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Canopy shading modulates seed yield, stem strength and soil quality of Paeonia ostii in a Ginkgo biloba agroforestry system, Jiangsu, eastern China

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Canopy shading modulates seed yield, stem strength and soil quality of *Paeonia ostii* in a *Ginkgo biloba* agroforestry system, Jiangsu, eastern China

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Abstract

Farmers on the Jianghuai Plain of eastern Jiangsu increasingly grow cash crops beneath ginkgo (*Ginkgo biloba* L.) canopies, yet field-scale evidence linking summer canopy density to the productivity, lodging resistance and topsoil status of the intercropped oil peony (*Paeonia ostii* 'Feng Dan') is scarce. We established five canopy-density treatments (0.0, 0.4, 0.6, 0.75 and 0.9) with three replicates inside an existing 12-year-old ginkgo stand near Taizhou and measured microclimate, leaf gas exchange, growth, seed yield, stem biomechanics and cell-wall chemistry; the experiment was established in 2022, and seed yield together with the mechanistic measurements (microclimate, gas exchange, stem traits) was recorded during the 2023 growing season, whereas topsoil properties were sampled after harvest in both years and are reported here as two-year means. Moderate shade (canopy density ≈ 0.6) relieved mid-summer heat stress: daily maximum air temperature fell by 4.2 °C and relative humidity rose by 11.8 percentage points relative to the open control, while photosynthesis and seed yield tended to peak. Seed yield at 0.6 was 27.5% higher than in the open field and 82.1% higher than under the heaviest shade (0.9); breaking force at 0.6 was 12.3% above the control (whole-plant breaking force; material strength per unit cross-section did not differ—the advantage is geometric). Under the heaviest shade, PAR fell to 21.3% of the open value, carbon assimilation and seed formation dropped, stems weakened, whereas soil organic carbon and available nutrients accumulated. Redundancy analysis suggested (exploratory RDA on treatment means, n = 5) that PAR, 10-cm soil temperature and alkali-hydrolyzable nitrogen were most closely associated with peony performance. We conclude that a summer canopy density near 0.6 best balances seed yield, stem strength and soil nutrient gains for ginkgo–peony agroforestry in this region, and we provide a quantitative pruning target that growers can use during the July–August period.

Keywords: *Paeonia ostii*; *Ginkgo biloba*; canopy density; stem mechanical strength; seed yield; soil quality

1. Introduction

Agroforestry integrates trees with understory crops and can raise both ecosystem services and farm income (Rao et al. 1997; Sun et al. 2017). Ginkgo biloba is planted widely around Taizhou, where it is valued for ecological, cultural and medicinal purposes. Most pure ginkgo stands leave the

understory idle, and the gap between that unused space and the economic potential of a managed understory is the rationale for intercropping cash crops under ginkgo crowns, an option increasingly practised in Jiangsu (e.g., ginkgo–tea systems; Tian et al. 2013). Oil peony (Paeonia ostii 'Feng Dan') is grown chiefly for seeds rich in unsaturated fatty acids. On open fields of the Jianghuai Plain, summer heat and intense sunlight can depress photosynthesis and final seed harvests, whereas moderate shading alleviates this (Shan et al. 2019; Han et al. 2019). Tree canopies modify the understory by intercepting light (Shafiq et al. 2021) and damping extreme temperature swings (Rao et al. 1997); a limited amount of shade can protect understory crops from heat damage, whereas excessive closure limits light capture and photosynthetic carbon gain.

It is important to distinguish the light regime imposed by a living tree canopy from that imposed by artificial shade cloth. Shade-cloth experiments control only irradiance, under a single even attenuation, and cannot reproduce the spatial heterogeneity, spectral filtering, root competition or litter input that accompany a real canopy. Yet much of what we know about shade effects on peony comes from cloth-based trials (Shan et al. 2019; Han et al. 2019, 2020), and the few agroforestry studies have relied on tree intercropping without an explicit, quantitative canopy target (Tang et al. 2022, with Carya), or across naturally occurring understory light positions without imposed canopy management (Zhang et al. 2026). Unlike these observational or intercropping-only studies, we imposed a replicated, quantitative canopy-density gradient and derived a management target. What is missing is tree-based, field-scale evidence that links a measurable canopy-density gradient to the seed yield, stem mechanical behaviour and soil status of the intercropped species and that ends in a management target growers can apply. The present study was designed to fill precisely that gap.

Most studies of P. ostii have addressed open-field cultivation, fertilizer management or dormancy control (Shan et al. 2019; Han et al. 2019), and the shading work on this species has likewise used shade cloth or controlled conditions rather than a real canopy gradient. Intercropping trials indicate that partial shade can reduce heat injury and improve photosynthesis in oil peony (Tang et al. 2022). Ginkgo agroforestry research has concentrated on ginkgo leaf and nut yield together with soil fertility (Tian et al. 2013; Wang et al. 2015). Quantitative field data for ginkgo–oil peony intercropping on the Jianghuai Plain, linking summer canopy density to microclimate, seed yield, stem mechanics and soil quality, remain scarce. We also lack a tested canopy target that protects yield, limits lodging and maintains soil health simultaneously.

