Erratum

Catalan P, López-Álvarez D, Bellosta C, Villar L. 2016. Updated taxonomic descriptions, iconography and habitat preferences of *Brachypodium distachyon*, *B. stacei* and *B. hybridum* (Poaceae). *Anales del Real Jardín Botánico de Madrid* 73 (1): e028 (doi: http://dx.doi.org/10.3989/ajbm.2428):

The original publication contains the following errors:

Spikelet length should always be in mm along the manuscript.

In page 2 (in Key to the species of the *Brachypodium distachyon* complex: *B. stacei*)

Replace “spikelet (13–)22(–41) cm” with “spikelet (13–)22(–41) mm”.

Replace “spikelet <22(–41) cm” with “spikelet <22(–41) mm”

In page 3

In Table 1: Trait 9, replace “Spikelet total length, without awns (cm)” with “Spikelet total length, without awns (mm)”.

In Table 1: Trait 10, replace “Spikelet length from the base to the apex of the fourth lemma, without awns (cm)” with “Spikelet length from the base to the apex of the fourth lemma, without awns (mm)”

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Updated taxonomic descriptions, iconography, and habitat preferences of *Brachypodium distachyon, B. stacei*, and *B. hybridum* (Poaceae)

Pilar Catalán[1,2]*, Diana López-Álvarez[1], Cristina Bellosta[1], and Luis Villar[3]

[1]Department of Agriculture and Environmental Sciences, High Polytechnic School of Huesca, University of Zaragoza, Ctra. de Cuarte km 1, 22071 Huesca, Spain
[2]Department of Botany, Institute of Biology, Tomsk State University, Lenin Av. 36, Tomsk 634050, Russia
[3]Instituto Pirenaico de Ecología (IPE-CSIC), Consejo Superior de Investigaciones Científicas, Av. de Nuestra Señora de la Victoria 12, 22700 Jaca (Huesca), Spain
pcatalan@unizar.es

Abstract

Catalán, P., López-Álvarez, D., Bellosta, C. & Villar, L. 2016. Updated taxonomic descriptions, iconography, and habitat preferences of *Brachypodium distachyon*, *B. stacei,* and *B. hybridum* (Poaceae). *Anales Jard. Bot. Madrid* 73(1): e028.

We present an updated morphological revision of the three annual species of the genus *Brachypodium* (Poaceae): *B. distachyon*, *B. stacei,* and *B. hybridum*, which were recently segregated as independent species from the single-species complex *B. distachyon* s.l. These three species have been proposed as a model system for grass polyploid speciation, and their genomes have been sequenced. However, despite the increasing number of genomic and population-genetic studies conducted for each of these species, no taxonomic updating has been done on them since their original descriptions. *B. stacei*, the rarest species of the complex, has a protologue based only on the study of specimens from its type locality in Torrent (Formentera, Spain). In this study we update the taxonomic descriptions of the three species using morphoanatomical data from specimens collected throughout their respective native circum-Mediterranean distributions as well as in other localities where they are non-autochthonous. We also provide icons for each species and information about their habitat preferences and geographic distributions.

Key words: annual model grass species, *Brachypodium*, ecology, illustrations, morphology, taxonomy.

Resumen

Catalán, P., López-Álvarez, D., Bellosta, C. & Villar, L. 2016. Actualización de las descripciones taxonómicas, iconografía y preferencias de hábitat de *Brachypodium distachyon*, *B. stacei,* y *B. hybridum* (Poaceae). *Anales Jard. Bot. Madrid* 73(1): e028.

Presentamos una revisión morfológica actualizada de las tres especies anuales del género *Brachypodium* (Poaceae), *B. distachyon*, *B. stacei* y *B. hybridum*. Estas dos últimas han sido recientemente segregadas como especies independientes dentro del complejo *B. distachyon* s.l. Las tres especies han sido propuestas como grupo modelo de especiación poliploide en gramíneas y sus genomas han sido secuenciados. Sin embargo, pese al incremento de estudios genómicos y genético-poblacionales desarrollados en poblaciones de estas especies, no se ha llevado a cabo todavía ninguna actualización taxonómica para las mismas desde que se describieron. El protólogo de *B. stacei*, la especie más rara del complejo, está basado únicamente en el estudio de especímenes de su localidad clásica en Torrent (Formentera, España). En este estudio actualizamos las descripciones taxonómicas de las tres especies, utilizando datos morfoanatómicos obtenidos de especímenes colectados a lo largo de sus respectivas áreas de distribución autóctona circunmediterráneas y en otras localidades donde no son autóctonas. Proporcionamos icones de cada una de las especies e información adicional sobre sus preferencias de hábitat y sus distribuciones geográficas conocidas.

Palabras clave: *Brachypodium*, ecología, gramíneas modelo anuales, ilustraciones, morfología, taxonomía.

INTRODUCTION

The genus *Brachypodium* P. Beauv. has received considerable attention since the selection of the annual species *B. distachyon* as a model functional plant for temperate cereals and biofuel grasses (IBI, 2010; Mur & al., 2011; Catalán & al., 2014). Recently, *B. distachyon* and the other segregated annual species of the *B. distachyon* complex (*B. stacei* and *B. hybridum;* Catalán & al., 2012) have been proposed as a model system for grass polyploid speciation (Catalán & al., 2014). The whole genus, containing taxa characterized by their small and compact genomes (Mur & al., 2011; Betekhtin & al., 2014), is also seen as an ideal candidate for comparative genomics of the monocots.

Brachypodium is a relatively small genus that contains ca. 18 taxa (17 species, 1 variety) distributed worldwide (Schippmann, 1991; Catalán & Olmstead, 2008; Catalán & al., 2012, 2015). According to the most recent systematic updating (Catalán & Olmstead, 2008; Catalán & al., 2012, 2015), three of them are annual species and 15 are perennials. Recently it has been demonstrated that the three annuals have wide distributions in their native circum-Mediterranean region (López-Álvarez & al., 2012, 2015). *Brachypodium hybridum* has also successfully colonized other non-native territories (cf. Catalán & al., 2012, and references therein). Phylogenetic studies of *Brachypodium* support the early splits of the annual and short-rhizomatose lineages (*B. stacei*, *B. mexicanum*, and *B. distachyon*) in the Holarctic region during the early Middle Miocene, and the allopolyploid origin of *B. hybridum* in the Pleistocene (Catalán & al., 2012, 2015).

The three annual species are characterized by a short life cycle, ephemeral habit and self-fertility (Catalán & Olmstead, 2000; Catalán & al., 2012). They consist of two diploids, each with a different chromosome base number [*B. distachyon* (x=5, 2n=10) and *B. stacei* (x=10, 2n=20)],

* Corresponding author.

and their derived allotetraploid *B. hybridum* (x=5+10, 2n=30). Phylogenetic analyses of two plastid (*ndh*F and *trn*LF) and five nuclear (ITS, ETS, CAL, GI, and DGAT) genes indicated that the more early-diverging *B. stacei* and the more recently evolved *B. distachyon* emerged from two independent lineages, confirming their contributions as genome donors to *B. hybridum* (Catalán & al., 2012, 2014, 2015). Further evidence from different molecular sources, like seed protein data (Hammami & al., 2011), nuclear SSRs (Giraldo & al., 2012), DNA barcoding (López-Álvarez & al., 2012), and isozymes (Jaaska, 2014) have also confirmed the co-occurrence of progenitor *B. distachyon* and *B. stacei* markers in the *B. hybridum* background.

Statistical analysis of morphometric traits showed that five characters (leaf stomatal guard cell length, pollen grain length, upper glume length, lemma length, and awn length) significantly discriminated among the three annual *Brachypodium* species when they were grown under controlled greenhouse conditions (Catalán & al., 2012). Although the three species can be differentiated through these phenotypic traits and through additional molecular and cytogenetic traits (Catalán & al., 2012; López-Álvarez & al., 2012), their direct identification is not always straightforward, as wild populations show overlapping phenotypic variation for some characters and a similar diploid genome size. This has led to taxonomic uncertainty, or even to taxonomic misclassifications of the model species and its close allies, when using currently employed identification methods such as morphology or flow cytometry (López-Álvarez & al., 2012). This is particularly problematic in natural admixed populations, where *B. hybridum* lives in sympatry with one or the other parental species (López-Álvarez & al., 2015). Furthermore, the current taxonomic description of *B. stacei*, the rarest species of the complex, is only based on specimens from the type locality (Spain, Balearic Islands, Formentera), the only known population at the time of the description (Catalán & al., 2012).

