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Drought meets nutrition: An integrated framework for *Eucalyptus* Responses to water deficit under warming and elevated CO_2

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Abstract
Eucalyptus is one of the world's most widely planted hardwood genera and is increasingly cultivated in environments where water availability constrains productivity. Research on eucalypt drought responses is extensive but fragmented across morphology, gas exchange, tissue water relations, hydraulics, nutrition, metabolites and molecular responses. This review integrates field, nursery and controlled-environment evidence to develop a multi-axis framework linking water access, stomatal regulation, tissue tolerance and xylem safety with potassium (K), phosphorus (P), sodium (Na), elevated CO_2 and heat. The synthesis indicates that drought performance cannot be represented by a single tolerance trait: genotypes may avoid dehydration through deep water access and stomatal control, tolerate low water potentials through osmotic or elastic adjustment, or maintain function through resistant xylem. K is a particularly important modifier because it can increase photosynthesis, leaf area, transpiration and water-use efficiency for stemwood production, while simultaneously increasing water demand and, under some conditions, narrowing hydraulic safety margins. P limitation can constrain growth and the response to elevated CO_2, whereas combined drought and heat generate responses that are not predictable from either stress alone. Across the literature, inference is weakened by short experiments, restricted root volume, single-clone comparisons, small sample sizes and limited integration of nutrition with hydraulics. We propose a research agenda centred on replicated factorial field experiments, explicit hydraulic endpoints, genotype × nutrition × water interactions, recovery and repeated-stress measurements, and process-based models that couple carbon, water and nutrient cycles.

Keywords: Eucalyptus, drought, water-use efficiency, hydraulic safety margin, potassium, phosphorus, sodium, osmotic adjustment, heatwave, elevated CO_2, root:shoot allocation

Introduction

Eucalyptus and its close relatives occupy a broad climatic range, from humid tropical margins to Mediterranean, semi-arid and cool-temperate systems. Their rapid growth and wood quality underpin major plantation industries, but high productivity is frequently accompanied by substantial water use. This makes the genus a useful model for examining how productivity, water limitation and nutrient supply interact under climate change.

Three pressures increasingly occur together: more frequent or severe drought, hotter episodes that raise atmospheric demand and leaf temperature, and nutrient constraints that can limit the capacity of trees to exploit elevated CO_2. Field studies linking drought to xylem embolism, together with plantation experiments manipulating K and throughfall, show that water availability and nutrition cannot be interpreted independently.

The purpose of this review is therefore not to rank species by a single drought-tolerance trait, but to integrate four functional axes—water access and avoidance, tissue tolerance, hydraulic safety and nutritional status—and to identify where their interactions alter growth, water use and survival.

- **Drought is intensifying.** The 2019 drought in eastern Australia produced canopy dieback that field work tied to xylem embolism (Nolan *et al*., 2021) [39].
- **Heatwaves are increasingly co-occurring with drought.** Heat can exacerbate drought-induced mortality risk (Prokopavicius *et al*., 2022; Correia *et al*., 2018) [7, 40].
- **Nutrients increasingly constrain the benefits of other global-change drivers.** CO_2 fertilisation, for instance, is limited by P in mature eucalypt forest (Ellsworth *et al*., 2017; Jiang *et al*., 2024) [24, 33].

Since the 2000s, studies from Australia, Portugal, Brazil, Argentina, India and Pakistan have documented drought effects on eucalypts. They have measured leaf water potential and stomatal conductance (White *et al*., 2000) [19], pressure–volume (P–V) parameters (White *et al*., 2000; Guarnaschelli *et al*., 2006) [11, 19], root hydraulics (Costa e Silva *et al*., 2004) [8], morphology (Susiluoto and Berninger, 2007; Yousaf *et al*., 2018; Varma *et al*., 2020) [16, 18, 20], metabolomes and transcripts (Correia *et al*., 2018; Amrutha *et al*., 2019) [1, 7], and nutritional modulation (Battie-Laclau *et al*., 2014a,b, 2016; Mateus *et al*., 2022; Santos *et al*., 2021) [5, 13, 15]. These bodies of work largely developed in parallel, and their conclusions are rarely placed side by side.

Highlights

- Eucalypt drought performance is a coordinated syndrome involving water access, stomatal regulation, tissue tolerance and xylem safety.

- Potassium can increase productivity and stemwood water-use efficiency while also increasing canopy water demand and hydraulic exposure.
- Hydraulic safety margins provide a useful bridge between stomatal behaviour, embolism resistance and drought mortality risk.
- Phosphorus availability constrains growth and can limit the benefits of elevated CO_2 in mature eucalypt systems.
- Field-scale, multi-factor experiments integrating water, nutrition, warming and CO_2 remain a major research priority.

Eucalyptus is the world's most widely planted hardwood genus, and it is increasingly grown where water, not light or temperature, sets the ceiling on productivity. Two decades of work have produced a large but fragmented literature on how eucalypts respond to drought. Most studies address a single level of organisation (leaf gas exchange, root allocation, hydraulics, metabolites or transcripts), a single stress, or a single nutrient status. This review synthesises 20 core studies, spanning field and nursery experiments, potassium (K) and phosphorus (P) manipulations, and CO_2, heat and combined-stress work. It complements them with recent hydraulic, nutritional and heatwave literature (2018–2025).

The synthesis leads to five conclusions.

- **Eucalypt drought strategies are best described as coordinated syndromes, not single traits:** Access to water (root depth and allocation), stomatal control, tissue-level tolerance (osmotic and elastic adjustment, turgor-loss point) and xylem safety combine differently in different species and clones. Rankings of "drought tolerance" therefore change with the trait, the stress duration and the level of organisation measured.

- **Species that appear "tolerant" or "susceptible" may be doing different things:** *E. camaldulensis* is a stomatally sensitive avoider in the field, yet its clone Ec226 wilted severely in a short nursery dry-down. *E. leucoxylon* and *E. platypus* tolerate very low water potentials with weak stomatal control. Many apparent contradictions between studies disappear once avoidance and tolerance are separated.

- **Nutrient supply is a first-order modifier of drought response, not a background variable:** K increases stomatal conductance, leaf area, transpiration and water-use efficiency for wood production (WUE_wood). In the field it also raises water demand, narrows hydraulic safety margins and can worsen water stress during prolonged dry spells. P limitation constrains growth and photosynthesis across Australian eucalypt systems and interacts with CO_2 and drought.

- **A "safety–efficiency–nutrition" trade-off appears to govern fertilised eucalypts:** Nutrient-replete trees operate closer to their hydraulic limits to maximise carbon gain. This reframes fertilisation as a risk-allocation decision, not only a yield decision.

- **Much of the evidence base is short-term, pot-based, single-clone or under-replicated:** Field-scale, multi-factor experiments in which water, nutrients, temperature and CO_2 vary together are rare, and process-based models lack K and P submodules.

We close with a research roadmap and a decision framework for matching genotype, nutrition and site water regime.

- Drought "tolerance" in eucalypts is multi-trait, so avoidance, tolerance and hydraulic safety must be assessed separately.
- K fertilisation raises photosynthesis and WUE_wood, but in the field, it increases water demand and hydraulic constraint.
- Partial K-for-Na substitution enhances embolism resistance in pots but narrows the hydraulic safety margin relative to K-deficient plants.
- Heat and drought together elicit metabolic responses (e.g. cinnamate accumulation) that are not the sum of either stress alone.
- Elevated CO_2 benefits are constrained by P availability in mature forest, and photosynthetic acclimation to warming is limited outside the native range.