Beyond light, a real ginkgo canopy may influence the understory through root exudates and litter. G. biloba produces bioactive compounds with allelopathic potential (Kato-Noguchi et al. 2013; Kato-Noguchi and Takeshita 2013), and its root exudates contain flavonoids and terpenoid lactones that can inhibit soil-borne fungi (Wang et al. 2024). We therefore treat ginkgo allelopathy as a potential confounder alongside root competition and discuss its possible contribution to our results.

We formulated three testable hypotheses: (H1) intermediate canopy density maximises seed yield by relieving mid-summer heat stress; (H2) heavy shade weakens stems by suppressing lignin and protopectin accumulation; and (H3) topsoil nutrient concentrations increase monotonically with canopy density, creating a trade-off between soil improvement and crop production. We tested these hypotheses across a summer canopy-density gradient in a ginkgo stand at Taizhou, Jiangsu, by measuring understory microclimate, leaf gas exchange, growth, seed yield, stem biomechanics, cell-wall chemistry and soil properties, and by using redundancy analysis to identify the environmental variables most closely associated with peony performance.

2. Materials and Methods

2.1 Study site and experimental design

The field trial was conducted near Taizhou, eastern Jiangsu, China, in a subtropical monsoon zone with a long-term mean annual temperature of 15.2 °C and mean annual precipitation of 1037 mm. The soil is loamy fluvo-aquic soil typical of the Jianghuai Plain. Plots were located within a 12-year-old Ginkgo biloba stand with a tree density of about 8 trees per 100 m², a mean diameter at breast height (DBH) of 14.6 ± 1.3 cm and a row spacing of 3.0 m × 4.0 m. The terrain was flat and baseline soil fertility was similar across plots.

Five canopy-density treatments were established during the summer full-leaf period (July–August): CK (0.0, open-field control), T1 (0.4, light shade), T2 (0.6, moderate shade), T3 (0.75, relatively heavy shade) and T4 (0.9, heavy shade). We first selected ginkgo plots whose natural crown closure spanned this range; where the natural canopy did not reach the target value, we pruned selected branches to adjust crown architecture. Pruning was performed in late winter, before peony budbreak and before any growth measurements in the same year, and affected 12 of the 15 plots; it removed on average 18% of the live crown volume, and the resulting gaps were concentrated in the upper crown so as not to shade the peony layer directly. We re-measured canopy density repeatedly through each summer and report the achieved values in Table S1; temporal variation within a treatment was small (coefficient of variation < 8%). Each treatment contained three independent 5 m × 5 m replicate plots. Uniform 3-year-old P. ostii 'Feng Dan' seedlings were planted at 0.8 m × 0.8 m spacing. Weeding and pest control followed the same schedule on every plot. Canopy density was measured with an LAI-2200C canopy analyser (Li-Cor, Lincoln, NE, USA) on sunny mornings between 09:00 and 11:00, and these readings confirmed the treatment levels. Because treatments were located within a single naturally varying stand, canopy density is confounded with any pre-existing spatial differences in tree age, root distribution or soil; we return to this limitation in Section 4.5 and stress that the present design does not separate above-ground shade from below-ground competition.

2.2 Microclimate monitoring

Photosynthetically active radiation (PAR) was recorded 1.5 m above the ground with an LI-190R quantum sensor (Li-Cor, Lincoln, NE, USA). Air temperature and relative humidity at peony canopy height were logged with an HOBO U23 Pro v2 logger (Onset, Bourne, MA, USA), and soil temperature at 10 cm depth with an ST-05 sensor (Beijing, China) connected to the same logger. All sensors were logged at 10-min intervals for three clear-sky days in mid-July of the second growing season, the hottest window of the summer; daily mean, daily maximum and minimum values were computed for statistical analysis. We acknowledge that three sunny days in mid-July may not capture the full seasonal course, and we discuss this in Section 4.5.

2.3 Plant growth, photosynthesis and seed yield

At full bloom, ten plants per plot were selected at random and tagged; the same plants were used throughout for growth, gas-exchange and yield measurements. Plant height, basal stem diameter and crown width were recorded at full bloom. Net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr) and intercellular CO_2 concentration (Ci) were measured on clear mornings (09:00–11:30, saturating PAR > 1200 μmol m^{-2} s^{-1}) with an LI-6800 portable photosynthesis system (Li-Cor, Lincoln, NE, USA) at a chamber CO_2 concentration of 400 μmol mol^{-1}, block temperature of 30 °C and flow rate of 500 μmol s^{-1}. SPAD readings were taken with an SPAD-502 Plus chlorophyll meter (Konica Minolta, Tokyo, Japan) on the same leaves. At seed maturity, pods on each tagged plant were counted, 1000-seed samples weighed, and per-plant seed yield calculated. Aboveground and belowground biomass were harvested, oven-dried at 80 °C to constant mass and weighed.