In order to increase the knowledge of phenotypic variation of the three annual *Brachypodium* species and to help in their identification, we have analyzed the morphology of a large collection of wild specimens of each species and have detected new traits useful for differentiating them. We provide an enlarged and updated taxonomic description of each species, their habitat preferences and current known distributions, and a dichotomous key to identify them. We also illustrate the three model species with their iconography.

MATERIALS AND METHODS

We studied 227 wild individuals (from 44 populations) of *B. distachyon*, 146 individuals (30 populations) of *B. stacei*, and 497 individuals (100 populations) of *B. hybridum*, covering a large range of distribution and ecological variability for each species (see Appendix 1). For most populations, geographic coordinates, altitude, geological substrate and habitat information was collected in the field or obtained from herbarium data. Taxonomic identity of each individual was confirmed through chromosome counting or DNA barcoding, following the procedures indicated in López-Álvarez & al. (2012). Recently collected materials have been deposited in the JACA herbarium.

Qualitative phenotypic data [leaf color (bright green, pale green, dark green), leaf softness (soft, unbendable), leaf shape (curled, straight), leaf hairiness (densely hairy, scarcely hairy or non-hairy), occasional presence of short rhizomes (presence, absence)] were recorded from living plants. Quantitative morphometric data were taken from both fresh and herbarium specimens. Measurements of vegetative and reproductive organs were done with a ruler under a dissecting microscope. Microanatomical analysis of culm leaf blade cross sections, pollen grain length and epidermal stomata guard cell length was done under a microscope. Approximately five individuals per population were used for the assessment of morphological character variation in each species.

Morphometric data from 15 potentially informative characters used to separate and identify the three species (Catalán & al., 2012; Table 1) were taken in all studied specimens. To this we added the information available for 180 specimens from individuals cultivated under standard greenhouse conditions [six inbred lines; *B. distachyon*: Bd21 (type) and ABR1; *B. stacei*: ABR114 (type); *B. hybridum*: ABR113 (type), ABR110 and ABR117; Appendix 1], which were used in the original descriptions of each species (cf. Catalán & al., 2012). Main results from the statistical analyses of the morphometric data, developed in a parallel study (López-Álvarez & Catalán, unpublished data), are discussed here (see Results and Discussion sections below). All materials examined in this study are indicated in Appendix 1.

Taxonomic descriptions, habitat preferences and geographic distributions of *B. distachyon*, *B. stacei*, and *B. hybridum*

Key to the species of the *Brachypodium distachyon* complex

1 Grass 44–76(150) cm, erect; culm leaf-blades soft, curled, patent, pale green; flag leaf overlapping and sometimes overtopping the panicle; panicle 5–6(–10) cm; spikelet (13–)22(–41) cm; lemma (6.1)8–9(–12.6) mm; awn (7.5–)12–13(–18.2) mm ..... **2. *B. stacei***

1 Grass to 44 cm, erect or spreading; culm leaf-blades unbendable, straight, erect (more rarely patent), bright or dark green; flag leaf not reaching or partially overlapping the panicle; panicle ≤ 3–4(–8) cm; spikelet <22(–41) cm; lemma <8–9(–12.6) mm; awn <12–13 (–18.2) mm 2

2 Short-tall, (2–)6–15(–56) cm, erect plant; culm with (1–)3–4 nodes; culm leaf-blades 3–7(–8.5) cm × (0.25–) 1.7(–4) mm, short, bright green; no. spikelets per panicle (1–)2(–4); caryopsis (3.8–)5–6(–7.2) mm; pollen grain (21–)30(–42) µm; stomata guard cell (17–)22.5 (–29) µm ..... **1. *B. distachyon***

2 Medium-tall, 30–40(–78) cm, erect or spreading plant; culm with 3–7(–18) nodes; culm leaf-blades 7–8(–16) cm × (0.7–)2–3(–4.3) mm, long, pale dark green; no. spikelets per panicle 3(–6); caryopsis (5–) 6–7(–8.9) mm; pollen grain (25–)38–40(–57) µm; stomata guard cell (20–)30(–40) µm ..... **3. *B. hybridum***

Table 1. Morphological traits analysed in the studied *Brachypodium distachyon, B. stacei*, and *B. hybridum* samples (see Appendix 1). 1-15: quantitative and discrete traits; 16-20: qualitative traits. Traits that significantly discriminate (e.g., quantitative and discrete traits) or separate (e.g., qualitative traits) among the three species, or between one species and the others. n-d: non-discriminant.

	Trait	Significant discrimination or separation
1	Leaf guard cell length (stomata) (mm)	*B. distachyon vs B. stacei vs B. hybridum*
2	Pollen grain length (mm)	*B. distachyon vs B. stacei vs B. hybridum*
3	Plant height (cm)	*B. distachyon vs B. stacei vs B. hybridum*
4	Number of nodes of tallest culm	*B. hybridum vs B. distachyon + B. stacei*
5	Second leaf length from the base of the plant (cm)	*B. distachyon vs B. stacei + B. hybridum*
6	Second leaf width (mm)	*B. distachyon vs B. stacei vs B. hybridum*
7	Inflorescence length (cm)	*B. distachyon vs B. stacei vs B. hybridum*
8	Number of spikelets per inflorescence	*B. distachyon vs B. stacei vs B. hybridum*
9	Spikelet total length, without awns (cm)	*B. distachyon vs B. stacei + B. hybridum*
10	Spikelet length from the base to the apex of the fourth lemma, without awns (cm)	*B. distachyon vs B. stacei + B. hybridum*
11	Number of flowers per inflorescence	n-d
12	Upper glume length (mm)	n-d
13	Lemma length from the basal floret (mm)	*B. distachyon vs B. stacei vs B. hybridum*
14	Awn length, the longest within the spikelet (mm)	*B. distachyon vs B. stacei vs B. hybridum*
15	Caryopsis length (mm)	*B. distachyon vs B. stacei + B. hybridum*
16	Occasional presence of rhizomes (presence vs absence)	*B. distachyon vs B. stacei + B. hybridum*
17	Leaf blade color (bright green vs pale green vs dark green)	*B. distachyon vs B. stacei vs B. hybridum*
19	Leaf blade shape (curled vs straight)	*B. stacei vs B. distachyon + B. hybridum*
18	Leaf blade softness (soft vs unbendable)	*B. stacei vs B. distachyon + B. hybridum*
20	Leaf blade hairiness (densely hairy vs scarcely hairy or glabrous)	*B. stacei vs B. distachyon + B. hybridum*

1. Brachypodium distachyon (L.) P. Beauv., Ess. Agrostogr. 101, 155, 156 (1812).
Bromus distachyos L., Fl. Palaest. 13 (1756).
Festuca distachya (L.) Roth, Catal. Bot. 1: 11 (1797).
Agropyron distachyon (L.) Chevall., Fl. Gén. Env. Paris 2: 196 (1827).
Trachynia distachya (L.) Link, Hort. Berol. 1: 43 (1827).
Zerna distachya (L.) Panz. ex B.D. Jacks., Index Kew. 2: 1249 (1895).
Iconography: Figures 1 and 4a.

TYPE: [Palaestina.] *Hasselquist s.n.* [neotype designated by Schippmann & Jarvis, Taxon 37: 158 (1988): LINN 93.48 photo!]. [Iraq.] Salah ad Din, 4 km from Salahuddin, in the road to Mosul. Col. No. K1202. USDA PI 254867, Bd21 inbred line, from seeds cultivated at Aberystwyth University, 2012, *Mur s.n*. [epitype designated by Catalán & al., Ann. Bot. (Oxford) 109: 401-402 (2012): MA 833764!; isoepitypes: JACA R298981!, JE!, K!].

