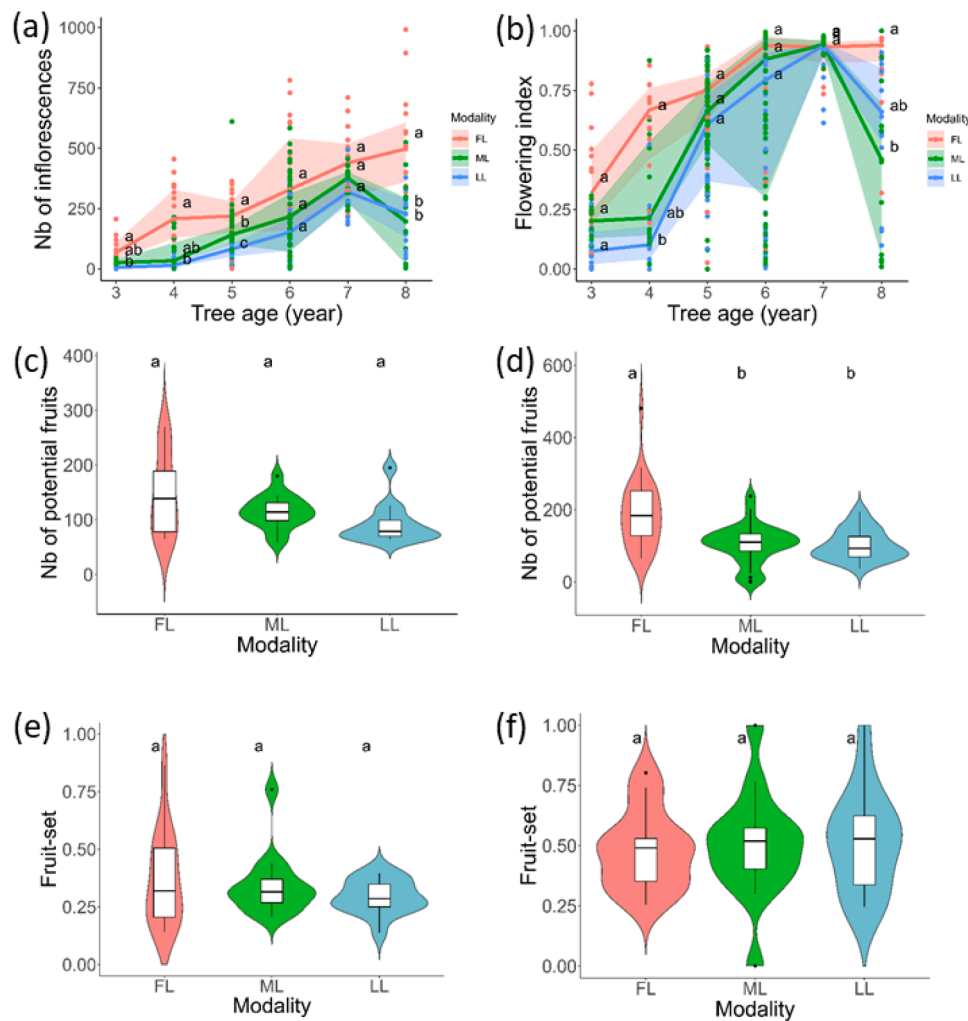


Fig. 4. Apple ‘Dalinette’ grafted on G202 rootstock, seven-year-old trees - Effects of the light treatment (FL, Full Light; ML, Moderate Light; LL, Low Light) on reproductive traits at the whole-tree scale (medians with interquartile intervals). Changes in (a) number of inflorescences and (b) flowering index on three- to eight-year-old trees; number of potential fruits (retained after physiological fruit drop) on (c) seven-year-old trees and (d) eight-year-old trees; fruit-set (Nb of potential fruits/Nb of inflorescences) on (e) seven-year-old trees and (f) eight-year-old trees. (c)(d)(e)(f) the width of the violin graph is proportional to the number of values. Medians with the same lowercase letters are not significantly different at $P < 0.01$ ($n = 15$). (a)(b) comparison is made for each year. (c)(d)(e)(f) width of the violin is proportional to the number of values.