2.4 Stem mechanical performance and cell-wall components

Stem diameter was measured 5 cm below the flower bud with a Vernier caliper and fresh stem tissue weighed on an electronic balance. Breaking force, our index of stem mechanical strength, was measured with an NK-2 strength tester (Hangzhou, Zhejiang, China) in a three-point bending configuration, with the two lower supports 40 mm apart and the load applied at a constant speed of 10 mm min^{-1}, following the protocol used in rice stem strength tests (Wu et al. 2017). We tested three plants per replicate plot (nine per treatment). We chose this sample size because breaking force varies little within a uniform plot and because destructive sampling had to be balanced against the need to keep enough plants for yield assessment; the within-plot coefficient of variation was < 6%. To separate size from material effects, we additionally computed a normalised index, breaking stress, as the ratio of breaking force to the cross-sectional area of the stem at the measured diameter.

For cell-wall analysis, basal internodes just below the flower buds were frozen in liquid nitrogen and stored at −80 °C until extraction. Cell-wall residues were prepared following Rose et al. (1998): stem material was ground to a fine powder under liquid nitrogen, extracted sequentially with 80% ethanol and chloroform/methanol (1:1, v/v), and the remaining pellet freeze-dried. To prevent starch interference with the cellulose assay, the pellet was treated with α-amylase (Sigma-Aldrich) at 37 °C

for 30 min before analysis. Soluble pectin and protopectin were quantified with the m-hydroxydiphenyl colorimetric method (Blumenkrantz and Asboe-Hansen 1973), cellulose with the anthrone–sulfuric acid method (Updegraff 1969), and lignin by the acetyl bromide spectrophotometric method, read at 280 nm. All biochemical assays were run in triplicate per sample.

2.5 Soil physicochemical analysis

After seed harvest in both 2022 and 2023, soil samples were collected from the 0–20 cm layer in each plot; the values reported here are plot-level means of the two sampling years. Three cores were taken per plot in each year, pooled and mixed to form a single composite sample per plot and year. Soil pH was measured by potentiometry (water:soil = 2.5:1). Soil organic carbon (SOC) was determined by potassium dichromate oxidation, total nitrogen (TN) by Kjeldahl digestion, total phosphorus (TP) by molybdenum–antimony colorimetry, alkali-hydrolyzable nitrogen (AN) by the alkali diffusion method, and available phosphorus (AP) by the Olsen method (Bray). Bulk density was measured with the core-cutter method.

2.6 Statistical analysis

Data were checked for normality (Shapiro–Wilk) and homogeneity of variance (Levene's test) before analysis; all variables satisfied these assumptions or were transformed. Because plots were nested within a single naturally varying stand, we treated plot as the experimental unit and, in addition to one-way ANOVA, fitted a linear mixed-effects model with canopy density as a fixed effect and plot as a random effect; results were consistent between the two approaches, so we report ANOVA with Duncan's multiple range test for mean separation at $\alpha = 0.05$. Pearson correlations between breaking force and cell-wall fractions were computed on plot-level data ($n = 15$). Redundancy analysis (RDA) was used to explore associations between environmental variables (PAR, soil temperature, AN and others) and peony growth, yield and stem traits; because RDA was run on treatment-level means ($n = 5$), we treat it as exploratory. Environmental variables were forward-selected, collinearity was checked by variance inflation factors (VIF < 10), and axis significance was assessed by permutation tests on treatment-level means. Analyses used SPSS 22.0 and Canoco 5.0; figures were built in Origin 2021.

3. Results

3.1 Understory microclimate along the canopy-density gradient

Canopy density strongly altered understory microclimate (Fig. 1). PAR declined steadily with increasing closure; at T4 it was 21.3% of the open CK value, a drop of 78.7%. Daily mean air temperature and soil temperature fell as canopy density rose, while relative humidity increased. Relative to CK, T2 reduced the daily maximum air temperature by 4.2 °C and soil temperature by 3.7 °C and raised relative humidity by 11.8 percentage points. T4 produced the strongest cooling and humidifying effect: peak daily air temperature was 6.5 °C lower than CK and humidity 17.2

percentage points higher. The cooling benefit approached saturation: T3 and T4 converged (daily maxima of about 32.5 and 32.0 °C), so additional canopy closure above 0.75 bought little further thermal relief (Fig. 1B). The diurnal temperature range under T2 was narrower than under CK, confirming that the ginkgo canopy damps extreme mid-summer temperature swings.