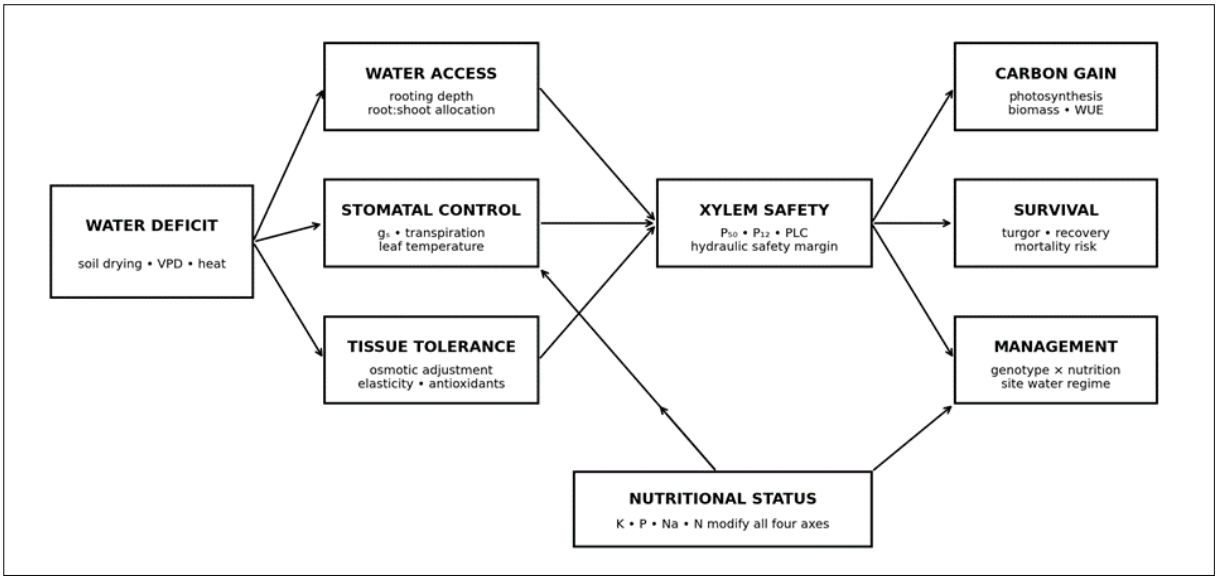


Fig 1: Integrated framework linking drought, nutrition and Eucalyptus performance

Scope and evidence base

The core evidence comprises the 20 studies supplied for this synthesis. These are experimental or review papers on eucalypt drought physiology, K/Na/P nutrition, CO_2 and heat. They were supplemented by targeted literature searches for recent work (2018–2025) on hydraulic failure, K/Na-embolism relationships, EucFACE (Eucalyptus Free-Air CO_2 Enrichment) P-limitation, and heatwave responses. This is a narrative synthesis, not a formal systematic review, and the recent literature was sampled selectively. Studies differ in scale (seedling to stand), stress type (withheld irrigation, imposed field-capacity levels, throughfall exclusion, PEG osmotic stress, natural drought) and duration (4 days to 3 years). Section 9 therefore weighs evidence by design quality instead of pooling effect sizes.

A conceptual framework for eucalypt drought responses

1. Avoidance, tolerance and hydraulic safety

We organise drought responses along three partly independent axes.

1.1 Water access and supply–demand balance (avoidance). This includes deep rooting, allocation to roots, leaf area adjustment and stomatal regulation. Tree water status is kept high by getting more water, using less, or both.

1.2 Tissue tolerance. Cells and tissues continue to function at low water potential through osmotic adjustment, elastic adjustment (lower bulk elastic modulus, ε), a low turgor-loss point and antioxidant capacity.

1.3 Hydraulic safety (xylem resistance and margins). The margin between the water potential at which stomata close (e.g. P_gs90) and the potential at which xylem embolism begins or reaches 50% (P_{12}, P_{50}) determines mortality risk (Choat *et al*., 2018; Brodribb *et al*., 2020). Mateus *et al*. (2024) [25, 26, 38] used this metric for eucalypts.

2. Why single-trait rankings mislead

Consider E. camaldulensis versus E. leucoxylon and E. platypus in Mediterranean Western Australia (White *et al*., 2000) [19]. Predawn leaf water potential (Ψ_pd) ranged only from −0.33 to −0.98 MPa in E. camaldulensis but from −1.07 to −4.07 MPa in E. platypus. (White *et al*., 2000) [19] interpret the narrow range as evidence of access to the capillary fringe of the water table (about 6 m depth), and they interpret the wide range as shallow-profile water use. E. camaldulensis was also about three times as stomatally sensitive to Ψ_pd (slope 225 versus 96 and 76 mmol m^{-2} s^{-1} MPa^{-1}). Its leaves were relatively inelastic and lost turgor at −2.4 to −2.9 MPa, whereas E. leucoxylon and E. platypus did not lose turgor until about −3.9 MPa. By tissue tolerance, the "wet-profile" species are the less tolerant. By avoidance, they are the better performers. A ranking on any one axis inverts on the other.

The same logic reconciles other apparent conflicts. Pot-grown E. camaldulensis clone Ec226 was "susceptible" in a nursery dry-down (Amrutha *et al*., 2019) [1], while field E. camaldulensis avoids drought by deep water access (White *et al*., 2000) [19]. The nursery comparison probes rapid dehydration in a confined root volume, where avoidance via rooting is impossible, and so exposes tolerance differences.

Morpho-physiological responses to water deficit

1. Growth and biomass allocation

Reduced growth and a shift of biomass toward roots are near-universal. Table 1 collates representative results.

Table 1: Representative growth and allocation responses to drought in the core studies

Study	Species / material	Stress design	Key morphological result
Costa e Silva *et al*. (2004) [8]	E. globulus clones CN5 (tolerant), ST51 (sensitive); pots	Water supplied = 50% of transpiration, 7 weeks	Total biomass ↓ ~46%, leaf area ↓ 63%; CN5 kept root growth (66% above controls at week 7) while ST51 root growth stopped after week 5
Guarnaschelli *et al*. (2006) [11]	E. globulus subsp. bicostata , 3 provenances	32-day graded preconditioning (50% → 10% of control water), then transplant	Total biomass ↓ ~20%, shoot/root ratio ↓ ~15%, RGR ↓ 32%
Susiluoto and Berninger (2007) [16]	E. microtheca seedlings	Greenhouse drought	Root allocation ↑; photosynthesis and g_s changed only modestly
Yousaf *et al*. (2018) [20]	E. camaldulensis , E. citriodora ; pots	Irrigation every 1, 5, 10, 15 days	Height, shoot fresh and dry weight fell with longer intervals; root length largest at 1 day (6.5 vs 6.1 cm)
Varma *et al*. (2020) [18]	E. tereticornis clone P-23	100/80/60/40% field capacity ± brassinosteroids (BR) ± sucrose	Shoot increment 35.7 → 12.5%; total dry weight 16.4 → 6.1 g; root length increased 5.51 → 6.59 cm
Santos *et al*. (2021) [15]	E. urophylla × camaldulensis (VM01), E. urophylla (AEC 0144)	60% and 40% field capacity × K level	With sufficient K, VM01 leaf and stem dry mass unchanged under severe stress; AEC 0144 lost 40% leaf and 52% stem dry mass
Mateus *et al*. (2022) [13]	E. urophylla × grandis seedlings, hydroponic	PEG-6000 to −1 MPa × 5 K levels	+PEG ↓ leaf area and dry matter; root/shoot ↑ ~50%

Two general lessons follow.

- Root allocation is a first-order response that is sustained or enhanced under water shortage. In Costa e Silva *et al*. (2004) [8], the more tolerant clone CN5 differed less in absolute response than in *persistence* of root growth, consistent with a lower leaf-to-root area ratio and more favourable balance of supply to demand. Susiluoto and Berninger (2007) [16] proposed that increased root/shoot ratio is the primary reaction that initiates a cascade of compensatory changes.
- Allocation shifts are not always growth-friendly. Guarnaschelli *et al*. (2006) [11] found that a month of conditioning reduced leaf area and shoot/root ratio and improved later survival, but it did not improve growth.

The survival advantage was correlated with shoot/root ratio (r^2 = 0.54) and midday relative water content (RWC; r^2 = 0.87) 36 days after transplanting.

2. Leaf-level adjustments

Reduced leaf area is the cheapest and most durable means of lowering canopy water demand. Its costs are lower light interception and carbon gain. In the rain-shielded K experiment of Battie-Laclau *et al*. (2014b), trees under 37% throughfall exclusion coped through stomatal closure, osmotic adjustment and lower leaf area index (LAI). Specific leaf area (SLA) responses are inconsistent: SLA fell in E. globulus (Costa e Silva *et al*., 2004) [8], was unaffected in preconditioned E. globulus subsp. bicostata (Guarnaschelli *et al*., 2006) [11], and declined marginally in E. tereticornis Et88 but significantly in E. camaldulensis Ec226 (Amrutha *et al*., 2019) [1]. Interpretation therefore requires knowledge of the evolutionary and environmental context, a point Amrutha *et al*. make with reference to broader SLA literature.