Plants annual, with 1–3(–8) reproductive culms. Culms (2–)6–15(–56) cm, erect, smooth and glabrous (or nearly so). Nodes (1–)3–4(–12), dense to minutely hairy. Leaf sheath margins open, fused at base, overlapping more than 2/3 the length below, glabrous to densely villose abaxially; auricles present; ligules (0.7–)0.9–1(–1.2) mm, scarious, sparsely hirsute, apex obtuse or truncate, dentate-erose, ciliate to laciniate. Leaf blades of culms (1–)3–7(–8.5) cm × (0.25–)1.5–2(–4) mm, erect, flat, unbendable, straigth, bright green, sparsely villose abaxially and adaxially, with short and long hairs (short hairs sometimes absent), the hairs 0.1–1(–1.5) mm; cross section (Fig. 4a) bearing up to 11 (or more) main veins, each with ribs adaxially alternating with smaller ribs on the secondary and tertiary veins, bulliform cells on valleys, sclerenchyma strands forming trabeculae or girders on most veins; stomata guard cells (17–)22–23(–29) µm; flag leaf (1–)1.5–2(–6.5) cm, usually not reaching the panicle. Panicles (0.9–)2–3(–5) cm, erect, with (1–)2(–4) spikelets; rachis smooth and glabrous. Spikelets (9.2–)14–15(–24) mm, (5–)10–12(–18.2) mm to the apex of the fourth lemma, (3–)6–9(–13)-flowered, lanceolate, bright green; glumes oblong-lanceolate, shorter (more than half) than the contiguous florets, abaxially glabrous to densely hairy, apex acute; lower glumes (2–)4–5(–6) mm, 5(–7)-veined; upper glumes (2.2–)5–7(–11) mm, 7(–9)-veined; lemmas (5.2–)7–8(–11) mm, 7-veined, lanceolate, abaxially nearly glabrous to densely hairy, awned; awn (5–)10–11(–15.2) mm, as long as or longer than lemma, hairy; paleas 5–6(–7) mm, scabrous on and between keels. Lodicules 1-1.5 mm. Anthers 2–3, 0.5–0.7 mm, non-exserted; pollen grains (21–)25–35(–42) µm. Ovaries oblong, hairy at apex. Caryopsis (3.8–)5–6(–7.2) mm, oblong. Flowering time in the native circum-Mediterranean range: Apr.–Jun. (Jul.). $2n=2x=10$; $x=5$.

Habitat—Growing in mesic Mediterranean ecosystems, clearings of evergreen and deciduous oak woodlands, maquis, and garriga shrubs, preferentially on calcareous substrates (such as limestone and calcareous loams), occasionally on siliceous schists, from mid to high altitudinal

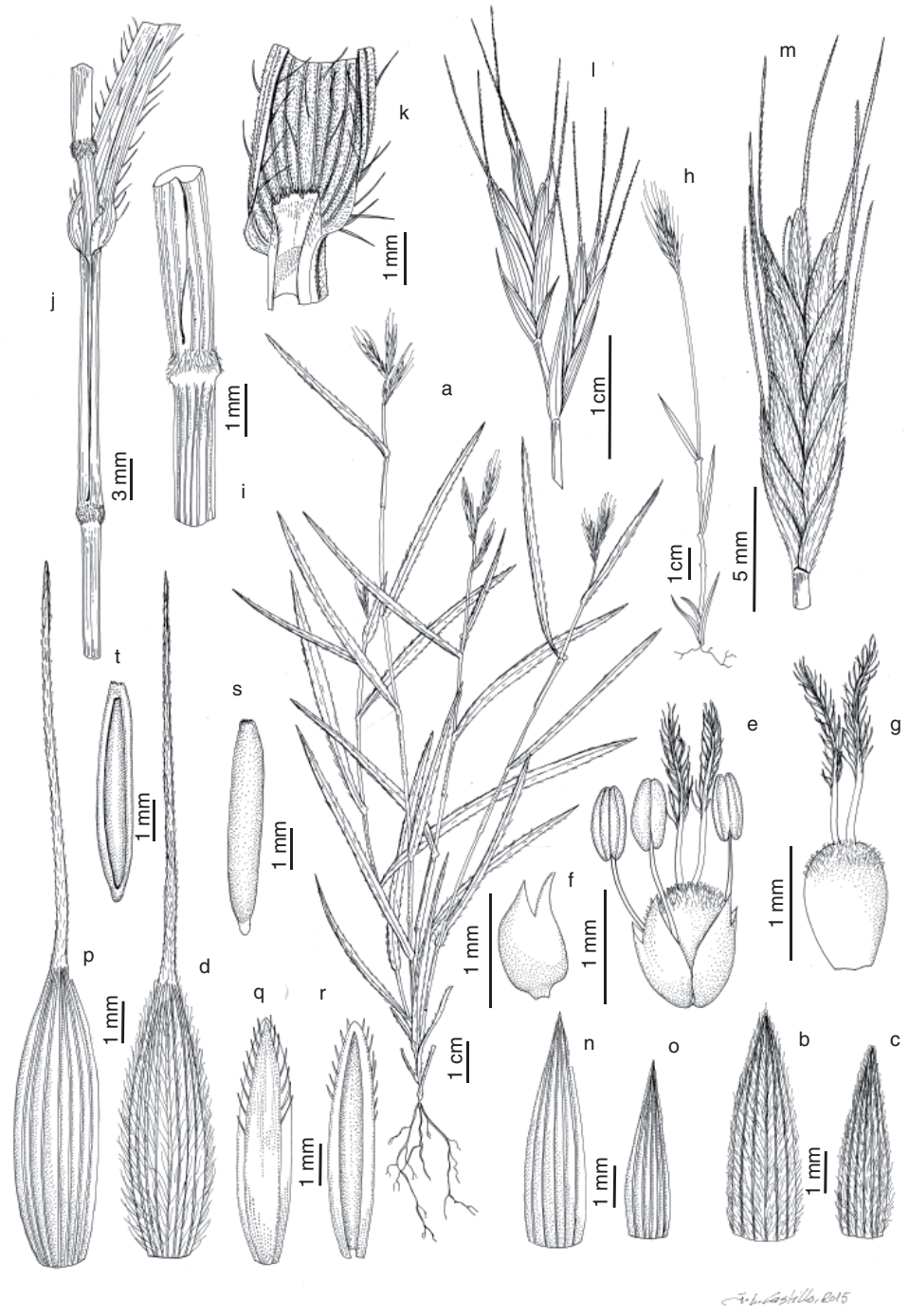

Fig. 1. *Brachypodium distachyon*: **a**, habit; **b**, upper glume, dorsal view; **c**, lower glume, dorsal view; **d**, lemma, dorsal view; **e**, lodicules, gynoecium, and stamens; **f**, lodicule; **g**, gynoecium; **h**, habit; **i**, culm node; **j**, flag leaf sheath and blade; **k**, sheath, ligule, and blade; **l**, panicle; **m**, spikelet; **n**, upper glume, dorsal view; **o**, lower glume, dorsal view; **p**, lemma, dorsal view; **q**, palea, dorsal view; **r**, palea, ventral view; **s**, caryopsis, dorsal view; **t**, caryopsis, ventral view. [a-g, *Mur s.n.*, (JACA 298981); h-t, *P. Catalán & L. Mur B19* (JACA R299007)].

ranges, between (50–)100–1500(–3196) masl, very rarely at lower altitudes.

Geographic distribution—Native to the circum-Mediterranean region [recorded in Albania, Armenia, France, Georgia, Greece, Iraq, Israel, Italy, Lebanon, Morocco, Spain (mainland: provinces Albacete, Almería, Badajoz, Cádiz, Cuenca, Granada, Guadalajara, Huesca, Jaén, Lérida, León, Logroño, Madrid, Navarra, Orense, Palencia, Soria, Teruel, Valencia, Valladolid, and Zaragoza; Balearic islands: Mallorca, Menorca), Tunisia, and Turkey; cf. Appendix 1 and López-Álvarez & al., 2015]. Its potential introduction into other regions where the species is non-native has yet to be confirmed.

Note—Schippmann & Jarvis (1988) designated a neotype for *Bromus distachyos* L. (LINN 93.48 photo!, see above); however, this neotype could not be confidently assigned to