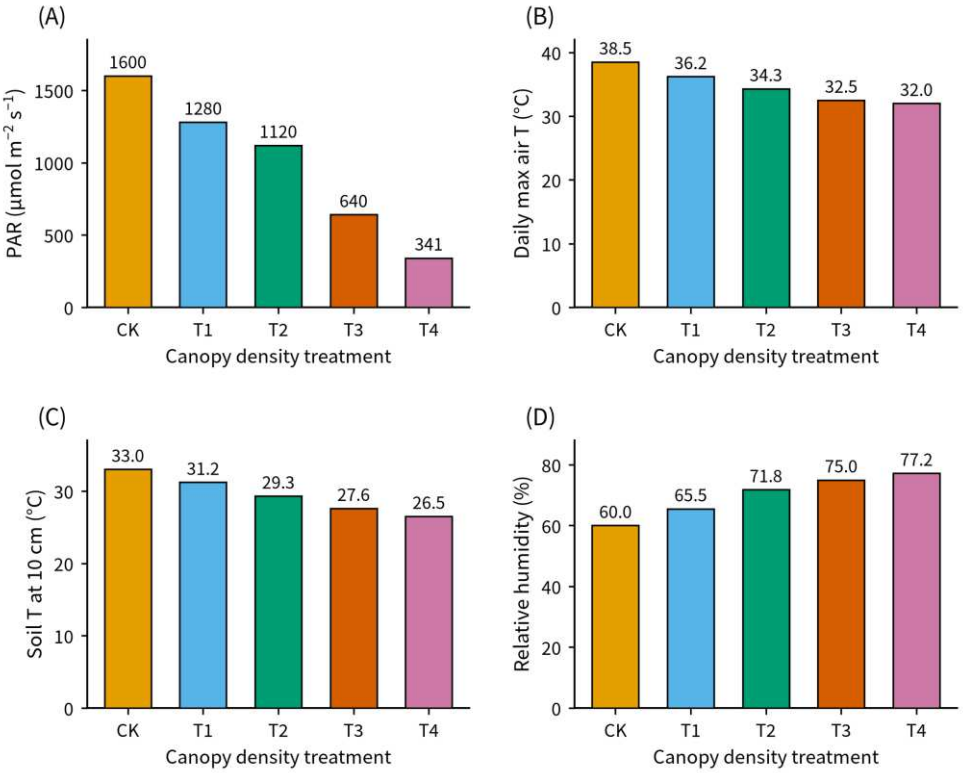


Fig. 1. Understory microclimate along the canopy-density gradient. (A) PAR; (B) daily maximum air temperature; (C) soil temperature at 10 cm depth; (D) relative humidity. Treatment codes: CK = 0.0, T1 = 0.4, T2 = 0.6, T3 = 0.75, T4 = 0.9. Values are treatment means.

3.2 Plant growth and photosynthetic characteristics

Plant height, basal stem diameter and aboveground biomass followed a unimodal curve across the gradient (Table 1), rising to a maximum at T2 and falling thereafter. Plant height at T2 was 12.5% higher than CK and 20.0% higher than T4; aboveground biomass at T2 was 19.4% higher than CK and 32.2% higher than T4. Photosynthetic parameters showed the same single-peak pattern. Pn, Gs and SPAD tended to peak at T2 and to decline under heavy shade; Pn at T2 was 16.2% above CK and 70.1% above T4. Ci was lowest at T2 and highest at T4 (Table 1), yet the differences among CK, T1 and T2 were small (268, 259 and 254 μmol mol^{-1}) and did not differ significantly. This modest rise in Ci at high shade is consistent with, but does not by itself prove, a non-stomatal limitation of photosynthesis; a single Ci measurement is weak evidence and we treat this as a tentative indication pending Pn/Ci or A–Ci data (see Section 4.1).

Table 1. Growth and photosynthetic traits of *Paeonia ostii* under different canopy densities.

Treatment	Plant height (cm)	Basal stem diameter (mm)	Aboveground biomass (g)	Pn (μmol m⁻² s⁻¹)	SPAD	Ci (μmol mol⁻¹)
CK	62.3±2.1b	12.1±0.5b	38.2±1.8b	14.2±0.6b	42.6±1.2b	268±8ab
T1	68.5±2.4a	13.3±0.6a	43.7±2.1a	15.8±0.7a	45.3±1.4a	259±7b
T2	70.1±2.6a	13.7±0.5a	45.6±2.3a	16.5±0.8a	46.1±1.3a	254±6b
T3	65.8±2.3ab	12.6±0.4ab	40.9±1.9ab	13.5±0.6b	43.8±1.1ab	275±9a
T4	58.4±2.0c	11.2±0.5c	34.5±1.7c	9.7±0.5c	39.2±1.0c	324±11c

Note: Different lowercase letters within a column indicate significant differences at P < 0.05 (Duncan's test, n = 3).

3.3 Seed yield

Yield traits also followed a unimodal distribution (Fig. 2, Duncan's test, n = 3 per treatment). Pod number per plant, 1000-seed weight and per-plant seed yield all tended to peak at T2. Pod number at T2 was 11.7% higher than CK and 52.3% higher than T4; 1000-seed weight at T2 was 8.2% higher than CK and 15.2% higher than T4. Seed yield at T2 was 27.5% higher than CK, whereas yield at T4 fell 30.0% below CK and reached only 54.9% of the T2 value. Moderate shade therefore tended to boost seed production, whereas excessive shade tended to suppress yield.

