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Shoot growth and development of *Berberis buxifolia* Lam. in Tierra del Fuego (Patagonia)

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ABSTRACT

Knowledge on the annual cycle of growth and development of several fruit species from temperate climate is available; however, few reports exist on fruit shrubs from cold climates like those of *Berberis* genus. The objective of this work was to study the shoot growth and development of the native Patagonian species *Berberis buxifolia* Lam., whose black blue fruits are of economic value. Data were recorded from adult plants that were planted in a representative area located near Ushuaia city, 54° 48′ SL, 68° 19′ WL, (Tierra del Fuego, Argentina). Shoots grown during the growing season developed vegetative and mixed buds in their nodes. Vegetative buds differentiated numerous leaves distributed around the central axis with the point of insertion nearly to the same height. In effect, when the bud sprouting starts, a rosette-like growth occurs. Flower differentiation started twelve weeks after bud breaks in coincidence with the end of the first fruit growth phase. In the following growing season, thirteen weeks later of sprouting, stamen primordial and a single carpel could be shown. Gamete differentiation occurred in a short period before sprouting for male gametes and during flowering time for female gametes. Blooming period occurred on spring and the length of the anthesis phase was closely related to the climatic conditions. While fruit growth followed a double sigmoid curve, shoot elongation showed a sigmoid curve. Knowledge of shoot growth and development of *B. buxifolia* is of great importance to understand its physiology, and when culture practices need to be incorporated like plant fertilization or when evaluating the impact of adverse climatic conditions on events as flowering and fruit set.

1. Introduction

In spite of the well-known importance of wild flora as source of food and medicinal substances, more studies on the diversity and the agronomic value of these plant species are still needed (Arena and Vater, 2005). Areas with indigenous flora offer non-domesticated plants (Monge et al., 2000), like *Berberis* genus in Patagonia (Orsi, 1984), which is well represented by 16 species of native shrubs, with a large distribution from Neuquén to Tierra del Fuego (Arena and Curvetto, 2008). Species of this genus belong to the so-called group of minor or under-utilized fruit tree species that are relevant for diversification of agro food production. At present, commercial barberry orchards are being planned due to this crop has economical potential for flavor and taste of the fruits. In fact, black blue berries are now consumed fresh, in marmalades and jams, in non-alcoholic beverages and in ice creams (Arena and Curvetto, 2008; Arena et al., 2012). *Berberis buxifolia* Lam., commonly named "calafate", is an evergreen shrub that may be semi-evergreen where winters are particularly cold and harsh, as it occurs in Tierra del Fuego. It is a spiny and erect shrub up to 4 m high, often growing in the magellanic subpolar forest Eco region (World Wildlife Fund et al., 2008), in coastal scrub, *Nothofagus* forest margins and clearings, moister areas in grass steppes, and along streams and rivers (Moore, 1983). *B. buxifolia* is one of the understory species in timber quality and associated non-timber quality stands of *Nothofagus* forests in Tierra del Fuego (Lencinas et al., 2008), being considered as a nontimber forest product. It can be propagated through seeds, rhizomes and *in vitro* culture (Arena and Martínez Pastur, 1994; Arena et al., 2000; Arena and Vater, 2005). Floral biology, fruit development and quality, and the assessment of morphological variability were studied in natural populations of *B. buxifolia* (Arena et al., 2003, 2011, 2013; Arena and Curvetto, 2008).

The annual cycle of growth and development is known to be determined by the climate (Billings and Mooney, 1968; Hänninen, 2004; Li et al., 2010). Knowledge on the annual cycle of growth and development of several fruit species from temperate climate

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is available; however, few reports exist on fruit shrubs from cold climates like those of *Berberis* genus. When referring to the annual cycle of growth and development of *B. buxifolia*, the rest period, which refers to successive events like growth cessation, bud set, dormancy and cold hardiness, as well as the high activity period, were not yet defined. In addition, several physiological processes like the shoot growth rhythm and development process are not known. The objective of this work was to study the shoot growth and development of *B. buxifolia* in Tierra del Fuego, Patagonia.

2. Materials and methods

2.1. Geographic and climatic description

The experiment was established in a representative area located near Ushuaia city, 54° 48′ SL, 68° 19′ WL, 30 MASL (Tierra del Fuego, Argentina), where *B. buxifolia* grows naturally. Climatic data were collected for mean air daily temperatures (°C) and rainfall (mm) by the Meteorological Station located at the Centro Austral de Investigaciones Científicas (CONICET, Argentina), from 2008 to 2011 years.

2.2. Plant material

B. buxifolia adult plants were obtained through clonal propagation and they were planted on 2007 (three years old) at 2 m × 1 m spacing (*n* = 24). Plants were not fertilized or pruned throughout the studied period so that they were conducted in a free growth form as they occur naturally. The weeding was done manually within the row and mechanically between the rows, three times during each growing season.