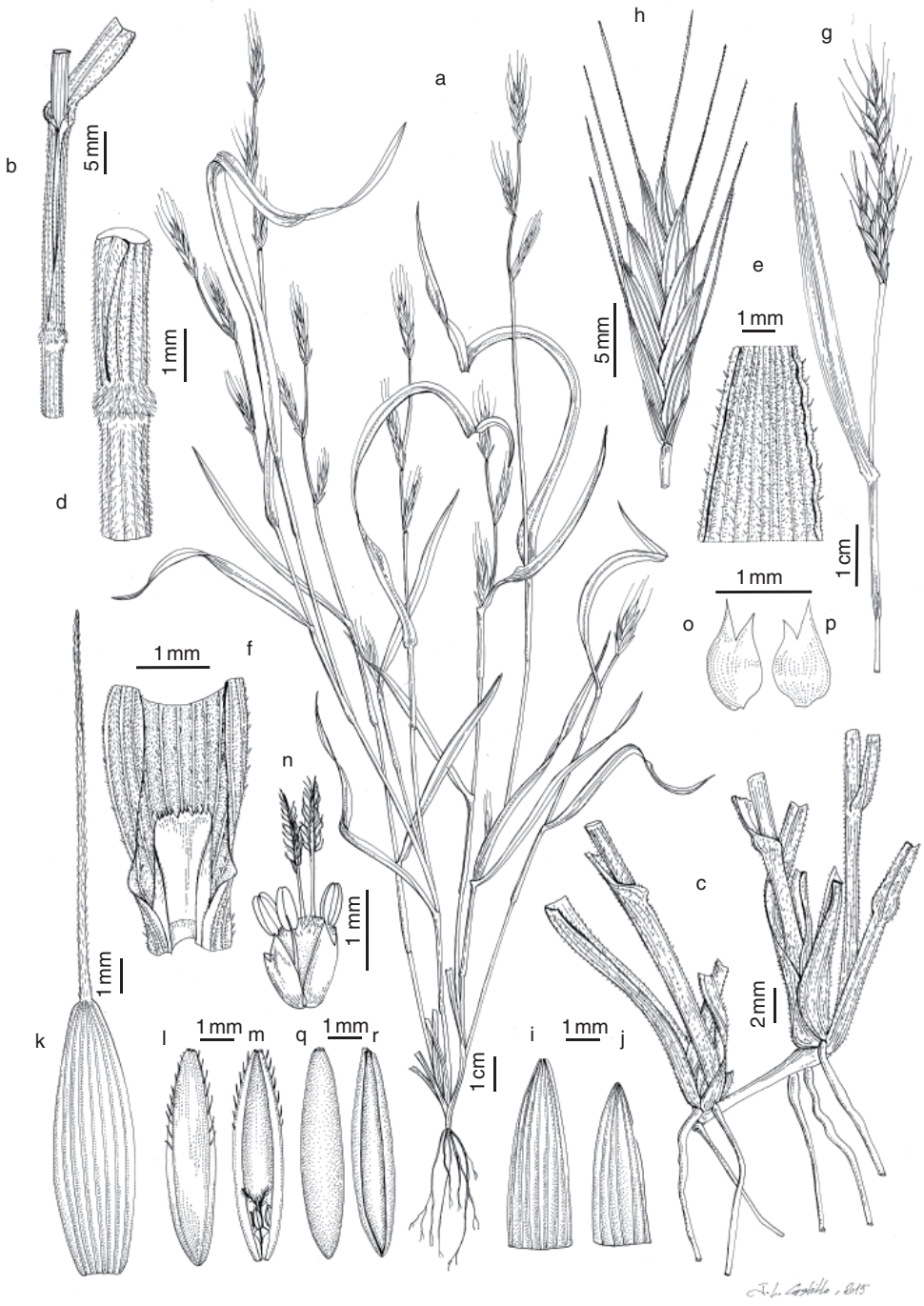

Fig. 2. *Brachypodium stacei*: **a**, habit; **b**, sheath, ligule, and blade; **c**, short rhizome; **d**, culm node; **e**, culm leaf blade, adaxial view; **f**, sheath, ligule, and blade; **g**, flag leaf and panicle; **h**, spikelet; **i**, upper glume, dorsal view; **j**, lower glume, dorsal view; **k**, lemma, dorsal view; **l**, palea, dorsal view; **m**, palea with gynoecium and stamens, ventral view; **n**, lodicules, mature gynoecium, and stamens; **o, p**, lodicules; **q**, caryopsis, dorsal view; **r**, caryopsis, ventral view. [a-b, *Mur s.n.*, JACA R298982; c-r, *D. López & P. Catalán B771* (JACA 299009)].

any of the three species of the complex because of its ambiguous diagnostic characteres. Besides, it was impossible to analyse this specimen cytogenetically and molecularly, and therefore we could not investigate its chromosome number and molecular barcode, characters also used to identify and discriminate the species. Consequently (cf. ICBN Art. 9.8, McNeill & al., 2005), we selected as epitype for *Bromus distachyos* L. the specimen MA 833764! (Catalán et al., 2012) that corresponds to the sequenced Bd21 ($2n$=10) reference genome.

2. Brachypodium stacei Catalán, Joch. Müll., Mur & Langdon, Ann. Bot. (Oxford) 109: 402 (2012).
Iconography: Figures 2 and 4b.

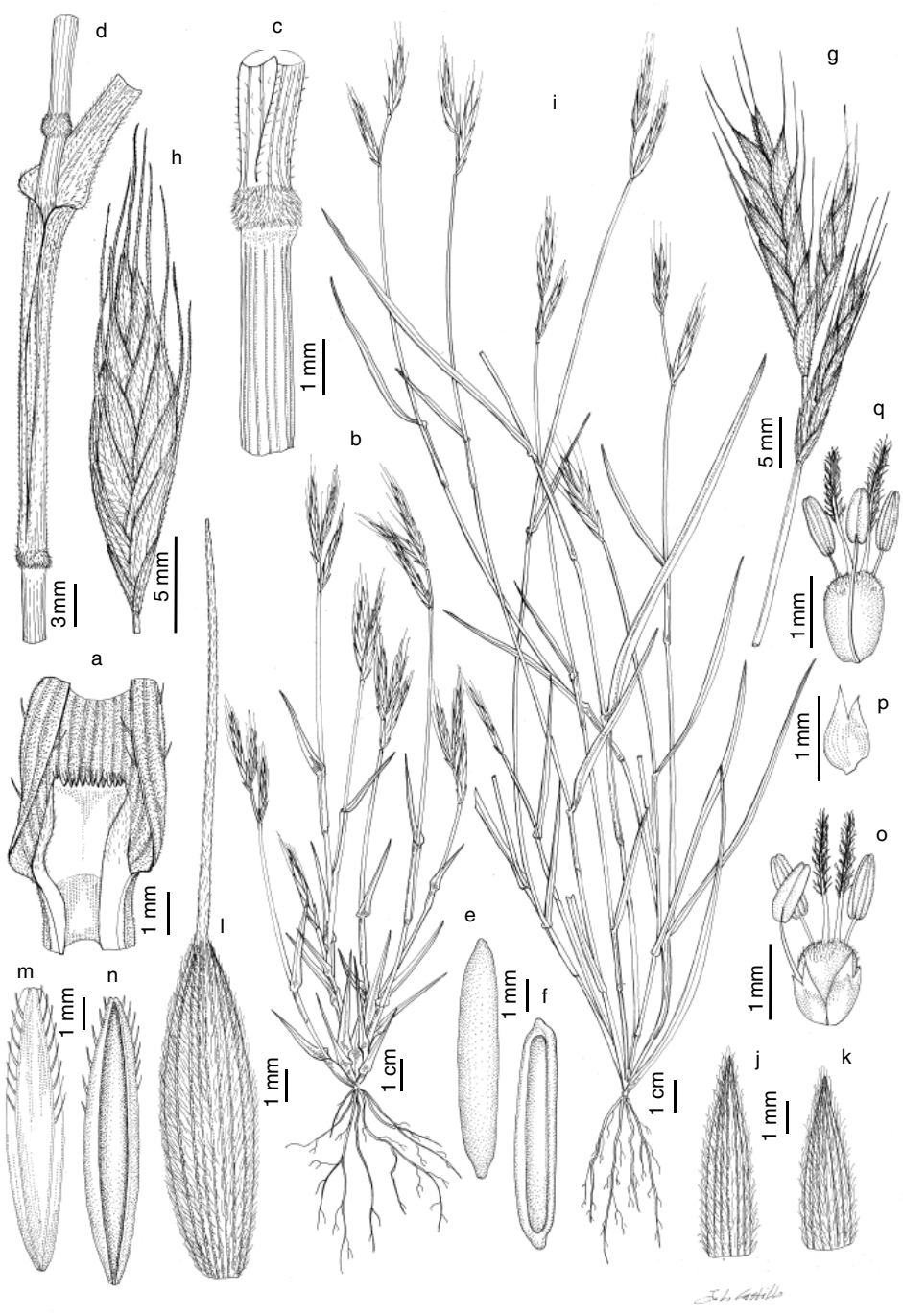

Fig. 3. *Brachypodium hybridum*: **a**, sheath, ligule, and blade; **b**, habit; **c**, culm node; **d**, flag leaf sheath and blade; **e**, caryopsis, dorsal view; **f**, caryopsis, ventral view; **g**, panicle; **h**, spikelet; **i**, habit; **j**, upper glume, dorsal view; **k**, lower glume, dorsal view; **l**, lemma, dorsal view; **m**, palea, dorsal view; **n**, palea, ventral view; **o**, lodicules, mature gynoecium, and stamens; **p**, lodicule; **q**, gynoecium and stamens. [a, *Mur s.n*. ABR113, (JACA 298983); b-f, *P. Catalán & L. Mur B40* (JACA R299010); g-h, *D. López & P. Catalán B831* (JACA R299012); i-q, Iran: Kalafabad, ABR100, JACA 299004].