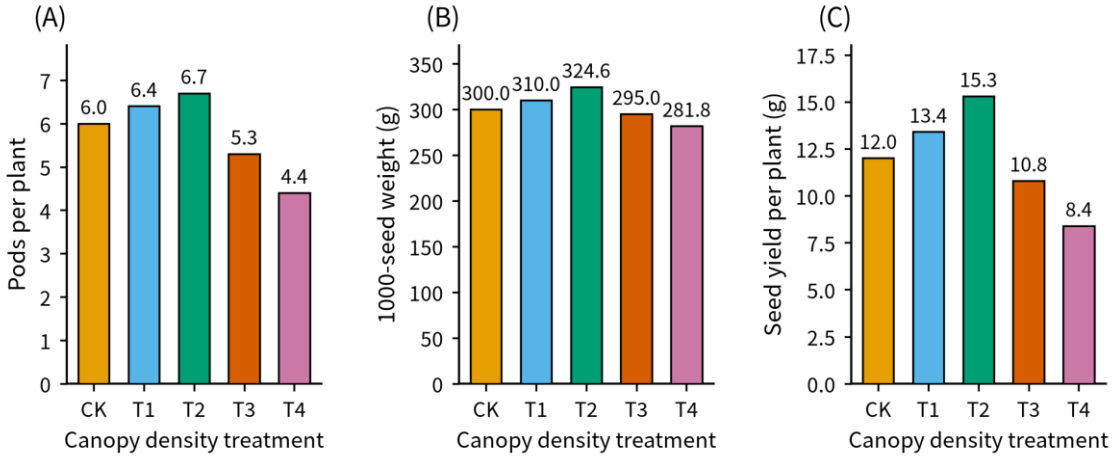


Fig. 2. Seed yield traits of *Paeonia ostii* under different canopy densities. (A) pods per plant; (B) 1000-seed weight; (C) seed yield per plant. Treatment codes as in Fig. 1. Values are treatment means (n = 3).

3.4 Stem mechanical performance and cell-wall components

Stem diameter, fresh weight and breaking force first increased and then decreased with rising canopy density (Table 2). Breaking force tended to be highest at T2 (12.3% above CK), and fell by 23.8% relative to T2 under the heaviest shade (T4), implying higher lodging risk. However, when breaking force was normalised to the stem cross-sectional area (Table 2), the values appeared similar in magnitude (range 0.82–0.88 N mm⁻²; not statistically tested). This shows that most of the variation

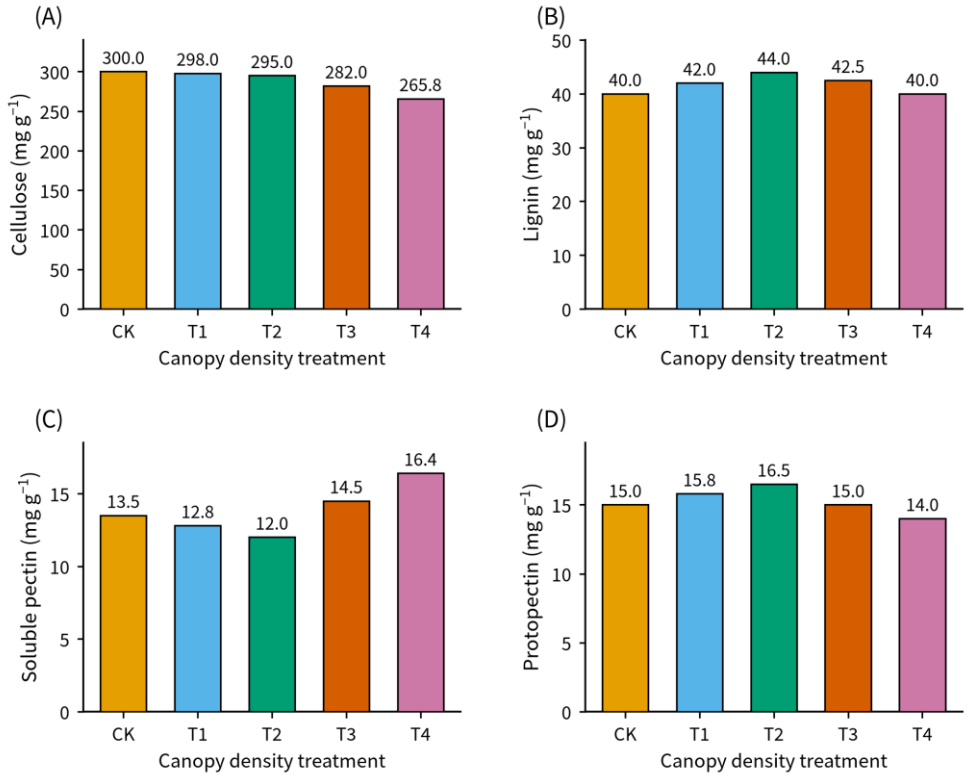
in breaking force arose from stem diameter, not from a change in material strength, and it qualifies the strength effect of shade.