3. Water relations and tissue tolerance

Osmotic and elastic adjustment. These are the classic tolerance mechanisms.

- Two mechanisms were distinguished in dry-zone eucalypts. *E. leucoxylon* has an inherently low osmotic potential, whereas *E. platypus* adjusted seasonally through elasticity: ε fell by 5.9 MPa from winter to summer (21.2 to 15.3 MPa), and relative water content at turgor loss (R_p) dropped to 0.73 (White *et al*., 2000) [19]. Elastic adjustment therefore lets a species lose more water before turgor is lost.

- In young *E. globulus* subsp. *bicostata*, only the Tumbarumba provenance showed true osmotic adjustment (0.25 MPa) after conditioning, whereas the other two showed passive lowering of osmotic potential that may reflect a larger apoplastic fraction (Guarnaschelli *et al*., 2006) [11]. This is a cautionary note: apparent osmotic adjustment from rehydrated-tissue measurements can be confounded by apoplastic water changes.

- Rehydration artefacts also matter. White *et al*. (2000) [19] found that osmotic potentials of rehydrated shoots were less negative than P–V estimates in *E. leucoxylon* and *E. platypus*, suggesting that solutes were lost or converted during 12–14 h rehydration. Osmotic potential at full turgor alone therefore missed elastic adjustment in *E. platypus*.

Water potential gradients and hydraulic conductance. Costa e Silva *et al*. (2004) showed that root hydraulic conductance and leaf-specific conductance (LSC) declined as stress developed, but the drought-tolerant clone CN5 maintained LSC 43% and 79% higher than ST51 at weeks 5 and 7. The authors attribute the difference to less cavitation-induced conductance loss and to greater root investment.

4. Stomatal control and gas exchange

Stomatal behaviour is the most visible axis of variation.

- Strong stomatal control (steep g_sm–Ψ_pd slope) in *E. camaldulensis*; weak control in *E. leucoxylon* and *E. platypus* (White *et al*., 2000) [19].

- Despite very different Ψ_pd, predicted maximum stomatal conductance varied far less among species than Ψ_pd did, supporting the hypothesis of similar transpiration per unit leaf area under water limitation (Hatton *et al*., 1998, as discussed by White *et al*., 2000) [19]. White *et al*. argue that this constancy is maintained by stomatal control *as well as* leaf area adjustment, which operate on different timescales.

- In a 4-day dry-down of five species, stomata began to close at roughly 50% of available soil water in most species, whereas *E. phaeotrica* (subgenus *Monocalyptus*) kept higher conductance and a more linear decline (Lima *et al*., 2003) [12]. This agrees with older observations that *Monocalyptus* species reach very low leaf water potentials before stomata close.

- Photosynthetic responses may not track conductance. In *E. microtheca*, changes in photosynthesis and g_s under drought were modest, while biochemical capacity (chlorophyll fluorescence, A–C_i measurements) actually increased (Susiluoto and Berninger, 2007) [16].

- Drought-induced photoinhibition varied among species and with CO_2 concentration. *E. camaldulensis* appeared slightly more sensitive by F_v/F_m (Lima *et al*., 2003) [12].

5. Hydraulic failure and mortality

Hydraulic failure is the leading mechanism of drought-induced tree death in many systems (Choat *et al*., 2018; Rowland *et al*., 2015) [26, 41], although carbon and hydraulic mechanisms interact. Reviews emphasise the need to integrate stomatal behaviour, embolism resistance and carbon dynamics (Li *et al*., 2022). Eucalypt-specific evidence includes:

- Retrospective embolism measurements linked to canopy dieback in *E. piperita* (Li et al., 2018).
- Trees with fully dead canopies had native embolism of 78–100%, versus 25–31% in relatively healthy trees during the 2019 Australian drought; small trees were disproportionately affected (Nolan *et al*., 2021) [39].
- A greenhouse and field study of *E. urophylla* reported loss of stem xylem conductance (PLC) of up to 84.4% under drought, with declines in whole-plant hydraulic conductivity and sap flux (Forest Ecology and Management, 2020) [44].
- Desiccation time during drought is predictable across eucalypt species from contrasting climates (Blackman *et al*., 2019) [23], which supports trait-based prediction.

Together with Costa e Silva *et al*. (2004) [8], who inferred greater cavitation-induced conductance loss in the sensitive clone from lower stem xylem pressures and K values, this literature supports treating xylem safety as the endpoint against which avoidance and tolerance traits are judged.

6. Biochemical and molecular responses

Metabolite and transcript work adds mechanistic depth but tends to be short-term and clone-specific.

- In *E. tereticornis* Et88 (tolerant) versus *E. camaldulensis* Ec226 (susceptible) under progressive nursery drought, leaf curling reached only 5.7% versus 96%, RWC 78.8% versus 40.1%, and photosynthesis

17.2 versus 8.4 μmol m^{-2} s^{-1}. Osmotin (*OSM34*) was induced 54-fold in Et88 versus 5-fold in Ec226. The DREB/CBF transcription factors *DREB*, *CBF1c* and *CBF2* were up-regulated 15–28-fold in Et88 and down-regulated 10–22-fold in Ec226 (Amrutha *et al*., 2019) [1]. Total sugars, proline, phenols, ABA and IAA increased in both genotypes.

- In drought-tolerant *E. globulus*, drought alone raised ABA, malondialdehyde and glutathione and shifted carbohydrate pools, whereas the combination with heat produced a distinct signature (Section 7.2; Correia *et al*., 2018) [7].

- Potassium supply modulated carbon and nitrogen isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) and leaf C/N under PEG stress (Mateus *et al*., 2022) [13], which supports the use of isotopes as integrative screening tools, although with the scale caveats discussed in Section 9.

Inter- and intraspecific variation: reconciling the evidence

Table 2: How "tolerance" rankings depend on the axis measured

Axis	Evidence	Implication
Avoidance (water access, stomatal control)	E. camaldulensis and E. saligna had narrow Ψ_pd ranges and steep stomatal sensitivity in the field (White *et al*., 2000) [19]; CN5 maintained root growth and conductance (Costa e Silva *et al*., 2004) [8]	Rankings are site-dependent (need a water source)
Tissue tolerance	E. leucoxylon / E. platypus lost turgor at ~−3.9 MPa; Et88 tolerated Ψ_w of −4.25 MPa (White *et al*., 2000; Amrutha *et al*., 2019) [1, 19]	Species without deep water require tolerance
Hydraulic safety	E. crebra (drought tolerant) had more negative P_{50} and wider safety margins than E. saligna (Mateus *et al*., 2024) [38]	Climate-of-origin predicts xylem traits (Bourne *et al*., 2017) [24]
Provenance-level	Osmotic adjustment differed among provenances but did not track site dryness (Guarnaschelli *et al*., 2006) [11]	Rainfall of origin is an imperfect proxy; test genotypes directly
Seedling establishment	Preconditioning gave temporary superiority in water status and g_s, with survival benefits (Guarnaschelli *et al*., 2006) [11]	Nursery practice can be as important as genotype

Three points deserve emphasis.

- **Subgenus effects:** Lima *et al*. (2003) [12] report that species of subgenus *Symphyomyrtus* (e.g. *E. grandis*, *E. urophylla*, *E. camaldulensis*) show stronger stomatal closure than *Monocalyptus* (*E. phaeotrica*). This is consistent with the conventional view that *Monocalyptus* species are poorly adapted to plantation outside Australia's climate zones with defined dry seasons.

- **Clone versus species:** Clonal contrasts (CN5 versus ST51; Et88 versus Ec226; VM01 versus AEC 0144) show large within-species variation. Single-clone comparisons cannot be generalised to species (Section 9).

- **Site-specific outcomes:** Because tolerance and avoidance interact with soil depth and water-table access, the same genotype can be "tolerant" at one site and "susceptible" at another.

