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Performance of Native Tree Species to Dry land Environmental Stresses

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မြန်မာနိုင်ငံအပူပိုင်းဒေသရှိ ပတ်ဝန်းကျင်ဆိုင်ရာ အခက်အခဲများအပေါ်
ဒေသမျိုးရင်းသစ်မျိုးများ၏ တုံ့ပြန်မှုကိုလေ့လာခြင်း

ဒေါက်တာညွန့်ခိုင်
လက်ထောက်ကထိက
သစ်တောတက္ကသိုလ်

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စာတမ်းအကျဉ်း

ဒေသမျိုးရင်းသစ်မျိုးများသည် အတူယှဉ်တွဲပေါက်ရောက်သည့် သစ်မျိုးများ၊ သားငှက်တိရစ္ဆာန်များနှင့် အပြန်အလှန် အကျိုးပြုခြင်းဖြင့် ဂေဟစနစ်တွင်အခြေခံအကျဆုံး အခန်းကဏ္ဍပါဝင်နေပါသည်။ သစ်ပင်များသည် ၎င်းတို့ရှင်သန်ပေါက်ရောက်ရာဒေသ၏ သဘာဝပတ်ဝန်းကျင်အခြေအနေအား ဖော်ပြနိုင်စွမ်း ရှိသောသက်ရှိများဖြစ်သောကြောင့်၊ ၎င်းတို့ရှင်သန်ပေါက်ရောက်ရာဒေသ၏ သဘာဝပတ်ဝန်းကျင်အခြေအနေအားလေ့လာအကဲဖြတ်ရန်နှင့် အပင်များ၏ဒေသရာဇီဥတုနှင့် လိုက်လျောညီထွေပေါက်ရောက်နိုင်စွမ်းအားတို့အားလေ့လာ အကဲဖြတ်ရာတွင် သစ်ပင်များအားညွှန်းကိန်းများအဖြစ် အသုံးပြုနိုင်ပါသည်။ ထိုသို့ ညွှန်းကိန်းအဖြစ်အသုံးပြုရာတွင်သစ်ပင်၏ခြောက်သွေ့ဒဏ်ခံနိုင်မှုနှင့် ဆားငံဓါတ်ခံနိုင်မှုများအား တိုင်းတာဖော်ပြနိုင်ပါသည်။ မြန်မာနိုင်ငံအပူပိုင်းဒေသသစ်မျိုးများ၏ ခြောက်သွေ့ဒဏ်ခံနိုင်မှုနှင့် ဆားငံဓါတ်ခံနိုင်မှုများအားဆန်းစစ်ရာတွင်အပင်များအတွင်း ရေရရှိသိုလှောင်နိုင်သောစွမ်းရည် (Plant Water Potential) နှင့်ဆားငံဓါတ် ဖျံ့နှံ့စိမ့်ဝင်နိုင်သောစွမ်းရည် (Plant Osmotic Potential)များတိုင်းတာခဲ့ပါသည်။ မြန်မာနိုင်ငံ အလယ်ပိုင်းဒေသတွင် သုတေသနလုပ်ငန်းဆောင်ရွက်ရန်နေရာ (၃)ခု (သန်း-ဒဟတ်တော၊ ရှားတောနှင့် အင်တိုင်းတော)၊ တောအမျိုးအစားအလိုက် ပေါများစွာတွေ့ရှိရသောသစ်မျိုးများနှင့် အတူယှဉ်တွဲပေါက်ရောက်သည့်သစ်မျိုးများ စုစုပေါင်း ကိုးမျိုးကို ရွေးချယ်စမ်းသပ်ခဲ့ပါသည်။ ရရှိလာသောကိန်းဂဏန်းအချက်အလက်များအား လေ့လာဆန်းစစ်ရာတွင် "Statistica" အားအသုံးပြုတွက်ချက်ထားပါသည်။ လေ့လာခဲ့သောဒေသမျိုးရင်းသစ်မျိုးများ (သန်း၊ ဒဟတ်၊ ရှား၊ ထနောင်း၊ ပျဉ်းကတိုး၊ အင်၊ သစ်ရာ၊ သစ်စေး၊ နဘဲ) အားလုံးတို့သည် မြေဆီလွှာအတွင်းရေဓါတ်ခန်းခြောက်ခြင်းအား သိသာစွာတုန့်ပြန်မှုရှိကြောင်းလေ့လာတွေ့ရှိရပါသည်။ သစ်စေးသစ်မျိုးသစ်မျိုးသည် မြေဆီလွှာရေဓါတ်ခန်းခြောက်ခြင်းနှင့် ဆားငံဓါတ်ခံနိုင်မှုတို့နည်းပါးကြောင်းလေ့လာတွေ့ရှိရပါသည်။ ယခုသုတေသနလုပ်ငန်းမှ သစ်မျိုးများ၏ခြောက်သွေ့ဒဏ်ခံနိုင်မှုနှင့် ဆားငံဓါတ်ခံနိုင်မှုတို့အား အတန်းအစားခွဲခြားခြင်း "Temperament Classification" သည် သစ်မျိုးများ၏ ဒေသပတ်ဝန်းကျင်၏အကျိုးသက်ရောက်မှုများအပေါ် ၎င်းတို့၏တုံ့ပြန်မှုများအား ၎င်းတို့ပေါက်ရောက်ရာမျိုးရင်းဒေသနှင့် နှိုင်းယှဉ်အတည်ပြုရာတွင် အသုံးဝင်သောကိရိယာ တစ်ခုအဖြစ်အသုံးပြုနိုင်ပါသည်။

Performance of Native Tree Species on Dryland Environmental Stresses

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Abstract

Native species play a fundamental role in the ecosystem by providing mutual interaction with the coexisting plant and animal species. Plants reflect the environmental conditions in which they grow and can thus be used as indicators to identify the ecological adaptation of the plants to the site. The ecological adaptation of plants to the environmental stresses can be examined through the measurement of plants internal potentials (i.e. water- and osmotic potential). The performance of predominant and dominated tree species to drought and salinity were analyzed through water- and osmotic potential measurements. Three research sites were chosen for the present study in central Myanmar. To provide a representation of the entire area in question, nine species of predominant and some associated trees from each forest type were selected. A total of six randomly selected trees per species per site were collected for water- and osmotic potential measurements. STATISTICA for Windows (Version 9.0, Statsoft, Inc., Tulsa, USA) was used in analysing leaf water- and osmotic potential. All native species revealed significant response patterns to the soil water deficit. Of the native tree species, *Acacia catechu*, *Tectona hamiltoniana*, and *Terminalia oliveri* are highly adaptable to drought and soil salinity. *Melanorrhoea usitata* is the most sensitive to the soil water deficits and soil salinity stress. This study suggests temperament classification is a useful tool to confirm the species' responses to the environmental stresses in reference to habitat preferences.

Keywords: Performance; Native tree species; Environmental stresses; Water potential; Osmotic potential

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Performance of Native Tree Species on Dryland Environmental Stresses

1 Introduction

The climate and soil conditions in central Myanmar are on the whole unfavorable to plant development. In the dryland environment, soil water availability and salinity influence plant physiological attributes, determining the plant's adaptability to stresses, productivity, and distribution within communities (Hayward 1954; Goodin and Northington 1979; Osmond et al. 1987; Mitlöhner 1997a, b; Bartels and Sunkar 2005; Singh 2005). Drought is particularly visible in the dryland, a result of scanty rainfall and evaporative demands (Reddy et al. 2004; Jaleel et al. 2009). In addition, soil salinity, one of the major problems encountered in the dryland, enhances physiological drought by decreasing soil water potential in the rhizosphere (Srivastava 2002). This has a detrimental effect on plant water uptake, nutrient absorption, growth, seed germination, and development. Plant distribution is, as a result, tremendously affected (Hayward 1954; Goodin and Northington 1979; Mitlöhner 1997a, b; Singh 2005).

