

A Thermal-Time Framework for S₁ Progenies of Medicinal *Cannabis sativa* L. under Tropical Conditions: Conserved Phenological Thresholds and Genotype-Specific Biomass Allocation

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Article

A Thermal-Time Framework for S₁ Progenies of Medicinal *Cannabis sativa* L. under Tropical Conditions: Conserved Phenological Thresholds and Genotype-Specific Biomass Allocation

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Abstract

Medicinal *Cannabis sativa* L. is expanding into tropical regions, but agronomic reference values derive from temperate or indoor environments. We evaluated thermal requirements, biomass partitioning, and morphometric predictors in three medicinal cannabis S₁ progenies under tropical conditions. Purple Wreck (THC-dominant), Doctor (CBD-dominant), and Schanti (balanced) were grown under a 20-h photoperiod during vegetative growth and then transferred outdoors under natural photoperiod. Organ dry biomass was sampled weekly and modeled against growing degree days (GDD) using three-parameter log-logistic functions. Thermal positioning did not differ detectably among progenies, whereas asymptotic biomass differed, indicating variation in biomass magnitude and reproductive allocation rather than developmental timing. Pooled thresholds occurred at 871 GDD for onset of active vegetative growth, 1329 GDD for stem elongation, 1425 GDD for flowering onset, 1543 GDD for onset of active floral biomass accumulation, and 1947 GDD for inflorescence formation. Harvest index was projected to stabilize at ~2263 GDD and onset of inflorescence maturation at ~2457 GDD, both beyond the sampled window. At a common developmental stage, morphometric descriptors added little to thermal time, although crown diameter showed the strongest within-stage association with floral biomass ($r = 0.31$). Thermal time reliably described growth and reproductive allocation once floral induction was photoperiodically permitted.

Keywords: *Cannabis sativa* L.; phenology; growing degree days; thermal time; biomass accumulation; biomass partitioning; harvest index; medicinal cannabis; tropical cultivation

1. Introduction

Medicinal cannabis and hemp cultivation have expanded rapidly, driven by the growing acceptance of cannabinoid-based therapies, industrial demand and regulatory advances [1]. Growth, flowering and biomass accumulation in *Cannabis sativa* L. arise from the interaction among genotype, sowing time and edaphoclimatic conditions, so cultivar choice and management must be established in the environment where the crop will be produced [2].

Most agronomic reference values and growth models, however, derive from temperate or indoor conditions [3–5], leaving tropical production systems without quantitative developmental references.

Thermal-time approaches based on growing degree days (GDD) predict development from accumulated temperature rather than calendar duration, provided that crop-specific base (T_{base}) and upper (T_{upper}) thresholds are defined [6,7]. Because these thresholds vary among crops, developmental stages, cultivars and estimation methods, they require crop-specific parameterization [7].

In *Humulus lupulus* L., the closest cultivated relative of *Cannabis* within the Cannabaceae, GDD reliably describes vegetative development and stage transitions under semi-arid, subtropical and Mediterranean conditions, and the choice of Tbase and of the calculation method measurably affects model fit [8,9]. Process-based models parameterised on thermal time reproduce phenology and organ-level biomass in tomato [10] and in maize, where genotype accounted for the largest share of harvest-index variance [11]; in soybean, elevated temperature reduced leaf area index, pod number, seed size and harvest index [12].

The first models for *Cannabis sativa* L. addressed fibre hemp in temperate regions [13–15], which limits their transfer to high-cannabinoid cultivars grown in the tropics. Temperature nonetheless governs carbon assimilation in the species: net photosynthesis peaks near 30 °C and declines at higher leaf temperatures, and this response differs between drug- and fibre-type varieties [16,17]. Under tropical daylengths, temperature and photoperiod jointly determine time to flowering, biomass accumulation and cannabinoid concentration, the dominant factor depending on the variety [18]. Whether these responses translate into reproducible thermal thresholds for medicinal cultivars under tropical field conditions has not been established.

In medicinal cannabis, the distribution of biomass among roots, stems, leaves and flowers governs growth efficiency and reproductive output [19]. Across seven hemp genotypes staged by the same decimal scale, inflorescence dry weight varied with genotype and growth stage, whereas leaf fractions did not [20]. Chemovars also differ in sink strength and assimilate allocation, one sustaining higher nutrient demand and greater floral biomass than the other under identical conditions [21].

Characterizing cultivars for medicinal production requires descriptors that reflect productive capacity, particularly floral biomass and resin yield. The test guidelines of the International Union for the Protection of New Varieties of Plants (UPOV) for *Cannabis sativa* L. [22] encompass the different end uses of the species, yet descriptors tailored to medicinal floral traits remain underdeveloped, and non-destructive morphometric proxies of yield are still poorly defined for this crop.

Morphometric–biomass relationships offer a route to estimating biomass without destructive sampling, and few studies have applied the approach to *Cannabis sativa* L. Carlson et al. [23] phenotyped 23 hemp families and identified basal stem diameter as the best single selection criterion for dry floral biomass, with stem diameter, canopy kite area and plant height together accounting for 67% of the explainable variation in floral yield. Naim-Feil et al. [24] evaluated 121 medicinal genotypes under controlled conditions and derived, from vegetative-stage measurements, a prediction equation for floral bud dry weight (adjusted $R^2 = 0.34$) that ranks candidate genotypes before the end of the cycle. Neither study related predictor performance to accumulated thermal time, and whether these descriptors retain predictive value under tropical field conditions remains untested.

Formal GDD-based phenological models have not been established for medicinal cannabis. We therefore tested the hypothesis that the thermal thresholds delimiting vegetative development and floral induction are conserved among genotypes, whereas the magnitude and rate of biomass accumulation and the partitioning of biomass to reproductive organs are genotype-specific. Three medicinal cultivars S1 progenies were grown under tropical field conditions to (i) describe growth dynamics as a function of GDD, (ii) quantify biomass accumulation and partitioning among organs, (iii) estimate the progression of harvest index, and (iv) assess morphometric and phenological descriptors, including UPOV traits, as predictors of growth and floral yield. Thermal thresholds proved conserved among the three progenies, whereas biomass magnitude and reproductive allocation did not, and morphometric descriptors added little to thermal time once developmental stage was accounted for.

2. Results

2.1. Growth Conditions

During the experimental period in Paty do Alferes, climatic conditions reflected a seasonal transition from late winter to early spring. This period was characterized by a gradual increase in photoperiod, with day length rising from early August to late October. Air temperature exhibited a progressive increase throughout the period. In August, the mean temperature was 17.2 °C, with maximum and minimum values of 33.4 °C and 4.2 °C, respectively. In September, the mean temperature increased to 21.2 °C, with maximum and minimum values of 34.1 °C and 9.9 °C. In October, the mean temperature reached 21.9 °C, with higher maximum temperatures (36.2 °C) and minimum values of 11.7 °C.

Rainfall distribution also varied markedly over time, with total precipitation of 41.0 mm in August and 12.4 mm in September, followed by a substantial increase to 138.2 mm in October, marking the onset of the rainy season. Notably, high-intensity rainfall events were recorded in late October, with precipitation totals of 71.0 mm and 43.8 mm on October 20 and 24, respectively. Regional climatic characterization was based on environmental monitoring data (Figure 1). Climatic data were obtained from the A637 – Paty do Alferes (Avelar, RJ, Brazil) automatic meteorological station of the Brazilian National Institute of Meteorology (INMET) [25].

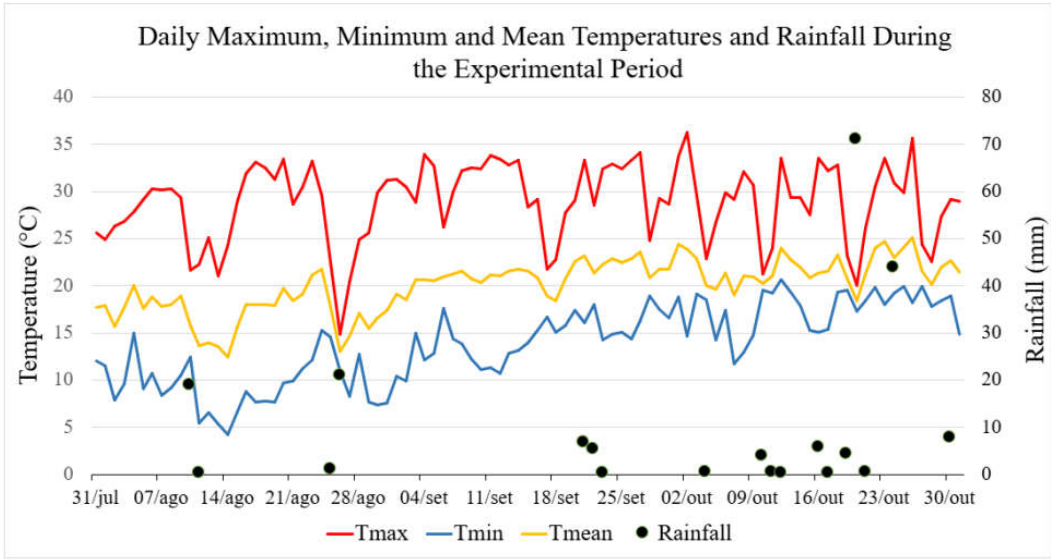


Figure 1. Daily maximum, minimum, and mean air temperature and rainfall during the experimental period.

2.2. Thermal Development and Phenological Thresholds

The thermal-time model identified discrete developmental thresholds that were largely uniform across the three S1 progenies (Table 1, Figure 2a). Thresholds up to and including the onset of active vegetative growth were reached under the constant 20-h photoperiod and reflect thermal accumulation and ontogeny alone; those from the flowering onset onward were reached after the common transfer to natural short days on 5 September 2024, and are therefore reference values conditional on that management sequence rather than intrinsic thermal requirements for floral induction. Development progressed through six phases. Propagation ended with the transfer to cultivation bags at ~456 GDD, a boundary set by management rather than estimated from the curves.