study, possible allelopathic effects of juglone produced by walnut could also be involved, for example related to the reduction of N mineralisation, as suggested in a previous study carried out on the same plot four years before our experimental design (Querné et al., 2017). However, as shown in the literature, these effects are far from being well established (Zubay et al., 2021). Therefore, we maintained the hypothesis that light remained a major factor explaining our results for FL but also for ML trees, in the latter case grown quite far from the walnut trees, with allelopathy possibly being a confounding factor for LL trees planted in the same rows as walnut trees.

Several studies have been conducted on the effect of shade on the vegetative and reproductive growth of apple trees, as well as on tree physiology. In addition to their higher specific leaf area (Pitchers et al., 2021), shade leaves have been shown to be more efficient than sun leaves at using low photosynthetic photon fluxes or sunspots (Corelli-Grappadelli, 2003). However, at the whole-canopy scale, carbon assimilation is quantitatively lower in shade-grown trees compared to sun-exposed trees, resulting in lower secondary growth of axes with a cumulative effect over successive years (Jackson and Palmer, 1977a; Pitchers et al., 2021). Shade also reduces fruit retention in both the year of shade and the following year (Jackson and Palmer, 1977b) and individual fruit weight (Dennis, 2003). Jackson and Palmer (1977b)

concluded that a shade intensity of 37% of full sun, corresponding to the moderate light modality studied here, would result in low total yield combined with biennial cropping. Our results generally confirmed these earlier statements and also indicated that tree management should be adapted to the shade context. For example, we can consider that the strong decrease in flowering in year 8 in ML and LL trees could have been reduced by a lower inflorescence load in year 7 on these trees (Fig. 4b). From a practical point of view, we could recommend a fruit load of 4 or even 3 fruits per cm^2 of TCSA on ML and LL trees instead of 5 as a rule of thumb used in our study in the three modalities.

4.1. The effects of light reduction on tree architecture and flowering at various scales

Trunk cross-sectional area (TCSA) is considered a relevant integrative trait to quantify vegetative growth of the whole tree. It is commonly used in studies of rootstocks effects on tree growth, provided the tree is maintained without excessive pruning (Fallahi et al., 2002). Both TCSA and, at a finer scale, branch cross-sectional area (BCSA) are considered good proxies for balancing fruit production with respect to vegetative growth, considering either inflorescences, as is usually done in fruit thinning (Lordan et al., 2019), or whole fruiting spurs, as is done in