Nutrition as a modifier of drought response

1. Potassium: mechanisms

K is the most abundant cation in plant tissue after N in photosynthetic organs (Sardans and Peñuelas, 2015) [14]. It regulates osmotic potential, stomatal movement, enzyme activation, phloem transport and cell expansion. Sardans and Peñuelas (2015) [14] reviewed evidence that K is as limiting as N and P for productivity, with some degree of K limitation in up to 70% of studied terrestrial ecosystems. They also flagged aridity, N deposition and other global-change drivers as raising the importance of K.

In eucalypts, Cornut *et al*. (2021) [6] review how K deficiency acts on both carbon source (leaf area, leaf lifespan, photosynthetic capacity, stomatal conductance) and sinks (phloem transport, wood formation). They conclude that K effects can be modelled independently of other nutrients and highlight the lack of process-based K submodules. Battie-Laclau *et al*. (2014a) showed that:

- net CO_2 assimilation rates were twice as high with K and 1.6 times as high with Na supply than in the control, through lower stomatal and mesophyll resistance and higher photosynthetic capacity;
- starch was higher and soluble sugar lower with K, which suggests that K starvation disturbed carbon storage and transport;
- SLA, leaf thickness, parenchyma thickness, stomatal size and intercellular air spaces increased with K and Na.

2. Potassium and drought: benefits

Growth and WUE_wood. In a large Brazilian throughfall-exclusion experiment, stemwood biomass three years after planting was 173% higher with K and 79% higher with Na than without either. K raised WUE for stemwood production by about 60%, with or without exclusion (Battie-Laclau *et al*., 2016) [5]. Later work found that K fertilisation also increased hydraulic redistribution and WUE for stemwood (Asensio *et al*., 2020) [22].

Seedling and clone experiments. With adequate K, drought-affected plants performed better across several controlled studies:

- In PEG-stressed hybrid seedlings, K supply raised dry matter by ~140% (non-PEG) and ~40% (+PEG), photosynthesis by 55% and 85%, and stomatal conductance by 100% and 400% (Mateus *et al*., 2022) [13]. K-supplied plants had leaf K near 27 g kg^{-1} under either condition.

- In two elite clones, sufficient K let VM01 (*E. urophylla* × *camaldulensis*) sustain photosynthesis, leaf water potential and dry mass under severe deficit, with instantaneous WUE two- to three-fold higher than in low-K plants. *E. urophylla* AEC 0144, by contrast, lost K from leaves and stems and dry mass under severe stress (Santos *et al*., 2021) [15]. Leaf and stem K concentration correlated positively with WUE and leaf water potential.

3. Potassium and drought: costs and the hydraulic trade-off

The benefits above are not the whole story. Three sets of evidence indicate that K enhances water demand and hydraulic risk.

- **Field water use and dry-spell stress.** In the rain-exclusion experiment, K and Na increased maximum stomatal conductance and, because fertilised trees have higher water requirements, increased water stress during dry periods. Excluding 37% of throughfall reduced above-ground biomass in the third year *only in K-supplied trees* (Battie-Laclau *et al*., 2014b). Canopy transpiration between years 1 and 3 rose from about 750 to 1300 mm yr^{-1} with K fertilisation (Battie-Laclau *et al*., 2016) [5]. The authors recommend revisiting fertilisation regimes for a drier climate.

- **Hydraulic constraint.** Guillemot *et al*. (2021) [32] report increased hydraulic constraints in K-fertilised plantations, and Cornut *et al*. (2021) [6] note that higher LAI in K-fertilised *E. grandis* lowers the sapwood-to-leaf-area ratio and leaf-specific conductance at the end of rotation.

- **Narrow safety margins.** In pots, K-supplied *E. saligna* and *E. crebra* had the narrowest hydraulic safety margins, K-deficient plants the widest, and partial K replacement by Na intermediate values (Mateus *et al*., 2024) [38]. Fertilised plants had also lower (more negative) P_{50} (greater embolism resistance), but they operated much closer to their P_gs90 to P_{50} margin. Total dry mass rose by up to 68% in *E. crebra* with partial K-by-Na replacement, and K-deficient plants showed almost no drought penalty on gas exchange.

This is the central tension of nutrient-drought interaction. A plant with abundant K opens stomata wider, builds more leaf area and grows faster, and it is therefore more exposed when soil water becomes limiting (Figure 1 conceptualises the trade-off in words below). The pattern is consistent with the broader observation that plants on fertile soils are often more sensitive to climate stress than those on infertile ones (Harrison *et al*., 2015, as discussed by Mateus *et al*., 2024) [38].

4. Sodium substitution and other ions

Partial replacement of K by Na is attracting interest because Brazil imports most of its K fertiliser and Na is cheaper (a 2025 greenhouse study of E. grandis and E. camaldulensis supports its use under varying water regimes. Laclau *et al*. (2024) [35] framed the question in a Forest Ecology and Management perspective on sodium in tropical plantations. Mateus *et al*. (2024) [38] found that 70/30 K/Na increased gas exchange, WUE and dry mass and lowered embolism thresholds. Points of caution:

- Effects vary among species and may be larger in drought-tolerant species that can sequester Na^+ in vacuoles (Mateus *et al*., 2024) [38].
- Cl^- from KCl and NaCl may contribute to observed effects, as chloride nutrition itself improves drought resistance in other species (Franco-Navarro *et al*., 2021) [31].
- Trees in the 'K-deficient' treatment may have carried nursery K reserves, which can mask deficiency symptoms (Mateus *et al*., 2024) [38].
- Transcriptomic responses of water-deficient *E. grandis* differ between K and Na fertilisation (Favreau *et al*., 2019) [30], which suggests non-identical mechanisms.

5. Phosphorus

Eucalypts are famous for efficient P acquisition, but P limitation is documented across contexts.

- **Seedlings:** Phosphorus was the principal factor limiting *E. grandis* seedling survival and growth in a North Queensland rainforest soil; P addition eliminated deficiency symptoms and produced growth and shoot dry weights similar to seedlings in *E. grandis* forest soil, and fumigation (a proxy for fire) improved survival (Tng *et al*., 2014) [17].

- **Mature woodland:** In a >80-year-old *E. tereticornis* woodland, adding 50 kg P ha^{-1} yr^{-1} increased leaf P by about 50% and stem basal-area growth by 54%, though photosynthetic capacity did not change (Crous *et al*., 2015) [10].

- **CO_2 interaction:** In the EucFACE experiment on a low-P soil, elevated CO_2 did not increase productivity (Ellsworth *et al*., 2017) [24]. Later work attributed the limited response to microbial competition for P (Jiang *et al*., 2024) [33], and P-cycle models overestimated the CO_2 response (Jiang *et al*., 2024) [33].

- **Drought:** P application has been reported to improve drought responses in *E. grandis* seedlings (Tariq *et al*., 2019) [42].

The drought-P link is far less studied than the drought-K link in eucalypts, and it is a clear gap.

Multiple stressors: CO_2, temperature and heat

1. Elevated CO_2 and drought

In five species, elevated CO_2 (700 versus 350 μmol mol^{-1}) did not alter the timing of stomatal closure during a 4-day dry-down but kept photosynthesis and WUE higher throughout (Lima *et al*., 2003) [12]. A recent study of E. grandis under elevated CO_2 and drought examined biomass, gas exchange and wood structure. Drought intensity alone strongly constrained photosynthesis, and the authors interpret their results in light of evidence that progressive drought and heat can largely eliminate CO_2 benefits. Any CO_2 compensation of drought is therefore short-lived and nutrient-dependent (Ellsworth *et al*., 2017; Jiang et al., 2024) [24, 33].

2. Heat, heatwaves and their combination with drought

- **Acclimation limits.** Planted 700 km closer to the equator than the nearest natural stand, *E. globulus* showed limited acclimation of photosynthesis: warming raised carboxylation and electron-transport capacity in winter but reduced both by 20–30% in summer, and the photosynthetic temperature optimum shifted by ~6 °C between winter and summer without further adjustment (Crous *et al*., 2013) [9]. The authors suggest that this

upper limit may define climatic zones where *E. globulus* plantations remain productive.