The subsequent thresholds were derived from the fitted models: to a second vegetative phase of active expansion (~871 GDD), stem elongation (~1329 GDD), flowering onset (~1425 GDD), onset of active floral biomass accumulation (~1543 GDD), and the onset of inflorescence maturation (~2457 GDD). Differences among genotypes of origin in these thresholds were minor and their 95% confidence intervals overlapped at every stage (Table 1), with no detectable difference in developmental timing among progenies. Confidence-interval width increased for thresholds near the end of the sampled window, from 118 GDD for SCH at stem elongation to 1,397 GDD for DOC at

onset of inflorescence maturation and 1,380 GDD for SCH at cessation of stem growth. The order of the thresholds was not identical across progenies. In DOC, the initial flower formation preceded the onset of active vegetative growth (865 versus 906 GDD). Each departure involves thresholds whose confidence intervals overlap, so the sequence reported here is the pooled one and progeny-level ordering at these three points is not resolved.

Whether the three progenies shared a common thermal positioning was tested directly by comparing nested log-logistic models (Section 4.5). For every organ, allowing the inflection parameter e to differ among progenies did not improve the fit over a model with a common e (total biomass $F = 0.58$, $p = 0.56$; above-ground biomass $F = 0.55$, $p = 0.58$; stem $F = 0.09$, $p = 0.92$; leaf $F = 1.34$, $p = 0.26$; flower $F = 1.11$, $p = 0.33$), whereas allowing the asymptote d to differ improved it in every case ($F = 3.24\text{--}22.93$, $p \leq 0.041$). Progeny-specific estimates of e for total biomass spanned 48 GDD (1422–1469). Bootstrap confidence intervals for the pairwise differences in e were wide (90% CI within ± 200 GDD for two of the three pairs), so the thresholds are statistically indistinguishable rather than demonstrably equivalent. Post-transfer thresholds also share ~ 1238 GDD of accumulation common to all progenies; referred to the interval that followed induction, the spread was 17–18% against 8% before induction.

The harvest index — the ratio of floral to total above-ground biomass — increased throughout reproductive development and was still rising, while decelerating, at the final sampling (~ 2120 GDD). The logistic model projected its stabilization at ~ 2263 GDD, cessation of stem growth at ~ 2409 GDD and onset of inflorescence maturation at ~ 2457 GDD, all beyond the sampled window.

Table 1. Thermal-time thresholds (accumulated growing degree days, GDD) associated with developmental phase progression in S1 progenies of *Cannabis sativa* L. Each threshold was defined as the GDD at which the fitted three-parameter log-logistic (LL.3) curve reached the stated percentage of its upper asymptote. Thresholds up to the onset of vegetative growth are pre-induction; those from the vegetative–reproductive transition onward followed the transfer to natural short days and are conditional on that management sequence. DOC, PW and SCH are progeny-specific fits, each shown with its 95% confidence interval; the pooled estimate was obtained from a single model fitted across all three progenies ($n = 210$) and is the reference value cited in the text. Confidence intervals overlap among progenies at every threshold. Thresholds are listed in the order given by the pooled estimates; progeny-level ordering differs at three points (Section 2.2). Stabilization of harvest index, cessation of stem growth and onset of inflorescence maturation lie beyond the last sampling point (~ 2120 GDD) and are model projections rather than observed values. Cessation of stem growth is defined at 99.5% of the asymptote, far beyond the sampled range, and its confidence intervals are correspondingly wide (1,213–1,380 GDD).

Developmental phase	Threshold criterion	DOC (95% CI)	PW (95% CI)	SCH (95% CI)	Pooled estimate (95% CI)
Early biomass accumulation	0.5% of total biomass	632 (463–802)	586 (448–724)	549 (419–679)	583 (491–674)
Onset of active vegetative growth	5% of total biomass	906 (787–1025)	881 (783–979)	840 (747–932)	871 (806–936)
Initial flower formation	0.1% of floral biomass	865 (746–983)	1015 (873–1157)	952 (839–1065)	937 (860–1014)
Stem elongation	50% of stem biomass	1325 (1265–1385)	1337 (1277–1397)	1326 (1267–1385)	1329 (1286–1371)
Flowering onset	5% of floral biomass	1422 (1327–1518)	1427 (1368–1487)	1456 (1402–1510)	1425 (1393–1457)

Onset of active floral biomass accumulation	10% of floral biomass	1562 (1424–1701)	1522 (1477–1568)	1578 (1506–1649)	1543 (1505–1580)
Inflorescence formation	50% of floral biomass	2059 (1709–2408)	1839 (1738–1940)	1997 (1801–2194)	1947 (1836–2057)
Stabilization of harvest index	95% of harvest-index asymptote	2250 (2098–2401)	2215 (2071–2358)	2333 (2147–2519)	2263 (2158–2368)
Cessation of stem growth	99.5% of stem biomass	2122 (1493–2751)	2479 (1873–3086)	2525 (1835–3215)	2409 (1946–2871)
Onset of inflorescence maturation	90% of floral biomass	2713 (2015–3411)	2222 (1978–2466)	2529 (2123–2935)	2457 (2220–2693)

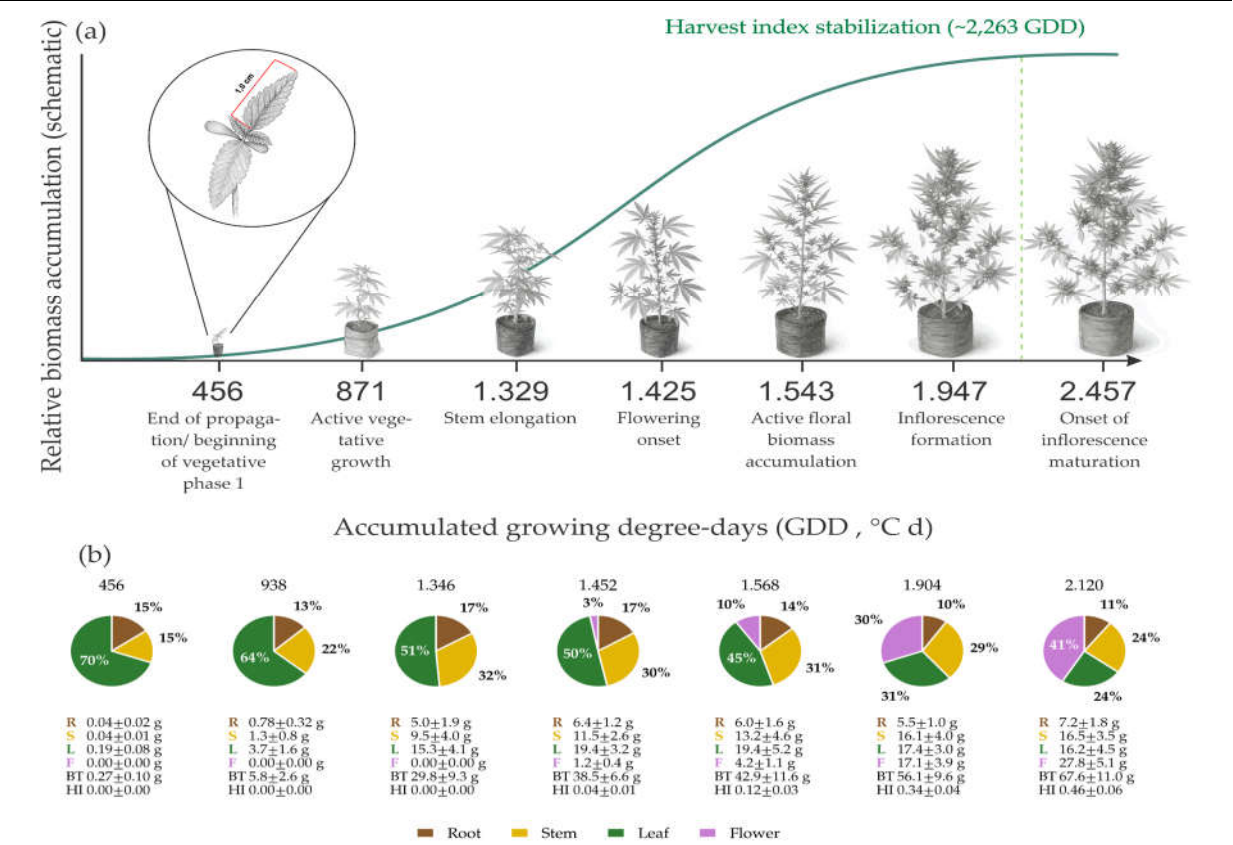


Figure 2. Sequential physiological development and dry-biomass partitioning of *Cannabis sativa* L. as a function of accumulated growing degree days (GDD). (a) Botanical illustrations depict key developmental stages: end of propagation (456 GDD), onset of active vegetative growth (871 GDD), stem elongation (1,329 GDD), flowering onset (1,425 GDD), onset of active floral biomass accumulation (1,543 GDD), inflorescence formation (1,947 GDD), and onset of inflorescence maturation (2,457 GDD); the first two are pre-induction, the remainder followed the transfer to natural short days. The dashed vertical line indicates the thermal threshold at which the harvest index stabilizes (~2,263 GDD), suggesting a decoupling between biomass accumulation and reproductive allocation during the final phase of the crop cycle. The sigmoidal curve is schematic and represents the general form of biomass accumulation; fitted models and parameter estimates are given in Figure 3 and Table A2. (b) Partitioning of dry biomass among root (R), stem (S), leaf (L) and inflorescence (F), expressed as a percentage of total plant dry biomass, at each of the seven destructive sampling dates nearest the developmental thresholds shown in panel (a); GDD values above each chart are the actual sampling dates (456, 938, 1,346, 1,452, 1,568, 1,904 and

2,120 GDD) and do not coincide exactly with the model thresholds in panel (a). Values beside each chart are organ means $\pm$ standard deviation; BT is total plant dry biomass and HI the harvest index (inflorescence dry mass / above-ground dry mass), both $\pm$ standard deviation. Destructive sampling comprised 15 plants per date across 14 dates (210 plants in total). No destructive sample was collected beyond 2,120 GDD, so no chart is shown for the 2,457 GDD threshold. Illustrations and charts are evenly spaced for legibility, so horizontal positions are schematic and do not scale with GDD. Inset: detail of a seedling at the end of propagation (scale bar, 1.0 cm).