Native species play a fundamental role in the ecosystem by providing mutual interaction with the coexisting plant and animal species. Under normal circumstances, native species are well-adapted to the environmental conditions in which they develop. Although these plants exhibit the ability to withstand drought (Hsiao and Acevedo 1974; Reddy et al. 2004; Hasanuzzaman et al. 2011), salinity (Munns and Tester 2008), and other environmental stresses to a certain extent, tolerance capacity varies greatly between and within the species. Plants experiencing environmental stresses generally adopt two adaptive mechanisms: (1) tolerance, and (2) avoidance (Osmond et al. 1987; Bartels and Sunkar 2005). These mechanisms help improve the plant's ability to resist environmental stresses as well as define the specific niche preference of the individual species.

In the soil-plant-atmosphere continuum, water moves along a gradient of potential energy (Kirkham 2008). Energy potential is a quantitative measure (Kirkham 2008) used to identify plant responses to drought and soil salinity and can be assessed via measurements of plants' internal potentials (i.e. plant water potential- Ψ_w and osmotic potential- Ψ_π) (Mitlöhner 1997a, b). Plant water potential is defined as the driving force for water movement between the plant and the soil (Barrs 1968) and signifies the amount of energy the plant requires to extract soil water (Boyer 1995). The lower the water potential, the more energy the plant must expend to absorb water from the root medium

(Kolay 2008) and the greater the influence on plant growth and developmental processes (Boyer 1995; Kolay 2008).

A predawn and midday measurement of the internal potentials can explain the species composition along with numerous important aspects of the vegetation structure under various environmental conditions (Mitloehner 1997a). Theoretically, plant water potential is in equilibrium with the soil water during the early morning hours (Klepper 1968; Mitlöhner 1997a; Ehlers and Goss 2003; Jones 2007), assuming the available water and evaporative demands are in balance (Klepper 1968). Water potential during the early morning hours is thus an indicator of soil water potential (Klepper 1968; Mitlöhner 1997a; Campbell and Norman 1998; Ehlers and Goss 2003; Jones 2007). Under less evaporative demands, the recovery process takes place at night, and the predawn water potential approaches 0 when the soil is fully hydrated (Campbell and Norman 1998). Inconsistencies, however, do occur, often when there is a strong wind either at night (Turner and Begg 1981), or during in the growing period (Boyer 1968), or when there is an extreme soil water deficit (Donovan et al. 2001). Tyree (1976) and Mitlöhner (1997a, b) report that the lowest midday water potentials measured during the dry period reveal the plant's maximum tolerance to water stress. In plant

water relation studies, remarkable diurnal variations of water potentials are observed as the result of fluctuations in evaporative demands during both the day and night (Klepper 1968; Turner and Begg 1981). In cases of extreme soil water deficit, the overnight recovery process slows, and the diurnal potentials ranges narrow.

The osmotic potential is determined by the concentration of solutes in soil water. This potential is always expressed in the negatives (Lambers et al. 2008), and its value is lower (i.e. more negative) when a concentration of higher solutes is present (Osborne 2000; Lambers et al. 2008; Ben-Menahem 2009). The internal negative osmotic potential ($\Psi\pi$) in a plant is equivalent to the concentration of dissolved salts, sugars, organic acids, etc. (Mitloehner 1997a, b) and is thus reliable tool to assess the ability of a plant to adapt to extreme osmotic stress in a particular site (Mitloehner 1997a, b).

2 Objectives

In the dry deciduous forests of central Myanmar, widely-distributed, predominant species *Tectona hamiltoniana*, *Terminalia oliveri*, *Acacia catechu*, and *Dipterocarpus tuberculatus* shared higher percentages of tree density, frequency, and basal area. Other species, such as *Diospyros burmanica*, *Shorea obtusa*, *Melanorrhoea usitata*, and *Hiptage candicans*, are considered parts of the dry forest ecosystem, that make up a much smaller percentage in, of tree density, frequency, and basal area. Until now, international publications concerning native tree species' responses to environmental stress in central Myanmar have not been available. This study evaluated native tree species' responses to water and salt stress using the Scholander apparatus and freezing point osmometry, with two main objectives: (1) to evaluate the predominant co-occurring species' responses to soil water shortage and soil osmotic stress, and (2) to examine the relationship between the dominance ability and stress adaptive ability of native tree species.

3 Materials and methods

3.1 Species study selections

To provide a representation of the entire area in question, the predominant and some associated species from each forest type were selected. These included *Tectona hamiltoniana* and *Terminalia oliveri* from the Terminalia forest; *Acacia catechu* and *Acacia leucophloea* from the Acacia forest; and *Dipterocarpus tuberculatus*, *Melanorrhoea usitata*, *Shorea obtusa*, *Xylia xylocarpa*, and *Buchanania lanzan* from the *Dipterocarpus* forest. *Tectona hamiltoniana* and *Terminalia oliveri* grew in association with *Acacia catechu* in the Acacia forest and were distributed throughout the region.

3.2 Field measurement and laboratory experiments

To measure water potential, a pressure chamber (“Scholander Apparatus”) was used (Scholander et al. 1965). This tool has been proven in the field as one of the most successful and widely-used methods to determine the total plant water potential (Turner 1988; Boyer 1995; Ehlers and Goss 2003; Kirkham 2005), relying on tension force in a measuring procedure described by Kreeb (1990) and Lassoie and Hinckley (1991). Developed by the cells’ potential to extract water from the soil through the xylem and root cells, tension force represents the applied pressure in the Scholander apparatus (Boyer 1967, 1995). When the plant parts were cut, xylem water drew back into the xylem; this method applied pressure around the leafy shoot to pull water out from the leaf cells until the xylem sap emerged at the cut surface of the shoot (Boyer 1967, 1995). This applied pressure corresponded to the negative pressure in the xylem and was assumed to be a direct measure of the water potential of leaf cells (Scholander et al. 1965; Boyer 1967).

Field measurements of leaf water- and osmotic potential were performed in January of 2010 during the late dry season. Leaf samples from the most dominant and associated species, *Terminalia oliveri*, *Tectona hamiltoniana*, *Acacia catechu*, *Acacia leucophloea*, *Dipterocarpus tuberculatus*, *Melanorrhoea usitata*, *Shorea obtusa*, and *Buchanania lanzan*, were collected for water potential measurement at a total of six randomly selected trees per species per site. Fully developed young leaves from the branches in the southward exposure at of 5-7 m insertion height were used to measure water potential at midday (12-14:30 pm) and predawn (3:30-6 am) (Mitlöhner 1997a, b).

Leaf samples from the same trees measured for water potential were collected to calculate osmotic potential (i.e 6 individuals per species per site). For midday osmotic potential measurement, fresh leaves (5-10 g) were weighed using a precision balance under field conditions. After balancing the weights, the leaf samples were dried in a stainless steel pan over a gas stove, a vitally important process to avoid leaf enzymatic changes. In drying the leaves, care must to be taken not to change the green color. The dry samples were packed, labelled, and stored for further analysis in Göttingen, Germany.

