

SHORT COMMUNICATION

Evidence for direct water absorption by the shoot of the desiccation-tolerant plant *Vellozia flavicans* in the savannas of central Brazil

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Our common view on water uptake by terrestrial plants is that it occurs via absorption by roots from the soil substrate. However, it has long been known that plants exhibit alternative water-absorption strategies, particularly in drought-prone environments. Examples include many tropical epiphytic orchids which use a specialized structure called *velamen radicum* around their aerial roots for moisture absorption directly from the air (Capesius & Barthlott 1975), specialized trichomes in bromeliads (Andrade 2003, Benzing 1990), uptake by hydathodes into leaves of species inhabiting dry desert ecosystems of Namibia (Martin & von Willert 2000) and foliar absorption by coastal California redwoods during the summer fog season (Burgess & Dawson 2004). One of the most intriguing and yet, least-studied examples of adaptations to severe water limitation is found with desiccation-tolerant plants (also called resurrection plants). During drought periods, the water content of these plants can equilibrate with the low relative humidity of the air to the point that the plants appear dead. However, when water is supplied, these plants fully rehydrate (Alpert 2000, Bewley & Krochko 1982) and become physiologically active. Desiccation-tolerant vascular plants are rare in most ecosystems but diverse in tropical inselbergs (granitic outcrops; Porembski & Barthlott 2000). Relatively little is known about inselberg species particularly from an ecophysiological perspective (see Lüttge 1997 and Klüge & Brulfert 2000 for reviews).

The white sand savannas and rock outcrops (campos rupestres) of central Brazil are a diversity centre for vascular species of desiccation-tolerant plants (Porembski & Barthlott 2000); most of these taxa are members of

the monocot family Velloziaceae (Menezes *et al.* 1994). Species within this family have distinct and rather unusual morphological and anatomical features: their trunks (pseudostems) consist mostly of persistent and fibrous leaf bases under which a massive sheath of adventitious roots is found (Menezes 1971, Owoseye & Sanford 1972; see Figure 1 for pseudostem morphology). Porembski & Barthlott (2000) described species of Velloziaceae as 'plants that grow like epiphytes upon the dead parts of their own pseudostems'. Porembski & Barthlott (1995) described the occurrence of *velamen radicum* in the adventitious roots of *Vellozia*, and hypothesized that this structure might be involved in rapid water uptake. At the time of their publication, experimental evidence determining the functional role of this structure in *Vellozia* was lacking and so it remained to be established whether it served as a water-uptake organ or perhaps conferred desiccation tolerance of some sort. In this study we provide the first evidence for the water-absorption capacity of the pseudostems of *Vellozia* in savannas of Central Brazil.

We used the heat ratio sap flow method (HRM; Burgess *et al.* 2001) to monitor water flow in the pseudostems of three individuals of *Vellozia flavicans* between August 2002 and September 2003. HRM was originally developed by Burgess *et al.* (1998) to measure slow rates of sap flow and reverse flows in roots of woody species. Recently it has also been used to measure reverse flow in the xylem of branches resulting from foliar uptake of fog water by redwood trees in coastal California (Burgess & Dawson 2004). HRM is described in detail in Burgess *et al.* (1998) and Burgess *et al.* (2001), but its principle is to measure the increase in temperature following a heat pulse at two points, above and below a central heater. One heater and a pair of

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Figure 1. *Vellozia flavicans* growing in the cerrado of central Brazil. Note the arborescent growth form, with branching stems covered with fibrous, persistent dead leaf bases under which adventitious roots are found and grass-like leaves in tufts at the apices.

copper–constantan thermocouples were inserted radially into the xylem tissue at the base of the pseudostem (at 30 cm height) of the three individuals. The diameter of the pseudostems at this height was wide enough (7–9 cm diameter) to hold these thermocouples. Each thermocouple had two junctions to measure sap velocity at two depths in the xylem tissue. A metal drill guide was used to ensure that the holes were parallel and spaced exactly 6 mm apart. This was necessary to minimize probe misalignment during insertion and therefore prevent violating the assumptions of the sap-flow calculations (see Burgess *et al.* 2001 for a full description). All probes were connected to an AM416 multiplexer (Campbell Scientific Inc. Logan, Utah, USA) by 8-m-long cable interfaced with a CR10x data logger (Campbell Scientific Corp., Logan, Utah, USA). Heaters were switched to send a pulse every 30 min and temperature ratios were recorded. The raw data were then analysed using the protocol outlined by Burgess *et al.* (1998, 2001). At the end of the study we cut all stems to stop sap flow. This procedure is required to obtain the most accurate reference velocity (zero flow, Burgess *et al.* 2001). Once zero flow was determined we were able to distinguish between reverse

flow (from the canopy to base of the trunk) and normal flow caused by transpiration (from the base of trunk to the canopy).