2.3. Biomass Accumulation and Partitioning

Logistic models fitted to organ-specific biomass as a function of accumulated GDD showed sigmoidal responses across all compartments, with clear separation among genotypes in asymptotic biomass (Appendix A, Table A2) (d) and slope (b) (Figure 3a–f). Across organs, genotypic differences were concentrated in the magnitude and rate of accumulation rather than in thermal timing, which did not differ detectably (Table 1, Figure 3).

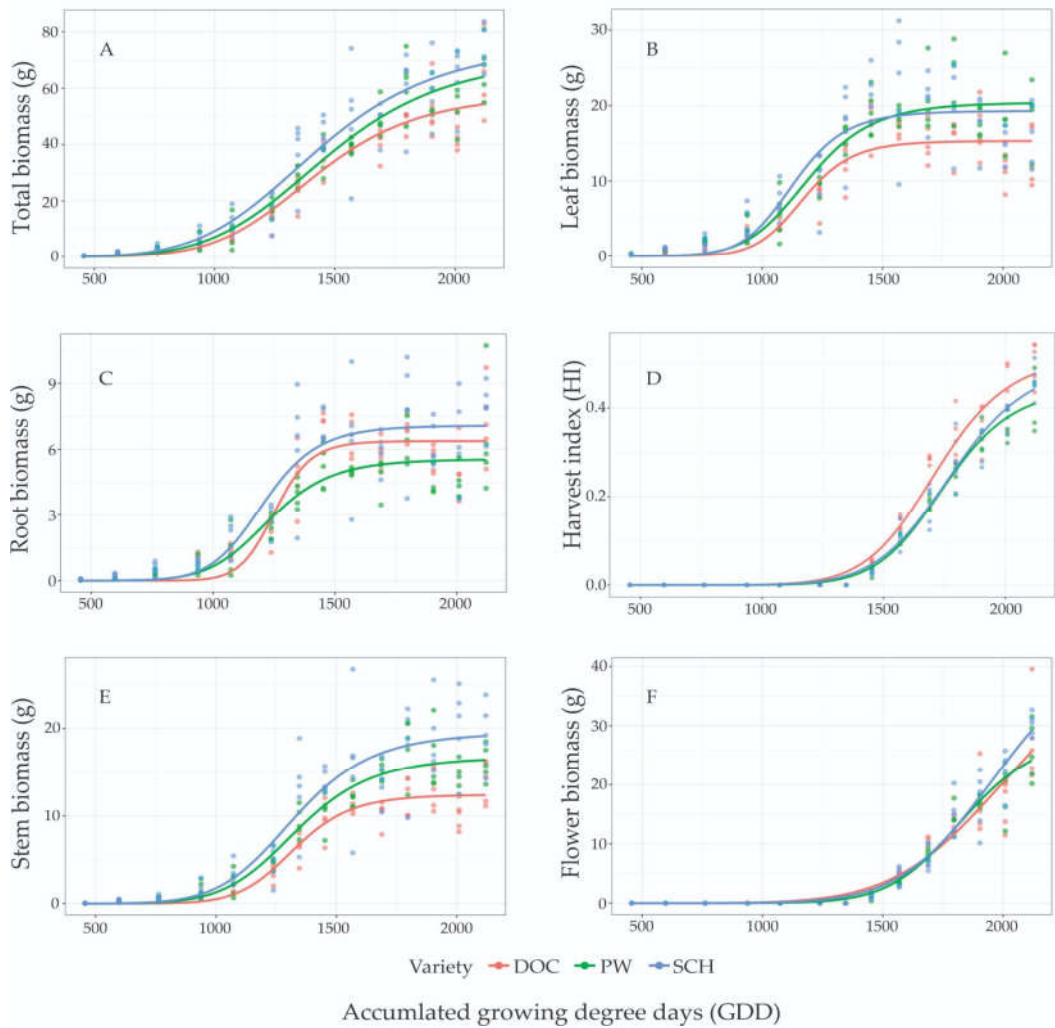


Figure 3. Logistic growth models of organ-specific biomass accumulation as a function of accumulated growing degree days (GDD) in three S1 progenies of *Cannabis sativa* L. Panels show (A) total biomass (roots included), (B) leaves, (C) roots, (D) harvest index (floral / above-ground biomass), (E) stems and (F) flowers. Points are observed values from weekly destructive sampling and lines are fitted three-parameter log-logistic (LL.3) curves (DOC – red; PW – green; SCH – blue).

Organs differed markedly in the timing of stabilization. Root biomass accumulated slowly until ~900–1000 GDD, accelerated between ~1100 and 1300 GDD, and plateaued early, around ~1500–1600 GDD, with SCH and DOC reaching higher asymptotes than PW (Figure 3c). Stem biomass remained low until ~1000 GDD, grew fastest between ~1200 and 1600 GDD, and plateaued between ~1900 and

2100 GDD, SCH attaining the greatest structural mass (Figure 3e). Leaf biomass intensified between ~1000 and 1500 GDD and stabilized from ~1500–1700 GDD, with SCH forming the largest canopy (Figure 3b).

In contrast, floral biomass showed a pronounced lag, remaining near zero until ~1400–1500 GDD, then rising sharply between ~1600 and 2100 GDD; unlike the vegetative organs, it continued to increase without reaching saturation within the observed GDD range, SCH showing the highest reproductive capacity (Figure 3f). Harvest index — the ratio of floral to above-ground biomass — rose steadily after the reproductive transition, increasing sharply between ~1600 and ~1900 GDD and decelerating toward the end of the cycle (Figure 3d). The curve approached but did not reach a plateau within the sampled window, with model-projected stabilization at ~2263 GDD. DOC showed the highest harvest index throughout the reproductive phase (0.50 at final sampling, versus 0.46 in SCH and 0.42 in PW), indicating the greatest proportional reproductive allocation, whereas SCH showed the highest absolute floral biomass.

Biomass partitioning shifted progressively across the cycle (Figure 2b). Leaves represented 70% of whole-plant dry biomass at the end of propagation and declined monotonically to 24% by the final sampling (2,120 GDD), whereas stem allocation rose from 15% to a plateau near 30% from ~1,346 GDD onwards and root allocation remained between 10% and 17% throughout. Inflorescence biomass was undetectable through 1,346 GDD, then rose from 3% at 1,452 GDD to 41% at the final sampling, a trajectory culminating in the final-harvest values reported below.

Across the reproductive-phase samplings (weeks 8–14; n = 35 per progeny), both progeny and thermal time affected harvest index (progeny F = 19.6, p < 0.001; sampling week F = 225.9, p < 0.001), with no interaction between them (p = 0.63). DOC exceeded both PW and SCH (Tukey, p < 0.001 in both cases), which did not differ from each other (p = 0.37).

At the final harvest (week 14, ~2120 GDD), floral tissue was the dominant sink across cultivars. In absolute terms, floral biomass averaged ~28 g plant⁻¹ in DOC and ~26 g plant⁻¹ in PW, reaching ~30 g plant⁻¹ in SCH, followed by stems (14–19 g), leaves (13–19 g) and roots (6–8 g) (Figure 4). In relative terms of whole-plant biomass, floral biomass represented the largest fraction — 44% in DOC, 41% in SCH and 38% in PW — while stems accounted for 23–26%, leaves for 21–28%, and roots for 10–12% (Figure 4b). Genotypic differences were concentrated in the reproductive and foliar compartments, whereas stem and root allocation remained comparatively uniform.

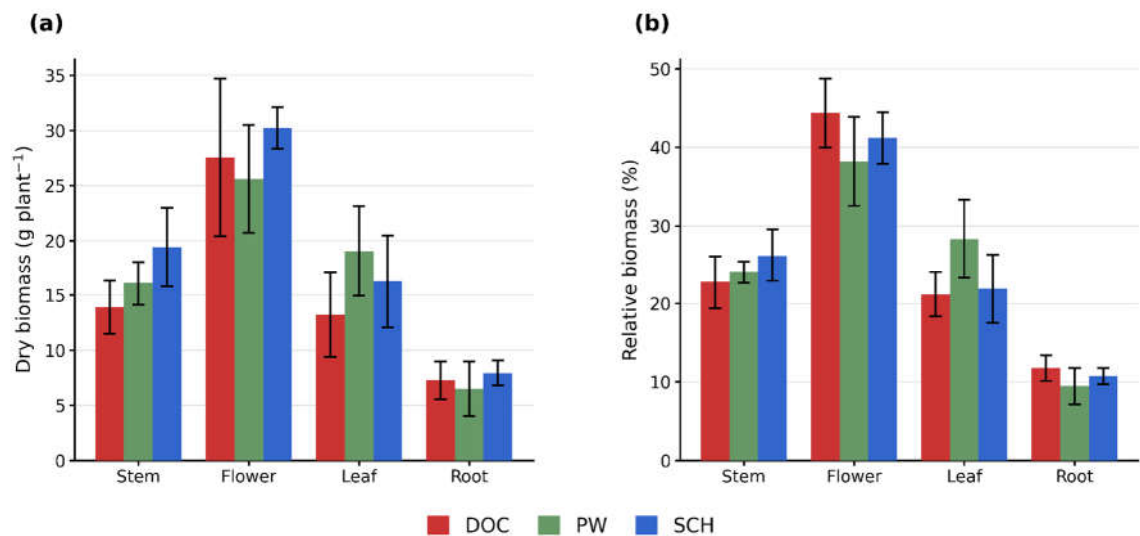


Figure 4. Absolute (a) and relative (b) biomass accumulation across plant organs at week 14 in three Cannabis sativa L. S1 progenies. Fractions in (b) are expressed on a whole-plant basis, roots included. Bars are means of five plants per progeny; error bars represent the standard deviation (n = 5).