- **Heatwave tolerance.** Among four *Eucalyptus* species, small-range species showed more damage than large-range species, and warm-grown seedlings were *more* susceptible than cool-grown ones. Species with less damage maintained higher g_s, lower leaf temperature, larger isoprene increases and less photosynthetic inhibition; species with more damage showed larger increases in heat shock proteins and respiratory thermotolerance (Aspinwall *et al*., 2019) [2].

- **Field-scale cooling.** In field-grown *E. parramattensis*, an extreme heatwave drove midday canopy photosynthesis near zero, but transpiration persisted and maintained canopy cooling; leaf thermal tolerance rose rapidly, and warming history conferred no added benefit (Drake *et al*., 2018) [28].

- **Repeated events and drought.** Repeated heatwaves led to greater thermal tolerance and safety margins through plasticity (Ahrens *et al*., 2021) [21], while extreme heat can increase stomatal conductance and drought-induced mortality risk in vulnerable species (Prokopavicius *et al*., 2022) [40].

- **Combined stress is qualitatively different.** In a drought-tolerant *E. globulus* clone, drought alone raised ABA, MDA and glutathione and reduced sugar phosphates. Heat alone increased RWC and Ψ_pd but reduced photosynthesis and WUE. Drought-stressed plants that were also heat-shocked showed lower Ψ_pd damage and MDA than drought alone, maintained a raised glutathione pool, and accumulated cinnamate as a novel response (Correia *et al*., 2018) [7].

Two implications follow. First, transpirational cooling, which depends on water availability and hence on stomatal strategy, links drought and heat. Stomatal closure that protects xylem in drought can raise leaf temperature in a heatwave. Second, single-stress screening cannot predict combined-stress performance.

Nursery and chemical mitigation

Preconditioning. One month of graded drought in E. globulus subsp. bicostata seedlings improved water status, g_s and survival after transplanting, but the advantage vanished under severe later drought and growth was not improved (Guarnaschelli *et al*., 2006) [11]. This illustrates that hardening trades growth for establishment survival and that the benefit is transient.

Brassinosteroids (BR) and sucrose. In E. tereticornis clone P-23, BR at 20 ppm raised total plant dry weight at 40% field capacity from 6.11 to 7.68 g (about 26%) and shoot increment from 7.83 to 12.95% in BR-only comparison; sucrose had non-significant effects (Varma *et al*., 2020) [18]. These are potentially attractive nursery treatments but need caution (Section 9). The interpretation that BR acts as a "master switch" for stress responses comes from the general literature cited by those authors and has not been tested at field scale in eucalypts.

Critical appraisal of the evidence

A review aiming for impact must state where the evidence is thin. We appraise the core studies below.

Table 3: Evidence quality and main limitations

Study	Scale / design	Principal strengths	Principal limitations for inference
White *et al*. (2000) [19]	Field, 4 allopatric species, 3 seasons	Multi-year, diurnal and P–V data; mechanistic link to soil water access	3 replicates, single site; species confounded with individual origin; stomatal data limited to 3 species
Costa e Silva *et al*. (2004) [8]	2 clones, pots (10 L), 7 weeks	Integrates growth, root and hydraulic measures	Two clones only; small containers restrict root growth; cavitation inferred, not measured directly
Guarnaschelli *et al*. (2006) [11]	3 provenances, pots, conditioning + transplant	Good factorial design; survival endpoint	Seedlings only; single dry-down; apparent osmotic adjustment may reflect apoplastic fraction
Lima *et al*. (2003) [12]	5 species, open-top chambers, 4-day dry-down	Species range; CO_2 × drought	Very short stress; seedlings (2.5-month-old); low temperatures (~13 °C mean) unlike plantation climate
Susiluoto and Berninger (2007) [16]	E. microtheca seedlings	Links allocation to biochemical capacity	Single species; greenhouse
Amrutha *et al*. (2019) [1]	1 clone per species, n = 3 ramets	Multi-level (morphology to transcripts)	Species conflated with clone; small n; stress assessed at day 5–6 only; leaf curling in Ec226 may reflect rapid pot desiccation rather than tolerance per se
Yousaf *et al*. (2018) [20]	2 species, pots, 4 irrigation intervals	Simple, transferable design	Five plants per treatment; text-figure inconsistencies (e.g. maximum plant height attributed to W1 versus W0); no volumetric moisture data; conclusions about planting on fertile land are not supported by the data
Varma *et al*. (2020) [18]	1 clone, pot, BR × sucrose × moisture	Interesting BR effect	Two plants per treatment yet tables state n = 80; unusually small SE on plant weights; internally conflicting statements on root length; sucrose units inconsistent (% vs ppm)
Mateus *et al*. (2022) [13]	Hydroponic seedlings, PEG	Isotopes + gas exchange + K gradient	PEG imposes osmotic, not soil, drought; limited hydraulic realism; 4 replicates
Santos *et al*. (2021) [15]	2 clones, pots, K × water	Uses two elite clones; K dynamics	Genotype-by-K-by-water design with n = 5; results depend on clone identity

Mateus *et al*. (2024) [38]	2 species, pots, K/Na, optical vulnerability	Direct P_{50} / safety margins	Pot-scale; high species–Cl^- confounding; nursery K reserves
Battie-Laclau *et al*. (2014a,b, 2016) [5]	Field throughfall exclusion, 3 years	Large scale, stand transpiration, WUE_wood	Site had deep soil water reserves that buffered drought; results may not generalise to shallow soils
Crous *et al*. (2013); Aspinwall *et al*. (2019) [2, 9]	Whole-tree chambers / controlled heatwave	Realistic heat and CO_2 manipulations	Limited species; temperate conditions
Tng *et al*. (2014); Crous *et al*. (2015) [10, 17]	Seedling; mature woodland	P manipulation with growth endpoints	Seed provenance mismatch (seedling study); no water treatment
Review papers (Cornut *et al*., 2021; Sardans and Peñuelas, 2015) [6, 14]	Syntheses	Broad, model-oriented	Rely on partial and sometimes unpublished data (Cornut *et al.*)

Three cross-cutting problems weaken current generalisations.

- **Scale mismatch:** Pot and hydroponic results (PEG, restricted root volume) exaggerate hydraulic constraint and cannot capture deep-water access, which the field studies show can dominate outcomes (Battie-Laclau *et al*., 2014b; Christina et al., 2017) [27].

- **Genotype confounding:** Species-level statements based on one clone per species (Amrutha et al., 2019; Costa e Silva *et al*., 2004) [1, 8] risk mislabelling clonal idiosyncrasy as species biology.

Toward an integrated synthesis

Integrating the evidence yields a hierarchical model with explicit prediction rules.

Rule 1: Water access sets the game. Where deep water or a capillary fringe exists (Battie-Laclau *et al*., 2014b; White *et al*., 2000) [19], avoidance dominates and trees can appear insensitive to moderate rainfall reduction. Tissue tolerance becomes decisive where roots cannot reach water.

Rule 2: Stomatal strategy must be read together with xylem safety. Early stomatal closure (steep g_s–Ψ slope) protects the xylem, but it costs carbon. Weak stomatal control demands either exceptional xylem resistance or deep water. P_{gs90} occurs at less negative potential than P_{12} in eucalypts (Mateus *et al*., 2024) [38], so the hydraulic safety margin is the appropriate integrated metric.

Rule 3: Nutrition shifts the operating point along the safety–efficiency axis. K-replete plants gain carbon and WUE_wood but reduce safety margins and deplete soil water faster; K-deficient plants are safe but unproductive (Mateus *et al*., 2024 [38]; Battie-Laclau *et al*., 2014b, 2016; Guillemot *et al*., 2021) [5, 32].

Rule 4: Additional stressors move the boundary. Heat raises evaporative demand and reduces carbon returns (Crous *et al*., 2013) [9], CO_2 gains are P-limited (Jiang et al., 2024) [33], and combined drought–heat generates distinct metabolic states (Correia *et al*., 2018) [7].

Rule 5: Allocation is the integrator. Across the studies, allocation to roots and lower leaf-to-root area ratio consistently accompany higher survival (Costa e Silva *et al*., 2004; Guarnaschelli *et al*., 2006; Susiluoto and Berninger, 2007) [8, 11, 16] and higher WUE for wood (Battie-Laclau *et al*., 2016 [5] concluded that allocation pattern was a major driver of WUE_wood).