Cell-wall fractions responded differently to shade (Fig. 3). At canopy densities above 0.6, lignin and protopectin declined with further shade. Lignin at T2 was 10.0% higher than at T4, and protopectin at T2 was 17.9% higher than at T4. Soluble pectin showed the reverse trend, lowest at T2 and 36.7% higher at T4. Cellulose fell slightly with shade, with T4 11.4% lower than CK; this difference was small in magnitude, and its biological significance is unclear. Pearson correlations on plot-level data ($n = 15$) linked breaking force positively with lignin ($R = 0.872$, $P < 0.01$) and protopectin ($R = 0.815$, $P < 0.01$) and negatively with soluble pectin ($R = -0.793$, $P < 0.01$). These correlations are correlative; because they were derived from destructive bulk assays at a single developmental stage and did not include stem anatomy, causation was not established (see Section 4.2).

Table 2. Stem morphological and mechanical traits of *Paeonia ostii* under different canopy densities.

Treatment	Stem diameter (mm)	Stem fresh weight (g)	Breaking force (N)	Breaking stress (N mm^{-2})
CK	9.2±0.4b	2.68±0.13b	58.3±2.4b	0.877
T1	9.8±0.5a	2.93±0.15a	63.5±2.7a	0.842
T2	10.1±0.4a	3.05±0.16a	65.5±2.9a	0.818
T3	9.4±0.4ab	2.76±0.14ab	59.7±2.5ab	0.860
T4	8.5±0.3c	2.41±0.12c	49.9±2.2c	0.879

Note: Different lowercase letters within a column indicate significant differences at $P < 0.05$ (Duncan's test, $n = 3$). Breaking stress was not tested separately; treatment means ranged 0.82–0.88 N mm^{-2}.



225

226 **Fig. 3.** Cell-wall components of *Paeonia ostii* stems under different canopy densities. (A) cellulose;
227 (B) lignin; (C) soluble pectin; (D) protopectin. Treatment codes as in Fig. 1. Values are treatment
228 means.

229 ***3.5 Soil physicochemical properties***

230 Soil properties improved partly with increasing canopy density (Table 3). SOC, TN, AN and AP
231 all rose as crown closure increased, while pH and bulk density fell slightly. Relative to CK, T2 raised
232 SOC by 14.9%, AN by 21.3% and AP by 18.3%. T4 held the largest nutrient stocks, with SOC 25.6%
233 higher than CK; whereas peony productivity at T4 was the lowest, limited by light. Bulk density at T4
234 was 9.4% lower than CK. We note that the decline in pH with canopy density (7.42 → 7.18) is
235 commonly attributed to litter decomposition, but we present no direct litter data; the pH trend is
236 therefore reported descriptively and its cause is left open (Section 4.3).

237 **Table 3.** Soil physicochemical properties under different canopy densities.

Treatment	pH	SOC (g kg⁻¹)	TN (g kg⁻¹)	AN (mg kg⁻¹)	AP (mg kg⁻¹)	Bulk density (g cm⁻³)
CK	7.42±0.08a	12.1±0.6c	1.08±0.05c	72.3±3.2d	8.2±0.4c	1.38±0.04a
T1	7.35±0.07ab	13.2±0.6b	1.17±0.06b	82.5±3.7c	9.1±0.4b	1.34±0.04ab
T2	7.29±0.06b	13.9±0.7ab	1.24±0.06ab	87.7±4.1b	9.7±0.5ab	1.31±0.03b
T3	7.24±0.06bc	14.5±0.7a	1.30±0.07a	93.2±4.3ab	10.2±0.5a	1.28±0.03bc
T4	7.18±0.05c	15.2±0.8a	1.36±0.07a	98.6±4.6a	10.8±0.6a	1.25±0.03c

Note: Different lowercase letters within a column indicate significant differences at P < 0.05 (Duncan's test, n = 3). Values are means of soil samples collected after harvest in 2022 and 2023.

3.6 Relationships between environmental factors and plant traits

RDA was used to explore associations between environmental variables and peony growth, yield and stem traits. Because the analysis was run on treatment-level means (n = 5), we interpret the ordination as exploratory. The first two constrained axes together explained 87.2% of the total variation (Fig. 4), with axis 1 and axis 2 accounting for 62.4% and 24.8% respectively. After forward selection, PAR, 10-cm soil temperature and alkali-hydrolyzable nitrogen were the environmental variables retained (all VIF < 10); a permutation test on treatment-level means (n = 5) indicated that the first axis captured a significant fraction of the constrained variation (P < 0.05). In the ordination, high PAR and warmer topsoil aligned with higher seed yield and stronger stems, whereas AN accumulated under dense canopies. This extra nitrogen could not offset severe light limitation, and peony performance collapsed at T4. Individual trait–predictor correlations are listed in Table S1.