2.4. Morphometric Predictors of Biomass

Descriptor-based models related each morphometric trait — plant height, stem diameters, leaflet number and dimensions, crown diameters, internode length and petiole length — to total or floral dry biomass as the response. Two functional forms were fitted: logistic models for height, basal stem diameter (D1) and crown diameters (dc1, dc2), and simple linear models for the remaining descriptors (Figures 5 and 6; Section 4.5).

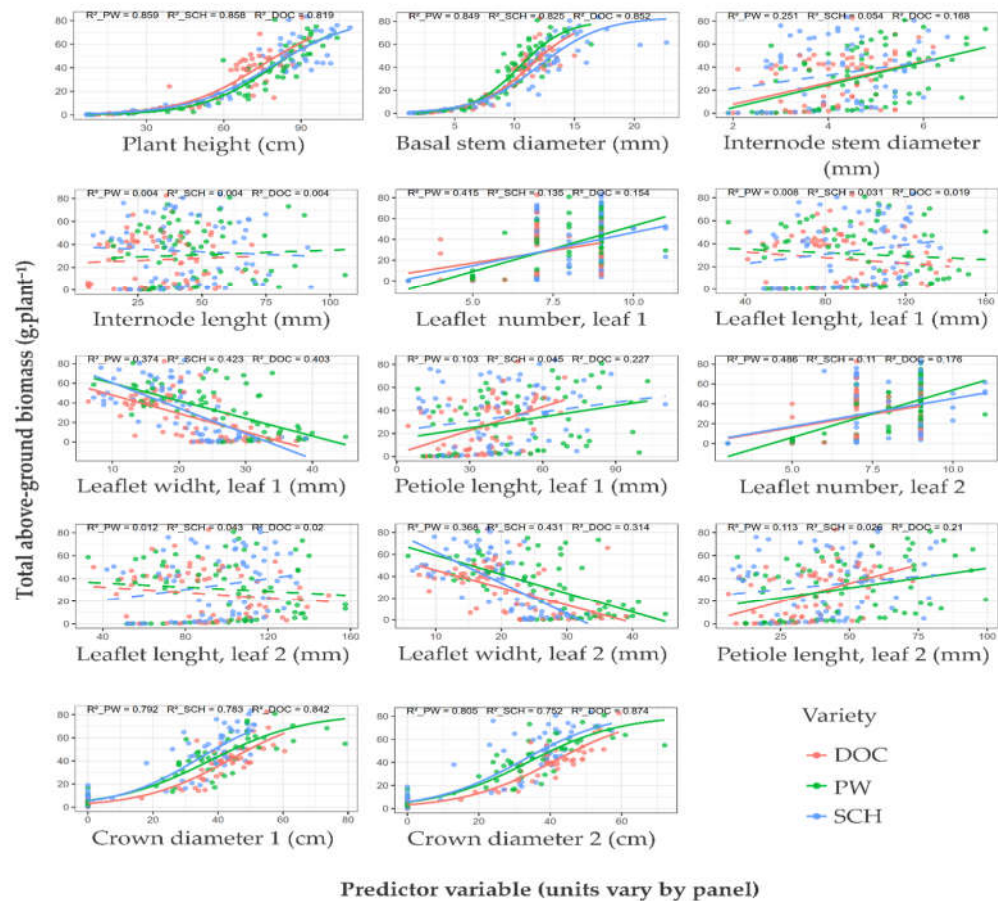


Figure 5. Relationships between total above-ground biomass and morphometric descriptors in three S1 progenies of Cannabis sativa L. (DOC – red; PW – green; SCH – blue). Points are individual plants from weekly destructive sampling (n = 70 per progeny); lines are fitted models, logistic for plant height, basal stem diameter and crown diameters and simple linear for the remaining descriptors. Parameter estimates, p-values and R² are given in Table A1.

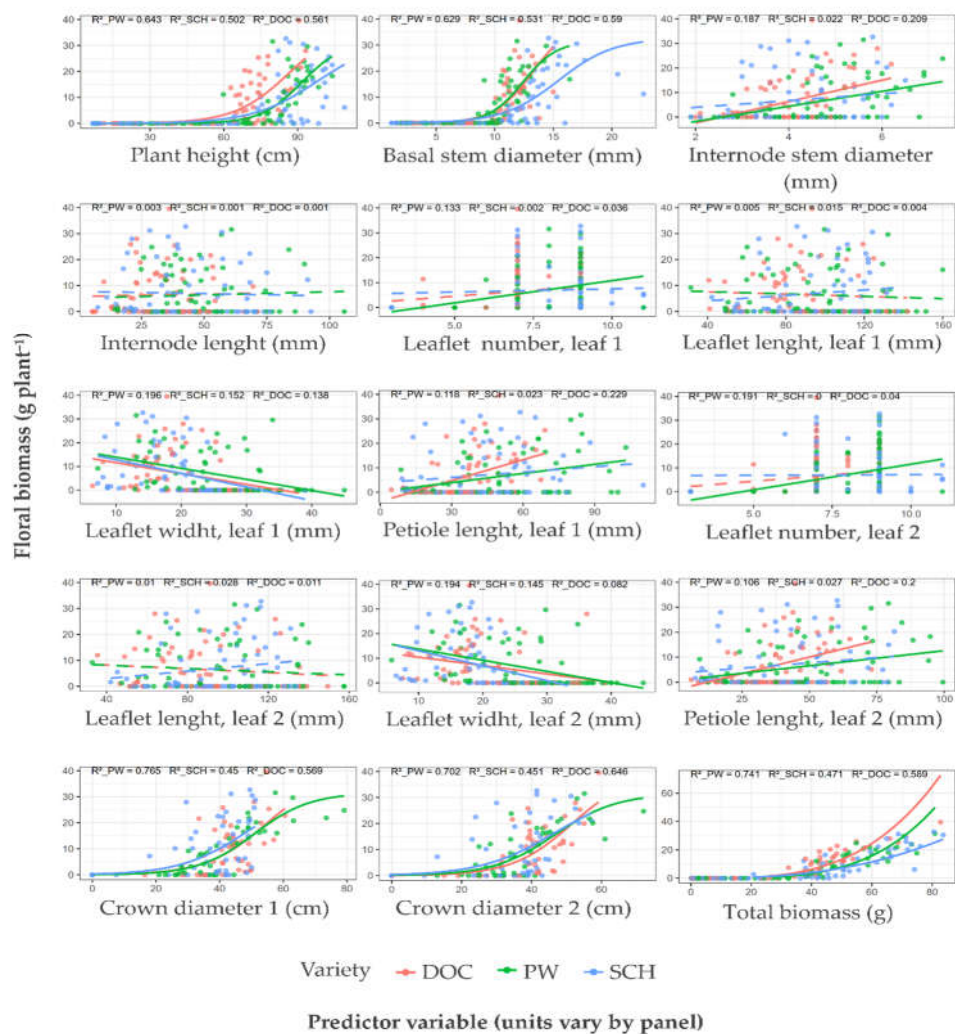


Figure 6. Relationships between floral biomass and morphometric descriptors in three S1 progenies of Cannabis sativa L. (DOC – red; PW – green; SCH – blue). Points are individual plants from weekly destructive sampling (n = 70 per progeny); lines are fitted models, logistic for plant height, basal stem diameter and crown diameters and simple linear for the remaining descriptors. Parameter estimates, p-values and R² are given in Table A1.

Plant height and basal stem diameter showed the strongest associations with total biomass ($R^2 \approx 0.82$ – 0.86 across genotypes; all $p \leq 0.001$), with crown diameter close behind ($R^2 \approx 0.75$ – 0.87), whereas internode length, leaflet traits and petiole length had limited predictive value (Figure 5). For floral biomass these associations weakened ($R^2 \approx 0.50$ – 0.64 for height and basal stem diameter), and the leading predictor became genotype-dependent: crown diameter ranked first in PW (dc1, $R^2 = 0.77$) and in DOC (dc2, $R^2 = 0.65$), exceeding height and basal stem diameter in both, whereas in SCH it fell below them ($R^2 \approx 0.45$) and basal stem diameter ranked first ($R^2 = 0.53$). Averaged across progenies, crown diameter gave the highest R^2 for floral biomass (0.60) and plant height the lowest (0.57), reversing the order they held for total biomass (Figure 6). Parameter estimates for all descriptor models – intercept, coefficient, p-value and R^2 against total and floral biomass – are given in Appendix A (Table A1).

Because both descriptors and biomass increase with thermal time, the models above confound trait variation with developmental stage. Two stage-controlled analyses were therefore added (Section 4.5). Within the reproductive window (weeks 8–14; n = 105), thermal time alone explained 86.5% of the variation in floral biomass, and adding a descriptor raised this by at most 0.6 percentage points; only crown diameter reached significance ($p = 0.028$), height, basal stem diameter and branch number did not ($p = 0.14$, 0.07 and 0.34). Under leave-one-week-out cross-validation, thermal time

alone gave $R^2 = 0.833$ and thermal time plus crown diameter 0.844. Within individual sampling weeks, the mean correlation with floral biomass was 0.31 for crown diameter, 0.26 for basal stem diameter, 0.17 for branch number and 0.09 for plant height.