Table 4: Prediction matrix for management-relevant scenarios (synthesised hypotheses to be tested)

Scenario	Predicted best-performing strategy	Supporting evidence	Key risk
Deep soils, rainfall moderate, K-poor	Fertilise K (or K + Na); select high-WUE_wood clones	Battie-Laclau *et al*. (2014b, 2016) [5]; Asensio *et al*. (2020)	Higher water demand; fertilised trees more affected in dry spells
Shallow soils, seasonal drought, K-poor	Moderate K; avoid maximal leaf area; choose clones with wide safety margins and proven tolerance	Mateus *et al*. (2024); Guillemot *et al*. (2021) [32, 38]	Hydraulic failure during prolonged dry spells
Establishment on dry sites	Nursery hardening (graded drought)	Guarnaschelli *et al*. (2006) [11]	Growth cost; benefit lost in severe drought
Hot-dry regions	Prefer genotypes combining stomatal cooling capacity with xylem safety	Drake *et al*. (2018); Aspinwall *et al*. (2019) [2, 28]	Combined heat–drought responses unpredictable
P-limited soils under rising CO_2	Manage P alongside K; do not assume CO_2 benefit	Ellsworth *et al*. (2017); Jiang *et al*. (2024) [24, 33]	Microbial competition for P

Implications for breeding and management

- Screen for the full syndrome. Evaluate root traits, hydraulic safety margins (optical vulnerability), stomatal sensitivity, and osmotic and elastic adjustment together. Include multi-trait indices instead of single traits. Isotope signatures ($\delta^{13}C$, $\delta^{15}N$) can assist but are not proxies for WUE_wood (Battie-Laclau *et al*., 2016) [5].

- Tune fertilisation to site water and genotype. Blanket K maximisation is unlikely to be optimal in drier climates. Fertiliser regimes, potentially with Na substitution, should be trialled by genotype × site water regime, monitoring hydraulic safety margins as well as growth.

- Use nursery hardening deliberately. Graded pre-transplant drought can raise survival, but it is a short-term insurance and does not substitute for genotype choice.

- Match plantation design to water budgets. Because fertilised, high-LAI stands transpire more, stocking and rotation decisions in water-limited catchments should account for K-driven water demand.

- Plan for compound stress. Do not assume that drought screening predicts heatwave or drought–heat performance.

- Treat chemical and hormonal mitigators (e.g. BR) as experimental until replicated field trials exist.

Knowledge gaps and a research roadmap

- Field-scale, factorial experiments crossing water, K/Na/P supply, temperature and CO_2 with genotype replication and hydraulic endpoints. The EucFACE and Brazilian throughfall-exclusion platforms show what is feasible; drought × P and drought × K × warming remain unexplored.

- Mechanisms linking K/Na to xylem safety. Hypotheses include pit-membrane structure and aquaporin-mediated refilling (Mateus *et al*., 2024) [38]. These need anatomical and molecular tests, and comparisons of K and accompanying anions (Cl^-).

- Long-term and recovery dynamics. Most studies end at the stress peak. Recovery, legacy effects and repeated drought are rarely followed (Correia *et al*., 2018 [7] is a partial exception).

- Genotype–environment–management interactions at scale, including modern hybrids (*E. urophylla* × *grandis*, *E. urophylla* × *camaldulensis*) and Indian and Pakistani plantation clones, where published rigour is currently weakest.

- Model integration. K and P submodules should be embedded in process-based models with hydraulic representation, following the priorities set out by Cornut *et al*. (2021) [6] and the evidence that models overestimate CO_2 responses when P is neglected (Jiang *et al*., 2024) [33].

- Reporting standards. Replication, effect sizes, raw-data availability, moisture-content data and unit consistency should be treated as minimum standards. Multi-site meta-analysis of eucalypt drought traits would substantially increase inferential power.

- Omics with ecological validation. Transcript and metabolite markers (osmotin, DREB/CBF, cinnamate) require validation across clones, developmental stages and field conditions before use in breeding.

Conclusions

Eucalypt drought responses cannot be understood, or predicted, from single traits, single stresses or single nutrient levels. The best-supported picture is a syndrome-based one. Water access, stomatal regulation, tissue tolerance and xylem safety combine in genotype-specific ways, and nutrition, especially K, shifts where a plant sits along a safety–efficiency continuum. Fertilised, fast-growing trees gain carbon and WUE_wood, but they consume soil water faster and operate nearer their hydraulic limits. Under a hotter, drier and CO_2-enriched climate, P limitation, heatwaves and combined stress add further constraints. The most valuable next steps are factorial field experiments with hydraulic endpoints, mechanistic work on nutrient–xylem interactions, and modelling frameworks that treat nutrition and hydraulics jointly. Better reporting and replication in the applied literature would substantially strengthen management guidance.

Acknowledgements

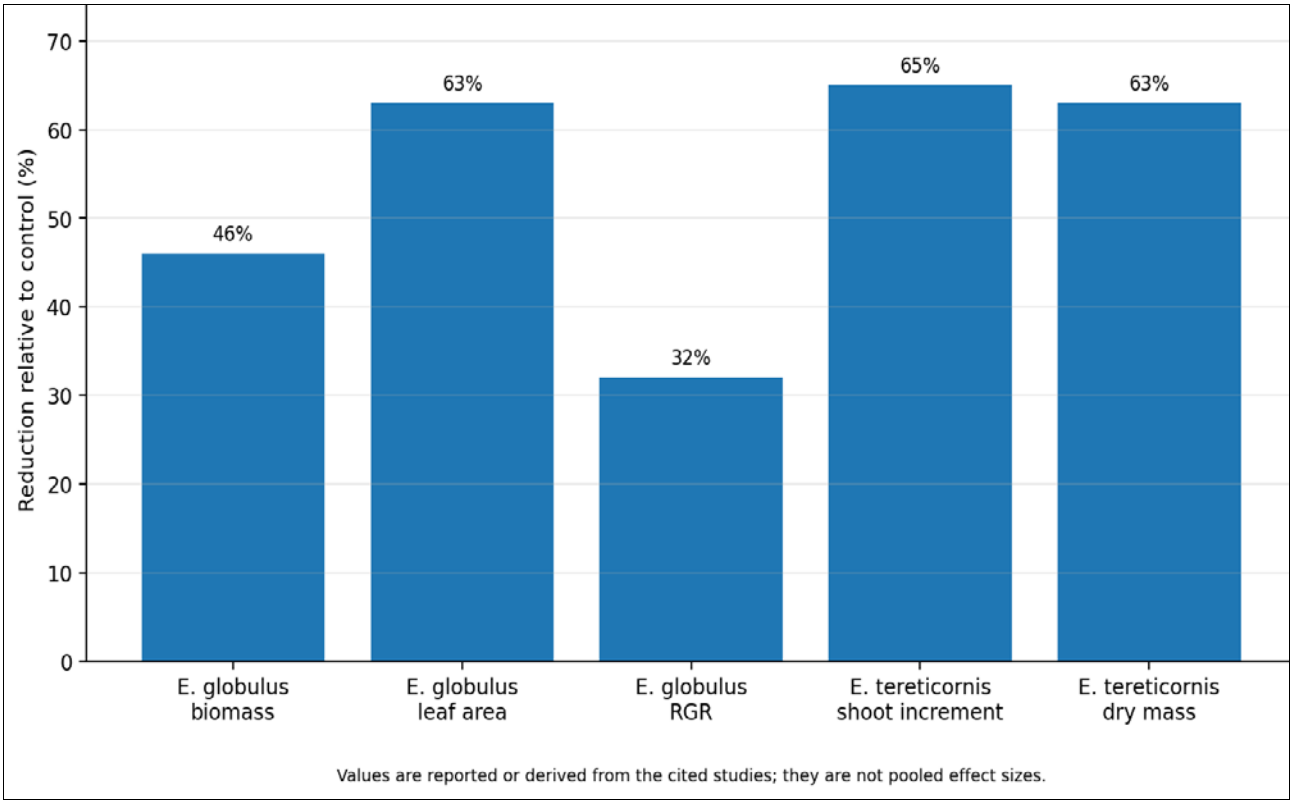


Fig 2: Selected reported reductions under drought. Values are reported or derived from the cited studies and are presented for comparison only; they are not pooled meta-analytic effect sizes.