To measure the saturated osmotic potential, 3-5 small branches per species were collected, labelled, and allowed to rehydrate overnight. Steponkus et al. (1982) and Mitlöhner and Köpp (2007) speculate that overnight rehydration may not affect the existing osmolytes in the leaf tissues, and little variation was expected among individuals of the sampled plants. Babu et al. (1999) suggests that the rehydration process is a qualitative measurement to quantify compatible solutes in stressed plants. The cutting edges of the branches were put into a water vessel by covering them with a black plastic bag to interrupt respiration during the rehydration process. The branches absorbed water and became re-saturated overnight; the saturated leaf samples were then cut from the branches, balanced, killed and dried under field conditions, labelled, and stored for further analysis. The procedures involved were as described in the calculation of the midday osmotic potential measurement.

In Göttingen, laboratory experiments were performed to measure the plants and soil osmotic potentials cryoscopically using semi-micro osmometer (Knauer, Germany). The leaf samples were well dried in an oven (Memmert, Germany) at 105 °C for 12 hours before being pulverized in a grinder (Fritsch, Germany). For osmotic potential measurement, each 1 g (\approx 1 g) of leaf powder was mixed with

demineralised water (dilution ×7) to make the solution dilute. Then, the output solution was stored in a water bath at 55 °C for 24 hours, and centrifuged with 4000 rpm for 15-20 minutes to separate the solute and solution. The finalized solution was stored for further analysis. About 0.15 ml solution for one sample was cryoscoped twice and its raw data from semi-micro osmometer (Knauer, Germany) was recalculated for late study. A total of 2-replications per sample sap were cryoscoped.

The results from the freezing point osmometry were recalculated using the following equations developed by Kreeb (1990) (Mitlöhner and Köpp 2007):

$$\Psi\pi = 0.1013 \times [0.021 (\Delta_t)^2 - 12.06 \Delta_t] \dots\dots\dots \text{(Kreeb 1990);}$$

$$\Psi\pi, t \text{ } ^\circ\text{C} = \Psi\pi, 0 \text{ } ^\circ\text{C} (1 + t \text{ } ^\circ\text{C}/273) \dots\dots\dots \text{(Kreeb 1990)}$$

Where: Δ_t is the depression at freezing point; $\Psi\pi, 0 \text{ } ^\circ\text{C}$ is the osmotic potential at 0 °C; and $\Psi\pi, t \text{ } ^\circ\text{C}$ is the osmotic potential at t °C. According to Kreeb (1990), the expected error in the whole measurement processes is approximately ± 2 bar (0.2 MPa).

3.3 Data analysis

STATISTICA for Windows (Version 9.0, Statsoft, Inc., Tulsa, USA) was used in analysing leaf water- and osmotic potential. The distribution of the samples was tested using the Chi-square goodness of fit test, and the differences between the species and sampling sites were studied using a one-way analysis of variance (ANOVA). Turkey’s test was used to rank the mean values after the significant results were revealed by ANOVA. The diurnal variation between midday and predawn water potential values were treated as the relaxation range of the plants from midday water stress. The midday and predawn values of the selected tree species were compared separately in graphs for a particular sampling site. A 45° bisecting line was created on the graph to mark the threshold value of tree species’ water stress.

The bisecting line approach was based on Slatyer’s (1957) model (Figure 3.1) which demonstrates the permanent wilting of the plant and soil. As a result of low water potential in soil, plant water potential progressively decreases while the predawn values rise to match the midday potential. At this point, the plant root ceases to extract water extraction from the soil mass (Slatyer 1957), and plant growth diminishes. In the case of dry forest plants in the dry season, available water is already restricted due to a soil water deficit; the remaining water is strongly bound to the soil particles, and the plants must expend energy in order to extract it. Midday water potential values consequently become more negative, the overnight recovery process slows, and the predawn water potential approaches midday potential. Here, both the predawn and midday values progress towards the bisecting line, potentially characterizing the ability of tree species of a particular forest stand to withstand water stress in the dry season.

The bisecting line also represents the permanent wilting point of the plant, where plant metabolism processes fail, causing the plants to die off (Mitlöhner 1997a) if there is no further rain or available water. Based on the relative position of the values on the bisecting line on the graph, the maximum negative water potential values of a tree species for a particular site can be described by extrapolation

(Mitlöhner 1997a). A paired t-test (Zar 2010) was used to compare the mean values of predawn and midday leaf water potential on the bisecting line.

4 Results

4.1 Plant water relations of the predominant co-occurring tree species

All indigenous species revealed significant response patterns to the soil water deficit (Table 4.1). The three predominant species, *Tectona hamiltoniana*, *Terminalia oliveri*, and *Acacia catechu*, exhibited lower midday and predawn water potentials, the former ranging from -3.1 to -3.2 MPa, the latter from -2.0 to -2.3 MPa. *Xylia xylocarpa* comprised minimum potentials at midday with -3.6 MPa, a value slightly lower than those of the three aforementioned species. Nonetheless, the predawn plant osmotic potentials among *Tectona hamiltoniana*, *Terminalia oliveri*, *Acacia catechu*, and *Xylia xylocarpa* were not significantly different. The midday and predawn water potentials of *Acacia leucophloea* were -2.6 and -1.3 MPa. Species such as *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Melanorrhoea usitata*, and *Buchanania lanzan* showed maximum predawn leaf water potentials ranging from -0.1 MPa to -0.6 MPa, although the potentials measured at midday were considerably higher than in the sampled species (i.e. -0.2 MPa to -1.2 MPa).

Diurnal fluctuations were wider in species such as *Tectona hamiltoniana*, *Terminalia oliveri*, and *Acacia catechu* (-0.6 MPa to -0.7 MPa) and narrower in *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Melanorrhoea usitata*, and *Buchanania lanzan* (-0.01 MPa to 0.6 MPa). Among the latter four species, the predawn water potential of *Melanorrhoea usitata* was slightly lower than the midday potential. The diurnal variation of *Acacia leucophloea* was relatively high (i.e. -1.0 MPa), although *Dipterocarpus tuberculatus* in the *Dipterocarpus* forest exhibited higher variations corresponding to the largest basal area per hectare (i.e. 28.6 m²ha⁻¹), which occupied 72% of total relative basal area. *Melanorrhoea usitata* was the second dominant species in this forest stand and contributed 15% to the total relative basal area.

The other associated species demonstrated a lower basal area per hectare with highly variable midday and predawn water potentials. A total of 88% of the relative basal area belonged to the predominant species in the *Acacia* forest, *Acacia catechu*. *Acacia leucophloea*, an infrequently-found species occupying less than 5% relative basal area in the same forest, exhibited relatively low plant water potentials at midday and predawn. The two predominant species of the *Terminalia* forest, *Tectona hamiltoniana* and *Terminalia oliveri*, had the lowest plant water potentials but amounted to 89% of total relative basal area per hectare.

The species-specific response to water stress was evaluated using the bisecting line approach (Figure 4.1). Leaf water potentials measured at predawn and midday were plotted on the x,y abscissas, with the extrapolation of the point position to the bisecting line reflecting both the species-specific adaptive ability to the soil water deficit and the permanent wilting percentage (i.e. threshold value) of the plants. The graphical depiction revealed two obvious groups of species that responded to the soil water deficit under similar environmental conditions. *Tectona hamiltoniana*, *Terminalia oliveri*, *Acacia catechu*, *Acacia leucophloea*, and *Xylia xylocarpa* all possessed a better ability to withstand midday water stress and indicated remarkable overnight relaxation.

The diurnal variations of these species were wider, and leaf water potentials were therefore distributed above the bisecting line. *Dipterocarpus tuberculatus*, *Shorea obtusa*, and *Melanorrhoea usitata* showed the highest midday and predawn water potentials. Of these three, the first two were able to effectively recover from midday water stress; most of the individuals from *Melanorrhoea usitata*, however, were under extreme water stress, with the severe water shortage experienced at midday resulting in an inability to fully recover at night. For this reason, the leaf water potentials were on the bisector while most individuals fell below it.