2.3. Anatomical and optical microscopy analysis

New shoots (*n* = 6) were manually and randomly harvested every two weeks from November 2010 to May 2011, and then continued during September and October 2011. Plant material was fixed in a 3% (v/v) glutaraldehyde solution in phosphate buffer (pH 7.4). Axillary bud groups were take-off and re fixed in the same phosphate buffer for 24 h and then post fixed in OsO_4 at 2 °C in the same buffer for 3 h. After this procedure, they were dehydrated in an ethanol series and embedded in Spurr's resin. Axillary bud groups were sectioned longitudinally, and serial thin sections (75–90 nm thick) were stained with uranyl acetate and lead citrate for the study under optical microscope. Photomicrographs were made by Leyca DM 2500.

2.4. Bud distribution on one year old shoots

The distribution of vegetative and mixed buds on one-year-old shoots (*n* = 15) was analyzed in relation to the spatial orientation (North, East, South and West) on October 2010. Data were statistically evaluated by one way ANOVA, and means were then separated using the Tukey multiple range test at $p \leq 0.05$. Coefficient correlations were performed between pairs of variables.

2.5. Vegetative growth

The length of all new shoots per each plant was evaluated each month since November to March for the 2008/09, 2009/10 and 2010/11 growing seasons. Shoots were classified as: (A) structural shoots: those that grow from buds formed on the shoots of the shrub. Mean number registered was 6.9, 47.2 and 115.9 for March 2009, 2010 and 2011, respectively. (B) Basal shoots: those that grow from buds formed on the shoots of the basal portion and rhizomes of the shrub. Mean number registered was 2.6, 16.0 and 11.1 for March 2009, 2010 and 2011, respectively); and (C) early shoots = those that grow early, in the same growing season, from buds formed on the shoots of the shrub. Mean number registered was 2.1, 2.5 and 43.5 for March 2009, 2010 and 2011, respectively.

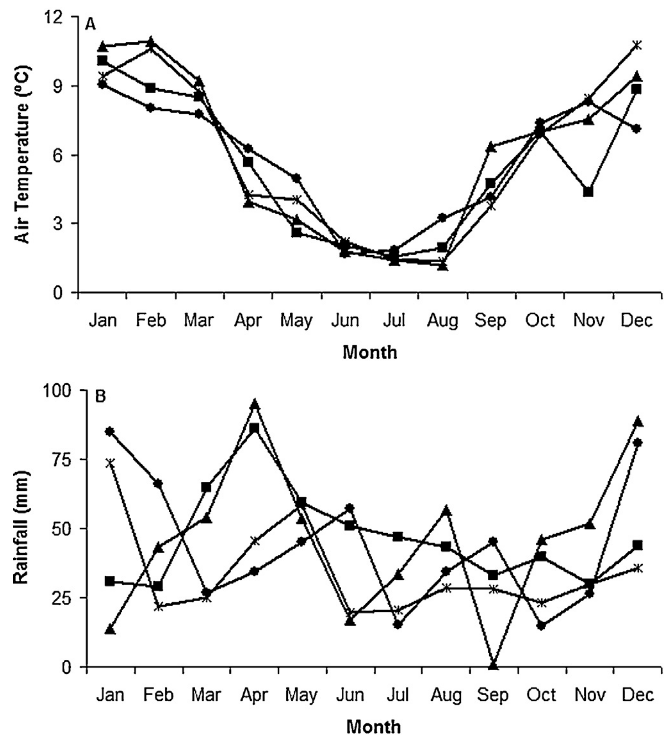

Fig. 1. Climatic data for the experimental region near Ushuaia city, 54° 48′ SL, 68° 19′ WL (Tierra del Fuego, Argentina). Mean air temperature, (A), and rainfall, (B), were recorded during 2008 (—▲—), 2009 (—■—), 2010 (—◆—) and 2011 (—✳—) by a Meteorological Station located at the Centro Austral de Investigaciones Científicas (CONICET, Argentina).

2.6. Fruiting

Fresh fruit weight was recorded on healthy and sun-exposed fruits (*n* = 30) that were manually and randomly collected every 14 days from November (14 days from full flower phase *DFFP*) to March (112 *DFFP*), during the 2008/09, 2009/10 and 2010/11 growing seasons.

3. Results

3.1. Climatic description

The mean air temperatures were 6.0, 5.5, 5.8 and 6.0 °C for 2008, 2009, 2010 and 2011 years, respectively (Fig. 1A). When considering the period from October to March for the 2008/09, 2009/10 and 2010/11 growing seasons, the mean air temperatures were 8.7, 7.5 and 8.6 °C, respectively, being the low air temperatures of November 2009 and January–February 2010 responsible for the low mean air temperatures during 2009/10 period. The rainfall from October to March for the 2008/09, 2009/10 and 2010/11 growing seasons were 311.4, 290.7 and 242.6 mm, respectively, being December and January the months with the highest rainfall (Fig. 1B). The registered values are comparable with those described earlier by Arena and Curvetto (2008). According to the climate classification of Köppen (Kottek et al., 2006), Ushuaia has a polar climate which is meanly characterized by a mean temperature of the warmest month among 0 and 10 °C.