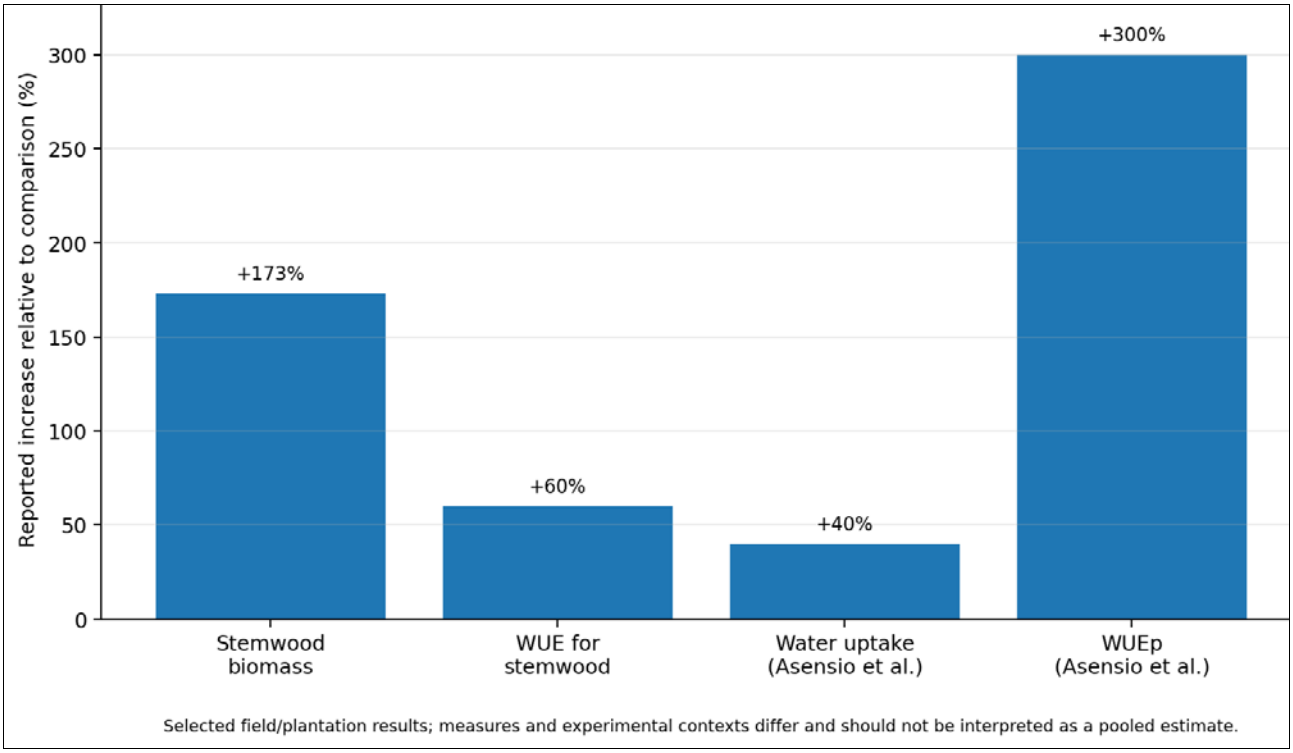


Fig 3: Selected reported responses to potassium supply. Experimental contexts and response variables differ among studies; values should therefore be interpreted as study-specific magnitudes rather than a common effect estimate.

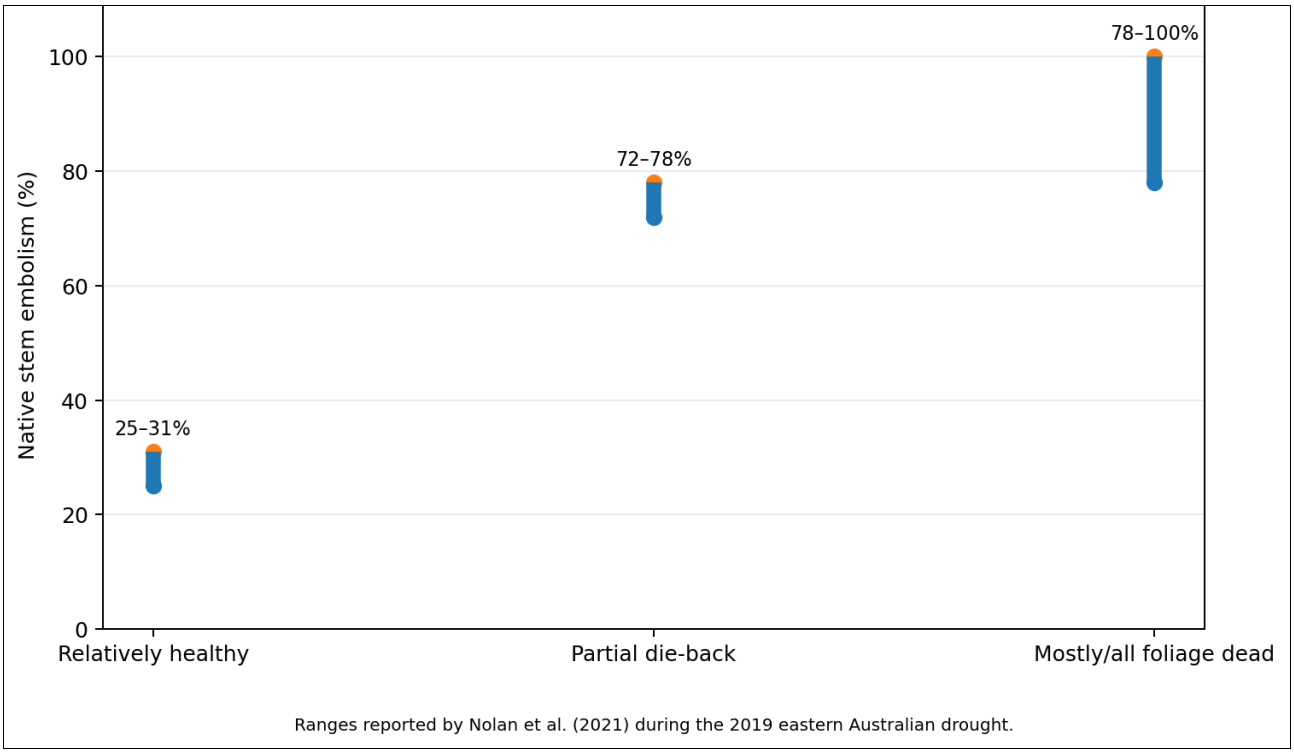


Fig 4: Native stem embolism associated with canopy die-back during the 2019 eastern Australian drought, based on the ranges reported by Nolan et al. (2021).

References

1. Amrutha S, Parveen ABM, Muthupandi M, Sivakumar V, Nautiyal R, Ghosh Dasgupta M. Variation in morpho-physiological, biochemical and molecular responses of two *Eucalyptus* species under short-term water stress. Acta Botanica Croatica,2019:78:125–134.
2. Aspinwall MJ, Pfautsch S, Tjoelker MG, et al. Range size and growth temperature influence *Eucalyptus* species responses to an experimental heatwave. Global Change Biology,2019:25:1665–1684.
3. Battie-Laclau P, Laclau JP, Beri C, et al. Photosynthetic and anatomical responses of *Eucalyptus grandis* leaves to potassium and sodium supply in a field experiment. Plant, Cell & Environment,2014a:37:70–81.
4. Battie-Laclau P, Laclau JP, Domec JC, et al. Effects of potassium and sodium supply on drought-adaptive