The significant differences of the points on the bisector were evaluated using a paired T-test. *Tectona hamiltoniana*, *Terminalia oliveri*, *Acacia catechu*, and *Acacia leucophloea* all responded to predawn and midday water stresses significantly, but no such differences were observed between potentials in *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Melanorrhoea usitata*, *Buchanania lanzan*, and *Xylia xylocarpa*.

4.2 Plant osmotic potentials for the predominant tree species

The leaf osmotic potentials for the indigenous species are described in table (4.2). The species *Tectona hamiltoniana*, *Terminalia oliveri*, and *Acacia catechu* revealed the lowest leaf osmotic potentials at midday, at -3.9 MPa, -3.8 MPa, and -3.9 MPa, respectively. The saturated leaf osmotic potentials of these species were relatively lower than in the other species. Leaf osmotic potentials measured at midday or saturated were not significantly different between the three; *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Melanorrhoea usitata*, *Buchanania lanzan*, *Acacia leucophloea*, and *Xylia xylocarpa*, however, responded differently, in that the corresponding midday and saturated leaf osmotic potentials were relatively high.

Shorea obtusa, *Melanorrhoea usitata*, *Acacia leucophloea*, and *Xylia xylocarpa* showed remarkably higher saturated osmotic potentials, ranging from -0.5 MPa to -0.7 MPa and corresponding to higher midday leaf osmotic potentials from -1.2 MPa to -1.6 MPa. *Dipterocarpus tuberculatus* and *Buchanania lanzan* exhibited the highest osmotic potentials, with saturated and midday leaf osmotic potentials for the former at a respective -0.9 MPa and -0.9 MPa and for the latter, at -0.5 MPa and -0.7 MPa.

Dipterocarpus tuberculatus was the most sensitive species to soil osmotic stress, with the narrowest diurnal potentials (-0.02 MPa); it nonetheless, demonstrated the highest basal area per hectare among the dry deciduous forest species in central Myanmar. *Tectona hamiltoniana*, *Terminalia oliveri*, and *Acacia catechu* responded to soil osmotic stress in much the same way they did to soil water deficit.

Melanorrhoea usitata expressed a considerably higher resistance to soil osmotic stress than to soil water shortage, registering a substantial relaxation in response to midday water stress unlike other species, such as *Shorea obtusa*, *Buchanania lanzan*, *Acacia leucophloea*, and *Xylia xylocarpa*. Additionally, it contributed a very low basal area per hectare in comparison with the predominant species. As references, the osmotic potentials of seawater (Collinson 1978; Lobban and Harrison 1997; Larcher 2003), and the midday osmotic potentials of cotton (*Gossypium hirsutum* L.) (Boyer 1965) and sorghum (*Sorghum bicolor* L. Moench) (Girma and Krieg 1992) are provided.

The adaptive ability of an individual was evaluated through the extrapolation of the positions of the point to the bisector (Figure 4.2); the closer the points to the bisector, the lower species' ability to withstand soil osmotic stress. As in plant water potentials, the osmotic potentials of native species revealed two clear groups. The predominant species of the dry deciduous forests, *Tectona hamiltoniana*, *Terminalia oliveri*, and *Acacia catechu* demonstrated better adaptability to the soil salinity with points distributed above the bisector. In the case of the species such as *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Buchanania lanzan*, and *Xylia xylocarpa*, some individuals were under severe stress and had points on the graph that fell below the bisecting line. Others, including *Xylia xylocarpa*, and some individuals of *Buchanania lanzan*, responded to soil osmotic stress differently than to water stress. These species registered a better ability to cope with soil water shortage, but were less adaptable to soil osmotic stress. This low ability notwithstanding, most of the individuals fully recovered from the midday osmotic stress, as demonstrated by points that lay farther from the bisector.

The paired T-test revealed significant differences between the midday and saturated leaf osmotic potentials for all species, with the exception of *Dipterocarpus tuberculatus* and *Buchanania lanzan*. The predominant and associated species *Tectona hamiltoniana*, *Terminalia oliveri*, *Acacia catechu*, *Melanorrhoea usitata*, and *Acacia leucophloea* exhibited effective relaxation from midday osmotic stress, showing relatively high saturated osmotic potentials significantly different from those at midday. *Shorea obtusa* and *Xylia xylocarpa* evidenced significant differences between midday osmotic potentials and saturated ones, but the diurnal variations were much narrower. The midday and saturated osmotic potentials of *Dipterocarpus tuberculatus* and *Buchanania lanzan* were insignificant at a $\alpha = 0.05$ level; the former experienced soil osmotic stress.

4.3 Species performance to dryland environmental stresses

Based on the plants' adaptability to soil water deficits and osmotic stress, the performances of native species were categorized into four different temperament classes (TC): TC-I, representing those species with both high water- and osmotic potentials; TC-II, corresponding to species with low water potentials but high osmotic potentials; TC-III, with both low water- and osmotic potentials; and TC-IV, referring to species with high water potentials but low osmotic potentials. The species-specific ecological niche preference is provided in table (4.3) as a reference of soil water availability and the solute/nutrient concentration in the root zone.

The predawn water potential is considered an indicator of soil water status (Mitlöhner 1997b; Ehlers and Goss 2003; Ackerly 2004; Jones 2007), whereas plant osmotic potential at full turgidity represents the osmotically active substances in the root zone (Bernstein 1961a, b; Kirkham et al. 1969; Bowman

and Roberts 1985; Stiles 1994). Based on these assumptions, the mean values of the predawn water potentials Ψ_w and saturated osmotic potentials Ψ_π for all species were plotted on the x,y axis in the graph. The temperament class determination was completed on the basis of mean potentials contributed by all species. The dash-dotted line parallel to the x-axis represented the mean value of the predawn plant water potential for all species; a similar line parallel to the y-axis corresponded to the means of the saturated plant osmotic potentials. From the interception of these two lines, the four temperament classes were assigned in an anti-clockwise direction. The graphical depiction of plant temperament classes is shown in figure (4.3).

The temperament classes in the graph are consistent with the information in table (4.4). The graph depicts *Tectona hamiltoniana*, *Terminalia oliveri*, and *Acacia catechu* as species of high adaptability to soil water deficits and osmotic stress, confirming the specific niche preference for those species. *Xylia xylocarpa* resisted soil water shortage well but had a relatively low ability to adapt to soil osmotic stress, explaining why the species rarely grows on saline soils. *Acacia leucophloea* exhibited an intermediate ability to withstand water stress but a remarkably low ability to resist high solute concentrations in the rhizosphere. Little variation was observed in the adaptations of *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Melanorrhoea usatata*, and *Buchanania lanzan*.

The plant rhizosphere salt concentration, estimated through the plant measurements (i.e. plant osmotic potential) is provided in the comparison of plant leaf salt concentration (Table 4.4). The former was estimated through the plant measurements. In response to the constraints and unreliability of the in situ measurement of soil osmotic potential at the root zones, Mitlöhner (1997a, b) established the concept of standardized plant osmotic potential to reflect the rhizosphere solute concentration for a specific species in a particular site. The resulting soil osmotic potentials in MPa were transformed into the molarity of NaCl solution (mM) using the equation described by Das (2004), Oriakhi (2009), and Zumdahl and Zumdahl (2011). For an electrolyte solution, the osmotic pressure based on both Van't Hoff laws (Das 2004; Zumdahl and Zumdahl 2011) and the molar concentration of the solution was calculated.