TYPE: [Spain.] Balearic Islands, Formentera, Torrent, ABR114 inbred line, from seeds cultivated at Aberystwyth University, 2012, *Mur s.n*. (holotype: MA 833765!; isotypes: JACA R298982!, JE!, K!).

Plants annual, with (1–)3–9 reproductive culms; occasionally producing short rhizomes. Culms (6.1–)44–76(–150) cm, erect (or twisted when growing inside shrubs), pubescent in the basal half. Nodes (1–)4(–9), densely to minutely hairy. Leaf sheath margins open, fused at base, overlapping more than 2/3 the length below, densely pubescent; auricles present; ligules (1–)1.3–1.6(–2) mm, scarious, densely hirsute, apex obtuse to truncate, dentate-erose, ciliate to laciniate. Leaf blades of culms (1.6–)7– 8(–15.1) cm × (0.26–)2–3(–7) mm, erect to patent, flat, soft, curled, pale green, densely villose abaxially and adaxially, with short and long hairs, the

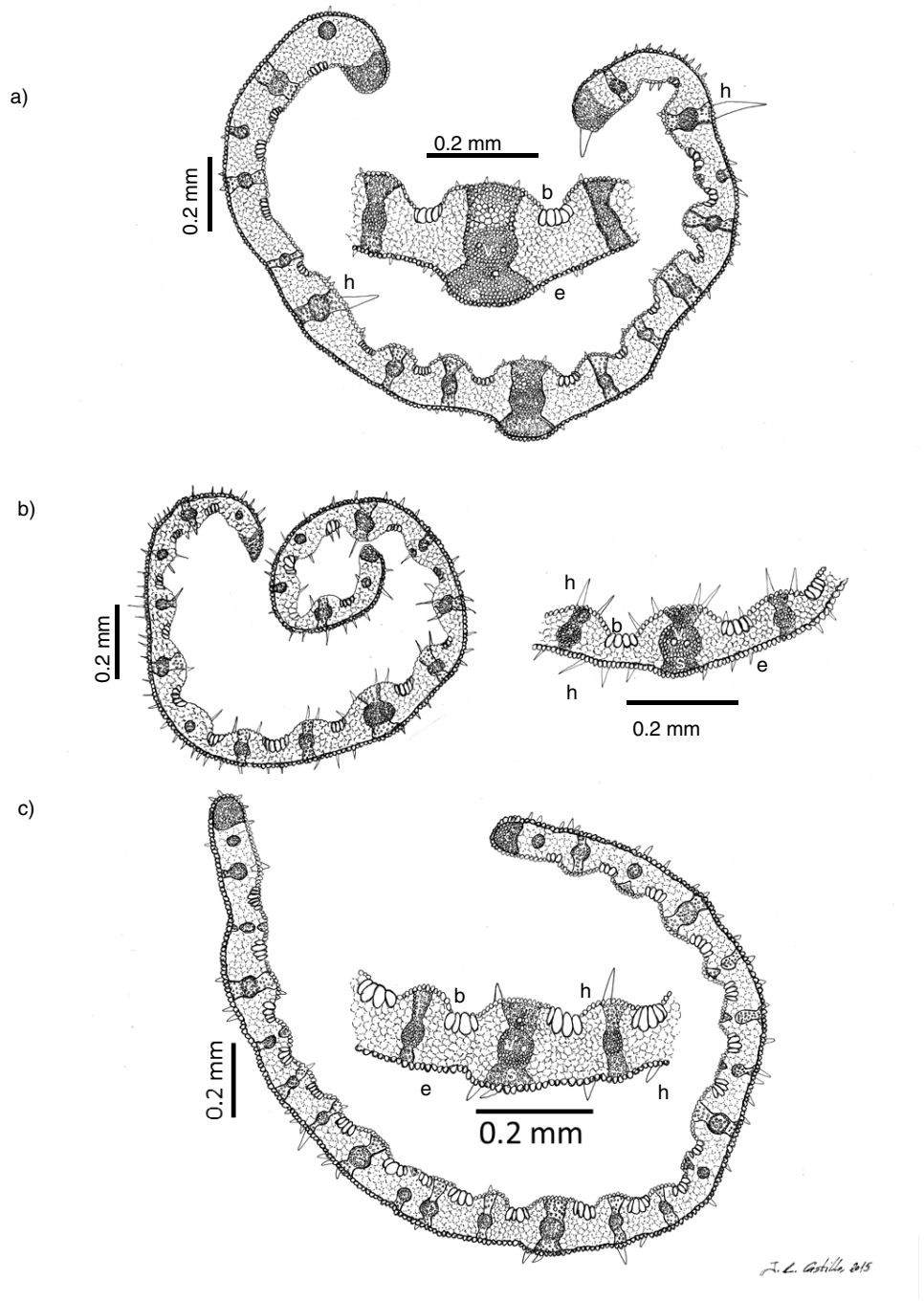

Fig. 4. Cross sections of culm leaves of a) *Brachypodium distachyon* [*P. Catalán & L. Mur B17* (JACA R299008)], b) *B. stacei* [*P. Catalán s.n.* (JACA 298995)], and c) *B. hybridum* [*P. Catalán & L. Mur B41* (JACA R299011)]: **v,** ribs with veins; **s**, sclerenchyma girders; **b,** valleys with bulliform cells; **e,** epidermal cells; **h,** adaxial and abaxial hairs.

hairs 0.1–0.7 mm; cross section (Fig. 4b) bearing up to 13 (or more) main veins, each with ribs adaxially alternating with smaller ribs on the secondary and tertiary veins, bulliform cells on valleys, sclerenchyma strands forming trabeculae or girders on most veins; stomata guard cells (16–)25(–38) µm; flag leaf (1.9–)5–6(–12.3) cm, usually reaching or overtopping the panicle, which is partly covered by the sheath. Panicles (2.1–)5–6(–10) cm, erect, with (1–)3–4(–5) spikelets; rachis smooth and glabrous. Spikelets (13–)21–23(–41) mm, (6.1–)12–16(–28) mm to the apex of the fourth lemma, (4–)8–9(–14)-flowered, lanceolate, pale green; glumes oblong-lanceolate, shorter (more than half) than the contiguous florets, abaxially glabrous or nearly so, apex acute to rounded; lower glumes (2.5–)4–5.5(–7) mm, 5(–7)-veined; upper glumes (2.9–)5–7(–8.7) mm, 7(–9)-veined; lemmas (6.1–)8–9(–12.6) mm, 7-veined, lanceolate, abaxially

glabrous or nearly so, though often with ciliate margins, occasionally pubescent, awned; awn (7.5–)12–13(–18.2) mm, as long as or longer than lemma, hairy; paleas 6–9 mm, scabrous on and between keels. Lodicules 1 mm. Anthers 3, 0.6–0.8 mm, non-exserted; pollen grains (22–)33–35(52) µm. Ovaries oblong, hairy at apex. Caryopsis (5.4–)6–7(–8.4) mm, oblong. Flowering time in the native circum-Mediterranean range: Apr.–Jun. (Jul.). $2n=2x=20$; $x=10$.

Habitat—Growing in arid Mediterranean ecosystems but in shady places, e.g., the understories of pine forests, juniper woods, and inside spiny shrubs, which protect the plant from direct insolation, preferentially on calcareous substrates (limestone, calcareous loams), but also on siliceous (schists, sand dunes) and volcanic substrates, in coastal and lowland ranges, between (1–)10–500(–900) masl.

Geographic distribution—Native to the circum-Mediterranean region [recorded in Greece, Iran, Israel, Italy (Sicily), Lebanon, Morocco, Palestine, Spain (mainland: Alicante, Almería, Granada, Jaén, and Murcia; Balearic islands: Formentera, Mallorca, and Menorca; Canary islands: Gomera and Lanzarote), and Tunisia; cf. Appendix 1 and López-Álvarez & al., 2015]. Its potential introduction into other regions where the species is non-native has yet to be confirmed.

3. Brachypodium hybridum Catalán, Joch. Müll., Hasterok & Jenkins, Ann. Bot. (Oxford) 109: 402 (2012).
Iconography: Figures 3 and 4c.
TYPE: [Portugal.] Lisboa, ABR113 inbred line, from seeds cultivated at Aberystwyth University, 2012, *Mur s.n.* (holotype: MA 833766!; isotypes: JACA R298983!, JE!, K!).