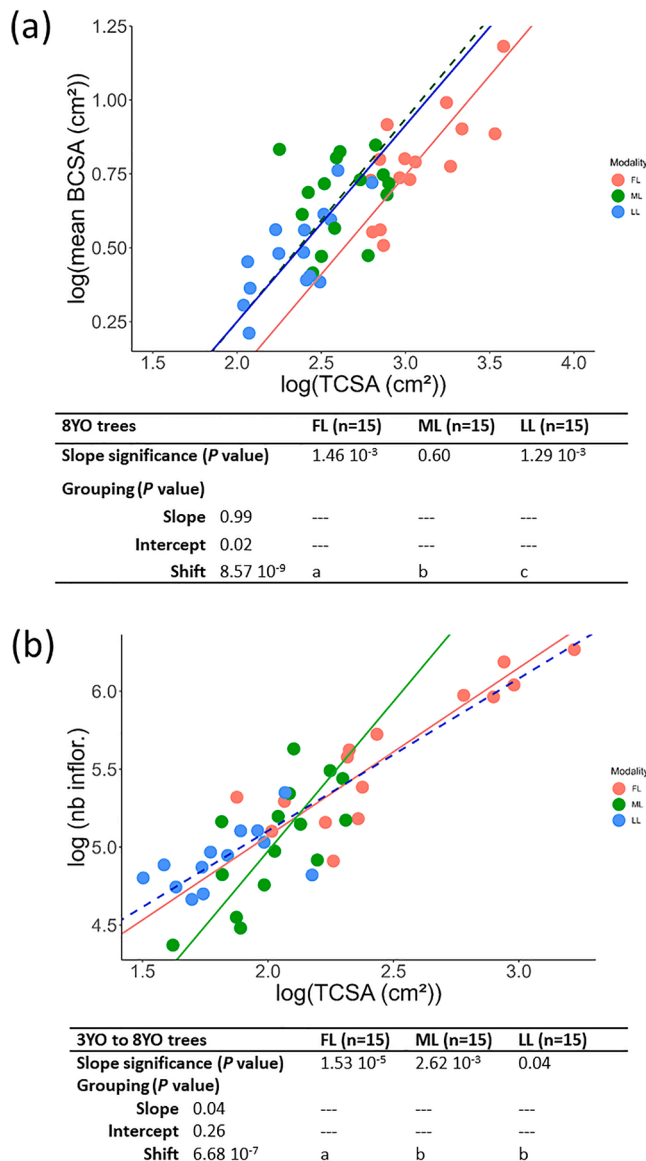


Fig. 5. Apple ‘Dalinette’ grafted on G202 rootstock - Effects of light treatment (FL, Full Light; ML, Moderate Light; LL, Low Light) on the covariation of trunk cross-sectional area (TCSA) and (a) mean branch cross-sectional area (BCSA) per tree on eight-year-old trees, and (b) number of inflorescences (Nb Inflor.) on a whole-tree scale. In (b) the data are averaged over six consecutive years, on three- to eight-year-old trees. All data have been log-transformed to meet the assumption of normal distribution. For each plot, the adjacent table shows the significance of the slopes (a non-significant slope is indicated by a dashed line on the plot) and the statistics for grouping the slopes, and where slopes were not significantly different at $P < 0.01$, differences were tested for intercepts and shifts along the common slope ($n = 15$).

artificial extinction procedures (Lauri et al., 2004; Tustin et al., 2011; Bound, 2019). Here it was shown that, despite similar tree height, apple trees in low and moderate light had thinner trunks and branches, confirming that the increased slenderness of one-year-old shoots (Pitchers et al., 2021) is also true at the tree scale. Furthermore, the relationship between TCSA and mean BCSA was well conserved across light modalities (no difference in slope and intercept; Fig. 5a), suggesting that this relationship is an invariant of tree architecture related to optimised biomechanical and hydraulic adaptations across years to cope with the amount of light received (Niklas et al., 2006; Jelonek et al., 2019).

The increase in the number of potential fruits (from about 140 to about 190) on FL trees between year 7 and year 8 was positively related

to the increase in the number of inflorescences. At the same time, the number of potential fruits on ML and LL trees varied little (about 100 on the two modalities in the two years). Interestingly, although fruit-set did not vary between light conditions within each year, despite high variability especially in year 8, it increased by about 20% between year 7 and year 8 regardless of the light modality. There was no obvious effect of the climatic context that would have affected the growth and development of the apple trees similarly regardless of the light conditions. Our hypothesis was that the balance between vegetative and reproductive growth at both the shoot and inflorescence scales was differentially affected by light conditions, involving not only shade intensity but also shade dynamics over the growing season in ML and LL trees.