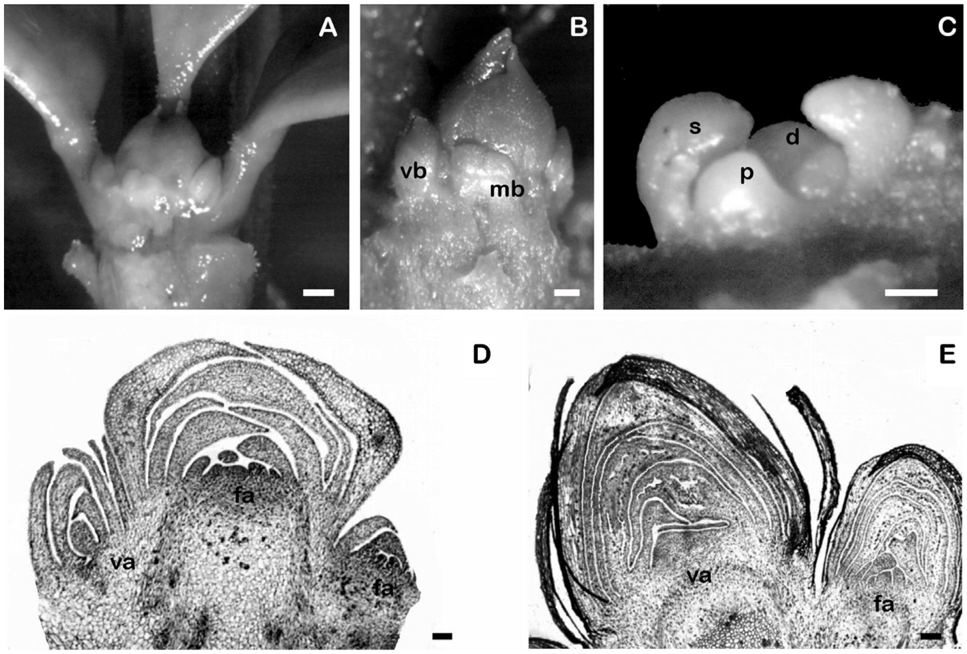

Fig. 2. (A)–(C) Buds of *Berberis buxifolia* observed by stereomicroscope. (A) Mixed and vegetative buds on axillary position; (B) detail of the mixed bud (*mb*) and vegetative bud (*vb*); (C) detail of a floral apex with sepals (*s*), petals (*p*) and dome (*d*). (D)–(E) Longitudinal section of group of buds grown at a node of *Berberis buxifolia.* Mixed and vegetative buds observed by optical microscope with floral apex (*fa*) and vegetative apex (*va*). Bars = (A) 10 μm; (B) 50 μm; (C)–(E) 10 μm. Buds collected on 2010–2011.

3.2. Anatomical analysis

Shoots grown during the growing season developed vegetative and mixed buds in their nodes. The number of axillary buds per node varied between 1 and 3. Buds were also formed in the apical region of the shoots, so they were called terminal or apical buds. At the end of the summer, during March, some lateral or axillary buds have already taken the shape of floral apex, broader than the acute elliptical shape of vegetative apex (Fig. 2A–C). Longitudinal section shows buds with a vegetative apex (Fig. 2E) or instead it can be differentiated into a floral apex (Fig. 2D).

Vegetative buds differentiated numerous leaves distributed around the central axis with the point of insertion nearly to the same height (Fig. 3A–D). In effect, when the bud sprouting starts, a little stem elongation occurs. So this rosette-like growth makes difficult the observation of the apical meristem.

Flower differentiation started twelve weeks after bud breaks in coincidence with the end of the first fruit growth phase (Fig. 4). Flowers developed from the mixed bud shoot apex, and are thus typically terminal. During the transition to flowering, the typical tunica-corpus organization of the vegetative apex may become modified, as also does cytohistological zonation, if it is recognized (Fig. 5A). In an early transition to flowering, the apex domed and has a two-layered tunica (Fig. 5A). Gradually the cells in the central core of the apex become highly vacuolated, in contrast to the meristematic cells which are smaller, densely staining and arranged on layers which form an outer covering or mantle (Fig. 5A). Mixed bud collected on December 16th shows an advance floral differentiation. In effect, the pistil which is the last organ to differentiate presents an active stigma formation (Fig. 6A–B) and the archesporial tissue shows sporogenous layers formation inside of the anthers (Fig. 6C). In the following growing season, thirteen weeks later the sprouting, stamen primordial and a single carpel can be shown (Fig. 5B). The developed carpel is occupying an apparently terminal position and the stigma formation is well recognized (Fig. 5B–F). The growth in volume of the carpel continues to twenty-eight weeks from sprouting (Fig. 5F). A period of active differentiation of floral parts can be observed from twelve to twenty eight weeks of rest completion (Fig. 4). Gamete differentiation occurred in a short period before sprouting for male gametes, while during flowering time for female gametes (data not shown, Fig. 4).