Plants annual, with (1–)3–7(–18) reproductive culms; occasionally producing short rhizomes. Culms (3.5–)30–40 (–78) cm, erect or spreading, pubescent in the basal half or for their full lengths. Nodes (1–)5–6(–11), densely to minutely hairy. Leaf sheath margins open, fused at base, overlapping more than 2/3 the length below, glabrous to pubescent abaxially; auricles present; ligules (0.5–)1.5–2 mm, scarious, sparsely to densely hirsute, apex obtuse or truncate, dentate-erose, ciliate to laciniate. Leaf blades of culms (1–)7–8(–16) cm × (0.7–)2–3(–4.3) mm, erect to patent, flat, unbendable, straigth, pale dark green, sparsely villose abaxially and adaxially, with scattered short and long hairs, the hairs (0.1–)0.5–1 mm; cross section (Fig. 4c) bearing up to 15 (or more) main veins, each with ribs adaxially alternating with smaller ribs on the secondary and tertiary veins, bulliform cells on valleys, sclerenchyma strands forming trabeculae or girders on most veins; stomata guard cells (20–)30(–40) µm; flag leaf (1.4–)3–4(–7.9) cm, not reaching or only partially reaching the panicle. Panicles (1–)3–4(–8) cm, erect, with (1–)3–4(–6) spikelets; rachis smooth, glabrous to densely hairy. Spikelets (10–)18–24(–41) mm, (5–)12–16(–30) mm to the apex of the fourth lemma, (4–)5–8(–17)-flowered, lanceolate, pale dark green; glumes oblong-lanceolate, shorter (more than half) than the contiguous florets, abaxially glabrous to densely hairy, apex acute; lower glumes (2–)4–5.5(–7) mm, 5(7)-veined; upper glumes (2.3–)5–6(–9.8) mm, 7(–9)-veined; lemmas (3–)8–10(–12.9) mm, 7(–9)-veined, lanceolate, abaxially glabrous to densely hairy, awned; awn (6.0–)11–12(18.9) mm, as long as or longer than lemma, hairy; paleas 6.5–8.5 mm, scabrous on and between keels. Lodicules 1.5 mm. Anthers 3, 0.5–1 mm, non-exserted; pollen grains (25–)38–40(–57) µm. Ovaries oblong, hairy at apex. Caryopsis (5–)6–7(–8.9) mm, oblong. Flowering time in the native circum-Mediterranean range: Apr.–Jun. (Jul.). $2n=4x=30$; $x=5+10$.

Habitat—Growing in both arid and mesic Mediterranean ecosystems, in sunny habitats, often in open disturbed places (roadsides, ditches) but also in natural or less disturbed niches, sometimes in sympatry with (or more likely near) *B. stacei* or *B. distachyon* parents, on calcareous (limestone, loams), siliceous (schists, sand dunes) and volcanic substrates, from coastal and lowland ranges to mid-high altitudes, between (1–)10–1200(–1881) masl.

Geographic distribution—Native to the circum-Mediterranean region [recorded in Afghanistan, Albania, Algeria, Armenia, France (mainland, Corsica), Greece (mainland, Aegean islands, Ionian islands), Iran, Iraq, Israel, Italy (mainland, Sardinia, Sicily), Jordan, Kuwait, Lebanon, Libya, Morocco, Portugal, Spain (mainland: Alicante, Albacete, Almería, Barcelona, Badajoz, Cádiz, Cáceres, Córdoba, Ciudad Real, Gerona, Granada, Huelva, Huesca, Jaén, Lérida, Madrid, Málaga, Murcia, Salamanca, Sevilla, Tarragona, Teruel, Valencia, and Zaragoza; Balearic islands: Ibiza, Mallorca, and Menorca; Canary islands: Fuerteventura, Gomera, Lanzarote, and Tenerife), Tunisia, Turkey, and Turkmenistan; cf. Appendix 1 and López-Álvarez & al., 2015]. The species has been introduced in other regions of central Europe, western-northern America (California), southern America (Uruguay and Argentina), South Africa and Oceania (Australia and New Zealand) (Jenkins & al., 2003; Garvin & al., 2008; Bakker & al., 2009; Catalán & al., 2012) and is considered an invasive plant in California and Australia.

TAXONOMY, ECOLOGY, AND EVOLUTION

Our morphological study of wild specimens of *B. distachyon*, *B. stacei*, and *B. hybridum* collected from their native circum-Mediterranean populations and some introduced populations (*B. hybridum*), has provided new data on both the interspecific and the intraspecific phenotypic diversity of these species. Our analysis has corroborated their phenotypic differentiation, with the number of species-specific discriminant traits increasing from five, in the study of Catalan & al. (2012), to 13 (López-Álvarez & Catalán, unpublished data, and current study; Table 1). Eight out of the 13 morphometric traits differentiate among the three species (leaf stomatal guard cell length, pollen grain length, plant height, culm leaf-blade width, panicle length, number of spikelets per panicle, lemma length, and awn length), four between *B. distachyon* vs. *B. stacei* and *B. hybridum* (culm leaf-blade length, total spikelet length, spikelet length —up to the 4th floret—, and caryopsis length), and one between *B. hybridum* vs. *B. distachyon* and *B. stacei* (number of culm nodes). Only two out of the 15 examined characters could not discriminate between the species (number of florets per spikelet, and upper glume length) (Table 1). Additionally, we found five new qualitative traits that helped to characterize and separate the three species (leaf blade color), *B. stacei* and *B. hybridum* from *B. distachyon* (occasional production of short rhizomes, but see comments below), and *B. stacei* from the other two species (leaf blade shape, softness and hairiness). We found 18 diagnostic characters out of 20 phenotypic characters studied (Table 1).

At the infraspecific level, most of the morphometric traits have increased measurement ranges for each species as a consequence of the enlarged number of specimens and populations analyzed. Notably, this has not affected the diagnostic value of these traits; on the contrary, more traits have been found to be useful to distinguish these species. Only one of the traits that discriminated among the three species in the study of Catalán & al. (2012) (upper glume length) was unable to separate them in our current study. The higher number of specimens and populations used in this study, compared to those in Catalán & al. (2012), makes these results more likely. In agreement with Catalán et al. (2012), our current results show that *B. stacei* and *B. hybridum* are, overall, taller and more robust plant species than *B. distachyon*, and that the allotetraploid shows larger measurements in several traits (leaf stomatal guard cell length, pollen grain length, and number of culm nodes) than either of its diploid parents, a likely consequence of polyploidy and heterosis. Correlation between increasing ploidy level and larger pollen grain and stomata guard cell sizes have been also found in other grasses and angiosperms [e.g., *Lolium* L., Speckman & al. (1965); *Bromus* L., Tan & Dunn (1973); *Dactylis* L., Bretagnolle & Lumaret (1995); *Eriotheca* Schott & Endl. (Malvaceae-Bombacoideae), Marinho & al. (2014)]. These two non-endoreduplicating plant cell types are commonly used as proxies to estimate ploidy level in plants (Nagl, 1978; but see Tate & Simpson, 2004).

A more detailed account of the habitat preferences of the three species has been also retrieved from our study. A recent environmental niche modeling (ENM) study, based on bioclimatic variables, was conducted for *B. distachyon*, *B. stacei*, and *B. hybridum* across their wide circum-Mediterranean native ranges as a way to predict the potential distribution of the species and to investigate the roles of geography and environment in the evolutionary diversification of the species (López-Álvarez & al., 2015). The environmental data indicated that *B. distachyon* grows in higher, cooler and wetter places than *B. stacei*, which grows in lower, warmer and drier environments, whereas *B. hybridum* grows in zones with intermediate values, but also in low altitudinal warmer and drier places, like its *B. stacei* progenitor (López-Álvarez & al., 2015). These results fit well the ecophysiological requirements of the species (e.g., vernalization for most of the *B. distachyon* accessions and lack of it for the *B. hybridum* and *B. stacei* accessions; cf. Vogel & al., 2009), which are crucial for the germination of seeds and survival of these annual species in their respective Mediterranean niches. Our current study has provided additional resource variables on the habitat preferences of the species. We have observed that the lowland *B. stacei* species grows in shady places, a fact that probably facilitates its tolerance to warm Mediterranean conditions, whereas the mostly highland B. *distachyon* species, and especially the lowland *B. hybridum* species, grow preferentially in open sunny places, suggesting a likely adaptation of the allotetraploid to more stressful arid conditions (Manzaneda & al. 2012).