Previous studies on different species have shown that there are parabolic relationships between shoot size, quantified as length, number of leaves or diameter, and flowering in apical position (Normand et al., 2009 and cited references). In apple, it has been shown that although parabolic relationships would well illustrate the behaviour of an irregular bearing cultivar, there was a linear and positive relationship for a regular bearing cultivar, i.e. one on which all shoot types are able to flower in apical position (Lauri and Trottier, 2004). Despite this cultivar specific determinism, we have shown here that light conditions can also modify these relationships between vegetative growth and apical flowering. Following the idea of a shoot-scale resource integration scheme proposed by Kawamura and Takeda (2006) on *Vaccinium hirtum* and the established positive relationship between shoot leaf area and shoot cross-sectional area (Brouat et al., 1998; Lauri, 2019; Fajardo et al., 2020), we could assume that shoots with larger girth in FL trees would be able to support the formation of an apical inflorescence, whereas this might not be true for the thinner shoots in agroforestry induced shade. Our results therefore confirmed that if the concept of topological distance is relevant to model activating and inhibiting factors for flower induction (Bellhassine et al., 2020) or fruit-set (Lauri and Térouanne, 1999), the light environment may play an important role in disrupting these relationships. Considering plants as ‘assemblages of semi-autonomous integrated physiological units’ (Watson, 1986), we hypothesised here that this concept was well defined at the shoot scale under full light conditions, whereas there was a shift to a larger scale of carbon allocation (including other shoots more or less close to the shoot under study) or more generally of activating and inhibiting signals under shade-induced agroforestry conditions.

The concept of flower and inflorescence quality usually refers to the ability to set fruit (May 1970; Abbott, 1977) and can be quantified by considering the number and size of spur leaves (Lauri et al., 1996), which play a crucial role in fruit-set and the onset of fruit growth (Lakso, 1980; Corelli-Grappadelli et al., 1994; Lauri et al., 1996). Our study showed that inflorescences had the same relationships between number of leaves and leaf area regardless of light modality, suggesting the same endogenous ability to set fruit, which was well confirmed at the tree level by similar fruit-set among the three light modalities (Fig. 4e-f).

Overall, it is likely that our results on the lower fruiting potential of apple trees grown in shade compared to apple trees grown in full light gave minimal production values considering that, in our experiment, ML and LL apple trees were planted under already well-developed walnut trees, which strongly influenced the establishment of the young apple tree architecture. We suggest that further studies could be developed considering other temporal and spatial plantation designs. At the temporal level, the concept of ‘dynamic agroforestry’ (Andres et al., 2016) could be of interest, for example including a co-planting or a slightly delayed planting of shade trees and apple trees, with the removal of the apple trees after 15–20 years, allowing the full development of the apple tree during the first years of tree growth, which, as shown here, strongly determines the fruiting potential of the mature apple tree. At the spatial level, the present study with an east-west row orientation suggests that a minimum distance of 6-7 m between the rows of shade trees and the rows of apple trees could be of interest. This allowed for moderate light conditions, i.e. with about 42% light reduction, reducing sunburn in