The study was carried out at the IBGE-RECOR ecological reserve, located 35 km south of Brasilia (15° 56'S, 47° 53'W, altitude 1100 m), in central Brazil. The 1350-ha reserve includes extensive areas of all major physiognomic forms of cerrado vegetation (Ribeiro & Walter 1995). The sap-flow investigation was carried out in a stand of cerrado *sensu stricto* (Ribeiro & Walter 1995), a seasonal savanna that represents the most common structural type in the cerrado area. This vegetation is characterized by a mixture of shrubs and trees of different phenological types and grasses that senesce during the dry season. The climate is seasonal with a distinct wet season (October–April) and dry season (May–September). Annual average rainfall is approximately 1450 mm and more than 90% of the precipitation falls during the wet season. The soil type is red oxisol with a very high clay content (> 70%). Mean monthly temperature ranges from 19 to 23 °C.

The sap-flow pattern measured on the pseudostem of three individuals of *Vellozia flavicans* during the transitional period from the dry to the wet season (2–12 September 2002) is shown on Figure 2. The first four days represent the end of a 5-mo dry period when no significant precipitation fell. A typical pattern of daytime transpiration was observed during this period, suggesting that despite the extensive drought period, *Vellozia* was still physiologically active. We also observed substantial night-time transpiration (positive sap flow during the night). This pattern was observed on nights with low atmospheric humidity (data not shown) when cuticular conductance and/or open stomata may have contributed to continued canopy water loss. This pattern was also observed by Labouriau (1963) for several other cerrado woody species. Nocturnal water loss in other cerrado species had also been documented by Bucci *et al.* (2004) and may be more common than has been previously acknowledged (see also Snyder *et al.* 2003).

During the first significant rainfall event of 36 mm, nocturnal transpiration stopped (Figure 2, dashed line). Simultaneously we observed reverses in stem sap flow or negative sap-flow values (first arrow on Figure 2). Such a pattern indicates absorption of water by the canopy. Therefore, following rainfall water began moving downwards, being redistributed to other parts of the plant. A heavier rainfall event of 56 mm occurred during daylight hours (starting at ~13h30) on 8 September (day 7) and we observed a sudden cessation of transpiration followed again by a reverse in stem sap flow (starting at ~14h00) that lasted for approximately 12 h (Figure 2).

The sap-flow pattern we observed for *V. flavicans* is consistent with water uptake by the canopy as recently