Although the three species are annual plants, the sporadic production of short rhizomes has been detected in wild individuals of *B. stacei* [SPAIN. Mallorca. Campanet (JACA 299009), Fig. 2; SPAIN. Jaén. Tíscar (JACA 298995)] and *B. hybridum* (A. J. Manzaneda, pers. com.). We haven't observed short-rhizomes in wild or cultivated individuals of *B. distachyon*; however secondary roots emerging from nodes could be artificially induced through cutting and planting tiller nodes in soil with 0.25% indole-3-acetic acid (Vinh-Ha & Chalhoub, pers. comm). The short-rhizomatose perennial *B. mexicanum* (Roem. & Schult.) Link is evolutionarily close to *B. stacei* and *B. distachyon* and shares biological (e.g., self-fertility) and genomic traits with them (Catalán & al., 1995, 2012; Catalán & Olmstead, 2000), suggesting the potential occurrence of perennial/annual switches within the earliest diverging *Brachypodium* lineages. A reverse trend from perenniality to annuality has been also observed in the more recently evolved core perennial *B. sylvaticum* (Huds.) P. Beauv., which is also self-fertile and produces very slender rhizomes (Khan & Stace, 1999; Catalán & Olmstead, 2000; Steinwand & al., 2013). Genomic investigations of evolutionary switches in this important trait are under way in *Brachypodium*, aiming to decipher the underlying mechanisms causing life-style changes and their respective adaptive speciation processes.

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Appendix 1. Geographical sources of *Brachypodium distachyon, B. stacei*, and *B. hybridum* specimens studied morphologically (see electronic copy)

Brachypodium distachyon

Iraq: Salah ad Din: 4 km from Salahuddin, on the road to Mosul. Col. No. K1202. USDA PI 254867, Bd21. MA 833764 (holoepitype), JACA 298981 (isoepitype).

France: Aude. USDA:W619177

Israel: Julis. AB&SE:BRA65

Spain: Albacete, Alcaraz. CS:Bd115F

Spain: Albacete, Bonillo. CS:Bd160F

Spain: Cádiz, Grazalema. AM:Graz

Spain: Cuenca, Sedóbriga. CS:Bd162F

Spain: Cuenca. CS:Bd484F

Spain: Granada, Sierra de Huétor, Puerto de la Mora. PC:B111

Spain: Granada, Sierra de Baza, Mirador de Narváez 1. PC: B128

Spain: Granada, Sierra de Baza, Mirador de Narváez 2. PC:B129

Spain: Granada, Sierra Nevada, Ctra al Veleta. PC:B136

Spain: Huesca, Jaca, Banaguás. PC&LM:B12

Spain: Huesca, Puente de la Reina. PC&LM:B14

Spain: Huesca, Arén. PC&LM:B18

Spain: Huesca, Adahuesca, San Jerónimo. PC&LM:B19, JACA R299007

Spain: Huesca, Barbastro. PC&LM:B20

Spain: Huesca, Benabarre. PC&LM:B17, JACA R299008

Spain: Huesca, Abizanda. PC&LM:B21

Spain: Huesca, Berdún. PC&LM:B22

Spain: Huesca, Bierge. PC&LM:B09

Spain: Huesca, Alquézar. PC&LM:B11

Spain: Huesca, Benabarre. PC&LM:B17

Spain: Huesca, Sariñena. PC&LM:B05

Spain: Huesca, San Miguel de Foces. PC&LM:B06

Spain: Huesca, San Martín de Rodellar. PC&LM:B10, JACA 298991

Spain: Huesca, Santa Cilia de Panzano. PC&LM:B07, JACA 298993

Spain: Huesca, Santa Cruz de la Serós. PC&LM:B13, JACA 298989

Spain: Huesca, Yaso. PC&LM:B08

Spain: Jaen, Sierra Segura, Cortijos Nuevos, El Contadero 1. PC B115

Spain: Jaen, Sierra Segura, Cortijos Nuevos, El Contadero 2. PC:B116

Spain: Jaén, Sierra de Jaén, Pitillos. PC:B134

Spain: Jaén, Sierra de Jaén, Puerto de Navalayegua. PC:B135

Spain: La Rioja: Ezcaray, monte Turgaiza. SALA 100198-1

Spain: Lleida, Fondedou. PC&LM:B30

Spain: Lleida, Castillo de Mur. PC&LM:B31

Spain: Lleida, Les Pallagues. PC&LM:B32

Spain: Madrid. CS:Bd480F

Spain: Navarra, Foz de Lumbier. PC&LM:B25

Spain: Navarra, Puerto del Perdón. PC&LM:B27

Spain: Navarra, Los Arcos. PC&LM:B28

Spain: Palencia, Cervera de Pisuerga. AM:Cer

Spain: Teruel, La Puebla de Valverde, Puerto del Escandón. PC:B142

Spain: Valladolid, Renedo de Esgueva. SALA 113171-1

Spain: Valladolid, Otero. INRA-V:Abrc7d

Spain: Zaragoza, Murillo de Gállego. PC&LM:B15

Spain: Zaragoza, Miramont. PC&LM:B23

Spain: Zaragoza, Sigüés. PC&LM:B24

Turkey: Kiresehir, Kaman. ABR1

Appendix 1. *(Continued)*

Brachypodium stacei
Spain: Balearic Islands: Formentera, Torrent. ABR114. MA 833765 (holotype), JACA R298982 (isotype).
Greece: Pelopponesos, Tyros. PC:G15
Greece: Pelopponesos, Trizina, tower Diateichisma. PC
Iran: Asalooyeh to Booshehr MRR:BdisIran1
Iran: 25 Km to Ramhorm from Ahwaz. MRR:BdisIran2
Iran: Fars, Kazeroon, Davan. MRR:B100-H141
Israel: Amazyia. AB&SE:BRA52
Israel: Lakhish. AB&SE:BRA135
Israel: Hawalid. AB&SE:BRA158
Israel: Bat Shelomo. AB&SE:BRA191
Israel: Yiftah. AB&SE:BRA286
Israel: Ziff junction. AB&SE:BRA89
Spain: Alicante, Xávea, Cabo La Nao. PC:B102
Spain: Alicante, Cabo de La Nao. CS:Bd483F
Spain: Almería, Cabo de Gata, Playa de Genoveses. PC B108
Spain: Almería, Cabo de Gata, Playa de Monsul. PC B109
Spain: Almería, Cabo de Gata. EB&PG:AL1
Spain: Almería, Cabo de Gata. EB&PG:AL5
Spain: Balearic Islands: Mallorca, Sa Dragonera, Gambes. DL&PC:B891
Spain: Balearic Islands: Mallorca, Banyalbufar, Mirador Ses Ánimes. DL&PC:B921
Spain: Balearic Islands: Mallorca, Alcúdia, c. Punta Negra. DL&PC:B621
Spain: Balearic Islands: Mallorca, Campanet, Coves. DL&PC:B771, JACA R299009
Spain: Balearic Islands: Mallorca, Felanitx, San Salvador. DL&PC:B109, JACA R298998
Spain: Balearic Islands: Mallorca, La Victoria. INRA:13498BGVA_Esp0
Spain: Menorca, Es Mercadal, Toro. DL&PC:B951
Spain: Canary Islands: Gomera, Agulo. INIA-CRF:BGE044241, NC050363
Spain: Canary Islands: Lanzarote, Teguise. INIA-CRF:BGE044249, NC050440
Spain: Granada, Moclín. CS:Bd129F
Spain: Jaén, Sierra de Cazorla, Ctra. de Cortijos Nuevos a Cazorla. PC:B117
Spain: Jaén, Baeza. CS:Bd114F
Spain: Jaén, Sierra de Quesada, Tíscar. ABR:18_1
Spain: Jaén, Sierra de Quesada, Monasterio Ntra Sra. Tíscar. PC, JACA R298995.
Spain: Murcia, Mar Menor, Calblanque. PC
Spain: Murcia, Portman. PC
Tunisia: Gouv. de Medénine: Ksar Hadada (NW Lfoum Tataouine). M 67243
Brachypodium hybridum
Portugal: Lisboa. ABR113. MA 833766 (holotype), JACA R298983 (isotype).
Afghanistan: Hauz-i-Mabat, Kandahar. USDA:PI219965
Afghanistan: 35 miles from Kandahar to Kahakai dam, 4,800 ft. USDA:PL219971
Afghanistan: USDA PI219965, ABR117
Australia: Crystal Brook, 3 km upstream from town. USDA:PL533015
France: Île Sainte Marguerite. INRA-V:Mar-1
Germany. USDA:PL422452
Greece: Crete, Metohi. M 201179
Greece: Crete. INRA:Cre0
Greece: Crete. INRA-V:Cre-1a
Greece: Crete. INRA-V:Cre-1b
Greece: Pelopponesos: Xiropigado.PC:G12
Greece: Pelopponesos: Korakovouni, Aghios Andreas.PC:G13