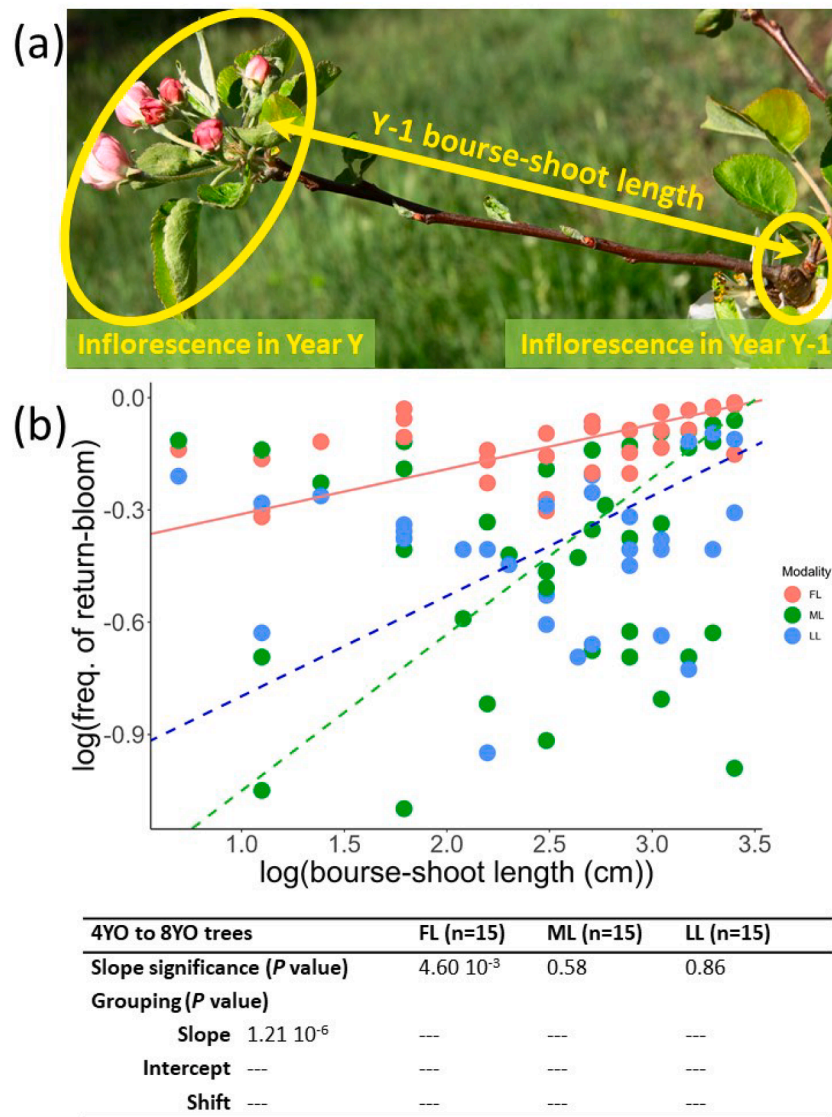


Fig. 6. Apple ‘Dalinette’ grafted on G202 rootstock - Effects of the light treatment (FL, Full Light; ML, Moderate Light; LL, Low Light) on return-bloom. (a) succession of an inflorescence in year Y-1 with its bourse-shoot of a given length and an inflorescence in year Y. (b) covariation between length of bourse-shoot in year (Y-1) and frequency of return-bloom in year Y. Data are mean values over four consecutive pairs of years, four- to five-year-old trees to seven- to eight-year-old trees and have been log-transformed to satisfy the assumption of normal distribution. Each symbol represents the relative frequency of at least five shoots. The adjacent table shows the significance of the slopes (a non-significant slope is indicated by a dashed line on the graph) and the statistics for grouping the slopes. As the slopes were significantly different between the three light modalities, no further analyses were performed.

case of excessive radiation (as shown in data collected in the same experimental plot after an extremely hot day with up to 44.3 °C on 28 June 2019; Lauri et al., 2022), while maintaining a satisfactory apple crop.

4.2. A dynamic architectural and functional interpretation of apple tree adaptation to agroforestry – elements for defining the shade adaptation syndrome

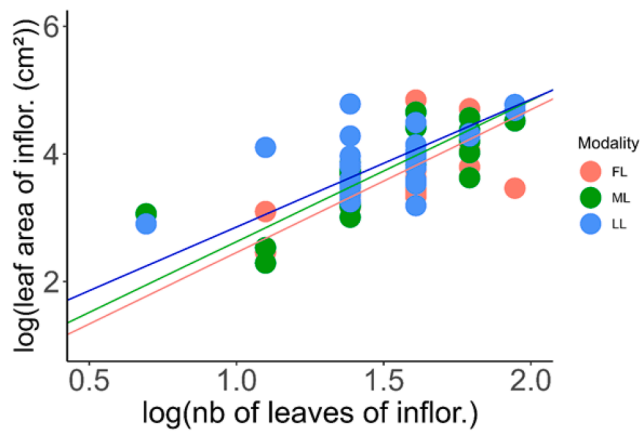
Our study of apple in agroforestry paves the way for conceptualising some key aspects of apple tree adaptation to shade-induced agroforestry conditions (Fig. 8).