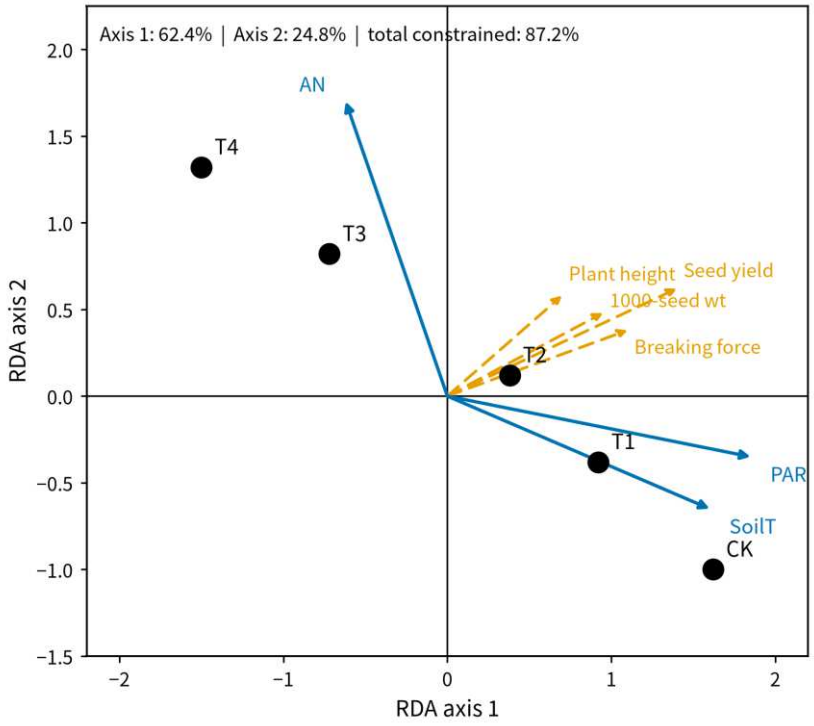


Fig. 4. Redundancy analysis (RDA) of environmental factors and peony traits under different canopy densities. Blue arrows, environmental variables: PAR, photosynthetically active radiation; SoilT, soil temperature at 10 cm depth; AN, soil available nitrogen. Orange dashed arrows, plant traits: seed yield, breaking force, 1000-seed weight, plant height. Treatment codes as in Fig. 1.

4. Discussion

4.1 Canopy shading regulates understory microclimate and photosynthesis

Tree canopy cover was the main factor reshaping the understory environment in our ginkgo stand. Canopy density of 0.6 relieved mid-summer heat stress, and this cooling benefit coincided with better

leaf gas exchange and higher seed yield at T2, consistent with earlier peony trials showing partial shade can reduce midday photosynthetic depression and lift yield potential (Shan et al. 2019; Han et al. 2019) and with the general observation that shade-tolerant understory crops reach maximum assimilation at intermediate light (Shafiq et al. 2021). The near-saturation of the cooling effect above 0.75 canopy density (Fig. 1B) is a useful practical point: beyond this, extra closure adds little thermal relief while sharply cutting light.

At canopy density 0.9, light supply became limiting and seed yield fell sharply. The higher Ci in heavily shaded plots is compatible with a non-stomatal restriction, but we emphasise that a single Ci measurement is not conclusive; leaf chlorophyll fluorescence or an A–Ci curve would be needed to confirm it. Likewise, the statement that low light slows chlorophyll synthesis and reduces photosynthetic enzyme activity is not directly measured here; it is offered as a plausible mechanism supported by the shading literature (Shafiq et al. 2021) rather than by our data.

4.2 Stem mechanical strength and cell-wall components

Stem strength matters for growers because lodging complicates mechanical seed harvest of oil peony. Moderate shade kept breaking force high, whereas heavy shade reduced it and raised lodging risk, echoing rice studies in which low light disrupts cell-wall biosynthesis and weakens stems (Wu et al. 2017; Zhu et al. 2023). Two qualifications temper this mechanistic reading. First, the higher breaking force at T2 was largely a size effect: once force was normalised to stem cross-sectional area, the treatment differences shrank (0.82–0.88 N mm^{-2}), so shade mainly altered stem geometry rather than material strength. Second, our cell-wall assays were destructive bulk measurements from a single developmental stage; they cannot localise compounds to the mechanical tissue, and they were not complemented by stem anatomy (sclerenchyma thickness, vascular bundle number). Shade-induced stem elongation (etiolation) could also change the proportion of mechanical tissue independently of cell-wall chemistry. The positive correlations between breaking force and lignin and protopectin are therefore suggestive, not proof of causation. Hypothesis H2 was therefore only partially supported: shade affected whole-stem breaking force, but per-unit-area stress did not differ among treatments.

The pattern is consistent with prior work on herbaceous peony identifying lignin as the main compound providing mechanical support to stems (Zhao et al. 2020) and with evidence that shade rebalances cell-wall fractions and alters stem rigidity. Lignin cross-links with cellulose and hemicellulose to confer stiffness (Salmén et al. 2016), and under low light plants allocate less carbon to structural tissue, suppressing lignin synthesis first. The shift from insoluble protopectin toward soluble pectin that we observed at T4 would, by analogy, tend to soften the wall. This conversion is consistent with weaker stems under heavy shade, but confirming a causal role would require anatomical localisation and multi-stage sampling.