Table 1
Minimum (Min), maximum (Max) and mean (Mean) number of mixed buds (*MB*) and vegetative buds (*VB*) registered on *Berberis buxifolia* one year old shoots according to their spatial orientation on October 2010.

Spatial orientation	MB			VB		
	Min	Max	Mean	Min	Max	Mean
East	5	24	13.36ab	1	29	8.36a
North	9	40	21.73a	0	15	5.27a
South	0	17	10.00b	1	31	11.55a
West	7	41	19.82ab	1	10	5.00a

Values followed by different letters in each column are significantly different (Tukey $p \leq 0.05$).

3.3. Bud distribution on one year old shoots

The number of mixed buds formed on one-year-old shoots was higher than vegetative buds. Spatial orientation of the shoots significantly affected ($p = 0.008$) the mixed bud number per shoot, being higher on shoots facing to north (21.7), which is statistically different to the mixed bud number on shoots facing to south (10.0) (Table 1). A high variability in mixed bud number among shoots could also be seen. The number of vegetative buds were not statistically different ($p = 0.117$) among shoot spatial orientations, although the highest values were found on shoots grown to South and East direction (11.55 and 8.36 respectively). The correlation between the number of vegetative and mixed buds differs according to the shoot spatial arrangement, being highly correlated both variables in the south ($r = 0.79$) and poorly correlated in the North and West spatial orientations ($r = 0.00$ and $r = 0.16$, respectively).

3.4. Vegetative growth

Structural and basal shoots began to elongate since November, when the flowering ended, while early shoots began to elongate

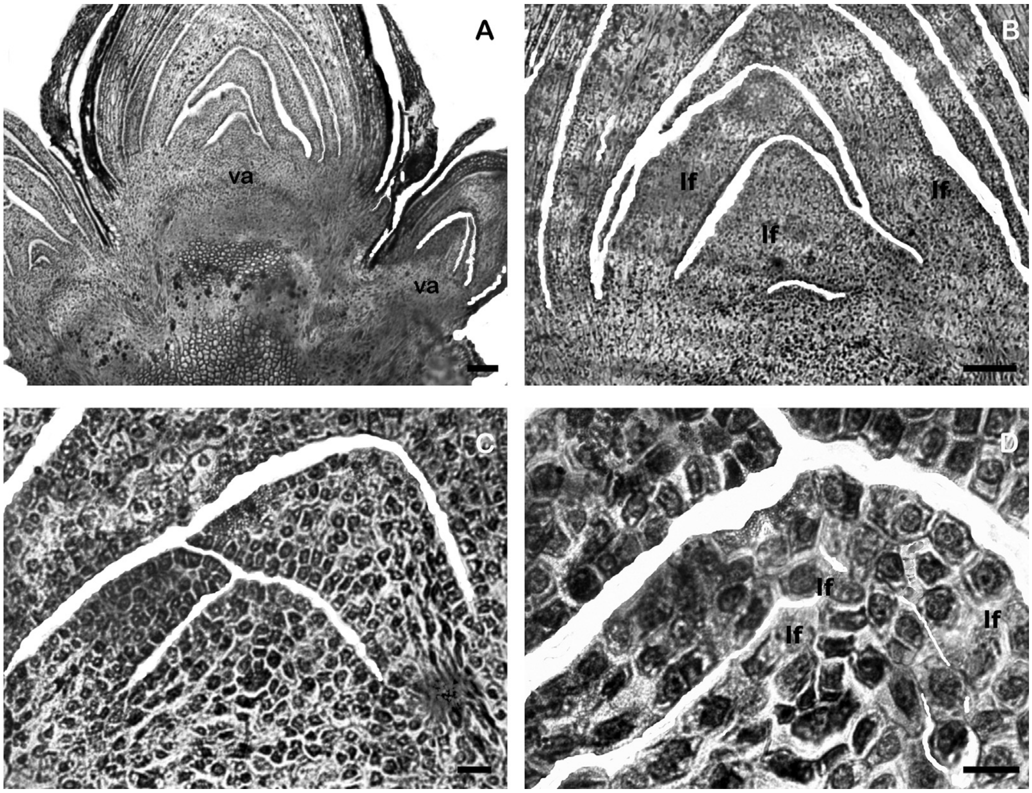

Fig. 3. Longitudinal section of a vegetative bud of *Berberis buxifolia.* (A)–(D) Different magnification of the vegetative apex (*va*). (B) and (D) Leaf (*lf*). Bars = (A) 10 μm; (B) 50 μm; (C) and (D), 10 μm. Buds collected on 2010–2011.