To better define a shade adaptation syndrome, this static scheme needs to include both spatial and temporal levels.

At the spatial level, the lower number of inflorescences and flowering rate in shade could be well explained by two factors, 1) the lower number of shoots, which consequently reduced the number of potential

sites for vegetative growth and flowering, and 2) the overall lower and more irregular flowering in the apical position on shoots, regardless of their length. These two factors at two different scales were related to tree architecture and shoot geometry respectively.

At the temporal level, our study showed that not only the intensity of shade, i.e. the three light conditions studied here, but also the duration of the shade and the position of the shade during the annual growing cycle of the apple tree need to be considered. In fact, the phenological delay between the apple tree and the overhanging walnut tree played an important role in the first stages of the apple tree’s annual growth, from bud burst onwards. Indeed, there was a delay of three to four weeks between apple bud burst at the beginning of April and walnut bud burst at the beginning of May. As a result, flowering and onset of fruit-set, which are key stages in apple reproductive development, were little affected by walnut trees. From a physiological point of view, this suggested that there were no significant changes in bud burst and inflorescence phenology, suggesting the same chilling accumulation



7YO trees	FL (n=30)	ML (n=30)	LL (n=30)
Slope significance (P value)	8.24 10 ⁻⁴	4.98 10 ⁻⁷	8.63 10 ⁻⁴
Grouping (P value)			
Slope 0.84	---	---	---
Intercept 0.05	---	---	---
Shift 0.64	---	---	---

Fig. 7. Apple ‘Dalinette’ grafted on G202 rootstock, seven-year-old trees - Effects of the light treatment (FL, Full Light; ML, Moderate Light; LL, Low Light) on the covariation of number of leaves and total leaf area of the inflorescence. The data were log-transformed to meet the assumption of normal distribution. The adjacent table shows that all slopes were significant and gives the statistics for grouping of slopes, intercepts and shifts along the common slope.

(Pitchers et al., 2021) and, as shown here, inflorescence growth (namely, number of leaves and leaf area) and fruit-set in the three light conditions. However, after this period of apple development when there was almost no shade on the apple trees, walnut growth had an increased effect on apple, particularly in reducing carbon acquisition and allocation to secondary shoot growth and axillary bud development (Pitchers et al., 2021). We therefore hypothesised that an earlier phenology of the overhanging tree relative to the apple could negatively affect

inflorescence development and fruit-set in the apple, as shown by artificial net shading before and during fruit set, which can greatly increase fruit drop by reducing carbohydrate assimilation (Morandi et al., 2011).

4.3. Further research

The present study was included in the general framework of agroforestry, which aims to optimise different productions on the same plot (here timber trees over several decades and fruit each year) and potentially provide other ecosystem functions and services, such as erosion reduction and pest and disease control (Lovell et al., 2018). However, knowledge of the effects of shade on apple yield components is part of other lines of research, such as those developed on apple crop productivity in agrivoltaic systems, which, in addition to producing electricity, may also protect orchard trees from extreme weather conditions, particularly excessive radiation (Juillion et al., 2022, 2023; Lopez et al., 2023). Such studies may pave the way for a better exploration of genetic diversity. Our analysis was limited to one cultivar grafted on one rootstock. In this case, the control trees had a rather regular fruiting pattern, as documented for this cultivar (Dalival, 2024). We encourage future research on different rootstock/cultivar combinations, including different flowering patterns (regular vs. alternate bearing) and fruit characteristics (e.g., skin colour), to develop a more generic set of traits that characterise the shade adaptation syndrome. This could help in the design of apple-based agroforestry systems that not only meet satisfactory yield targets, but also provide other ecosystem services (Lauri and Simon, 2019).