The Van't Hoff equation (Das 2004; Zumdahl and Zumdahl 2011) is as follows:

$$\Pi = iMRT; M = \frac{\Pi}{iRT}$$

Where: Π is the osmotic pressure, i is the number of particles/ions, M is the molar concentration of the solution, R is the universal gas constant ($0.00831 \text{ L MPa mol}^{-1} \text{ K}^{-1}$) (Wills 2007), and T is the absolute temperature (at 25°C). At cell maximum hydration (full turgidity), the osmotic pressure (Π) is equal to the osmotic potential (Ψ_π), showing different signs of positive and negative (Karamanos 2008).

The solute concentration in the root zone was the highest at the time of the field measurement due to a prolonged drought. The categorization into sensitive, moderately tolerant, and tolerant species was based on Atwell et al. (1999) and Heuperman et al. (2002). The rhizosphere solute concentrations were lower for *Acacia leucophloea*, *Dipterocarpus tuberculatus*, *Shorea obtusa*, *Melanorrhoea usatata*, *Xylia xylocarpa*, and *Buchanania lanzan*, in direct contrast to predominant tree species *Tectona hamiltoniana*, *Terminalia oliveri*, and *Acacia catechu*, which were highly resistant to high root medium solute concentrations. *Buchanania lanzan* revealed the lowest adaptability to soil salinity, and *Acacia*

leucophloea, despite a higher resistance to water stress, had a relatively low ability to adapt to soil osmotic stress.

5 Discussion

Plant responses to environmental stress vary greatly between and within species, depending on the site conditions and the plant's inherent physiological traits. The indigenous species in this study responded in significant ways to soil water deficits. *Xylia xylocarpa* depicted the lowest midday and predawn leaf water potentials, followed by *Acacia catechu*, *Terminalia oliveri*, *Tectona hamiltoniana*, and *Acacia leucophloea*. The midday water potential for *Xylia xylocarpa* reached up -3.6 MPa, and the minimum water potentials for the other species decreased to -3.2 MPa, implying a high adaptability to soil water stress during periods of drought. The lowest midday plant water potential is considered an indicator of maximum drought resistance (Ladiges 1975, DeLucia and Schlesinger 1991, Gebrekirstos et al. 2006, Kirkham 2008), a suggestion confirmed in this study. Nevertheless, the lowest midday plant water potential is not recommended for best plant development (Boyer 1995). In the case of *Xylia xylocarpa*, a widely-distributed ironwood tree of Myanmar, well-drained, sandy soils are a requirement for the tree to thrive and attain larger dimensions and height (Troup 1921b); in dry forests with shallow, poor soil, stunted stems are the rule. This species contributes about 2% of the total relative basal area per hectare in the *Dipterocarpus* forest.

Terminalia oliveri and *Tectona hamiltoniana*, characteristic species of the dry forests in central Myanmar, grow especially well in clay soils (Troup 1921a, b; Kermode 1964) and occupy over 85% of the total relative basal area per hectare. *Acacia catechu* grows on a variety of soil types, from alluvium sandy soil along river beds to the poorest soil in the dry areas. Along river banks in the *Acacia* forests, this species can contribute up to 90% of the total relative basal area per hectare. Altogether, these three species exhibit minimum midday water potentials of about -3.2 MPa with maximum predawn potentials of -1.5 MPa. Their diurnal water potential ranges, however, are relatively wide (-0.7 MPa), the results of the overnight relaxation processes. This suggests that *Terminalia oliveri*, *Tectona hamiltoniana*, and *Acacia catechu* are not only tolerant to drought, but can also fully recover from midday soil water stress during the dry season. Good growth can therefore be expected under adequate water conditions.

Acacia leucophloea, an associated species of *Acacia catechu*, grows on poor, shallow soil in drought-prone areas. It is at present very difficult to find in the natural forest, but is more likely to be spotted along roadsides. This species occupies a total relative basal area of no more than 5% in the *Acacia* forest. In central Myanmar, *Terminalia oliveri*, *Tectona hamiltoniana*, *Acacia catechu*, and *Acacia leucophloea* can grow together in the shallow, poor soils of drier tracts, and no significant differences in midday water potentials were observed. Nevertheless, this does not mean all the species have similar inherent ecophysiological attributes—rather, micro-site conditions and/or root architecture influences water uptake and the regulation of the plant's water status. Based on our results, it appears that *Xylia xylocarpa*, *Terminalia oliveri*, *Tectona hamiltoniana*, *Acacia catechu*, and *Acacia leucophloea* are resistant to drought.

Dipterocarpus tuberculatus, *Shorea obtuse*, and *Melanorrhoea usitata* revealed the highest midday and predawn leaf water potentials, implying that these species experience no water stress and water access

is certain. Troup (1921b) and Kermode (1964) note that *Dipterocarpus tuberculatus* and *Shorea obtusa* grow well in areas with higher rainfall and are less resistant to drought. It is possible that the remarkably high leaf water potentials measured at midday and predawn characterize the species-specific niche preference for these species. *Melanorrhoea usitata*, the commonly associated species of the *Dipterocarpus* forests, is the most sensitive to the soil water deficits. *Buchanania lanzan*, which grows in association with *Dipterocarpus tuberculatus*, *Shorea obtusa*, and *Melanorrhoea usitata*, is drought sensitive (Troup 1921a, b), although less so than *Melanorrhoea usitata* given its intermediate potentials measured at midday and predawn. It appears that the micro-site requirements for *Melanorrhoea usitata* and *Buchanania lanzan* are similar to those of *Dipterocarpus tuberculatus* and *Shorea obtusa*.

Mitlöhner (1997a, b) reports that the midday water potentials of dry forest species can decrease to -8.0 MPa. Gebrekirstos et al. (2006) found that *Dichrostachys cinerea* (L.) Wight & Arn. in Abernosa, Ethiopia had a minimum water potential of about -5.8 MPa. Wai (2005) describes the midday water potentials of *Tectona hamiltoniana* Wall., which can reach as low as -4.2 MPa, and *Terminalia oliveri* Brandis, at -3.4 MPa; his findings are slightly lower than our results. The lower midday water potentials of the same species may be due to the differences in site conditions as well as genetic variations between individuals.

Plant osmotic potentials at full cell hydration corresponds to solute concentrations at the root zone (Bernstein 1961a, b; Kirkham et al. 1969; Bowman and Roberts 1985; Stiles 1994; Mitlöhner 1997a, b; Mitlöhner and Köpp 2007), while the minimum those at midday during the dry season are suggested to be the plants' maximum adaptability to soil osmotic stress (Mitlöhner 1997a, b). Seawater has an osmotic potential of ≈ -2.5 MPa (Collinson 1978, Lobban and Harrison 1997, Larcher 2003); however, the soil osmotic potentials in the driest areas can be considerably lower than those of seawater (Collinson 1978). Cotton (*Gossypium hirsutum* L.) (Cothren 1999) and sorghum (*Sorghum bicolor* L. Moench) are salt-tolerant crops (Cothren 1999, Vlek et al. 2008) with a midday plant osmotic potential at about -1.2 MPa for the former (Boyer 1965) and -2.8 MPa for the latter (Girma and Krieg 1992). Herbaceous plants have an osmotic potential of ≈ -1.5 MPa, and xerophytes, at the permanent wilting point, can be at less than -10 MPa (Mohr and Schopfer 1995). Halophytes (e.g., *Atriplex* spp.) can reach as low as -20 MPa (Collinson 1978). The species studied in central Myanmar have midday plant osmotic potentials ranging from -0.7 to -3.9 MPa and saturated osmotic potentials from -0.5 to -2.9 MPa.