4.3 Soil quality under the agroforestry system

SOC and available nutrients rose with canopy density across our plots. Two mechanisms may contribute. Denser canopies produce more leaf litter, and a mild, stable understory may accelerate microbial turnover and nutrient cycling, as reported in other ginkgo agroforestry work (Tian et al. 2013; Wang et al. 2015). Alternatively, part of the trend may be a concentration or dilution effect: under heavy shade, peony biomass and nutrient uptake fall, so, with similar inputs, less nutrient removal leaves higher residual concentrations in the topsoil. Our dataset cannot separate these pathways; future work should quantify litterfall, fine-root turnover and plant nutrient removal. We therefore caution that the higher nutrient content at T4 does not necessarily represent a genuine improvement in soil quality — it may partly be an uptake artefact. The decline in pH with canopy density is reported descriptively and its cause (likely litter decomposition) was not measured here.

The central insight is that T4 had the best soil chemical status yet the lowest peony yield. Expressing yield per unit of soil nitrogen exposes the trade-off: the moderate-shade treatment converted available nitrogen into seed far more efficiently than the heavy-shade treatment. Soil fertility alone is therefore an inadequate criterion for judging agroforestry performance; crop yield and lodging risk must be weighed alongside.

4.4 Multi-dimensional trade-off and management implications

Balancing seed yield, lodging resistance and soil improvement is the core practical challenge for ginkgo–peony canopy management. Low canopy density delivers ample light but exposes peony to mid-summer heat and limits soil improvement. At canopy density near 0.6 we observed a balanced outcome: solid seed yield, good lodging resistance and clear soil nutrient gains. Above this density, soil quality continues to rise, but yield falls and lodging becomes more likely. Our data support earlier reports that intercropping is a promising cultivation mode for oil peony (Zhang et al. 2021; Tang et al. 2022) and that well-managed ginkgo agroforestry can deliver both ecological and economic benefits (Sun et al. 2017).

We recommend a summer canopy density near 0.6 for ginkgo–peony systems on the Jianghuai Plain, achievable by selective thinning and crown pruning. This recommendation carries three qualifications. It is site- and age-specific, derived from 12-year-old ginkgo and 3-year-old peony; it applies only to the July–August full-leaf period of the deciduous ginkgo, when canopy cover is at its seasonal maximum; and it does not account for ginkgo leaf and nut yield, which is the primary income for many growers. Where ginkgo production is economically decisive, the target may need to shift to protect tree yield, and an explicit assessment of that trade-off lies outside the scope of this paper.

4.5 Limitations of the study

Several caveats constrain the interpretation. First, the treatments were established by selecting plots that naturally differed in crown closure and then pruning to target. Canopy density is therefore confounded with pre-existing spatial variation in tree age, root distribution and soil, and, because we

did not install root barriers, above-ground shade cannot be separated from below-ground competition between ginkgo and peony. The RDA, run on treatment-level means (n = 5), cannot disentangle these correlated factors; it is exploratory, and the "PAR–soil temperature–AN" attribution must be read accordingly. Second, cell-wall components were sampled at a single developmental stage (full bloom) and by bulk assays; we do not know how these compounds shift later, and we made no anatomical measurements. Third, the intensive microclimate and gas-exchange campaign, together with the seed-yield and stem measurements, covered only the 2023 growing season (the first season after treatment establishment), which may not capture year-to-year variation; topsoil properties, by contrast, were sampled after harvest in both 2022 and 2023 and are reported as two-year means. Fourth, our canopy gradient describes only the summer full-leaf stage; ginkgo is deciduous, so canopy cover disappears from late autumn to early spring, and we did not cover this seasonal shift. Fifth, all peony plants were 3-year-old seedlings; older or younger stands may respond differently to the same canopy density. Finally, we report no ginkgo yield data, so the economic balance between tree and understory income remains open.

5. Conclusion

Ginkgo canopy density altered understory microclimate, peony seed yield, stem strength and topsoil properties for intercropped Paeonia ostii. At a summer canopy density of about 0.6, shade reduced mid-summer heat stress, raised photosynthetic efficiency, maximised seed yield, maintained high whole-plant breaking force (a geometric rather than a material advantage) and improved soil nutrient status. Heavy shade (0.9) imposed severe light limitation, weakened stems and cut seed output while still enriching topsoil nutrients. Managing summer canopy density near 0.6 offers a practical way to balance crop productivity, low lodging risk and soil health in ginkgo–oil peony agroforestry across eastern China, subject to the site-, age- and season-specific qualifications described above.

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Declarations

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Competing interests: The authors declare that they have no competing financial or non-financial interests.

Availability of data and material: Datasets generated and analysed in the current study are available from the corresponding author on reasonable request; the primary dataset will be deposited in a public repository before publication.

Code availability: Not applicable; no custom code or software was used beyond the commercial packages listed in the Methods.

Authors' contributions: Zongqing Jiang conceived and designed the experiment, performed the data analysis and wrote the original manuscript. Le Yu carried out field sampling and laboratory measurements and helped to draft and revise the manuscript. Both authors read and approved the final manuscript.

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