5. Conclusions

Our study demonstrated the interest of the multiscale (tree, shoot, inflorescence) approach to analyse how the architecture of young and fruiting apple trees adapts to shade. We showed here that growing apple trees in the shade of overhanging walnut trees reduced branch and trunk diameter and the number of growing shoots, both vegetative and flowering. We also showed that at the shoot scale, the frequency of return-bloom was globally lower and less predictable in shade than in full light. However, at the inflorescence scale, there was no difference in leaf number and total leaf area with similar fruit-set regardless of light

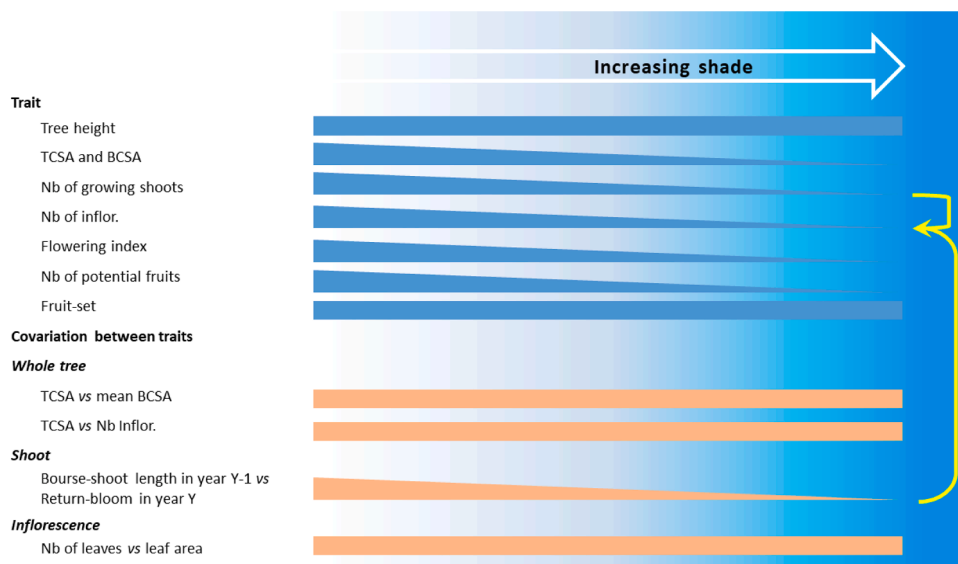


Fig. 8. Adaptation of apple trees to shade-induced agroforestry conditions - Conceptual scheme of the effect of increasing shade on main vegetative and reproductive traits and on the covariation between traits. A rectangular shape indicates similar values or allometric laws (same slope), whereas a slanted shape indicates changes in values or allometric laws (different slopes), for trait analysis or covariation between traits, respectively. The reduced number of inflorescences in the shade results from both a reduced number of shoots (‘Nb of growing shoots’) and a reduced capacity of individual shoots to initiate flowering (‘flowering index’) in the terminal position (vertical yellow arrows on the right).

condition. We hypothesised that these latter results were due to delayed leafing of the overhanging walnut trees. Our study also showed that the vegetative and reproductive behaviour of apple is dependant on different time scales, involving the architectural development of the tree over consecutive years (branching density, TCSA, BCSA), and the growth of the shoot and inflorescence over two consecutive years (flowering initiation in one year and inflorescence growth and possibly fruit-set in the following year). Our study therefore provides further support for the importance of considering the temporal scale when seeking a comprehensive view of how plants adapt to the environment (Cui, 2024). It opens up practical considerations for the implementation of apple-based agroforestry systems, both in terms of the timing of plantation of overhanging shade trees and apple trees and the distances between them, and in terms of crop load management of apple to optimise regular flowering in the shade.

CRedit authorship contribution statement

Pierre-Éric Lauri: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Anna Gautier:** Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Lauri reports financial support was provided by DEPHY EXPE, Research Program ALTO, France. Lauri reports financial support was provided by Département de l'Hérault, Research program PIRAT, France. Gautier reports financial support was provided by Groupement d'intérêt scientifique (GIS) fruits, France. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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