The native tree species in central Myanmar have significant responses to soil osmotic stress, although in different ways than to soil water stress. *Acacia catechu* demonstrated the lowest midday and saturated osmotic potentials, followed by the predominant species *Terminalia oliveri*, *Tectona hamiltoniana*, *Acacia leucophloea*, and *Xylia xylocarpa*. The adaptive response abilities seem to be analogous, and there are no significant differences in plant osmotic potentials between *Acacia catechu*, *Terminalia oliveri* and *Tectona hamiltoniana*. For all species, the lowest midday osmotic potential was around -3.9 MPa whereas the highest saturated osmotic potential was -2.3 MPa. All species depicted lower plant osmotic potentials with parallel decreases in plant water potentials.

Acacia leucophloea and *Xylia xylocarpa* responded to soil osmotic stress differently than they do to soil water shortage. Additionally, their saturated osmotic potentials ranged from -0.7 to -1.2 MPa, reflecting a rhizosphere osmotic potential (Bernstein 1961a, b; Kirkham et al. 1969; Stiles 1994; Mitlöhner 1997a, b) that is remarkably higher than that of *Terminalia oliveri*, *Tectona hamiltoniana*, and *Acacia catechu*.

The micro-site requirements for *Acacia leucophloea* and *Xylia xylocarpa* involve less soil salinity, and the two are thus referred to as salt-sensitive species. The occurrence of *Acacia leucophloea* along the roadsides is possibly due to the rain, which washes salt particles to lower parts of the soil, thus resulting in less amounts of overall salinity. *Dipterocarpus tuberculatus* and *Buchanania lanzan* exhibited the highest midday and saturated leaf osmotic potentials, indicating that the former is the least resistant species to soil osmotic stress. *Shorea obtusa* and *Melanorrhoea usitata* are intermediate species, as evidenced by their measured intermediate saturated and midday potentials.

The saturated plant osmotic potentials between *Dipterocarpus tuberculatus*, *Buchanania lanzan*, *Shorea obtusa*, and *Melanorrhoea usitata* are significantly different. These differences are the result of species-specific physiological and morphological attributes, rooting depths, and a variety of solute concentration in the root zones. In the case of *Melanorrhoea usitata*, the species responded differently to soil water shortages and soil osmotic stress. Most *Melanorrhoea usitata* individuals are under extreme water stress conditions, but exhibit a better adaptation to soil osmotic stress.

Dipterocarpus tuberculatus exhibits the highest plant water potential, corresponding to the largest basal area per hectare. This suggests that the species dominance ability is proportional to higher plant water potentials in areas with good access to water. *Dipterocarpus tuberculatus*, which grows gregariously in higher rainfall areas at the boundary of central Myanmar, also shares a higher percentage in terms of stem numbers and basal area per hectare. Kirkham (2008) found that crops sensitive to drought yielded better than in areas with good water access than their drought-resistant counterparts. Our results are in accord with Kirkham's (2008) findings, and we speculate that higher plant water potentials in areas with good water access relate closely to the dominant ability of the species.

Acacia catechu, *Tectona hamiltoniana*, and *Terminalia oliveri* demonstrate both the lowest plant water- and osmotic potentials among the indigenous species. They resist drought and soil salinity well, and can thus be found across all of central Myanmar dominating specific forest. This suggests that their resistance to adverse environmental stresses helps improve their ability to dominate the area.

Temperament class categorization permits a comparison between the species' ability to adapt to drought/soil salinity and their habitats, which could characterize the species' physiological and morphological attributes. The findings revealed that the temperament class of a particular species is consistent with the species-specific niche preference. This study suggests temperament classification is a useful tool to confirm the species' responses to the environmental stresses in references to habitat preferences.

6 Conclusion and Recommendations

There is a clear relation of plant drought tolerance to domination ability in drought prone areas. Of the native tree species, *Acacia catechu*, *Tectona hamiltoniana*, and *Terminalia oliveri* are highly adaptable to drought and soil salinity. *Melanorrhoea usitata* is the most sensitive to the soil water deficits and soil salinity stress. This study suggests temperament classification is a useful tool to confirm the species' responses to the environmental stresses in reference to habitat preferences.

Dry deciduous forests play an exceptionally important role from both an ecological and socio-economic point of view. Until now, these forests have been the most critical and principal suppliers of the resources that local communities depend on for their subsistence. For these reasons, the following options are recommended.

1. The protection of dry deciduous forests is of vital importance to maintaining the soil water regime and solute concentration as normally as possible, since the regeneration, growth, and development of native tree species are only certain under forest conditions with minimal anthropogenic disturbances.
2. Of the native tree species, *Acacia catechu*, *Tectona hamiltoniana*, and *Terminalia oliveri* are highly adaptable to drought and soil salinity.
3. Additional scientific research on native species' germination and seedling establishment in relation to various salinity levels is recommended.

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Tables

Table 4.1. The leaf water potentials of the predominant tree species in the dry deciduous forests in central Myanmar.

Sites and species	n	Leaf water potential Ψ_w [MPa]*			g**
		Minimum	Midday	Predawn	
<u>Terminalia forest</u>					
<i>Tectona hamiltoniana</i>	6	-3.1	-2.7 ± 0.1 (a)	-2.0 ± 0.1 (a)	38
<i>Terminalia oliveri</i>	6	-3.2	-2.8 ± 0.1 (a)	-2.1 ± 0.1 (ad)	51
<u>Acacia forest</u>					
<i>Acacia catechu</i>	6	-3.2	-2.9 ± 0.1 (a)	-2.3 ± 0.1 (ad)	88
<i>Acacia leucophloea</i>	6	-3.1	-2.6 ± 0.2 (a)	-1.3 ± 0.3 (b)	5
<u>Dipterocarpus forest</u>					
<i>Dipterocarpus tuberculatus</i>	6	-0.2	-0.2 ± 0.01 (b)	-0.1 ± 0.01 (c)	72
<i>Shorea obtusa</i>	6	-0.3	-0.2 ± 0.03 (b)	-0.2 ± 0.02 (c)	0.2
<i>Melanorrhoea usitata</i>	6	-0.4	-0.2 ± 0.03 (b)	-0.3 ± 0.04 (c)	15
<i>Buchanania lanzan</i>	6	-2.6	-1.2 ± 0.4 (c)	-0.6 ± 0.1 (c)	1
<i>Xylia xylocarpa</i>	6	-3.6	-3.1 ± 0.2 (a)	-2.7 ± 0.1 (d)	2

* Means \pm standard errors are shown for each variable. Within a parenthesis, means followed by different letters were statistically different at $P < 0.05$ (Tukey test).

**g= Relative tree basal area (%), n= Number of replications.

Table 4.2. The leaf osmotic potentials of the dominant tree species in the dry deciduous forests, in central Myanmar.

Sites and species	n	Leaf osmotic potential $\Psi\pi$ [MPa]*			g**
		Minimum	Midday	Saturated	
<u>Terminalia forest</u>					
<i>Tectona hamiltoniana</i>	6	-3.9	-3.4 \pm 0.1 (a)	-2.6 \pm 0.1 (a)	38
<i>Terminalia oliveri</i>	6	-3.8	-3.4 \pm 0.1 (a)	-2.7 \pm 0.1 (a)	51
<u>Acacia forest</u>					
<i>Acacia catechu</i>	6	-3.9	-3.8 \pm 0.1 (a)	-2.9 \pm 0.1 (a)	88
<i>Acacia leucophloea</i>	6	-2.0	-1.6 \pm 0.1 (c)	-0.7 \pm 0.1 (bc)	5
<u>Dipterocarpus forest</u>					
<i>Dipterocarpus tuberculatus</i>	6	-1.5	-0.9 \pm 0.2 (b)	-0.9 \pm 0.1 (b)	72
<i>Shorea obtusa</i>	6	-1.6	-1.2 \pm 0.2 (bc)	-0.7 \pm 0.04 (bc)	0.2
<i>Melanorrhoea usitata</i>	6	-1.6	-1.3 \pm 0.1 (bc)	-0.5 \pm 0.04 (c)	15
<i>Buchanania lanzan</i>	6	-0.9	-0.7 \pm 0.4 (b)	-0.5 \pm 0.1 (c)	1
<i>Xylia xylocarpa</i>	6	-2.0	-1.6 \pm 0.1 (c)	-1.2 \pm 0.1 (bd)	2

* Means \pm standard errors are shown for each variable. Within a parenthesis, means followed by different letters were statistically different at $P < 0.05$ (Tukey test).