later, since December and January (Fig. 7). The rate of absolute shoot growth and shoot length varied with the type of shoot, month and growing season. Structural shoots attained the highest rates of absolute growth on December (0.21 cm/day) for the 2008/09 growing season, while for the 2009/10 and 2010/11 growing seasons, the highest rates of absolute growth were reached later on January (0.26 and 0.22 cm/day respectively) (Fig. 7A). Length of structural shoots was of 10.9, 13.0 and 11.0 cm on March 2009, 2010 and 2011, respectively. Basal shoots attained the highest rates of absolute growth on January (0.27, 0.67 and 0.78 cm/day for the 2008/09, 2009/10 and 2010/11 growing seasons, respectively) (Fig. 7B). Length of basal shoots was of 19.3, 32.8 and 38.5 cm on March 2009, 2010 and 2011, respectively. Finally, early shoots attained the highest rates of absolute growth on February (0.19 cm/day) for the 2008/09 growing season, while for the 2009/10 and 2010/11 growing seasons, the highest rates of absolute growth were reached early on January (0.14 and 0.17 cm/day respectively) (Fig. 7C). Length of early shoot was of 6.2, 6.9 and 8.1 cm on March 2009, 2010 and 2011, respectively.

3.5. Fruiting

The rate of growth of the fruits varied with the month and the growing season (Fig. 8). For the 2008/09 and 2010/11 growing seasons, the first highest rates of absolute growth of the fruits were of 7.1–6.3 mg fresh weight/day, for December 2nd fortnight, determining the end of the first phase of rapid increase (day 42 *AFFP*). Then the rates of absolute growth of the fruits decreased to minimum values of 3.2–2.8 mg fresh weight/day for January 1st fortnight, determining the plateau phase (second lag phase), which was extended by 14 days. Finally, new increments in the rates of 11.5–12.7 mg fresh weight/day were observed at the end of the fruiting period (third phase of rapid increase) until March 1st fortnight (112 days *AFFP)*, time when the fruits also ripen.

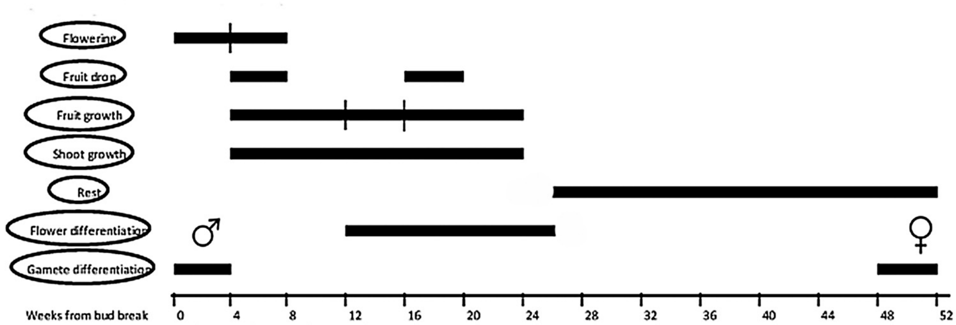

Fig. 4. Physiological cycle of *Berberis buxifolia*.

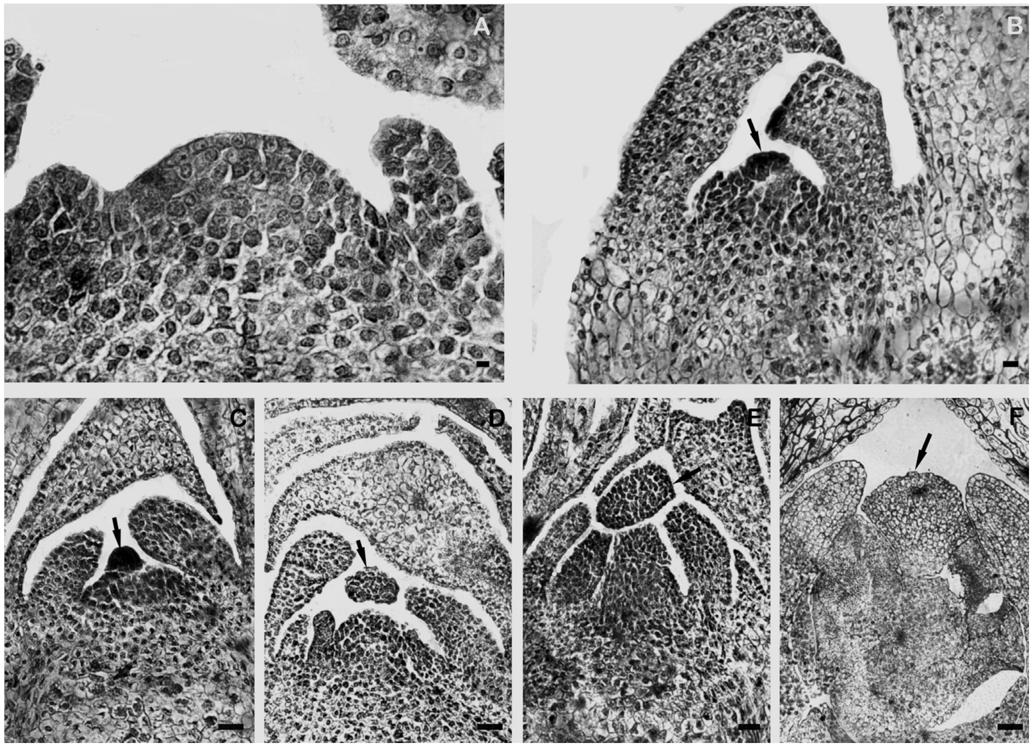

Fig. 5. Longitudinal section of a mixed bud of *Berberis buxifolia* with pistil development. (A) Floral apex in the first stage of development (December); (B) pistil with rudimentary stigma (*arrow*). (C) and (D) Pistil growth from January to April. Arrows indicate the stigma evolution. Bars = 10 μm. Buds collected on 2010–2011.