mechanisms in *Eucalyptus grandis* plantations. New Phytologist,2014b:203:401–413.
5. Battie-Laclau P, Delgado-Rojas JS, Christina M, et al. Potassium fertilization increases water-use efficiency for stem biomass production without affecting intrinsic water-use efficiency in *Eucalyptus grandis* plantations. Forest Ecology and Management,2016:364:77–89.
6. Cornut I, Le Maire G, Laclau JP, et al. Potassium limitation of wood productivity: a review of elementary processes and ways forward to modelling illustrated by *Eucalyptus* plantations. Forest Ecology and Management,2021:494:119275.
7. Correia B, Hancock RD, Amaral J, Gomez-Cadenas A, Valledor L, Pinto G. Combined drought and heat activates protective responses in *Eucalyptus globulus* that are not activated when subjected to drought or heat stress alone. Frontiers in Plant Science,2018:9:819.
8. Costa e Silva F, Shvaleva A, Maroco JP, Almeida MH, Chaves MM, Pereira JS. Responses to water stress in two *Eucalyptus globulus* clones differing in drought tolerance. Tree Physiology,2004:24:1165–1172.
9. Crous KY, Quentin AG, Lin YS, et al. Photosynthesis of temperate *Eucalyptus globulus* trees outside their native range has limited adjustment to elevated CO_2 and climate warming. Global Change Biology,2013:19:3790–3807.
10. Crous KY, Ósvaldsson A, Ellsworth DS. Is phosphorus limiting in a mature *Eucalyptus* woodland? Phosphorus fertilisation stimulates stem growth. Plant and Soil,2015:391:293–305.
11. Guarnaschelli AB, Prystupa P, Lemcoff JH. Drought conditioning improves water status, stomatal conductance and survival of *Eucalyptus globulus* subsp. *bicostata* seedlings. Annals of Forest Science,2006:63:941–950.
12. Lima W de P, Jarvis P, Rhizopoulou S. Stomatal responses of *Eucalyptus* species to elevated CO_2 concentration and drought stress. Scientia Agricola,2003:60:231–238.
13. Mateus NS, Ferreira EVO, Florentino AL, et al. Potassium supply modulates *Eucalyptus* leaf water-status under PEG-induced osmotic stress: integrating leaf gas exchange, carbon and nitrogen isotopic composition and plant growth. Tree Physiology,2022:42:59–70.
14. Sardans J, Peñuelas J. Potassium: a neglected nutrient in global change. Global Ecology and Biogeography,2015:24:261–275.
15. Santos EF, Mateus NS, Rosário MO, Garcez TB, Mazzafera P, Lavres J. Enhancing potassium content in leaves and stems improves drought tolerance of eucalyptus clones. Physiologia Plantarum,2021:172:552–563.
16. Susiluoto S, Berninger F. Interactions between morphological and physiological drought responses in *Eucalyptus microtheca* . Silva Fennica,2007:41:221–233.
17. Tng DYP, Janos DP, Jordan GJ, Weber E, Bowman DMJS. Phosphorus limits *Eucalyptus grandis* seedling growth in an unburnt rain forest soil. Frontiers in Plant Science,2014:5:527.
18. Varma S, Beniwal RS, Daneva V, Jangra M. Effect on morphological characters in *Eucalyptus tereticornis* Sm. at juvenile stage under the influence of moisture stress and mitigation by brassinosteroids and sucrose. International Journal of Chemical Studies,2020:8(3):2825–2829.
19. White DA, Turner NC, Galbraith JH. Leaf water relations and stomatal behavior of four allopatric *Eucalyptus* species planted in Mediterranean southwestern Australia. Tree Physiology,2000:20:1157–1165.
20. Yousaf MS, Farooq TH, Ahmad I, et al. Effect of drought stress on the growth and morphological traits of *Eucalyptus camaldulensis* and *Eucalyptus citriodora* . PSM Biological Research,2018:3:85–91.
21. Ahrens CW, Challis A, Byrne M, Leigh A, Nicotra A, Tissue D, et al. Repeated extreme heatwaves result in higher leaf thermal tolerances and greater safety margins. New Phytologist, 2021.
22. Asensio V, Domec JC, Nouvellon Y, et al. Potassium fertilization increases hydraulic redistribution and water use efficiency for stemwood production in *Eucalyptus grandis* plantations. Environmental and Experimental Botany,2020:176:104085.
23. Blackman CJ, Li X, Choat B, et al. Desiccation time during drought is highly predictable across species of *Eucalyptus* from contrasting climates. New Phytologist,2019:224:632–643.
24. Bourne AE, Creek D, Peters JMR, Ellsworth DS, Choat B. Species climate range influences hydraulic and stomatal traits in *Eucalyptus* species. Annals of Botany,2017:120:123–133.
25. Brodribb TJ, Powers J, Cochard H, Choat B. Hanging by a thread? Forests and drought. Science,2020:368:261–266.
26. Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE. Triggers of tree mortality under drought. Nature,2018:558:531–539.
27. Christina M, Nouvellon Y, Laclau JP, et al. Importance of deep water uptake in tropical eucalypt forest. Functional Ecology,2017:31:509–519.
28. Drake JE, Tjoelker MG, Vårhammar A, et al. Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. Global Change Biology,2018:24:2390–2402.
29. Ellsworth DS, Anderson IC, Crous KY, et al. Elevated CO_2 does not increase eucalypt forest productivity on a low-phosphorus soil. Nature Climate Change,2017:7:279–282.
30. Favreau B, Denis M, Ployet R, et al. Distinct leaf transcriptomic response of water deficient *Eucalyptus grandis* submitted to potassium and sodium fertilization. PLoS ONE,2019:14:e0218528.
31. Franco-Navarro JD, Díaz-Rueda P, Rivero-Núñez CM, et al. Chloride nutrition improves drought resistance by enhancing water deficit avoidance and tolerance mechanisms. Journal of Experimental Botany,2021:72:5246–5261.
32. Guillemot J, Asensio V, Bordron B, et al. Increased hydraulic constraints in *Eucalyptus* plantations fertilized with potassium. Plant, Cell & Environment,2021:44:2938–2950.
33. Jiang M, Crous KY, Carrillo Y, et al. Microbial competition for phosphorus limits the CO_2 response of a mature forest. Nature,2024:630:660–665.
34. Jiang M, Medlyn BE, Wårlind D, et al. Carbon–phosphorus cycle models overestimate CO_2 enrichment

response in a mature *Eucalyptus* forest. Science Advances,2024:10:eadl5822.
35. Laclau JP, Gonçalves JLM, Bouillet JP, Nouvellon Y. Perspectives: can we apply sodium in tropical plantations to reduce the need of potassium fertilizer? Forest Ecology and Management,2024:553:121643.
36. Li X, Blackman CJ, Rymer PD, et al. Xylem embolism measured retrospectively is linked to canopy dieback in natural populations of *Eucalyptus piperita* following drought. Tree Physiology,2018:38:1193–1199.
37. Li X, Xi B, Wu X, Choat B, Feng J, Jiang M, et al. Unlocking drought-induced tree mortality: physiological mechanisms to modeling. Frontiers in Plant Science,2022:13:835921.
38. Mateus NS, Perez-Martinez V, Lavres J, Tissue DT, Choat B. The double-edged sword of potassium and sodium fertilization in xylem embolism resistance of two *Eucalyptus* species under drought stress. Journal of Experimental Botany,2024:75:5641–5654.
39. Nolan RH, et al. Hydraulic failure and tree size linked with canopy die-back in eucalypt forest during extreme drought. New Phytologist,2021:230:1354–1365.
40. Prokopavicius R, et al. Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species. Global Change Biology,2022:28:1133–1146.
41. Rowland L, da Costa ACL, Galbraith DR, et al. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. Nature,2015:528:119–122.
42. Tariq A, Pan K, Olatunji OA, et al. Impact of phosphorus application on drought resistant responses of *Eucalyptus grandis* seedlings. Physiologia Plantarum,2019:166:894–908.
43. Effect of elevated CO_2 and drought on biomass, gas exchange and wood structure of *Eucalyptus grandis*. Plants,2023:12:148. doi:10.3390/plants12010148.
44. Chen X, Zhao P, Ouyang L, Zhu L, Ni G, Schäfer KVR. Whole-plant water hydraulic integrity to predict drought-induced *Eucalyptus urophylla* mortality under drought stress. Forest Ecology and Management,2020:468:118179. https://doi.org/10.1016/j.foreco.2020.118179.
45. Mateus NS, Florentino AL, Taghavi D, Santos EF, Ferreira EVO, Lavres J. Partnering with the enemy: How partial potassium substitution by sodium optimizes *Eucalyptus* nutrient dynamics and resilience to drought stress. Journal of Soil Science and Plant Nutrition,2025:25(3):7961–7977. https://doi.org/10.1007/s42729-025-02645-z.