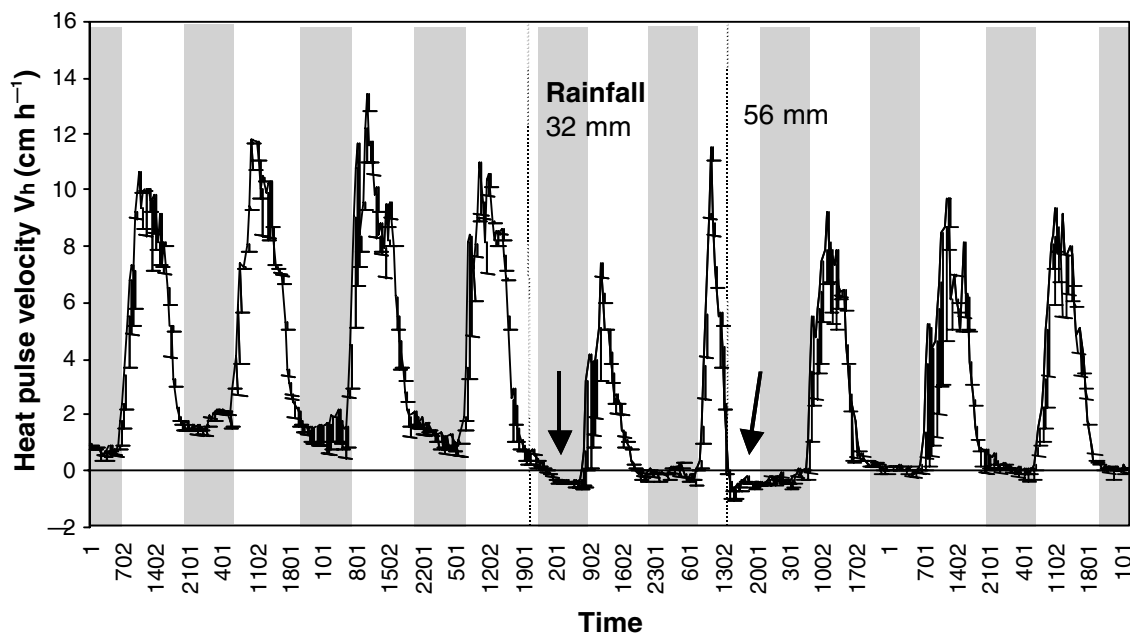


Figure 2. Sap velocity (V_h) in the pseudostem of three *Vellozia flavicans* individuals during the dry–wet season transition (2–12 September 2002) at the RECOR-IBGE ecological reserve. Each data point represents the average of data from three individuals \pm SE. Nocturnal transpiration (positive sap flow during the night) was observed before rainfall. A major rainfall event occurred the night of day four and we observed reverses in sap flow (indicated by the first arrow), suggesting water uptake by the pseudostem. Grey bars represent nights. Arrows indicate reverse in flow. Dotted lines indicate rainfall events.

described by Burgess & Dawson (2004) for coastal redwood trees exposed to heavy fog events in California and demonstrates direct uptake. We believe that canopy water uptake in *Vellozia* occurred through the pseudostem and not through the foliage because pseudostems of *Vellozia* possess adventitious roots with *velamen radicum*, which is a hydrophilic structure and thus likely more conductive to water than the wax-covered leaves; this is the case seen for several epiphytic orchids (Capesius & Barthlott 1975).

Although the two flow reversal events shown in Figure 2 were short in duration and relatively small in magnitude, the fact that water absorption by aerial parts of the plant has been demonstrated in *Vellozia* opens up the possibility that small, but regular inputs of water from dewfall that is common during the dry season in the cerrado, could be an important component of this species' water relations. It is also important to realize that if it is the stems that absorb water, they would have done so above and below our sensor positions; i.e. net migration of water toward the roots will be less than overall absorption.

Dewfall has been suggested as an important moisture input for several ecosystems and thus relevant to the water economy and survival of several species (Andrade 2003, Gouvra & Grammatikopoulos 2003, Haines 1953, Munne-Bosch *et al.* 1999). However, as far as we know, no experimental evidence is available to support the

hypothesis of dewfall absorption by the aerial part of cerrado plants.

The uptake of water by aerial parts may be particularly advantageous for *Vellozia* species, because it may help reduce water stress and play a critical role in cavitation repair. Cavitation is probably common in *Vellozia* because of its profligate water use during the dry season and lack of a deep root system (Oliveira 2004). The rapid water uptake observed in *Vellozia* may also confer competitive advantage in an environment where water is limiting during several months and several shallow-rooted species coexist very close to each other.

Most of the species of *Vellozia* occur in environments where water is even more limiting than at our study site (e.g. bare rocks on inselbergs or white sands in the central/eastern part of Brazil; Mello-Silva 1990, Menezes *et al.* 1994, Porembski & Barthlott 2000). Under such conditions, we believe that rapid water absorption by the pseudostem must be especially important for the survival and persistence of *Vellozia* species, because it may constitute the only gateway for water into the canopy. The ability to absorb water directly into the pseudostem may be a key trait influencing the ecological distribution and explain the dominance of *Vellozia* in these harsh, drought-prone, environments. Our findings add to the understanding of the diversity of physiological strategies exhibited by tropical plants inhabiting water-limiting

environments that may have important implications for potential niche differentiation and species coexistence.

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