3. Discussion

3.1. Thermal-Time Control of Phenological Progression in *Cannabis sativa* L.

The thermal-time framework adopted here builds on the phenological models of Amaducci et al. (2008, 2012), in which post-emergent development is governed by temperature and photoperiod rather than by chronological time. All progenies were transplanted on a common date and reached the photoperiodic switch at near-identical thermal time, so the convergence at the onset of flowering (1422–1456 GDD) reflects the management sequence and is reported as a reference value for it. Beyond induction, threshold estimates remained statistically indistinguishable among progenies, their 95% confidence intervals overlapping at every stage.

Floral development proceeds in two steps under distinct control, where vegetative growth and reproductive differentiation overlap. Solitary axillary flowers are initiated at the juvenile-to-adult transition through age-dependent, photoperiod-independent signals, differentiating even under long days [27,28]. Short days then act on the shoot apex in two successive phases: internodes and the main stem first elongate rapidly, after which elongation of newly formed internodes ceases and the condensed inflorescence is assembled through intense apical branching and shortening of internodes and petioles [27,29]. This second step requires short days in photoperiod-sensitive genotypes such as those evaluated here; autoflowering types flower independently of daylength [30,31].

The progenies evaluated here reproduced this sequence. Following Mediavilla et al. [26], flower primordia and the first solitary flowers (codes 2001–2201) appeared between 938 and 1073 GDD while plants were still under the 20-h photoperiod, whereas condensed inflorescences (2202) and measurable floral biomass followed only after transfer to natural short days, from 1346 and 1452 GDD respectively. Trichome maturation — glandular heads shifting from clear to milky and amber, with head senescence and dehiscence [32] — proceeds on a longer timescale and was not assessed; the maturation threshold reported here is defined on floral biomass.

This two-step structure conditions what thermal time explains in the present dataset. Vegetative progression occurred entirely under a constant, non-inductive photoperiod, so its timing depended on thermal accumulation and ontogeny alone, yielding the closest agreement among progenies of the whole cycle (stem elongation differing by 12 GDD).

Point estimates of the later thresholds did not rank consistently across progenies, and their confidence intervals were wide and mutually overlapping — reaching 1,397 GDD for DOC at inflorescence maturation and 1,380 GDD for SCH at cessation of stem growth — so the ordering is not statistically supported. Precision decreased as thresholds approached the end of the sampled window (~2120 GDD). At the latitude of the site (22°25' S), sunrise-to-sunset daylength ranges from ~11.1 h in early August to ~12.9 h in early November and does not exceed 13.5 h, while the shortest critical photoperiod among the 27 cultivars screened by Zhang et al. [33] was 13 h 45 min.

Prevailing daylengths therefore fall below the inductive threshold of every genotype surveyed, and civil twilight, which extends the effective photoperiod, narrows this margin in late spring without closing it. Because a one-hour difference at tropical daylengths alters time to flowering, biomass and cannabinoid concentration [18], unmanaged plants would be induced shortly after establishment, making the supplemental 20-h photoperiod a precondition for vegetative development. Photoperiod is thus permissive for inflorescence development, whereas thermal time sets its rate; genotype acts on biomass magnitude and reproductive allocation, not on timing.

Separating genotype from management in the reproductive thresholds would require staggering the transfer date among progenies or including photoperiod-insensitive genotypes; the present design fixes that sequence for all three. Conservation was nonetheless not confined to the vegetative phase — a common inflection parameter sufficed for every organ, flower included — and the pre-

inductive thresholds were reached with no shared trigger. What remains open is generalisation to other photoperiod regimes, not the agreement itself.

3.2. Thermal-Time-Based Modeling of Biomass Accumulation

The biomass accumulation patterns observed here are corroborated by Schober et al. [5], who studied medicinal *Cannabis sativa* L. in a greenhouse using growing degree days (GDD) as the explanatory variable. They fitted logistic functions to organ-level biomass during flowering ($R^2 = 0.89\text{--}0.97$) and used phase-specific base temperatures (1.9 °C vegetative, 11.3 °C generative). The resulting logistic trajectory has three segments matching the subdivision of the flowering phase proposed in this study. The full correspondence between the phases delimited here, the decimal code of Mediavilla et al. [26] and the GDD thresholds is given in Appendix A (Table A3). In the same work, inflorescence and cannabidiol (CBD) yield rose linearly with GDD while harvest index stayed equivalent across growing media (≈ 0.56) — indicating that allocation tracks development rather than the growing environment.

The step change in T_b from 1.9 °C to 11.3 °C at flowering onset introduces a discontinuity in the accumulation rate: at a mean daily temperature of 21 °C, the same day contributes 19.1 °Cd before the transition and 9.7 °Cd after it. This is a modelling convention rather than a physiological threshold. In Amaducci et al. [14] the two values belong to a beta-function response to hourly temperature accumulated as physiological development days, with 11.3 °C assigned to the photo-inductive and flower-development phases; their own sensitivity analysis showed the model to be weakly responsive to T_b , and the authors note the limited experimental basis for the post-juvenile value. Transposing both values into a linear degree-day sum, as done here and by Schober et al. [5], is therefore an operational approximation: thermal sums before and after the transition are not strictly commensurable, and comparison with studies using a single T_b requires caution.

In the present study, three-parameter log-logistic (LL.3) models described organ-level biomass accumulation as a function of GDD, with R^2 between 0.76 and 0.98. Differences among cultivars lay in the magnitude (asymptotic biomass) and rate of accumulation, not in thermal timing: the thermal thresholds did not differ detectably among the S1 progenies, whereas productive capacity was set by genotype.

Evidence of a different kind comes from Reichel et al. [34], who grew three medicinal cannabis cultivars under contrasting light spectra. Despite the difference in light, each cultivar retained its characteristic morphology and growth pattern; the only marked response to spectrum was stem elongation under a low red/far-red ratio (shade avoidance). Thus, in an experiment where the manipulated environmental factor was light rather than temperature, genotypic traits again prevailed over the environment — the same genotype-over-environment pattern observed here across the GDD axis.

Process-based modeling converges with these results. Hopf et al. [35], adapting the CROPGRO framework, simulated above-ground biomass (Willmott's $d = 0.91$) and flowering timing ($\pm 4\text{--}5$ days). This capacity to simultaneously capture both phenological transitions and biomass dynamics validates the use of thermal-time-based sigmoidal models as a well-supported framework for accurately evaluating genotypic performance and growth trajectories under tropical conditions.

3.3. Biomass Partitioning and Harvest Index Dynamics

Across treatments, the harvest-index values estimated here fall within the range reported for medicinal *Cannabis sativa* under favourable conditions. Alden and Faust [19] recorded stable values of $\approx 0.60\text{--}0.65$ across management treatments, and Simonutti et al. [36] found no response to supplemental phosphorus and potassium during flowering, indicating that allocation to flowers is largely insensitive to agronomic and nutritional intervention. Pena et al. [37] qualified this stability: harvest index was equivalent between contrasting genotypes under non-stress conditions but declined in the CBD-dominant genotype under drought. Water supply was non-limiting here, so the

present values correspond to their non-stress condition; whether the thresholds hold under deficit remains open.

Harvest index differed among progenies, DOC exceeding both PW and SCH, and the absence of interaction with sampling week indicates that this ranking held throughout the reproductive phase (Section 2.3). Because developmental timing did not differ detectably (Section 2.2), the difference reflects genotype-dependent partitioning to floral biomass rather than a phenological shift.

Comparison of these values with the literature depends on where the boundary of the floral compartment is drawn, and that boundary is not standardised for the species. Ahrens et al. [38] obtained 0.57–0.60 in two THC-dominant cultivars grown indoors, counting sugar leaves as part of the inflorescence; here sugar leaves were assigned to the leaf compartment, which places the numerator lower for the same plant. Naim-Feil et al. [24] report 0.10–0.30 for a controlled-environment panel, but their inflorescences were trimmed and refined before weighing, so the material removed in trimming leaves the numerator and enters the denominator. Values obtained under different conventions are therefore not interchangeable, and the convention adopted should be stated whenever harvest index is reported for this crop.

Whereas these studies treat harvest index as a final value, the present results show that its formation is a continuous, thermally regulated process. Harvest index rose throughout reproductive development, with weekly increments declining toward the end of the cycle and then rising again at the final sampling (~2120 GDD); a plateau was not observed, as plants were harvested earlier, and stabilization was estimated by the model at ~2263 GDD, beyond the sampled window. This continuous accumulation, without an early plateau, is consistent with Alden and Faust [39], and the late-stage rebound is consistent with the canopy senescence reported during late flowering [40].

These findings indicate that harvest index alone cannot define physiological maturity or optimal harvest timing, and that similar thermal accumulation does not guarantee equivalent reproductive yield: Thongplew et al. [41] reported nearly identical cumulative thermal time at harvest across contrasting seasons, yet reproductive yield and biomass partitioning differed substantially. Harvest index should therefore be interpreted together with the thermal trajectory of floral biomass accumulation.

3.4. Morphometric Predictors Support Indirect Selection for Total and Floral Biomass

The descriptor most closely associated with biomass changes with the tissue considered. Axial traits — plant height and basal stem diameter — led for total biomass, whereas crown diameter led for floral biomass in two of the three progenies (Section 2.4). The reordering is consistent with where inflorescences are borne: height and stem diameter integrate cumulative axial growth, whereas crown expansion integrates the lateral branching that carries the flowers. The same ordering held within individual sampling weeks.

The fall in explanatory power between total and floral biomass locates the point at which size ceases to track yield. Floral biomass depends not only on how much a plant grows but on the fraction of that growth directed to inflorescences, which differed among progenies (Section 3.3). Selection on size alone therefore favours large plants rather than plants that partition strongly to flowers, and crown diameter sits closer to that partitioning step. Naim-Feil et al. [24] likewise found floral bud dry weight uncorrelated with days to maturation.

Carlson et al. [23] reached a comparable position from different material, identifying basal stem diameter as the best single selection criterion for floral biomass in field-grown hemp, with canopy kite area among their three leading predictors. Which descriptor ranks first differs — basal stem diameter there, crown diameter in two of three progenies here — as expected when material and environment differ, and calibration within the target population accommodates that difference.