Appendix 1. *(Continued)*

Greece: Pelopponesos: Tyros.PC:G14
Greece: Pelopponesos: Kosta1. PC:G3
Greece: Pelopponesos: Ano Fanari.PC:G8
Iran: Fars, Kazerun, 12 miles E of Kazerum, 3,800 ft. USDA:PL226629
Iran: Juzestan, between Ahwaz and Shushtar, near Abe-e Gonji. USDA:PL227011
Iran: Kalafabad. ABR100, JACA R299004.
Iran: Susa, SW Iran. USDA:PL239715
Iran: Khūzestān, Kalafabad. ABR100
Iran: Kohkiloyeh, Gchaemich T.Chogan. MRR:B99-H138
Iran: Kohkiloyeh, Yasooj. MRR:B98-H137
Iraq: As Sulaymānīyah, Arbet, 30 km S of Arbet. USDA:PL254868
Israel: Lehavim. AB&SE:BRA7
Israel: Gilbo'a. AB&SE:BRA26
Israel: Nahal Bokek. AB&SE:BRA57
Israel: Petah Tikwa. AB&SE:BRA143
Israel: Amirim. AB&SE:BRA146
Israel: Tel Fares. AB&SE:BRA160
Israel: Brachyia. AB&SE:BRA221
Israel: Sion. AB&SE:BRA293
Israel: Tel Aviv Univ, Botanical Garden. AB&SE:BRA299
Italy: Sardinia: Cagliari. M 55806
Italy: Sicily, Punta Longa. SH:PLA_1
Italy: Sicily, Santa Marina. SH:SMN_1
Italy: Sicily, Cappella Palatina. SH:VCP_1
Lebanon: INRA-V:Aja-1
Morocco: E Morocco,Oujda,34°41'N 1°54'O 34.683, -1.9, near Algeria. USDA:PL253334
Pakistan: Khyber Pakhtunkhwa, Pabbi. USDA:PL250647
Portugal: Tras-os-Montes, Mogadouro. AM:Mog
South Africa: E Cape, near Darling. USDA:PL208216
Spain: Alicante, Xávea, playa La Barraca. PC:B101
Spain: Almería, Cabo de Gata, Playa de Genoveses 1. PC:B103
Spain: Almería, Cabo de Gata, Playa de Genoveses 2. PC:B104
Spain: Almería, Cabo de Gata, Playa de Genoveses 3. PC:B105
Spain: Almería, Cabo de Gata, Playa de Genoveses 4. PC:B106
Spain: Almería, Cabo de Gata, Playa de Genoveses 5. PC:B107
Spain: Balearic Islands: Mallorca, Pto. Pollensa. DL&PC:B600
Spain: Balearic Islands: Mallorca, Pto. Pollensa, Formentor. DL&PC:B681
Spain: Balearic Islands: Mallorca, Pto. Pollensa, Mal Pas. DL&PC:B701
Spain: Balearic Islands: Mallorca, Pto. Pollensa, St Vicent. DL&PC:B731
Spain: Balearic Islands: Mallorca, El Toro. DL&PC:B861, JACA R299003.
Spain: Balearic Islands: Mallorca, Pollensa-Sóller, Temenia. DL&PC:B741
Spain: Balearic Islands: Mallorca, Escorca, Tossels, Cuvert. DL&PC:B781
Spain: Balearic Islands: Mallorca, Escorca, Pico del Tossel. DL&PC:B791
Spain: Balearic Islands: Mallorca, Escorca, Cuvert. DL&PC:B811
Spain: Balearic Islands: Mallorca, Deià. DL&PC:B831, JACA 299012
Spain: Balearic Islands: Mallorca, Escorca, Sa Calobra. DL&PC:B851
Spain: Balearic Islands: Mallorca, Paguera, Cala Fornell. DL&PC:B871
Spain: Balearic Islands: Mallorca, Valldemosa, Sa Marina. DL&PC:B931
Spain: Balearic Islands: Mallorca, Llucmajor, Algaida. DL&PC:B1101
Spain: Balearic Islands: Menorca, Fornells, Torre de Fornells. DL&PC:B1001

Appendix 1. *(Continued)*

Spain: Balearic Islands: Menorca, Ciutadella, Port. DL&PC:B1011
Spain: Barcelona, Montjuich.PC&LM:B37
Spain: Barcelona, Prat de Llobregat.PC&LM:B38, JACA R299001.
Spain: Canary Islands: Fuerteventura, Puerto del Rosario.INIA-CRF:BGE044244
Spain: Canary Islands: Fuerteventura, Betancuria. INIA-CRF:BGE044245
Spain: Canary Islands: Fuerteventura, Betancuria.INIA-CRF:BGE044246
Spain: Canary Islands: Gomera, Vallehermoso, Tamargada. INIA-CRF:BGE044242
Spain: Canary Islands: Gomera, Arure-Vallehermoso 3km NE. INIA-CRF:BGE044243
Spain: Canary Islands: Lanzarote, Teguise. INIA-CRF:BGE044247
Spain: Canary Islands: Lanzarote, Teguise.INIA-CRF:BGE044248
Spain: Canary Islands: Tenerife, Buenavista del Norte, Las Canales. INIA-CRF:BGE044238
Spain: Canary Islands: Tenerife, Buenavista del Norte, Masca. INIA-CRF:BGE044239
Spain: Canary Islands: Tenerife, El Rosario, La Esperanza. INIA-CRF:BGE044240
Spain: Ciudad Real, Puertollano, Sierra de Cerro del Castellar. SALA 87745-2
Spain: Córdoba, Córdoba. CS:176F
Spain: Córdoba, Guadalcázar. INRA:Esp1
Spain: Girona, Cap de Lladró. PC&LM:B36
Spain: Girona, Roses, Castell de Trinitat. PC&LM:B33, JACA R298998
Spain: Granada, Sierra de Huétor, Puerto de la Mora1. PC:B112
Spain: Granada, Sierra de Huétor, Puerto de la Mora2. PC:B130
Spain: Huelva. CS:333F
Spain: Huesca, Graus. PC&LM:B16
Spain: Jaén, Sierra de Segura, Cortijos Nuevos. PC:B113
Spain: Jaén, Sierra de Segura, Cortijos Nuevos, Finca La Vaquilla. PC:B114
Spain: Jaén, Sierra de Cazorla, Cazorla, Paso del Aire, Mirador de las Palomas. PC:B118
Spain: Jaén, Hinojares, Hinojares 2. PC:B122
Spain: Jaén, Fontanar, Los Cotos2. PC:B124
Spain: Jaén, Fontanar, Los Cotos, río Guadiana Menor. PC:B125
Spain: Jaén, Universidad de Jaén. PC:B131
Spain: Jaén, Sierra de Jaén, Salto de la Cabra. PC:B132
Spain: Jaén, Sierra de Jaén, Quiebrajano. PC:B133
Spain: Jaén, Cazorla, Sierra Quesada, Tíscar, Monasterio de Ntra. Sra. de Tíscar. PC:B119bis
Spain: Jaén. CS:137F
Spain: Málaga, Abdalajís. CS:260F
Spain: Málaga, Estepona. INRA-V: Estepona-0
Spain: Murcia, Espuña. AM: Espuña
Spain: Murcia, Alhama de Murcia, Sierra de Espuña1. PC:B137
Spain: Murcia, Alhama de Murcia, Sierra de Espuña2. PC:B138
Spain: Murcia, Alhama de Murcia, Sierra de Espuña3. PC:B139
Spain: Tarragona, Amposta. PC&LM:B39
Spain: Tarragona, Poble Nou del Delta. PC&LM:B40. JACA R299010
Spain: Teruel, Calaceite. PC&LM:B41, JACA R299011
Spain: Zaragoza, Belchite. PC&LM:B42
Uruguay. USDA:PL372187

Collectors: AB: Adina Breiman, AM: Antonio Manzaneda, CS: Consuelo Soler, DL: Diana López-Álvarez, EB: Elena Benavente, PC: Pilar Catalán, PG: Patricia Giraldo, LM: Luis Mur, MRR: Mohammad Reza Rahiminejad, SE: Smadar Ezrati, SH: Samuel Hazen.
Herbaria: JACA (Jaca), M (München), MA (Madrid), SALA (Salamanca).
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