The maximum fruit weight varied among 0.44 and 0.50 g for the mentioned growing seasons, and then a decrease in fresh biomass occurred toward the end of the fruiting period. However, for the 2009/10 growing season, the first highest rates of absolute growth of the fruits were of 9.1 mg fresh weight/day for January 1st fortnight (day 56 *AFFP*). Then the rates of absolute growth of the fruits decreased to minimum values of 1.8 mg fresh weight/day for January 2nd fortnight, determining the plateau phase (second lag phase), which was extended by 14 days. Finally, new increments in the rates of 5.5 mg fresh weight/day were observed at the end of the fruiting period (third phase of rapid increase) until March 1st fortnight (112 days *AFFP)*. The maximum fruit weight was of 0.41 g, and then a decrease in fresh biomass occurred toward the end of the fruiting period. Fruit growth measured

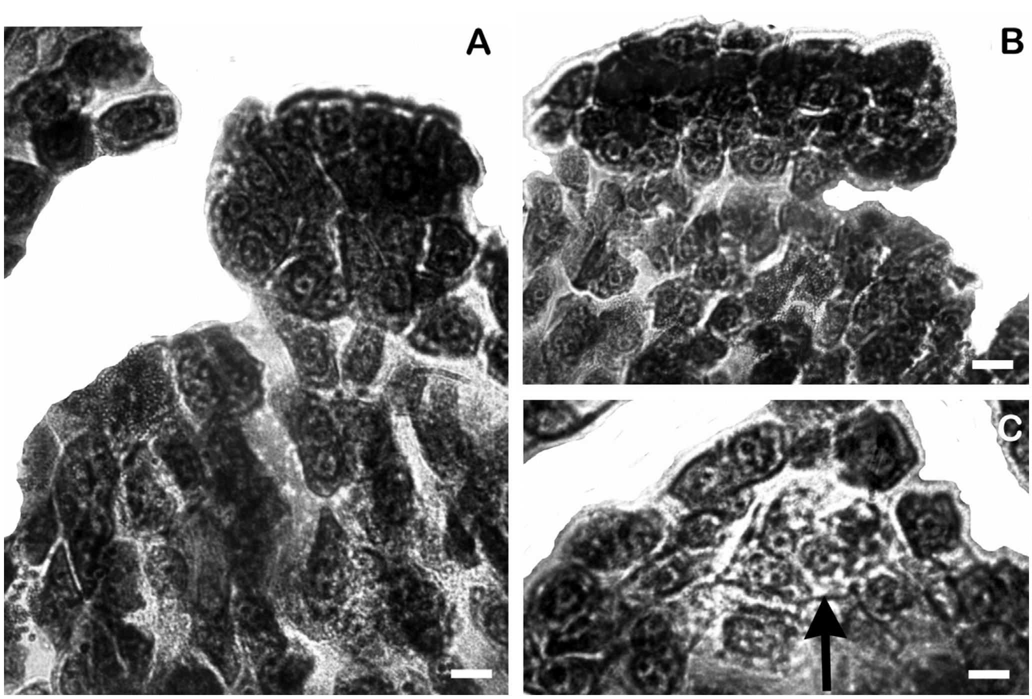

Fig. 6. Details of stigma and anther of flowers collected in mid-February. (A) and (B) Longitudinal section of stigma and style; (C)–(F) start of the archesporium development on the anther (*arrow*). Bars = 10 μm. Buds collected on 2010–2011.