Crown diameter is measured with a tape on an intact plant, before harvest, drying and weighing, so it could screen plants before the costliest phenotyping steps. Its reach is set by the stage-controlled results: at a common stage it added 0.6 percentage points to what thermal time already explained, with a mean within-week correlation of 0.31 — enough to rank plants within a cohort, but not to

replace measurement of the harvested product. Any such use requires calibration within the family under selection, since coefficients differed among progenies, and a measurement window fixed developmentally rather than by calendar date, supplied by the thermal thresholds reported here (Section 2.2) in growing degree-days, which transfer across environments as days after transplanting do not.

Crown diameter predicts how much floral biomass a plant produces, not how much active resin that biomass carries. Four attributes define productive capacity in medicinal cannabis, and the available descriptors cover them unevenly. Cannabinoid concentration is scored by UPOV TG/276/2 [22] as THC, CBD and CBG content. Cannabinoid yield per plant — the product of concentration and floral biomass — has no standardised descriptor, although it is what breeding programmes ultimately select for. Trichome density is sometimes proposed as a morphological proxy, but it does not consistently predict cannabinoid content across genotypes, since gland size, maturity and biosynthetic enzyme activity contribute independently [42]. Inflorescence productivity per plant is the attribute crown diameter addresses here; TG/276/2 introduced separate variety types for horticultural cultivation in its 2025 revision, yet plant height remains its only characteristic of whole-plant size. Descriptors selected for distinctness, uniformity and stability need not capture productive capacity, so a complementary set is required for medicinal breeding.

4. Materials and Methods

4.1. Location

The experiment was conducted at a medical cannabis patient association, APEPI (Association for the Support of Research and Patients Using Medical Cannabis), located in the rural area of the municipality of Paty de Alferes, Rio de Janeiro State, Brazil (22°25'44" S, 43°24'08" W; 624 m above mean sea level).

According to the Köppen climate classification system, the study area is classified as Cfa (humid subtropical climate), characterized by hot and humid summers, mild winters, and well-distributed annual precipitation, representing typical climatic conditions of southeastern Brazil [43]. The classification refers to long-term climatic normals; rainfall during the 2024 experimental season was below the local normal, particularly in September. The Cfa classification reflects the elevation of the site (624 m); at 22°25' S the site lies within the tropics, and the daylength regime is that of a tropical latitude. References to tropical conditions throughout this work denote this photoperiodic regime rather than the thermal classification.

4.2. Plant Material and Photoperiod Conditions

Seeds used in this study were obtained through chemical sex reversal of female mother plants via the application of a 3 mM silver thiosulfate (STS) solution, an ethylene-action inhibitor that induces the formation of viable male flowers in genetically female (XX) plants [44]. Ethylene-mediated sex reversal in *Cannabis sativa* is well established and involves early transcriptional reprogramming preceding floral development [45]. Three S1 progenies, derived from selfed clonal cultivars and consisting exclusively of female plants, were evaluated, one from each of the cultivars Purple Wreck (THC-dominant), Doctor (CBD-dominant) and Schanti (balanced THC:CBD ratio). Chemotype refers to the parent cultivar; cannabinoid content was not determined in the S1 individuals evaluated here.

The three medicinal cannabis S1 progenies were cultivated under greenhouse conditions during the vegetative phase under supplemental lighting providing a 20-h photoperiod. Artificial lighting was supplied using 9 W LED lamps arranged in a linear configuration and spaced at 1 m intervals, resulting in an approximate power density of 3.6 W m⁻².

This corresponds to an estimated photon flux density of ~6 μmol m⁻² s⁻¹ at canopy level, assuming a conversion efficiency of 1.7 μmol s⁻¹ W⁻¹ for white LED lamps. This light intensity promotes photoperiod maintenance (night interruption) in photoperiod-sensitive species and is

sufficient to suppress floral induction, without significantly contributing to net photosynthetic carbon assimilation.



Figure 7. Medicinal *Cannabis sativa* L. plants during the vegetative phase grown in a greenhouse under supplemental lighting (20-h photoperiod). (a) Young plants at the third week of vegetative growth. (b) Plants at the fourth week of the vegetative stage.

On 5 September 2024 all three progenies were transferred to open-field conditions and exposed to the natural, non-supplemented photoperiod throughout the spring season (September to November). The transfer changed photoperiod, incident radiation, vapour pressure deficit, wind and rainfall exposure, and the thermal environment simultaneously. Thresholds reached after this point therefore describe developmental progression following a defined management transition and are not attributed to temperature in isolation.



Figure 8. Flowering phase of medicinal cannabis cultivated under open-field conditions during the 2024 growing season. (a) General view of the experimental area with plants at the flowering stage. (b) Detailed view of the crop rows, arranged in a uniform and aligned spatial configuration.

4.3. Crop Management Practices

Dry seeds were initially subjected to water imbibition overnight and subsequently germinated on moist germination paper. During the propagation phase, seeds exhibiting radicle protrusion were transplanted into 1 L pots filled with a simplified acclimatization substrate composed of Carolina Soil (inert matrix, 70%), cured manure (10%), organic compost (10%), and earthworm humus (10%).

As vegetative development progressed, plants were subsequently transferred to 19 L cultivation bags containing a vegetative substrate consisting of earthworm humus (10%), organic compost (20%), clay soil (5%), cured manure (20%), sand (10%), raw rice husk (10%), coconut fiber (15%), and bagasse or leaf litter (10%).

Fertilization was performed using powdered fertilizer applications throughout plant development. During the vegetative phase, 250 grams of incorporated fertilization were applied per plant, consisting of thermophosphate (58%), castor cake (12%), potassium sulfate (8%), bone meal (6%), Ekosil® (6%; 8% K₂O), cured manure (7%), and rice husk (5%). A second topdressing application was performed at mid-flowering, totaling 120 g per plant and composed of potassium sulfate (43%), bone meal (29%), and rice husk (29%).

Throughout the experiment, plants were irrigated manually with continuous flow to field capacity, observed by the runoff, four times per week; during the final three weeks of flowering, irrigation frequency was reduced to twice per week. During the flowering stage under open-field conditions, plants were also subjected to natural rainfall, which influenced water availability. For phytosanitary management, matrine was applied three times at the end of the vegetative phase, at five-day intervals.

4.4. Experimental Design and Sampling Procedures

A completely randomized design was adopted, with plants spaced 0.7 m apart within rows and 1.2 m between rows. Destructive sampling was performed at weekly intervals, with five plants collected from each S1 population (corresponding to one genotype), totaling 15 individuals per sampling event. Over the 14-week experimental period, 210 plants were individually evaluated. Following collection, plants were partitioned into roots, stems, and leaves during the vegetative phase, whereas flowers were included only during the reproductive phase, when inflorescences were present.

Bracts were weighed as part of the inflorescence, whereas sugar leaves were assigned to the leaf compartment. The harvest index was calculated as floral dry biomass divided by total above-ground dry biomass (flowers, stems and leaves); roots were excluded from the denominator.

The plant material was placed into separate breathable bags and properly labeled according to individual plant and organ type. Samples were then oven-dried at 65 °C in a forced-air chamber for at least 24 h, or until constant weight was achieved, indicating complete moisture removal, and subsequently weighed to determine the dry biomass of each organ

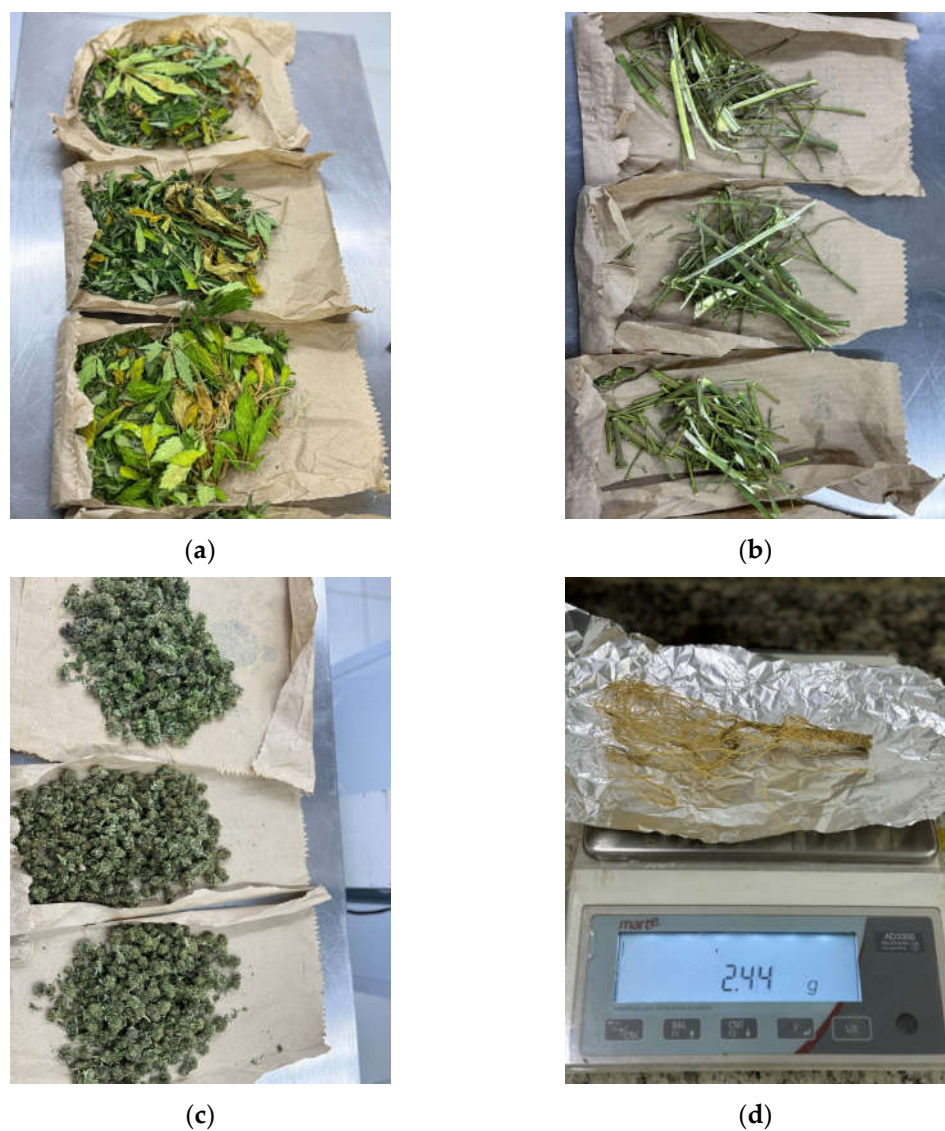


Figure 9. Processing and weighing procedures for plant organ biomass determination. Dried plant organs arranged and properly labeled by individual plant and organ type; (a) leaves, (b) stems, (c) inflorescences, and (d) weighing of cleaned root samples.