**g= Relative tree basal area (%), n= Number of replications.

[Reference: seawater $\Psi\pi \approx -2.5$ MPa (Collinson 1978; Lobban and Harrison 1997; Larcher 2003), cotton $\Psi\pi = -1.2$ MPa (Boyer 1965), sorghum $\Psi\pi = -2.8$ MPa (Girma and Krieg 1992)]

Table 4.3. The classification of temperament classes based on the species adaptability to soil water deficit (predawn Ψ_w) and salinity stress (saturated $\Psi\pi$), the dry deciduous forest species in central Myanmar.

Species	High Ψ_w	Low Ψ_w	High $\Psi\pi$	Low $\Psi\pi$	TC	ecological niche preference*
<i>Dipterocarpus tuberculatus</i>	X		X		I	Sandy, gravelly, laterite soils
<i>Shorea obtusa</i>	X		X		I	Sandy, gravelly, laterite soils
<i>Melanorrhoea usitata</i>	X		X		I	Sandy, gravelly, laterite soils
<i>Buchanania lanzan</i>	X		X		I	Laterite soils
<i>Acacia leucophloea</i>		X	X		I-II	Poor shallow soils,
<i>Xylia xylocarpa</i>		X	X		II	Deep sandy loam, laterite soils
<i>Tectona hamiltoniana</i>		X		X	III	Clay soils

<i>Terminalia oliveri</i>	X	X	III	Clay soils
<i>Acacia catechu</i>	X	X	III	Sandy alluvium, loam with varying clay content

*Troup (1921a, b), Kermode (1964)

Table 4.4. The native species performance in response to soil salinity, which is expressed as the molar concentration of NaCl (mM).

Category ⁺	Salt conc.- Soil solution* (mM) NaCl**	Salt conc.- Plant leaf (mM) NaCl	Species	Family
Sensitive	82	102	<i>Buchanania lanzan</i>	Anacardiaceae
	102	102	<i>Melanorrhoea usitata</i>	Anacardiaceae
Moderately sensitive	123	143	<i>Shorea obtusa</i>	Dipterocarpaceae
	123	143	<i>Acacia leucophloea</i>	Fabaceae
	164	184	<i>Dipterocarpus tuberculatus</i>	Dipterocarpaceae
Moderately tolerant	204	245	<i>Xylia xylocarpa</i>	Fabaceae
	450	530	<i>Tectona hamiltoniana</i>	Verbenaceae
Tolerant	429	552	<i>Terminalia oliveri</i>	Combretaceae
	530	593	<i>Acacia catechu</i>	Fabaceae

* Salt concentration in the soil solution was estimated on the basis of standardized leaf osmotic potential after Mitlöhner (1997a, b).

**10 mM NaCl \approx 1 dSm⁻¹ (Cramer 2002); 40 mM NaCl \approx 0.2 MPa (Munns and Tester 2008; Shabala and Munns 2012)

⁺ after Atwell et al. (1999) and Heuperman et al. (2002)

[For comparison: *Eucalyptus tereticornis* and *E. camaldulensis* have the ability to withstand the soil salinity of 400+ (mM) LD₅₀ (i.e. at which 50% of the seedling population die); *E. camaldulensis* in the De Grey River in Western Australia provenance is tolerant to soil salinity up to 636 (mM) (i.e. at which mortality of all individuals are expected) (Lambert & Turner 2000)]

Figures

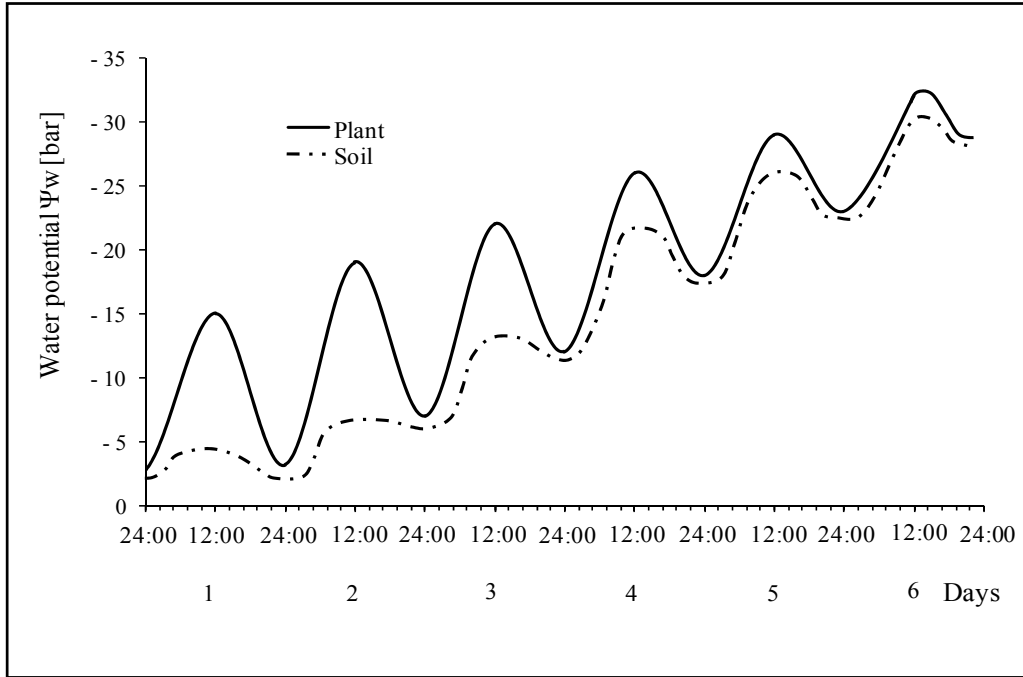


Figure 3.1.

Slatyer's (1957) model, showing the diurnal relationship between plant water potential and soil water potential based on increasing drought within a week, modified [after Mitlöhner (1997a, 1999)].