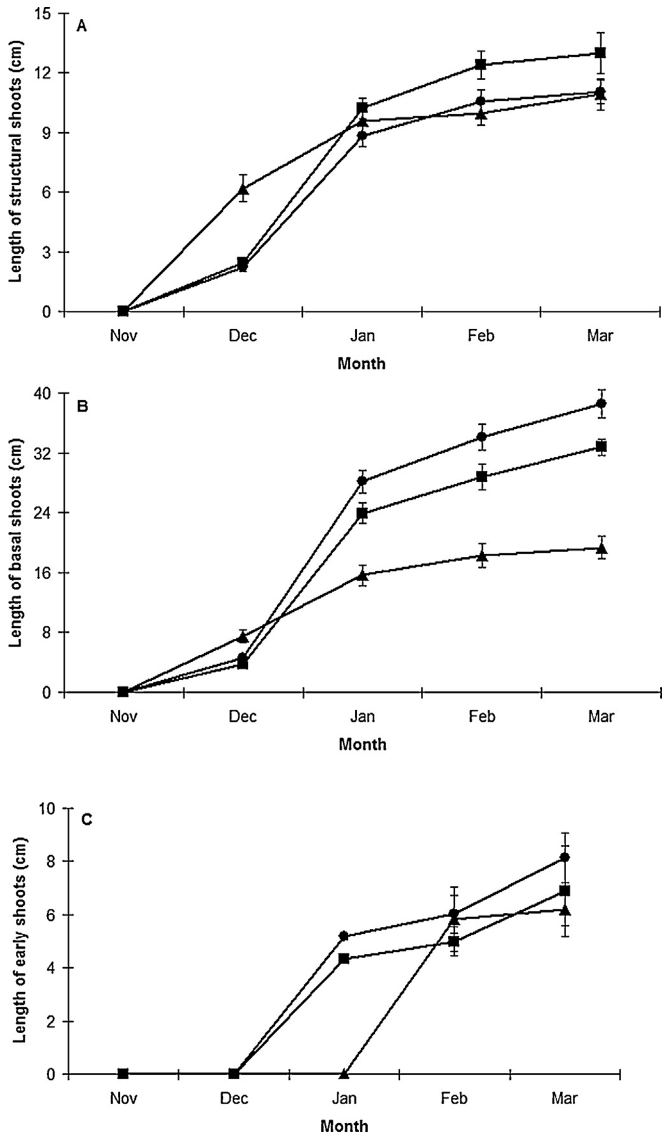

Fig. 7. Structural (A), basal (B) and early (C) shoot length of *Berberis buxifolia* along the 2008/09 (—▲—), 2009/10 (—■—) and 2010/11 (—●—) growing seasons. Bars represent ± standard error of the mean.

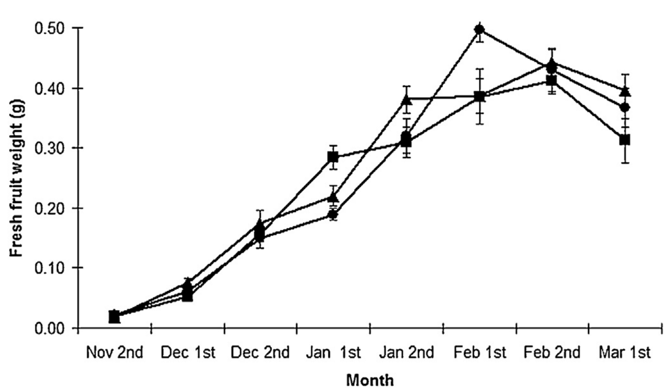

Fig. 8. Fresh fruit weight of *Berberis buxifolia* along the fruiting period during the 2008/09 (—▲—), 2009/10 (—■—) and 2010/11 (—●—) growing seasons. 1st: first fortnight, 2nd: second fortnight. Bars represent ± standard error of the mean.

by fresh weight increase was accomplished in approximately 98 days.

4. Discussion

To maintain the normal physiology throughout the life, also called the annual activity cycle, temperate and cold climate species require an annual period of low activity (Billings and Mooney, 1968; Hänninen, 2004), called in this manuscript rest, which refers to successive events like growth cessation, bud set, dormancy and cold hardiness (Tanino et al., 2010). The onset of rest is related to day length as well as decreasing temperatures in many plants (Bidwell, 1974). In *B. buxifolia* this period coincided with the beginning of autumn and winter, and can be extended up to the spring. During this period the plants showed no activity and no apparent vegetative growth or flowering. However, some physiological processes, such as root absorption, vascular translocation, respiration, photosynthesis, transpiration (Kramer and Kozlowski, 1979) as well as some changes in flower buds can occur slowly at the beginning and end of the rest period. The keys to time of starting of new growth are the melting of the snow-cover or, on snow-free areas, the increase of soil and air temperatures (Billings and Mooney, 1968) or both, as occurs in Tierra del Fuego. According to the theory that has prevailed until recently, air temperature has been considered to be the most important environmental factor regulating the bud break of trees in the boreal and temperature zone (Hänninen, 2004). Prolonged exposure to comparatively high temperatures causes bud break, but only after a sufficient long period of chilling has conditioned the buds to respond to the high temperatures. A relatively long photoperiod appears to be important in breaking the dormancy of vegetative buds in some species but without positive temperatures there is no photoperiodic effect (Billings and Mooney, 1968). In Ushuaia, Tierra del Fuego, at the time when the mean air temperatures had the highest increases along September and October, microsporogenesis process developed during the end of rest period as similarly occurs on stone fruit species (Ontivero et al., 2005; Radice and Galati, 2006). Microsporogenesis occurred when external buds seemed to be in dormancy. Then, vegetative and mixed buds began to swell and later became the bud break. In fact, growing season last no more than 6 months, a period slightly shorter than occurs in temperature zones (Davenport, 2000). Later, leaves of both vegetative and mixed buds began to unfold and expanded early in the spring at the time that flowering became in mixed buds. On the other hand, the time necessary from floral initiation to fruit maturity was up to 1 year in these conditions. Nevertheless, the initiation and development of flower buds occurred in summer and fell of one season, while the flowering process itself occurred in early spring the next season, as was found on stone fruits (Faust, 1989). It is well known that auxin contributes to floral meristem initiation but it remains to elucidate some molecular, genetic and biochemical aspect to explain how this process is triggered (Liu et al., 2009). Shoot apical meristems typically initiate leaves that subtend either branches or flowers. Branches initiate from the axillary meristems that form at the base of leaves during vegetative development, while flowers initiate from floral meristems which form at the base of the leaves called bracts during reproductive development as described by Grbić (2005). A distinctive feature of angiosperm flowers relative to the other reproductive shoots in seed plants is that they are telescoped into the shoot apical meristem. In effect, as has been observed in the floral apex of *B. buxifolia*, this compression of the floral apex is accomplished in two distinct aspects of development, the termination of the shoot apical meristem through its consumption by reproductive structures and reduced internode length near the shoot apex (Baum and Hileman, 2006). Flowering of *B. buxifolia* has been well explained by Arena et al. (2011) and it is important to remark that seven floral phenological phases have been recognized during the blooming period, being the length of the anthesis phase closely related to the climatic conditions. Consequently, fruiting is also subject to climate. Fruit set occurred at the beginning of November, when the first fruit growth phase initiated. The fruit growth exhibited a typical double sigmoid curve, as was reported previously for this species (Arena and Curvetto, 2008). Nevertheless, this pattern of growth has been influenced by the climatic conditions, with the lag phase occurring later when the climate was adverse, like happened on 2009/10 growing season, highlighting the fact that the fruit growth rate greatly varies among seasons and environmental conditions as was stated for *Prunus* sp. (Predieri and Dris, 2005). *B. buxifolia* fruit growth is similar to that observed on peach fruit (Nyéki and Soltész, 1996), grapes (Coombe and McCarthy, 2000) and currants (Wright, 1956; Toldam-Andersen and Hansen, 1997).