In addition to biomass quantification, phenotypic characterization was conducted using internationally recognized Cannabis descriptors to document morphological variation throughout plant development.

4.5. Statistical Analysis

Growing degree-days (GDD) were calculated by the simple average method with an upper cut-off, summed cumulatively from the onset of propagation (10 July 2024). Daily maximum and minimum air temperature were recorded by a Tinytag data logger throughout the experimental period (10 July – 31 October 2024), inside the greenhouse during propagation and vegetative growth and in the field after the greenhouse-to-field transition described in Section 4.2. The logger was not fitted with a meteorological radiation shield, so maximum readings on clear days can overestimate true air temperature; the ceiling temperature (Tc) of 40.0 °C limits the influence of this effect on the reported GDD values. Data from the A637 – Paty do Alferes – Avelar meteorological station [25] were used exclusively for the regional climatic characterization presented in Section 4.1 and did not enter the calculation of thermal time. Daily thermal time (DTT) on day t was obtained as

$$DTT_t = \min(T_c) - T_b, \tag{1}$$

where $T_{max,t}$ and $T_{min,t}$ are the daily maximum and minimum air temperatures (°C) on day t , T_c is the ceiling temperature and T_b the base temperature, both in °C. Cardinal temperatures were adopted from Amaducci et al. [14] rather than estimated from the present data: $T_b = 1.9$ °C for the propagation and vegetative phases and 11.3 °C from flowering onward, with $T_c = 40.0$ °C applied throughout the experiment. Schober et al. [5] applied the same two base temperatures and ceiling to medicinal cannabis under greenhouse conditions.

Biomass accumulation curves were modeled as a function of accumulated growing degree-days (GDD) using a three-parameter log-logistic function (LL.3), expressed as

$$f(x) = \frac{d}{1 + \exp(b(\log(x) - \log(e)))} \tag{2}$$

where, in Equation (2), x is the accumulated GDD. Parameter d represents the upper asymptote (maximum biomass), e corresponds to the inflection point (ED50), indicating the GDD at which biomass reaches 50% of d , and b defines the slope around the inflection point. Models were fitted by nonlinear regression independently for each S1 progeny and to the pooled dataset comprising all three progenies ($n = 210$), and goodness-of-fit was evaluated through residual analysis and visual inspection of observed versus fitted values.

Phenological thresholds were derived from the fitted curves, each transition being defined as the accumulated GDD at which a given curve reached a fixed proportion of its upper asymptote d , obtained by inverting the LL.3 function. Onset of active vegetative growth was set at 5% of total biomass and stem elongation at 50% of stem biomass. The decimal code of Mediavilla et al. [26] subdivides the vegetative stage by node number rather than by physiological phase; the division adopted here between an early vegetative phase and a phase of active vegetative growth is therefore an operational criterion of the present study, defined by the point at which total biomass reaches 5% of its asymptote. The midpoint of the fitted stem-biomass curve marks maximum stem elongation within that second phase. The flowering onset, onset of floral biomass accumulation and inflorescence formation were set at 5%, 10% and 50% of floral biomass, respectively, and onset of inflorescence maturation at 90%. Stabilization of the harvest index was defined as 95% of the asymptote of the fitted harvest-index curve, beyond which further gain per unit of thermal time is negligible. Ninety-five percent confidence intervals for each threshold were obtained by the delta method from the covariance matrix of the fitted parameters. These proportions are conventions rather than physiological constants, and the thresholds are only moderately sensitive to them: replacing the 5% criterion for the vegetative–reproductive transition by 3% or 8% shifts the pooled estimate by about 80 GDD in either direction, while the spread among progenies remains between 34 and 46 GDD and within the confidence intervals in every case. The choice of proportion therefore affects the absolute reference values, not the conclusion that the progenies are statistically indistinguishable.

Destructive sampling ended at approximately 2120 GDD. Thresholds estimated beyond this value, namely stabilization of the harvest index and inflorescence maturation, are extrapolations of the fitted models and are reported as projections throughout the text.

Relationships between morphometric descriptors and biomass were modelled separately for each S1 progeny, with total or floral dry biomass as the response and a single descriptor as the predictor. Plant height, basal stem diameter (D1) and crown diameters (dc1, dc2) approached saturation over the observed range of the descriptor and were fitted by nonlinear least squares to a three-parameter logistic function, with the upper asymptote K fixed at the maximum biomass observed in the dataset rather than estimated. The remaining descriptors were fitted as simple linear regressions by ordinary least squares.

Fixing K constrains the fitted curve to the observed range of biomass and stabilizes the two remaining parameters, but the asymptote is then taken from the same data it describes. Fit statistics

of the logistic models are therefore conditional on that value and are not directly comparable with those of the linear models. The p-value reported for each model tests the null hypothesis that the descriptor term is zero — the regression slope, by F test, in the linear models, and the rate parameter, by Wald test, in the logistic models — and R^2 is the ordinary coefficient of determination for the former and a pseudo- R^2 ($1 - SS_{res}/SS_{tot}$) for the latter.

Harvest index was compared among progenies by two-way analysis of variance with progeny and sampling week as fixed factors, restricted to the reproductive-phase samplings in which floral biomass was present in every plant (weeks 8–14; $n = 35$ per progeny). Homogeneity of variances was confirmed by Levene's test ($p = 0.85$), and means adjusted for sampling week were separated by Tukey's HSD.

Two additional analyses supported the interpretation of these models. First, the hypothesis of a common thermal positioning among progenies was tested by comparing nested log-logistic models in which the inflection parameter e , the asymptote d , or both were allowed to vary among progenies, using F tests on the residual sums of squares; pairwise differences in e were bootstrapped (2000 resamples, stratified by progeny and sampling week) to obtain confidence intervals for an equivalence assessment. Second, because descriptors and biomass both increase with thermal time, descriptor effects were re-estimated with developmental stage held constant: floral biomass was regressed on accumulated GDD with and without each descriptor over the reproductive window, the increment in explained variation was assessed by leave-one-week-out cross-validation, and within-week Pearson correlations between each descriptor and floral biomass were computed.

5. Conclusions

Thermal time described the development of medicinal *Cannabis sativa* L. under tropical conditions reliably, growth following a sigmoidal trajectory with transitions at well-defined GDD thresholds. Under the well-watered conditions of a single season, thresholds were statistically indistinguishable among the three S1 progenies: allowing thermal positioning to differ among progenies did not improve fit for any organ, whereas allowing the asymptote to differ did. Progenies therefore differed in biomass magnitude, accumulation rate and reproductive allocation rather than in developmental timing. Pre-induction thresholds were reached under the constant 20-h photoperiod and reproductive thresholds followed a common transfer to short days, making the latter management-conditional reference values rather than intrinsic requirements for induction. Floral biomass and harvest index were still rising at the end of sampling (~2120 GDD); their projected stabilization points lie beyond the sampled window and the floral asymptote was imprecisely estimated (standard errors of 2.7–17.5 g). Crown diameter, absent from UPOV TG/276/2, showed the strongest association with floral biomass, yet at a common developmental stage no descriptor added appreciably to thermal time.

Together, these results establish thermal accumulation as a reliable predictor of growth and reproductive allocation in medicinal cannabis. They further indicate that breeding and cultivar registration for this end use will require descriptors tailored to tropical medicinal production — inflorescence productivity per plant, resin yield per gram of dried inflorescence, resin potency and quality (terpenes and minor cannabinoids), and plant-architecture and maturity-group descriptors — complementing the thermal-time framework and reference GDD values developed here.

6. Patents

This section is not mandatory but may be added if there are patents resulting from the work reported in this manuscript.

Author Contributions: Conceptualization, R.T.T. and D.J.H.S.; methodology, R.T.T. and D.J.H.S.; validation, M.M.F., T.O.V.K., A.F.S.R. and L.U.L.S.; formal analysis, A.F.S.R. and H.M.T.; investigation, R.T.T. and M.M.F.; resources, M.M.F.; data curation, R.T.T. and H.M.T.; writing—original draft preparation, R.T.T. and H.M.T.;

writing—review and editing, R.T.T., D.J.H.S., H.M.T. and L.U.L.S.; visualization, R.T.T., D.J.H.S., H.M.T. and L.U.L.S.; supervision, D.J.H.S.; project administration, R.T.T.; funding acquisition, M.M.F. and D.J.H.S. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

APEPI	Associação de Apoio à Pesquisa e Pacientes de Cannabis Medicinal
CBD	Cannabidiol
CBG	Cannabigerol
dc1, dc2	Crown diameters (first and second measurement axes)
D1	Basal stem diameter
D2	Internode stem diameter
DOC	Doctor (cultivar)
GDD	Growing degree days
HI	Harvest index
INMET	Instituto Nacional de Meteorologia (Brazilian National Institute of Meteorology)
LL.3	Three-parameter log-logistic model
PW	Purple Wreck (cultivar)
S1	First selfed generation
SCH	Schanti (cultivar)
Tb	Base temperature
Tc	Ceiling temperature

THC Δ9-Tetrahydrocannabinol

UPOV International Union for the Protection of New Varieties of Plants

Appendix A

Table A1. Parameter estimates of descriptor-based models for total above-ground biomass and for floral biomass in three S1 progenies of Cannabis sativa L. (DOC, PW, SCH). n = 70 per descriptor and progeny in every model.