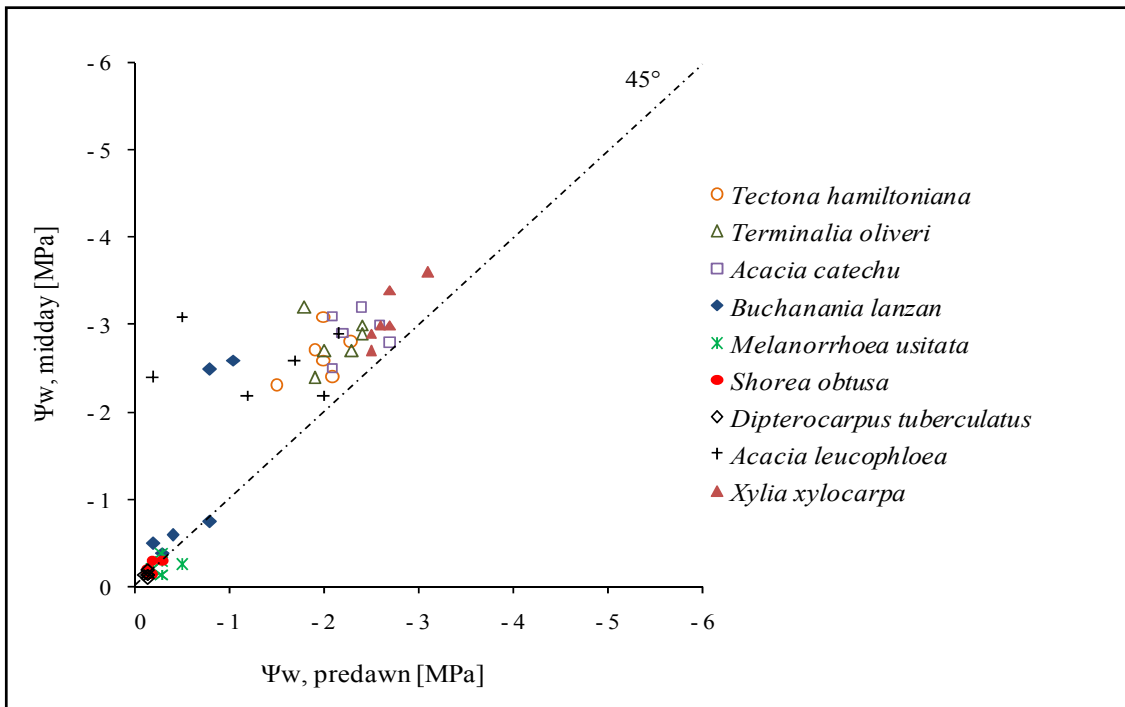


Figure 4.1. Midday and predawn leaf water potentials Ψ_w (MPa) of the predominant tree species in the dry deciduous forests, in central Myanmar.

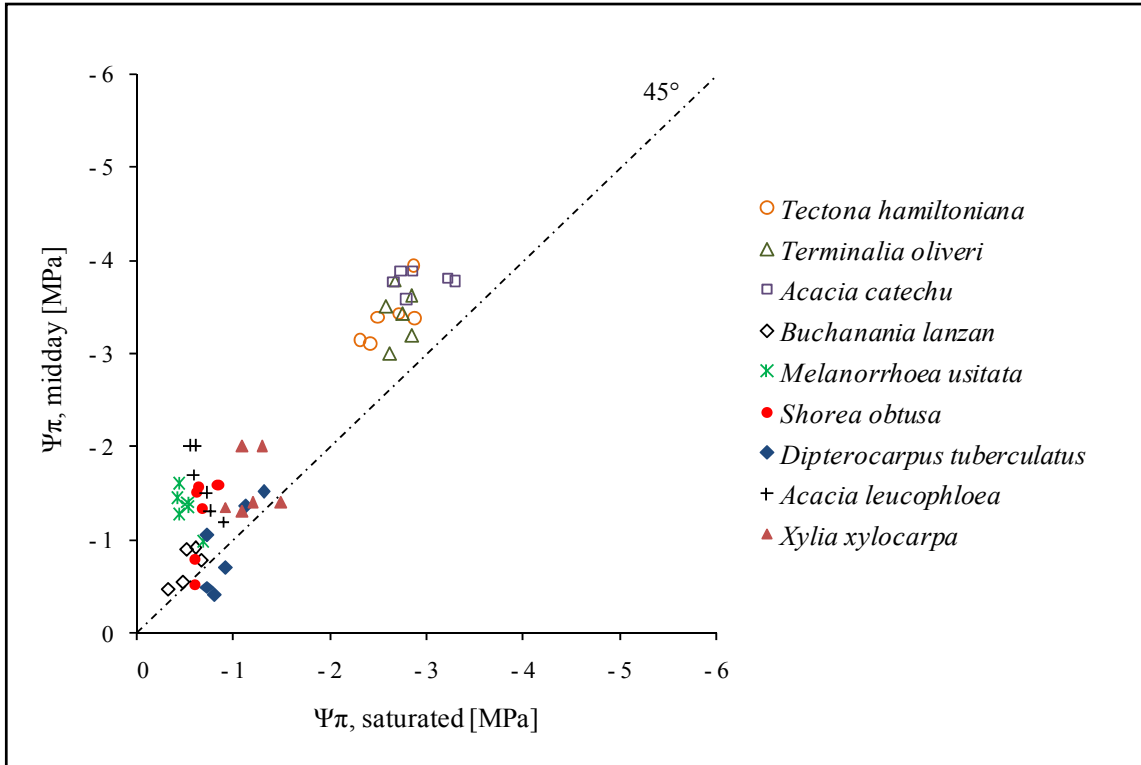


Figure 4.2. Midday and saturated leaf osmotic potentials Ψ_{π} (MPa) of the predominant tree species in the dry deciduous forest, in central Myanmar.

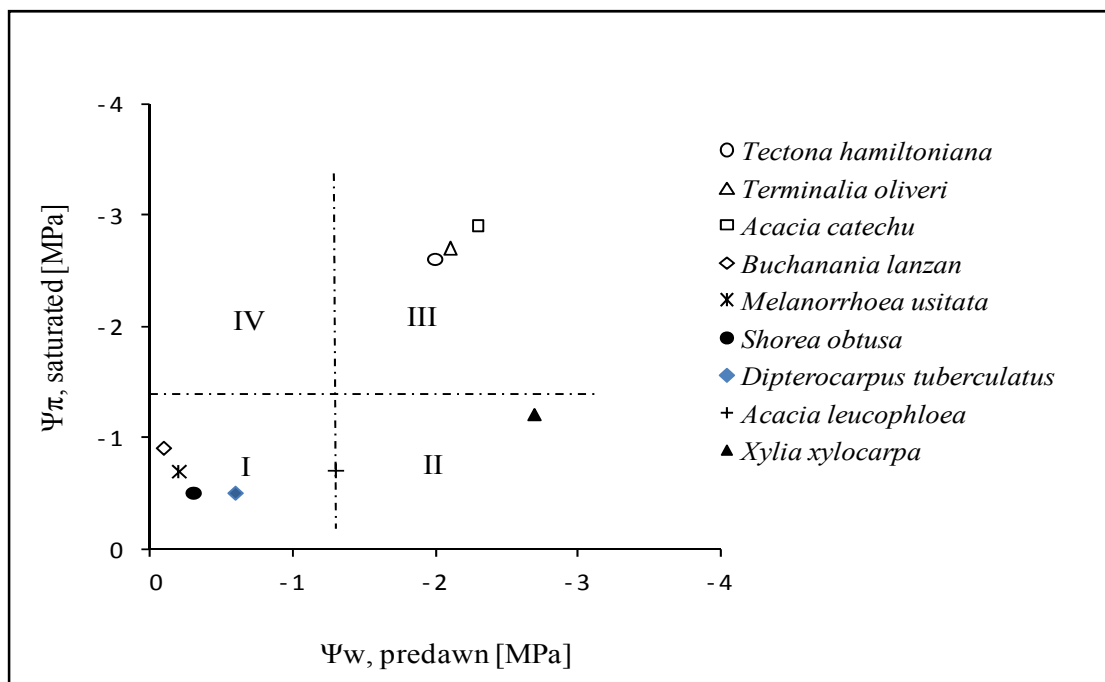


Figure 4.3. The classification of temperament classes based on the plant respective predawn water potentials Ψ_w and plant saturated osmotic potentials Ψ_{π} ; mean potentials are included, temperament classes (TC-I, II, III, and IV) classification follows the means of all species, 6-individuals per species were tested.