When the flowering ended, shoot elongation became in vegetative buds. Most of the vegetative growth occurred at the beginning and middle of the summer, when the air temperatures were the highest. In spite of the low temperatures, the carbohydrates stored in roots and rhizomes are rapidly translocated to the young shoots and leaves (Billings and Mooney, 1968), being the growth of shoots very fast, as was observed in *B. buxifolia*. In the bright light days with low temperatures after snowmelt, carbohydrates must be incorporated not only into new tissue but a considerable amount into anthocyanins, so that the *B. buxifolia* young vigorous shoots are often dark purple. Anthocyanins promote a protective mechanism through the effective absorption of solar UV, thus preventing damage to tissues (Billings and Mooney, 1968). Shoot elongation seems to follows a sigmoid curve, although it was affected by the climatic conditions along the growing season. A first phase of slow growth (one month at the end of the spring) was followed by a phase of fast growth (beginning of the summer). Then, a new phase of slow growth (two months at middle and the end of summer) was observed for the 2009/10 and 2010/11 growing seasons. However on 2008/09 growing season, the first phase of growth was characterized by a high rate of absolute growth. These differences could be due to the higher air temperatures on November and December of 2008 respect to the same months of the following years. The pattern of shoot growth observed in *B. buxifolia* during the studied period could be explained by the prevailing climatic conditions during the growing season. These results are not coincident with those observed in sweet cherry growing in a warmer climate, where a double sigmoid curve was observed for shoot length (Li et al., 2010). After all, the 81.9 and 75.6% of the final shoot length was attained on January for structural and basal shoots respectively, while the 80.3% of its final length was attained later on February for early shoots. These results show that during the last phase of slow growth of early shoots, they are still elongating and cannot become lignified before the rest period. On the other hand, length of basal and early shoots increased with the plant age, *i.e.* with the growing seasons, while length of structural shoots was maximum on 2009/10 growing season, which could not been correlated with climatic conditions, plant age nor fruit growth and production, due to yield per plant increased with the growing season during the studied period (data not published). However, a negative effect of the excessive growth of the structural shoots on 2009/10 growing season over the shoot length on the following growing season could not be discarded.

5. Conclusions

The annual cycle of growth and development of the native Patagonian fruit species *B. buxifolia* was studied. Flower differentiation started twelve weeks after bud breaks in coincidence with the end of the first fruit growth stage. In the following growing season, gamete differentiation occurred in a short period before sprouting for male gametes and during flowering time for female gametes. While fruit growth followed a double sigmoid curve, shoot elongation shows a sigmoid curve, both being influenced by the climatic conditions. Knowledge of shoot growth and development of *B. buxifolia* growing in a free growth form in its native zone is of great importance to understand its physiology and when comparing these events on commercial cultures that are being planned in other zones. On the other hand, these findings are of crucial relevance when in a commercial orchard the plants need to be fertilized or pruned, or when evaluating the impact of adverse climatic conditions as well as global change on events like flowering and fruit set.

Acknowledgments

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