Descriptor	Model	Total above-ground biomass				Floral biomass			
		Interce pt	Coeffic ient	p- value	R ²	Interce pt	Coeffic ient	p- value	R ²
Plant height – DOC	logistic	-4.919	0.066	0.001	0.819	-7.743	0.089	0.010	0.561
Plant height – PW	logistic	-5.651	0.072	<0.001	0.859	-11.046	0.121	0.004	0.643
Plant height – SCH	logistic	-4.921	0.062	<0.001	0.858	-7.429	0.076	0.004	0.502
Basal stem diameter (D1) – DOC	logistic	-5.085	0.449	0.001	0.852	-7.952	0.600	0.008	0.590
Basal stem diameter (D1) – PW	logistic	-5.356	0.515	<0.001	0.849	-8.577	0.691	0.002	0.629
Basal stem diameter (D1) – SCH	logistic	-4.589	0.379	<0.001	0.825	-6.523	0.422	0.002	0.531
Internode stem diameter (D2) – DOC	linear	-11.083	9.389	<0.001	0.168	-11.151	4.362	<0.001	0.209
Internode stem diameter (D2) – PW	linear	-14.936	9.886	<0.001	0.251	-7.932	3.069	<0.001	0.187
Internode stem diameter (D2) – SCH	linear	9.586	5.861	0.052	0.054	1.157	1.389	0.216	0.022
Internode length – DOC	linear	23.933	0.083	0.617	0.004	5.843	0.017	0.806	0.001
Internode length – PW	linear	27.205	0.079	0.619	0.004	5.176	0.024	0.675	0.003
Internode length – SCH	linear	38.074	-0.088	0.605	0.004	7.744	-0.017	0.784	0.001
Leaflet number (leaf 1) – DOC	linear	-7.163	4.872	0.001	0.154	-0.370	0.975	0.117	0.036
Leaflet number (leaf 1) – PW	linear	-34.960	8.793	<0.001	0.415	-7.099	1.788	0.002	0.133
Leaflet number (leaf 1) – SCH	linear	-17.348	6.396	0.002	0.135	4.884	0.261	0.738	0.002
Leaflet length (leaf 1) – DOC	linear	37.739	-0.124	0.249	0.019	8.365	-0.022	0.625	0.004
Leaflet length (leaf 1) – PW	linear	38.222	-0.075	0.466	0.008	8.494	-0.022	0.544	0.005
Leaflet length (leaf 1) – SCH	linear	14.505	0.205	0.145	0.031	1.947	0.052	0.314	0.015

Descriptor	Model	Total above-ground biomass				Floral biomass			
		Intercept	Coefficient	p-value	R ²	Intercept	Coefficient	p-value	R ²
Leaflet width (leaf 1) – DOC	linear	66.832	-1.883	<0.001	0.403	16.189	-0.459	0.002	0.138
Leaflet width (leaf 1) – PW	linear	78.141	-1.799	<0.001	0.374	18.590	-0.468	<0.001	0.196
Leaflet width (leaf 1) – SCH	linear	86.512	-2.594	<0.001	0.423	18.541	-0.573	0.001	0.152
Petiole length (leaf 1) – DOC	linear	2.309	0.680	<0.001	0.227	-3.780	0.284	<0.001	0.229
Petiole length (leaf 1) – PW	linear	15.078	0.322	0.007	0.103	0.207	0.124	0.004	0.118
Petiole length (leaf 1) – SCH	linear	22.239	0.275	0.078	0.045	3.807	0.073	0.206	0.023
Leaflet number (leaf 2) – DOC	linear	-11.029	5.427	<0.001	0.176	-1.058	1.074	0.097	0.040
Leaflet number (leaf 2) – PW	linear	-41.683	9.564	<0.001	0.486	-10.081	2.158	<0.001	0.191
Leaflet number (leaf 2) – SCH	linear	-10.708	5.602	0.005	0.110	6.583	0.050	0.947	0.000
Leaflet length (leaf 2) – DOC	linear	37.355	-0.119	0.247	0.020	9.656	-0.036	0.396	0.011
Leaflet length (leaf 2) – PW	linear	39.812	-0.091	0.375	0.012	9.352	-0.031	0.399	0.010
Leaflet length (leaf 2) – SCH	linear	11.217	0.240	0.085	0.043	0.102	0.072	0.163	0.028
Leaflet width (leaf 2) – DOC	linear	61.690	-1.606	<0.001	0.314	13.832	-0.341	0.016	0.082
Leaflet width (leaf 2) – PW	linear	76.577	-1.734	<0.001	0.368	18.218	-0.453	<0.001	0.194
Leaflet width (leaf 2) – SCH	linear	90.623	-2.833	<0.001	0.431	19.055	-0.606	0.001	0.145
Petiole length (leaf 2) – DOC	linear	3.012	0.653	<0.001	0.210	-3.214	0.265	<0.001	0.200
Petiole length (leaf 2) – PW	linear	14.301	0.347	0.005	0.113	0.516	0.121	0.006	0.106
Petiole length (leaf 2) – SCH	linear	24.747	0.228	0.183	0.026	3.456	0.085	0.177	0.027
Crown diameter (dc1) – DOC	logistic	-3.250	0.074	0.001	0.842	-5.729	0.105	0.016	0.569
Crown diameter (dc1) – PW	logistic	-2.592	0.069	<0.001	0.792	-5.815	0.114	0.001	0.765

Descriptor	Model	Total above-ground biomass				Floral biomass			
		Interce pt	Coeffic ient	p- value	R ²	Interce pt	Coeffic ient	p- value	R ²
Crown diameter (dc1) – SCH	logistic	-2.725	0.080	<0.001	0.783	-4.641	0.096	0.006	0.450
Crown diameter (dc2) – DOC	logistic	-3.204	0.078	<0.001	0.874	-6.059	0.118	0.010	0.646
Crown diameter (dc2) – PW	logistic	-2.608	0.077	<0.001	0.805	-5.292	0.113	0.001	0.702
Crown diameter (dc2) – SCH	logistic	-2.593	0.080	<0.001	0.752	-4.435	0.095	0.004	0.451

Model type indicates the functional form fitted for each descriptor: logistic models (three-parameter, K fixed at the observed maximum) for height, stem diameter (D1) and crown diameters (dc1, dc2); and simple linear models for the remaining descriptors. Intercepts and coefficients are expressed on the scale of each model and are therefore not directly comparable across model types. p-values test the null hypothesis that the descriptor term is zero: the regression slope, by F test, in the linear models, and the rate parameter, by Wald test, in the logistic models. All models contain a single predictor, so the adjusted R² differs from R² by less than 0.02 throughout and is not reported. For the logistic models R² is a pseudo-R² computed as 1 – SSres/SStot, conditional on the fixed K.

Table A2. Parameter estimates of three-parameter log-logistic (LL.3) models of organ-specific biomass accumulation and harvest index as a function of accumulated growing degree days (GDD) in three S1 progenies of Cannabis sativa L. b, slope at the inflection point; d, upper asymptote (g, or dimensionless for harvest index); e, GDD at the inflection point. Standard errors in parentheses. R² is calculated as 1 – SSres/SStot; RMSE is on the scale of the response.

Organ	Progeny	b (SE)	d (SE)	e (SE), GDD	n	R ²	RMSE
Total biomass	DOC	-6.54 (0.98)	58.29 (3.79)	1422 (42)	70	0.918	6.30
Total biomass	PW	-5.76 (0.77)	71.80 (5.23)	1469 (51)	70	0.935	6.33
Total biomass	SCH	-5.54 (0.98)	76.23 (7.06)	1429 (66)	70	0.889	9.12
Root biomass	DOC	-17.18 (4.09)	6.38 (0.20)	1255 (18)	70	0.878	1.02
Root biomass	PW	-9.68 (2.14)	5.56 (0.25)	1231 (31)	70	0.829	1.03
Root biomass	SCH	-10.87 (2.71)	7.08 (0.32)	1207 (32)	70	0.797	1.48
Stem biomass	DOC	-11.16 (1.86)	12.42 (0.43)	1325 (21)	70	0.911	1.64
Stem biomass	PW	-8.49 (1.24)	16.77 (0.68)	1338 (25)	70	0.920	1.96
Stem biomass	SCH	-8.22 (1.83)	19.56 (1.22)	1326 (39)	70	0.833	3.49
Leaf biomass	DOC	-11.56 (2.50)	15.32 (0.56)	1172 (27)	70	0.837	2.77
Leaf biomass	PW	-8.95 (1.56)	20.42 (0.75)	1191 (26)	70	0.874	3.06
Leaf biomass	SCH	-10.40 (2.81)	19.29 (0.90)	1130 (35)	70	0.757	4.37
Flower biomass	DOC	-7.97 (1.62)	45.96 (17.47)	2058 (195)	70	0.903	2.84
Flower biomass	PW	-11.62 (1.53)	28.80 (2.74)	1839 (39)	70	0.949	2.01
Flower biomass	SCH	-9.32 (1.24)	46.01 (8.96)	1997 (89)	70	0.954	2.15
Harvest index	DOC	-11.43 (1.18)	0.520 (0.027)	1721 (24)	70	0.965	0.035
Harvest index	PW	-12.33 (0.99)	0.448 (0.018)	1750 (17)	70	0.979	0.023
Harvest index	SCH	-11.10 (1.07)	0.507 (0.031)	1783 (27)	70	0.970	0.029

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